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EVOLUTION OF THE THERIAN MAMMALS IN THE LATE CRETACEOUS OF ASIA. PART IV. SKULL STRUCTURE IN *KENNALESTES* AND *ASIORYCTES*

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Skulls of Late Cretaceous eutherian genera: *Asioryctes* and *Kennalestes* from Mongolia are described and figured. The following features characteristic of both genera are regarded as symplesiomorphic therian character states: inclination of occipital plate forwards from the condyles, a basisphenoid wing, homologous with basiptyergoid process, f. rotundum confluent with sphenorbital fissure, ectotympanic inclined to the horizontal, medial internal carotid and stapedia arteries present, no promontory artery, no entotympanic, long jugal, a subsquamosal foramen, no paroccipital process, medial inflection of angular process. Lack of evidence for presence of promontory artery in *Asioryctes* and *Kennalestes* supports PRESLEY's (1979) idea that the primitive mammalian morphotype with two vessels (medial internal carotid and promontory) should be revised. Family Kennalestidae nov. and subfamily Asioryctinae nov. within Palaeoryctidae are erected, both assigned to Proteutheria ROMER.

Key words: Mesozoic mammals, Eutheria, Cretaceous, *Asioryctes*, *Kennalestes*, braincase, alisphenoid, ectotympanic, internal carotid, lower jaw.

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Streszczenie. — Czaszki górnokredowych ssaków łóżyskowych należących do rodzajów *Asioryctes* i *Kennalestes* z pustyni Gobi w Mongolii zostały opisane i zilustrowane. Wykazano, że chociaż *Asioryctes* i *Kennalestes* różnią się uzębieniem oraz szczegółami anatomii czaszki, zasadniczy schemat budowy czaszki jest u obu rodzajów taki sam. Porównania z cynodontami, z różnymi grupami ssaków mezozoicznych, z torbaczami oraz z przedstawicielami prymitywnych ssaków łóżyskowych pozwoliły na wyróżnienie zespołu cech, które są charakterystyczne dla *Asioryctes* i *Kennalestes*, a jednocześnie mogą być wyróżnione jako zespół symplezjomorficzny dla ssaków właściwych (Theria). Zespół ten obejmuje następujące cechy: nachylenie potylicy od kłykci potylicznych ku górze i ku przodowi; długi region mezocefaliczny, związany z dużymi rozmiarami skrzydła skroniowego kości klinowej; podział części podstawowej kości klinowej na część środkową i skrzydło boczne, przypuszczalnie homologiczne processus basiptyergoideus gadów, otwór okrągły złyany z otworem klinowo-oczodołowym; otwór owalny umieszczony daleko w tyle, arteria carotis interna media i arteria stapedia obecne, brak śladu po arteria promontorii, brak entotympanicum, ectotympanicum tworzące 3/4 pierścienia, ustawione skośnie w stosunku do poziomu; wyrostek zapanewkowy przedłużony ku przodowi i dośrodkowo jako grzebień przechodzący w kość skrzydłową; długa kość jarzmowa dochodząca do dołu żuchwowego, który położony jest daleko w tyle, naprzeciw przedniej części promontorium; obecny otwór podskroniowy; brak wyrostka przypotylicznego; wyrostek kątowy żuchwy zagięty dośrodkowo, szczątkowa kość coronoideum zachowana, zrosnięta z kością zębową.

Brak arteria promontorii u *Kennalestes* i *Asioryctes* potwierdza pogląd PRESLEYA (1979), że należy poddać rewizji morfotyp, uznany w literaturze paleontologicznej od czasów MATTHEW

(1909) za prymitywny dla ssaków, w którym występują dwa niezależne naczynia krwionośne: arteria carotis interna media i arteria promontorii. Utworzono następujące nowe jednostki systematyczne: rodzina Kennalestidae dla rodzaju *Kennalestes* i podrodzina Asioryctinae (zaliczona do Palaeoryctidae WINGE) dla *Asioryctes*. Kennalestidae i Palaeoryctidae zaliczono do rzędu Proteutheria ROMER, 1966.

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INTRODUCTION

The braincase is a part of the mammalian skeleton that is rarely preserved in the fossil state and until recently has been virtually unknown in Cretaceous therian mammals. All the early Cretaceous therians so far described (see KIELAN-JAWOROWSKA, BOWN and LILLEGRAVEN 1979, KIELAN-JAWOROWSKA, EATON and BOWN 1979, and CLEMENS 1979 for reviews) are known from isolated teeth or occasionally from fragments of jaws with teeth.

The rich Late Cretaceous therian faunas of North America (CLEMENS 1966, 1973, CLEMENS and RUSSELL 1965, FOX 1970, 1971, 1972, 1974, LILLEGRAVEN 1969, 1972, 1976, SAHNI 1972, SLOAN and VAN VALEN 1965, VAN VALEN and SLOAN 1965, and others) consist almost

exclusively of teeth and jaws. The exceptions are three fragments of marsupial braincases; one is a small part of the ventrolateral corner of the skull of *Eodelphis browni* from Judith River Formation described by MATTHEW (1916); two others are two fragments of braincases of *Didelphodon vorax* from Lance Formation described by CLEMENS (1966). In addition numerous isolated eutherian petrosals from the Hell Creek Formation of Bug Creek in Montana referred to as Bug Creek petrosals are known. These are not identified at the generic or specific level, but have been described in detail by MACINTYRE (1972). The Late Cretaceous therian mammals have also been found in Peru (GRAMBAST *et al.* 1967, SIGÉ 1972) as isolated teeth, and in Southern France (LEDOUX *et al.* 1966) as a single lower molar. The Cretaceous therian mammals are unknown so far from Africa and Australia.

In contrast with these scattered records of Late Cretaceous therian mammals from various continents is a collection of Late Cretaceous mammals from Asia, consisting of skulls often preserved with their braincases. The first of the Late Cretaceous eutherian skulls were found in Mongolia in the rocks of the Djadokhta Formation by members of the Central Asiatic Expeditions of the American Museum of Natural History. These specimens, though comparatively complete were poorly preserved and destroyed during preparation, and did not provide useful information on braincase structure (GREGORY and SIMPSON 1926, SIMPSON 1928a).

The collection of Late Cretaceous therian mammals from Mongolia assembled by members of the Polish-Mongolian Palaeontological Expeditions embraces new and better preserved material of numerous skulls. Of the seven therian genera known from these beds only four (*Kennalestes*, *Asioryctes*, *Zalambdalestes* and *Barunlestes*) have been identified as undoubted eutherian mammals (KIELAN-JAWOROWSKA 1975a, 1975b, 1975c); the remaining genera (*Deltatheridium*, *Deltatheroides* and *Hyotheridium*) are classified as Theria of metatherian-eutherian grade.

In the present paper I describe the skulls of *Kennalestes* and *Asioryctes*. They allow the braincase of Cretaceous eutherian mammals to be reconstructed for the first time. The skulls of *Zalambdalestes* and *Barunlestes* will be described in a forthcoming publication.

The two genera are monotypic, *Kennalestes* being represented by *K. gobiensis* KIELAN-JAWOROWSKA, 1969 and *Asioryctes* by *A. nemegetensis* KIELAN-JAWOROWSKA, 1975. For the sake of brevity in the descriptions I use only the generic names. *Kennalestes* occurs in the Djadokhta Formation, the age of which has been determined as ?late Santonian and/or ?early Campanian, *Asioryctes* occurs in the Barun Goyot Formation, recognized as of ?middle Campanian age (GRADZIŃSKI *et al.* 1977, KIELAN-JAWOROWSKA 1974).

Preliminary descriptions of the skulls and dentition of *Kennalestes* and *Asioryctes* were published by KIELAN-JAWOROWSKA (1969, 1975a), the structure and occlusion of the molars by CROMPTON and KIELAN-JAWOROWSKA (1978) and the postcranial skeleton by KIELAN-JAWOROWSKA (1977). The descriptions, photographs and drawings published in these papers are not repeated here (except when emended) and therefore the present paper should be read in conjunction with the earlier ones.

It appears from the studies on the dentition of *Kennalestes* and *Asioryctes* (KIELAN-JAWOROWSKA 1969, 1975a, CROMPTON and KIELAN-JAWOROWSKA 1978) that *Kennalestes* which is assigned to the Kennalestidae nov. is in various respects more primitive than *Asioryctes* assigned to the Palaeoryctidae (subfamily Asioryctinae nov.) and should be described before *Asioryctes*. As, however, the skull of *Asioryctes* is more complete and the braincase better preserved, making a more complete reconstruction possible, it is described first, and the skull of *Kennalestes* is then compared with it.

The terminology used in the present paper for the description of the skull is mostly that of McDOWELL (1958) and MACINTYRE (1972) and for the description of the teeth the terminology of VAN VALEN (1966).

The following new terms in the description of the skull have been introduced:

basisphenoid wing — lateral part of the basisphenoid arranged lateroventrally, and oblique to the medial part of the basisphenoid. The free lateral margin of the basisphenoid wing is fused with the medial margin of the alisphenoid to form the pterygoid ridge.

mesocranial region of the skull — the part of the cranium between the end of the palate and front of the promontorium. The mesocranial region is especially elongated in *Asioryctes* and in the Tenrecidae.

recessus fenestrae cochleae — a funnel-like, ovoid structure in the promontorium, in which lies the fenestra cochleae. The recessus fenestrae cochleae occurs in *Kennalestes* and is less distinct in *Asioryctes*.

Abbreviations used:

- AMNH American Museum of Natural History, New York
 BSM Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich
 GSP Geological Institute, Academy of Sciences of the Mongolian People's Republic, Ulan Bator
 MCZ Museum of Comparative Zoology, Harvard University, Cambridge
 USNM United States National Museum, Washington
 ZPAL Institute of Paleobiology, Polish Academy of Sciences, Warsaw

The specimens housed in the Institute of Paleobiology, described in the present paper have long numbers, e.g. ZPAL MgM-I/98; for the sake of brevity, throughout the descriptions only the last term of the number is used, e.g. instead of ZPAL MgM-I/1 only no. 1 is used; in the discussion usually the full numbers are given.

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Mrs. K. BUDZYŃSKA and the remainder by Miss E. OSIŃSKA; Mr. W. SICIŃSKI arranged the plates. The SEM micrographs were made at the Laboratory of Electronic Microscopy of the Nencki's Institute of Experimental Biology in Warsaw. To all these persons and institutions I would to express my sincere thanks and gratitude.

MATERIAL

Asioryctes nemegetensis KIELAN-JAWOROWSKA, 1975

ZPAL MgM-I/56, holotype, Barun Goyot Formation, Nemegt (Southern Monadnocks), Nemegt Basin, Gobi Desert, Mongolia. Almost complete skull with both lower jaws in occlusion, incomplete atlas and axis. For details see KIELAN-JAWOROWSKA (1975a: 6). Skull figured by KIELAN-JAWOROWSKA (1975a, pl. 1), atlas and axis by KIELAN-JAWOROWSKA (1977, fig. 1A and B, pl. 15). Figured in this paper in figs. 1–3 (2 and 3 reconstructed) and on pls. 3, 4:1, 5:2, 6, and 7:1.

ZPAL MgM-I/70, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia. Incomplete skull without anterior part of the face, with choanal region preserved; incomplete right and left lower jaws in occlusion, right and left P^4-M^3 and P_4-M_3 preserved. Figured in this paper on pl. 8.

ZPAL MgM-I/71, same horizon and locality, anterior part of the face of a juvenile individual; both lower jaws in occlusion; almost complete dentition. Figured in this paper on pls. 9:1 and 10:2.

ZPAL MgM-I/73, same horizon and locality, fragment of right maxilla with M^1-M^3 , in occlusion with partial right lower jaw with M_2-M_3 , associated with partial left lower jaw with P_3-M_3 . Figured by KIELAN-JAWOROWSKA (1975a: pls. 3 and 4; there is a mistake in the enlargement of SEM photographs on these plates, which should be $\times 20$ and not $\times 17.5$, as it has been published) and by CROMPTON and KIELAN-JAWOROWSKA (1978: fig. 6).

ZPAL MgM-I/74, same horizon and locality, fragment of left lower jaw with P_3-M_2 , figured in this paper on pls. 18:2 and 19:2.

ZPAL MgM-I/87, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, fragment of left maxilla with P^3-M^3 in occlusion with left lower jaw with P_3-M_3 ; figured in this paper on pl. 10:1.

ZPAL MgM-I/98, same horizon and locality, almost complete skull, with complete dentition, strongly compressed laterally with right and left lower jaws in occlusion and fragments of postcranial skeleton. For details of the postcranial skeleton see KIELAN-JAWOROWSKA 1977: 67. Skull figured by KIELAN-JAWOROWSKA (1975a, pl. 2), postcranial skeleton by KIELAN-JAWOROWSKA (1977, figs. 2, 3A, 4A, pl. 15: 3a–b, pl. 16: 2a–b, pls. 17 and 18). Figured in this paper on pl. 5:1.

ZPAL MgM-I/134, Barun Goyot Formation, Nemegt (Eastern Sayr), Nemegt Basin, Gobi Desert, incomplete face, strongly compressed laterally, bones of the cranial roof badly damaged, with left P^1-M^3 and right P^2-M^3 , in occlusion with incomplete right and left lower jaws, both with P_3-M_3 ; figured in this paper on pl. 11.

ZPAL MgM-I/144, Khermeen Tsav red beds of, Khermeen Tsav II, Gobi Desert, right and left damaged maxillae, each in occlusion with incomplete lower jaws; right P^2-M^3 and P_4-M_3 , left P^3-M^3 and $C-M_3$; figured in this paper on pl. 9:2.

ZPAL MgM-I/148, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, incomplete left lower jaw, alveoli for I_2-I_4 and $C-M_3$; figured in this paper on pls. 4:2, 7:2, 18:3 and 19:3.

ZPAL MgM-I/166, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, incomplete right maxilla with P^2-M^3 ; figured in this paper on pls. 18:1 and 19:1.

Kennalestes gobiensis KIELAN-JAWOROWSKA, 1969

All the specimens are from the Djadokhta Formation, Bayn Dzak (Main Field), Gobi Desert, Mongolia.

ZPAL MgM-I/1, an almost complete skull of a juvenile individual, with lower jaws in occlusion, associated with atlas and fragment of axis; cranial roof damaged. Dentition see p. 53. Figured by KIELAN-JAWOROWSKA (1975*d*, fig. 8 and 1977, pl. 16: 1) and by CROMPTON and KIELAN-JAWOROWSKA (1978, fig. 12); figured in this paper in figs. 4-6 (figs. 5 and 6 reconstructed) and on pls. 7:3, 12-15, 16:3 and 17:3.

ZPAL MgM-I/2, nearly complete face, with fragment of cranial roof showing partial endocranial cast and isolated right petrosal found in the same piece of rock; for details see KIELAN-JAWOROWSKA (1969: 177), figured by KIELAN-JAWOROWSKA (1969, fig. 1E and pl. 24); the petrosal figured in this paper in fig. 8 and on pl. 16:1.

ZPAL MgM-I/3, holotype, almost complete, somewhat distorted skull, without posterior portion of the cranium with lower jaws in occlusion; for details see KIELAN-JAWOROWSKA (1969: 177). Figured by KIELAN-JAWOROWSKA (1969, fig. 1D, pl. 22 and pl. 23:1*a-g*); figured in this paper in fig. 11.

ZPAL MgM-I/5, partial face with partial lower jaws in occlusion, for details see KIELAN-JAWOROWSKA 1969: 177. Figured by KIELAN-JAWOROWSKA 1969, pl. 23:2*a-d* and pl. 25.

ZPAL MgM-I/44, posterior part of the cranial roof with incomplete occipital plate and right petrosal, figured in this paper in fig. 7 and on pl. 16:2.

ZPAL MgM-I/55, fragment of right maxilla with P³-M³.

DESCRIPTIONS

SKULL

ASIORYCTES

(Figs. 1-3, 10, 12; pls. 3, 4:1, 5:1 and 2c, 8:1*a*, 9:1*a* and 2, 10:1*a-1c* and 2, 11:1*a*)

The skull as a whole. — The length of the skull is about 30 mm. The snout is very narrow anteriorly, widening opposite P³. There is a conspicuous interorbital constriction but no postorbital process. The zygomatic arch is comparatively deep. The mesocranial region is narrow, strongly elongated, and comprises nearly one third of the entire skull length. The occipital surface lies at an angle of about 75° to the plane of the teeth, the occipital condyles strongly protrude behind. The lower jaw is slender, with a very large coronoid process.

Snout and anterior part of zygomatic arch. — The course of the naso-frontal suture cannot be traced with full certainty. In the preliminary description I stated (KIELAN-JAWOROWSKA 1975*a*: 7): "Nasals expanded posteriorly, in contact with lacrimals...", however, reexamination of all the skulls referred to *Asioryctes* shows that it is more probable that the nasals do not contact the lacrimals. The naso-frontal suture, as now tentatively recognized, is placed above the infraorbital foramen and directed roughly transversely. The nasals widen only slightly behind. The premaxilla is relatively extensive, with an incurved anterior margin. The lateral wall of the maxilla is concave, the infraorbital foramen is extensive, placed above P³. The lacrimal foramen is placed near the edge of the margin of the orbit. The lacrimal is provided with a facial wing, probably pointed anteriorly (in contrast to my previous reconstruction, see KIELAN-JAWOROWSKA 1975*a*, fig. 1B). The jugal is very extensive and forms almost

the entire zygomatic arch, posteriorly reaching the anterior margin of the glenoid cavity. The maxilla does not contribute to the zygomatic arch. The jugal is somewhat thickened along the lower margin of the orbit, which it surrounds. It contacts the lacrimal anteriorly and contributes extensively to the structure of the lateral wall of the snout, meeting the maxilla with an undulating suture.

Palate. — The palatal part of the premaxilla has not been preserved, but in no. 56 the course of the premaxillary-maxillary suture can be traced. This is placed just in front of the canine and directed roughly transversely. There is a distinct, small foramen, identified as incisive foramen, in the middle of either side of the premaxillary-maxillary suture. The palatal part of the maxilla is concave on either side and the palatine groove was probably present. The course of the palatino-maxillary suture cannot be traced and hence the extension of the horizontal part of the palatine bone is not known. In the posterior part of the hard palate there are a few foramina, which may, however, be caused by damage and none can be recognized with certainty as the anterior palatine foramen. A weak postpalatine torus is present, more prominent laterally than medially. The posterior margin of the palatal process of the maxilla, lateral to the postpalatine torus is notched on both sides of no. 56. It is probable that the posterior palatine foramen was developed as a notch.

Cranial roof and posterior part of zygomatic arch (fig. 1). — The supraorbital crest turns dorsally opposite M^2 - M^3 embrasure and its end is visible in the dorsal view of the skull. The fronto-parietal suture cannot be discerned with any certainty and it is tentatively recognized as extending more or less across the postorbital constriction.

The parietals are extensive and form the whole cranial roof posteriorly, except for the lateral parts where the squamosals contribute. It is difficult to state with any certainty whether the sagittal crest was present, as the posterior part of the cranial roof is damaged in all the specimens. However, in no. 98, which is strongly flattened laterally, a very weak sagittal crest is present along the anterior part of the parietals, which suggests that it also continued posteriorly. The lambdoidal crests are present, probably weak medially and somewhat more extensive lateroventrally. A faint ridge extends dorsally and then anteriorly from the dorsal edge of the base of the zygomatic arch, to the anterior orifice of the sinus canal, and borders the temporal fossa dorsally. It runs across the squamosal and parietal, roughly parallel to the upper border of the skull; as it ends at the sinus canal foramen, it possibly reflects the course of the sinus canal.

The squamosal is extensive, in lateral view roughly triangular, with a pointed anterior end, inserted between the parietal and the alisphenoid. Its suture with the parietal is convex dorsally; the suture between the squamosal and petrosal is not discernible: the suture between the squamosal and the mastoid extends along the lateral mastoid flange (MACINTYRE 1972). The temporal crest is very prominent. The posterior root of the zygomatic arch is placed far posteriorly. When seen from the side (fig. 1) it is roughly triangular in shape and embraced by two crests: the temporal crest, and posteriorly by the lateral mastoid flange. Dorsally the two crests meet and continue as a lambdoidal crest. The most posterior part of this structure extends ventrally as a posttympanic process. The surface of the squamosal between the postglenoid and posttympanic processes, forming the recess for the external auditory meatus, is strongly concave. In its ventral part a very large, roughly rectangular tympanohyal is superimposed on the squamosal. It is well preserved on the left side of no. 56, although its medial edge which covers the fossa muscoli stapedii ventrally is broken off. It cannot be excluded that the missing medial part of the tympanohyal was pointed as in *Kennalestes*. The zygomatic lamina, although incompletely preserved, appears to be extensive, and is somewhat concave in dorsal view.

A single postparietal foramen is present on the parietal and three small postsquamosal foramina on the squamosal close to the temporal crest, the most anterior situated above the

posterior margin of the postglenoid process. A large fissure-like subsquamosal foramen opens on the lateral surface of the zygomatic arch, above and very slightly to the rear of the postglenoid process.

Occiput. — The occipital plate is roughly semicircular (fig. 2). The occipital condyles are prominent, extending to about the mid-height of the foramen magnum. Dorsolaterally the foramen is surrounded by weak protuberances of the exoccipitals. The suture between the supraoccipital and exoccipitals is tentatively recognized as extending dorsolaterally between the protuberances of the exoccipitals and supraoccipital. The suture between the exoccipital and mastoid is more distinct, discernible on both sides of the skull. It extends from the lower margin of the occipital plate, roughly parallel to the occipital condyle and close to it, in a furrow which surrounds the condyle laterally. The paroccipital process is absent.

The mastoid seen from behind is large, more rectangular than triangular, although it narrows somewhat dorsally. It is very extensive and occupies a large part of the occipital plate. It sends out the tympanic process ventromedially, only the base of which has been preserved, and a mastoid process ventrolaterally. The promontorium and tympanohyal are visible in this view. On the mastoid there are two distinct foramina, the smaller, upper one situated in the dorsomedial corner, recognized as a mastoid foramen (COPE 1882), and the lower large one, situated more laterally, near the base of the tympanic process. The latter does not, as far as I know, occur in the skulls of modern therian mammals; it is also absent in *Kennalestes*. It is designated herein as the lower mastoid foramen.

Orbit. — The orbit is confluent with the temporal fossa and there is no trace of a postorbital process (fig. 1). The upper rim of the orbit is probably made by the frontal. A small flange is developed on the lacrimal, around the anterior edge of the orbit, concealing the lacrimal foramen, which thus opens into the orbit. This flange is continuous dorsally with a very weak supraorbital crest, and ventrally with the upper edge of the zygoma (made by the jugal). The supraorbital crest continues posteriorly up to a point opposite the M²-M³ embrasure where it turns dorsally and can be seen ending in the dorsal aspect of the skull. The dorsal rim of the temporal fossa is completely smooth and rounded.

It is impossible to determine the arrangement of the sutures in the orbital region. The maxillary foramen is present medially and below the lacrimal foramen, separated from it by a prominent bar. Extending posteriorly from the maxillary foramen through the floor of the orbit to the notch of the posterior margin of the maxilla, is a very shallow groove. The suture between the maxilla and the palatine within the orbit probably extends medially to this groove.

The floor of the orbit is comparatively large, triangular in dorsal view. The suture between the palatine and the frontal cannot be traced within the orbital wall. The suture between the palatine and orbitosphenoid is distinguished on both sides of no. 56. It starts immediately in front of the optic foramen and continues anterodorsally (in lateral view) around the ethmoidal foramen. There is a large, round recess at the posteroventral corner of the palatine, in front of and slightly above the optic foramen. The recess may house the sphenopalatine foramen, but the foramen itself has not been identified.

Temporal fossa (fig. 1). — *The orbitosphenoid* is relatively small by comparison with the large alisphenoid. From the side it appears roughly trapezoidal, elongated in the posteroventral — anterodorsal direction. In ventral view it appears wider, with rounded anterior, lateral and posterior margins and straight medial margin. It is pierced by four foramina, well preserved on both sides of no. 56 but possibly somewhat enlarged by preparation. They are also distinguishable (although less clearly) on the left side of no. 98 and on the right side of no. 70. The ethmoidal foramen is in the anterodorsal corner of the orbitosphenoid, the sinus canal foramen posterior to it, the optic foramen in the anteroventral corner, and the sphenorbital fissure

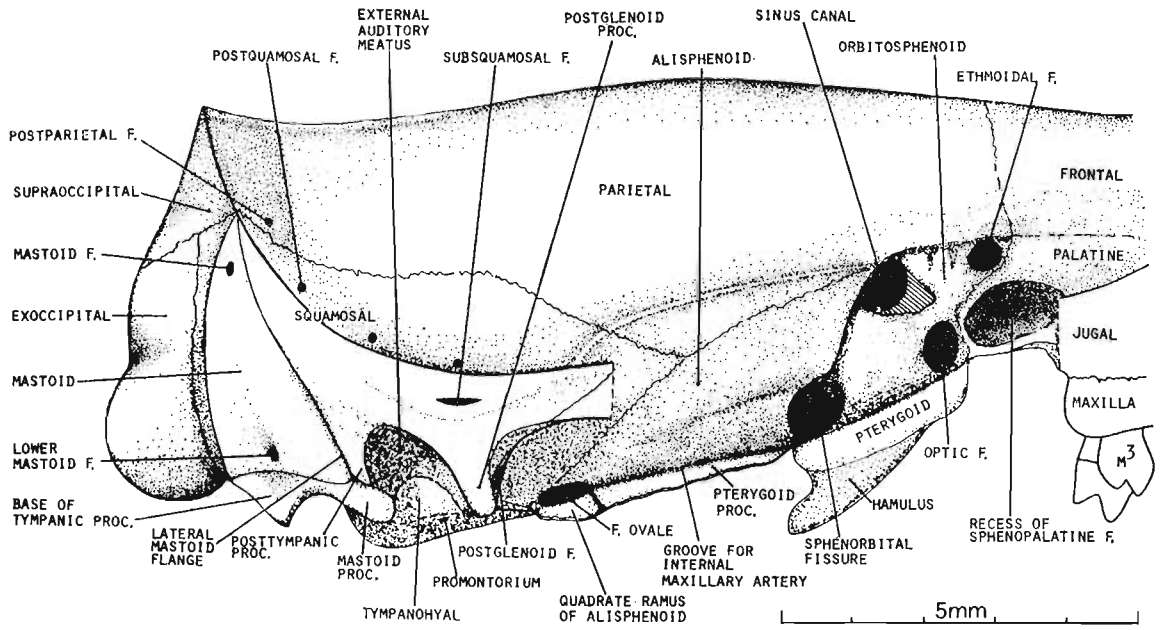


Fig. 1

Asioryctes nemegetensis KIELAN-JAWOROWSKA, reconstruction of the braincase in lateral view based upon ZPAL MgM-I/56 and partly upon ZPAL MgM-I/98.

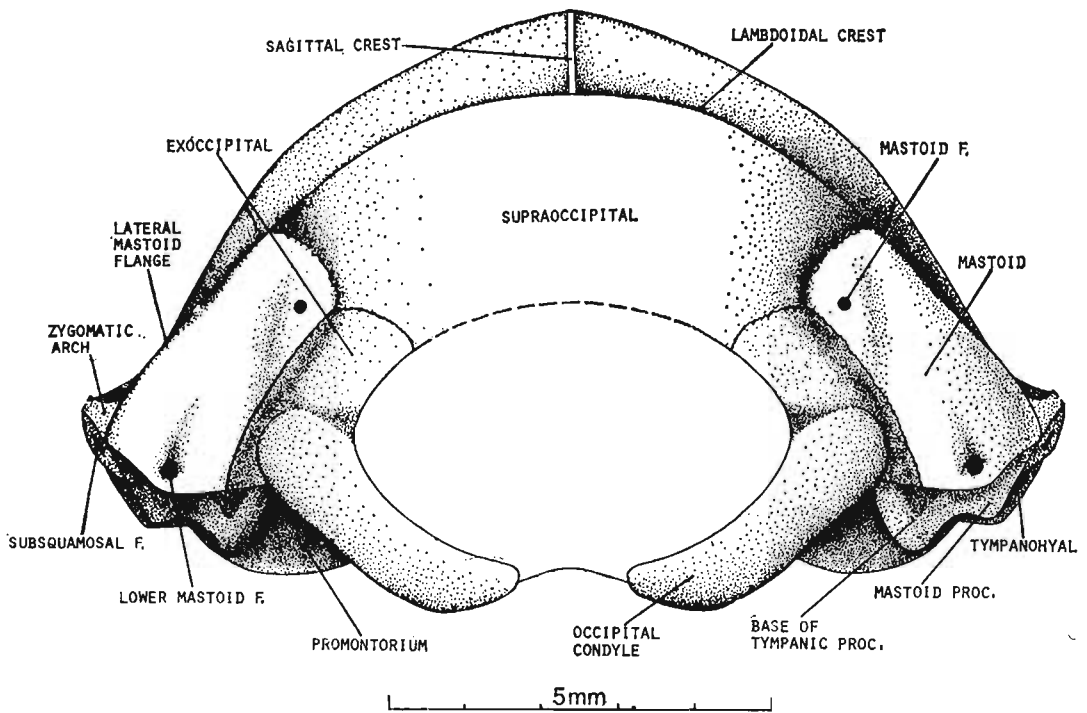


Fig. 2

Asioryctes nemegetensis KIELAN-JAWOROWSKA, reconstruction of the skull in occipital view based upon ZPAL MgM-I/56.

(united with foramen rotundum) at the posteroventral corner, at the boundary with the alisphenoid which forms only its lateral wall. The optic foramen is seen in lateral view to be relatively low, very close to its counterpart, with which it probably communicates. In no. 56 which is very well preserved, the surface of the orbitosphenoid on both sides of the specimen has a different appearance from those of the other bones, being much whiter and smoother. The anterior margin of the alisphenoid on both sides of no. 56. projects somewhat over the surface of the orbitosphenoid, which extends in front of it. Its edge appears to be broken. In all the specimens in which this region is preserved, the frontal also projects over the dorsal surface of the orbitosphenoid, but one cannot be sure whether this is not due to damage. The peculiar appearance of the orbitosphenoid (characteristic also of no. 98), and the broken anterior edge of the alisphenoid suggest that in life the posterior part of the orbitosphenoid was covered by a thin sheet of bone, extending anteriorly from the alisphenoid, as in the Tenrecidae and in some creodonts. If so, some of the foramina recognized in the orbitosphenoid were probably covered in life by the alisphenoid, and the nerves running through them left the area between the double walls of the braincase by a common fissure. It is, however, impossible to reconstruct the presumed position on this opening and of the free end of the alisphenoid.

Ventrally the orbitosphenoid is bounded by a prominent ridge of the pterygoid, which separates it from the presphenoid.

The pterygoid process. Opposite the sphenorbital fissure in no. 56 the surface of the pterygoid is broken off on both sides, however, the base of the pterygoid process is preserved on the right side. The entire pterygoid process is well preserved on the right side of no. 98, in which the posterior part of the right mandible has been removed, to display the temporal fossa. Because of the strong lateral flattening of the specimen, the bones of the lateral wall of the braincase have been badly crushed and partly displaced. The hamulus is, however, well preserved. It is a roughly triangular process with pointed and elongated posteroventral tip; the base of the hamulus extends between the optic foramen and fissura sphenorbitalis.

The alisphenoid seen from the side is roughly triangular, longitudinally elongated, and has a pointed anterodorsal corner that is higher anteriorly than posteriorly. Its sutures with the parietal and squamosal are reconstructed in figs. 1 and 3. The ventral part of the anterior margin of the alisphenoid, behind the sphenorbital fissure is inflated. Ventrally the alisphenoid is bordered by a prominent pterygoid ridge, built by the free edges of the alisphenoid and basi-sphenoid wing (see next section). At the posteroventral corner of the alisphenoid is a large foramen, elongated longitudinally, which I recognize as a foramen ovale. Although the posterior margin of the foramen touches the alisphenoid-squamosal suture, the foramen lies virtually within the alisphenoid, and it is for this reason that I call it foramen ovale and not pseudoovale. In ventral view this foramen is situated opposite the anterior part of the glenoid fossa. It is rimmed ventrally by the flange — a continuation of the pterygoid ridge. The flange, coming from the quadrate ramus of the alisphenoid, is strongly inflated in this region and protrudes somewhat posteriorly beyond the foramen (see next section).

At first sight it may seem incorrect to call the described foramen — f. ovale, as in no. 56 it is situated too far posteriorly with respect to the petrosal (and hence the probable position of the semilunar ganglion), to carry the mandibular branch of the fifth nerve. However, in spite of its good state of preservation, specimen no. 56 is somewhat distorted. It has been broken across the basioccipital, and the middle part of the basicranium (including both petrosals) was pushed forward, more so the right petrosal than the left one. In the undistorted skull, therefore, it seems likely that the foramen was anteromedial to the position of the semilunar ganglion. Another problem in the identification of this foramen is caused by the fact that on both sides of no. 56 the foramen does not lead directly into the braincase, but into the middle ear cavity, which is an impossible course for the Vth nerve. However, in *Tenrec* the part of the mandibular branch of the Vth nerve is separated from the middle ear cavity only by a thin sheet of bone that forms the roof of the cavity. If we imagine that this bone is broken on both

sides of no. 56, one can conclude that the path of V_3 in *Asioryctes* was more or less similar to that in *Tenrec*. Another indication that this foramen is the foramen ovale is provided by study of the position of the lower jaw in *Asioryctes*: the foramen points directly into the mandibular foramen in the lower jaw.

The alisphenoid canal is absent. Extending anteriorly from the foramen ovale, along the ventral margin of the alisphenoid, parallel to the pterygoid ridge, is a narrow, but distinct groove. Anteriorly the groove is pierced by small nutrient foramina distributed at random. The position of the groove and the absence of alisphenoid canal indicate that the groove may house the internal maxillary artery.

Choanae and basicranium (fig. 3). — *The vomer*. Because the choanal channels in no. 56 and in no. 70 are damaged and the sutures obliterated, it is impossible to state to what extent the vomer has been preserved. The elongated bone, forming the anterior part of the choanal roof in no. 56 is recognized tentatively as the vomer. The fragments of bone, preserved lateral to it, that are more complete on the left side, are identified as belonging to the palatine.

The pterygoid bones in no. 56 are probably completely broken off in the anterior part of the choanae, in front of the optic foramen. The fragments of the pterygoids are preserved in the posterior part of the choanae, opposite the presphenoid. They were described in the preceding section. It is not possible to say whether the maxillae extend backwards along the pterygoid laminae, as is characteristic of the Tenrecidae.

The narrow and concave *presphenoids* extend to the rear of the bone tentatively determined as a vomer. The lateral margins of the presphenoids are broken off. The length of the presphenoid is ca. 2.5 mm, and width ca. 1.9 mm. Just opposite the indefinite suture between the presphenoid and the basisphenoid there is a foramen, well preserved on both sides of no. 56, which might be a vidian foramen. The posterior margin of the presphenoid undulates markedly; along the margin on the left side of no. 56 two distinct tubercles of unknown function are distinguishable, between which the vidian foramen is situated. The presphenoid extends exactly between the optic and vidian foramina.

The basisphenoid consists of two parts: medial and lateral. The medial part is horizontal and of roughly triangular shape; it is flanked by the two lateral basisphenoid wings which are subrectangular, arranged obliquely with regard to the median part and project ventrolaterally. The wings are slightly concave in ventral view. On the right side of no. 56 the basisphenoid wing is somewhat displaced, arranged very steeply downwards and covering the medial part ventrally. On the left side of the same specimen the basisphenoid wing occupies more or less its natural position. The length of the median part is ca. 3.7 mm, the greatest width (one side) ca. 1.4 mm. The line which I identify as a basisphenoid-basioccipital suture extends transversally, nearly in line with the postglenoid process. To the rear of the suture there is another transverse line across the basisphenoid, which is probably a break. It might be, however, that the latter line is the basisphenoid-basioccipital suture, the posterior part of the basisphenoid forming a narrow, roughly rectangular plate, fitted snugly between the petrosals. The medial part is slightly concave. Extending posteriorly along the medial suture between the basisphenoids is a narrow, median ridge, prominent anteriorly and disappearing just before the basisphenoid-basioccipital suture. The lateral wing of the basisphenoid undulates irregularly. Its anteromedial corner embraces the posterior part of the vidian foramen. The anterolateral corner projects somewhat anteriorly beyond the medial part and contacts the presphenoid. It is also in contact with the pterygoid, but as the posterior ends of the pterygoids are broken on both sides of no. 56, this contact cannot be traced. Posteriorly the basisphenoid wing widens laterally; in its posterolateral corner there is an oval, concave area, which probably supports the ectotympanic. The posterior margin of both parts of the basisphenoid is strongly emarginated, embracing the promontorium anteriorly. This margin undulates, probably to house the carotid foramina, described below.

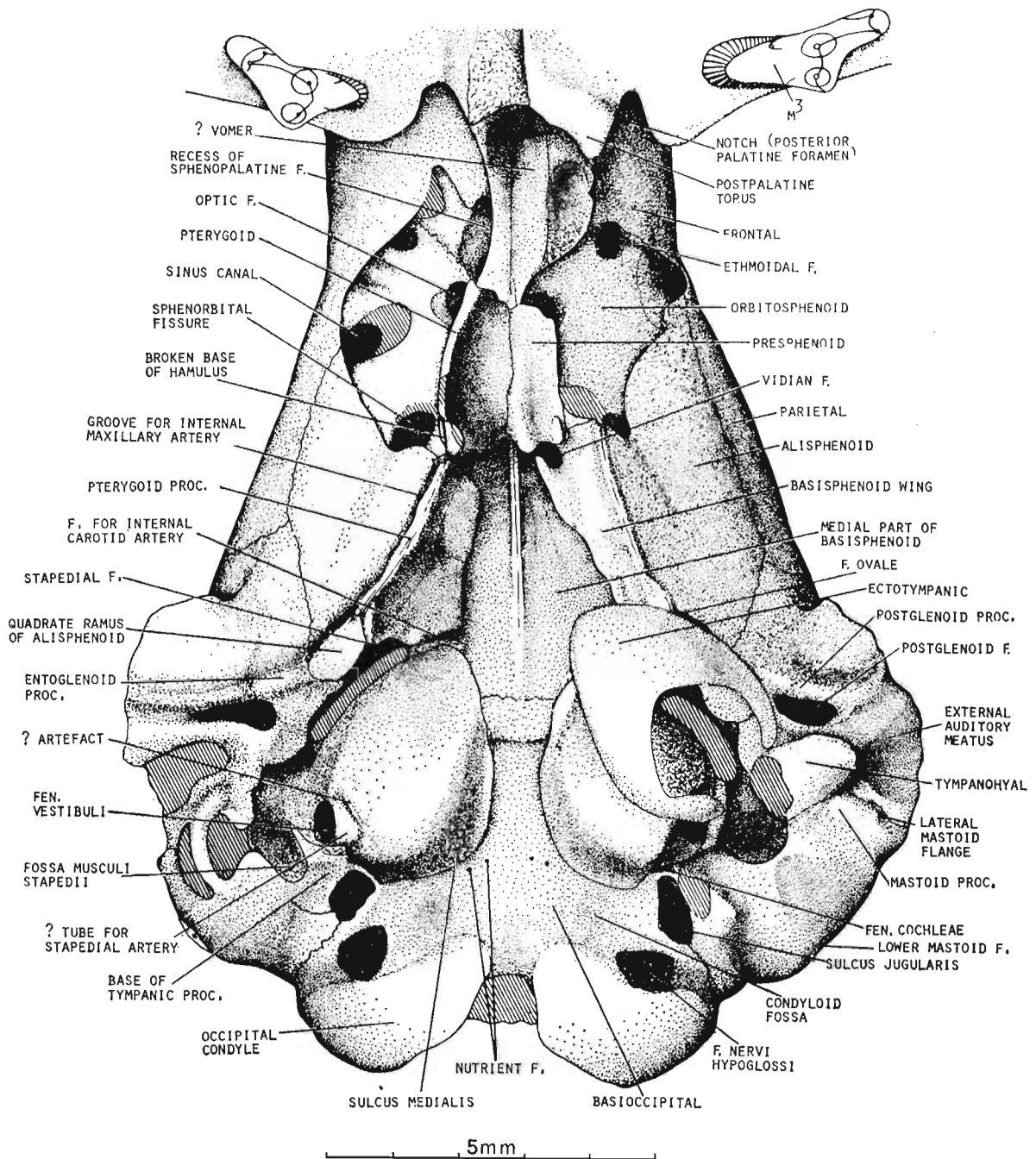


Fig. 3

Asioryctes nemegetensis KIELAN-JAWOROWSKA, ZPAL MgM-1/56, ventral view of the braincase, the right ectotympanic has been removed.

The lateral margin of the basisphenoid wing and the medial margin of the alisphenoid form together a prominent pterygoid ridge. This ridge is part of a continuous flange, which extends anteromedially from the medial border of the glenoid fossa, as a prolongation of the postglenoid process; the most anterior part of this flange is built up by the pterygoid bone. It is impossible to state how far the pterygoid bone extends posteriorly and to what extent it covers the pterygoid process of the basisphenoid and alisphenoid. Part of the flange, medial to the foramen ovale recalls the quadrate ramus of the eipterygoid (alisphenoid) of therapsids (BROILI and SCHRÖDER 1934, KEMP 1972) and triconodonts (e.g. *Morganucodon* see KERMACK

and KIELAN-JAWOROWSKA 1971). The quadrate ramus of the alisphenoid in therapsids and triconodonts is a slender bone tapering posteriorly; in *Asioryctes*, however, the corresponding part is strongly inflated.

CROMPTON and JENKINS (1979) demonstrated that the principal innovation in the structure of this region in triconodonts, in comparison with that of cynodonts is the formation of a floor to the cavum epiptericum. The floor is built of the quadrate ramus of the alisphenoid and the area occupied by cavum epiptericum is greatly reduced in triconodonts. Further reduction takes place in therian mammals. Unfortunately it was impossible to study the inside of the braincase of *Asioryctes* and because of the partial damage of the periotic in this region it is impossible to reconstruct the size and shape of the remnant cavum epiptericum. It should, however, be stressed that the inflation and relatively large size of the bone determined as quadrate ramus of the alisphenoid is a characteristic feature of the skull of *Asioryctes*. As it is so big it might mean that the remnant cavum epiptericum was still present in *Asioryctes*. The suture between the alisphenoid and the petrosal in this region is obliterated; it cannot be excluded that the remnant of the lateral flange of the petrosal was fused with the quadrate ramus of the alisphenoid.

The basioccipital (except for the anterior process inserted between the promontoria) is comparatively flat and wide. The occipital condyles are not very prominent. The condyloid fossae are shallow. F. nervi hypoglossi is situated posterolaterally to the condyloid fossa in a deep sulcus and has possibly become enlarged by preparation. Two small (possibly nutrient) foramina are present anteromedial to the condyloid fossa, the anterior one situated more medially. The basioccipital is clearly separated from the petromastoid by a distinct suture, well preserved on both sides of no. 56 and discernible also in no. 98. The suture extends anteromedially. It is situated very close to the occipital condyle posteriorly and reaches the medial edge of the sulcus jugularis anteriorly.

The squamosal. The glenoid fossa is situated lateral to the anterior part of the promontorium; it is gently concave, the postglenoid process protrudes weakly. Details of this are described under: "The promontorium". Lying posteromedially to the postglenoid process is a large, transversely elongated postglenoid foramen possibly greatly enlarged by preparation or preservation. The concave area of the external auditory meatus, described under "Cranial roof and posterior part of zygomatic arch" is well exposed in this view.

Ear region (fig. 3). — *The mastoid*, as seen in ventral view is an extensive bone; the suture which separates it from the squamosal is very distinct in no. 56 and no. 98. The tympanic process of the petromastoid which in *Kennalestes* is very prominent and rounded, protruding strongly ventrally, was probably also present in *Asioryctes*. It is completely broken off in no. 56, while in no. 98 on the right side the tip is missing, but the extensive, triangular base of the process is present. Lateral to the tympanic process of the petromastoid is a deep sulcus, which houses the foramen stylomastoideum primitivum. The lateral part of the mastoid is developed as a very weakly inflated rather large mastoid process, which abuts against the tympanohyal. The posterior part of the mastoid, behind the sulcus for the stylomastoid foramen, undulates markedly. The exact shape of the fossa musculi stapedii cannot be recognized with full certainty. It appears to be rather more oval than tear drop-shaped (as in *Kennalestes*), but the difference may be due to the damage of the *Asioryctes* specimens. The fossa is distinctly separated from the recessus fenestrae cochleae (see below) and from the fenestra vestibuli by a bony wall, which probably forms the basal strut of the tympanic process.

The ectotympanic. — In nos. 56 and 98 the ectotympanics were preserved on both sides. In no. 56 they were separated during preparation to show the details of the petrosal structure; their original position is shown on the photographs taken during preparation (see KIELAN-JAWOROWSKA 1975a, pl. I). In no. 98 the ectotympanics were left in their original position on both sides. Both the skulls were found with lower jaws in occlusion. I separated the lower jaws of no. 56, but not of no. 98. The photographs of both specimens with lower jaws preserved in

their original position (KIELAN-JAWOROWSKA 1975a, pls. 1 and 2) show the relation of the ectotympanic to the posterior part of the dentary. It can be seen from the above mentioned photographs that the ectotympanic does not lie to the rear of the dentary, as is characteristic of all mammals except the monotremes (BOLK *et al.* 1936, DABELOW 1928) but its anteromedial part is concealed by the angular process of the dentary. This position of the tympanic bone, which more or less fits the emargination in the posterior part of the dentary, clearly demonstrates that we are dealing here with the bone homologous to the angular of reptiles: i.e. with the ectotympanic and not the entotympanic. The ectotympanic in the Cretaceous forms studied preserves a very primitive anterior position.

The ectotympanic, when completely preserved, is a large bone (fig. 3), forming about 3/4 of a ring, open at its posterolateral-dorsal end. The ring is the widest at its anteromedial edge, strongly diminishing in width on both sides posterolaterally. Its posterior limb (homologue of the reflected lamina of the angular) is somewhat wider again, inflated and rounded. The anterior limb is also somewhat inflated and rounded, but not so conspicuous as the posterior one. The posterior and anterior limbs of the ectotympanic embrace the tympanohyal on both sides (fig. 3), the anterior limb abuts against the tympanohyal, while between the posterior limb and the tympanohyal, there is a short break. In *Asioryctes* the ectotympanic is inclined at about 45° to the horizontal plane. In no. 98 which is strongly compressed laterally, the ectotympanic occupies an almost vertical position due to distortion, but in no. 56 it appears to be in nearly the original position. In lateral view (KIELAN-JAWOROWSKA 1975a, pl. 1:1c, 1d) the rounded opening (porus acusticus externus) in the middle of the ectotympanic, occupied in life by the tympanic membrane is placed posteroventrally with respect to the glenoid fossa, just as in most mammals. The ectotympanic is less strongly inclined than the posterior part of the dentary, but the difference in the angle is not very great.

The horizontal position of the ectotympanic, observed in some modern mammals (in the monotremes and among the eutherians in e.g. the Soricidae) was regarded as a primitive character (van KAMPEN 1905, GREGORY 1910, van der KLAUW 1931). The position of the ectotympanic in *Asioryctes* demonstrates that this is not the case. Theoretically one can presume that the angular of the reptiles, when released from the lower jaw, primitively occupied an inclined position, being more or less parallel to the posterior part of the dentary. The position of the ectotympanic in *Asioryctes*, where this bone is situated still more anteriorly than in the more advanced mammals, shows that the inclined position (at least in the eutherian mammals) must be regarded as a primitive character.

The promontorium. — The promontorium is very large, pear-shaped, very strongly convex, highest posteromedially, with narrow, but rounded rostral apex. The promontorium bulge slopes gradually toward the rostral apex, more steeply posterolaterally towards the mastoid apex, and very steeply posteromedially toward the paroccipital apex. The promontorium is surrounded medially and anteromedially by a relatively wide, almost flat rim. The fenestra vestibuli is a comparatively large, oval opening on the lateral face of the promontorium; because of its state of preservation its dimensions cannot be given. The fenestra cochleae is probably situated in a large, ovoid, funnel-like structure, which I call the recessus fenestrae cochleae. This structure is better preserved in *Kennalestes*; in *Asioryctes* the details cannot be seen clearly. Probably the recess is somewhat smaller than in *Kennalestes*. The sulcus jugularis is clearly visible on both sides of no. 56. The contact of the petrosal with the basioccipital is well seen on the right side of no. 56. On the left side of the same specimen the medial edge of the petrosal is somewhat turned downwards and the crista promontorii is clearly visible, but the sulcus for the inferior petrosal vein is not discernible on either side of the specimen.

At the posteromedial corner of the promontorium, just medial to the very high slope of the posteromedial bulge, the promontorial surface is gently concave. This concavity extends as a groove anteriorly, along the medial margin of the promontorium and may be interpreted as a sulcus medialis, possibly for the medial internal carotid artery. The identification is to

some extent tentative, as the described groove is poorly defined, much less clearly than in Bug Creek petrosals (MACINTYRE 1972).

Lying medially to the fenestra vestibuli (on the right side of no. 56) is a distinct, roughly triangular inflation on the promontorium; the sulcus arteriae stapediae is absent. Posterior to this inflation the bone is missing on the right side. On the left side a larger piece of bone is missing medial to the fenestra vestibuli. The state of preservation of right promontorium suggests that the inflation is not an artefact; it cannot be excluded that this is a tube in which the stapedial artery was encased. However, any opening to the tube is hidden. It is either crushed on both sides of the skull, or open to the rear and almost confluent with fenestra cochleae. It might be situated in the recessus fenestrae cochleae. In front of the inflation there is a faint, extremely narrow furrow that extends anterolaterally. This is probably an artefact. The sulcus arteriae promontorii is absent.

On the lateral side of the promontorium, on both sides of no. 56 is a large opening in the roof of the middle ear, which separates the promontorium from the flange described above. It seems that in *Kennalestes* (no. 1) the middle ear roof is partially preserved in this region. A large vacuity (pyriform fenestra) occurs in the middle ear roof in the Solenodontidae and the Soricidae (MCDOWELL 1958). VAN VALEN (1966) recognized a small pyriform fenestra in *Palaeoryctes puercensis*, (AMNH 15923). It is certain that at least a part of a large vacuity in *Asioryctes* is due to distortion: therefore there is no basis for deciding whether the pyriform fenestra was present or not. As the lateral sides of both petrosals are destroyed in no. 56, the hiatus fallopi and the apertura externa canalis facialis are not preserved.

The rostral apex of the promontorium abuts against the basisphenoid. Lateral to the rostral apex is a sulcus on the medial part of the posterior margin of the basisphenoid wing (better preserved on the left side in no. 56), which might be a foramen for the internal carotid artery. On the right side of the same specimen the basisphenoid wing has been displaced somewhat medially and the foramen for internal carotid lies opposite rather than medial to the rostral apex.

Immediately lateral to the foramen for the internal carotid artery there is another sulcus in the posterior border of the basisphenoid wing, which I identify as a foramen for ramus inferior of the stapedial artery. A large foramen situated at the end of presphenoid transmitted a branch of stapedial artery. This has been identified as a vidian foramen.

On the right side of no. 56 there are two depressions in the postglenoid process. The first one is situated just behind the quadrate ramus of the alisphenoid, the other in front of the medial side of the postglenoid foramen, which was probably greatly enlarged by preparation. These two depressions are marked in fig. 3. If these are not artefacts the first one presumably housed the ramus superior of the stapedial artery, which could have joined (or become) the internal maxillary artery and proceeded along the groove in the alisphenoid in front of the foramen ovale (see figs. 1 and 3). The second groove may transmit the chorda tympani. If so, the part of the process bordering the glenoid fossa posteromedially, enclosed between the two grooves, would form the entoglenoid process.

KENNALESTES

(Figs. 4-9 and pls. 12-16)

The skull of *Kennalestes* has been described (KIELAN-JAWOROWSKA 1969) on the basis of less material than is now available. The braincase has not been described. Those parts already described are now described only in a few cases where new details are known.

The skull as a whole. — The skull of *Kennalestes* is somewhat smaller and less robust than of *Asioryctes*. The general shape and proportions are similar, except that the zygomatic

arch is less deep in *Kennalestes*. The length of the adult skull is about 26 mm, the length of the juvenile skull, in which the braincase is preserved, is 21 mm. The snout is narrow anteriorly, widening opposite the infraorbital foramen. The interorbital constriction is conspicuous, there is no postorbital process. The mesocranial region, which is comparatively short in a juvenile skull was probably longer in adult individuals, as in *Asioryctes*. The occipital plate lies at an angle of ca. 75° with regard to the plane of the teeth. The lower jaw is very slender, the coronoid process large, but smaller than in *Asioryctes*.

Snout, anterior part of zygoma, palate and orbit — see KIELAN-JAWOROWSKA (1969).

Cranial roof and posterior part of zygomatic arch (fig. 4). — *The parietals* are extensive and form the whole cranial roof posteriorly. In a previous publication (KIELAN-JAWOROWSKA 1969: 183) I stated that in no. 2: "A large part of the interparietal bone, separated from the parietals by a discernible suture is preserved..." The shape of the interparietal bone has been reconstructed in fig. 1E of the same paper. A comparison with a better preserved specimen, in which the posterior part of the cranial roof has been preserved (no. 44) shows that the line interpreted as a suture in no. 2 is an artefact, the interparietal bone being absent. The sagittal crest is very distinct, the lambdoidal crest slightly overhang the occipital plate medially. Lateroventrally opposite the mastoid the lambdoidal crest passes into the lateral

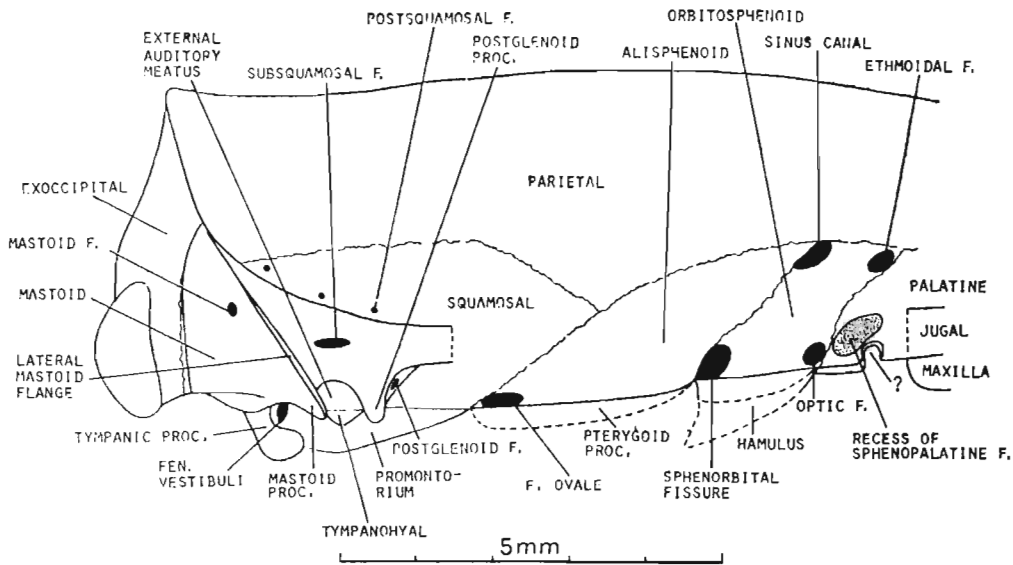


Fig. 4

Kennalestes gobiensis KIELAN-JAWOROWSKA, diagrammatical reconstruction of the lateral wall of the braincase based upon ZPAL MgM-I/1, ZPAL MgM-I/3 and ZPAL MgM-I/44.

mastoid flange (MACINTYRE 1972), which is very prominent and crescent-shaped. The suture between the parietals and supraoccipital (well seen in no. 44) extends to the very end of the cranial roof, just in front of the lambdoidal crest and parallel to it. The suture between the mastoid and the squamosal is not discernible, but probably extends along the ventral part of the lateral mastoid flange.

The squamosal contributes extensively to the structure of the lateral wall of the braincase. The posterior root of the zygomatic arch is placed far back (fig. 4). The zygomatic lamina which extends between the lateral wall of the braincase and the temporal crest is wide, roughly

triangular, and somewhat concave when seen in dorsal view. The temporal crest is very prominent opposite the zygomatic lamina; in the posterior part it forms a low ridge. The two crests (temporal and lateral mastoid flange) embrace the posterior triangular root of the zygomatic arch. A fissure-like subsquamosal foramen opens at the base of this triangle; in lateral view it is seen above and between the postglenoid and posttympanic processes, more posteriorly than in *Asioryctes*. The posttympanic process is very small, relatively smaller than in *Asioryctes*. In the ventral prolongation of the concave part of the squamosal, between the postglenoid and posttympanic processes, forming a recess for the external auditory meatus, lies the tympanohyal, described on p. 44. It is relatively smaller than in *Asioryctes*. The postparietal foramina cannot be distinguished with any certainty, although there are possible traces in no. 1; three (or four) postsquamosal foramina are recognized on the left side of no. 1, just above the temporal crest, as in *Asioryctes*. The suture between the squamosal and parietal looks as if it follows a similar course to that in *Asioryctes*.

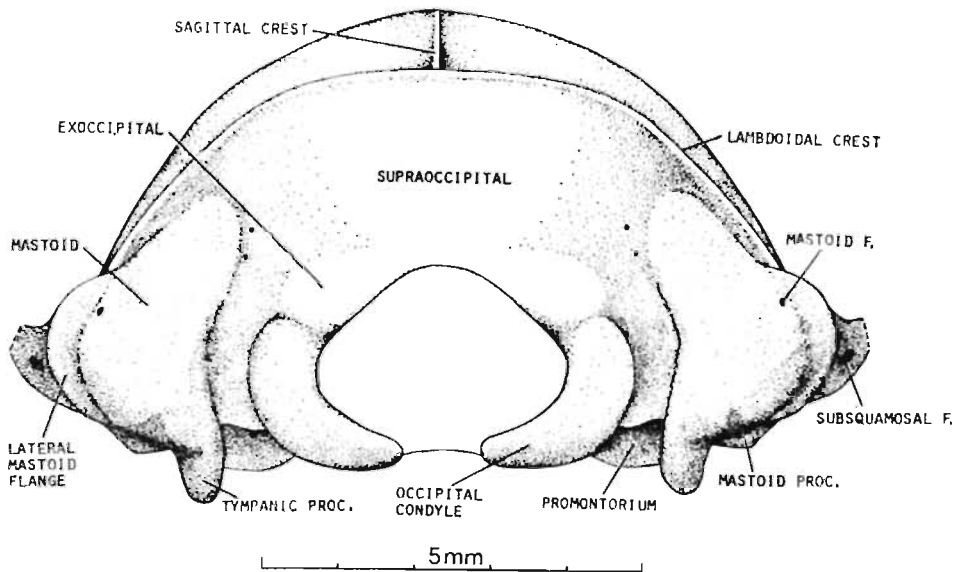


Fig. 5

Kennalestes gobiensis KIELAN-JAWOROWSKA, reconstruction of the skull in occipital view based upon ZPAL MgM-1/1 and ZPAL MgM-1/44.

Occiput. (fig. 5) — The occipital plate is fragmentarily preserved both in no. 1 (see KIELAN-JAWOROWSKA 1977, pl. 16:1) and in no. 44 (pl. 16:2d). The semicircular outline of the occipital plate is deranged by the ventral parts of the mastoid flanges, which protrude laterally as prominent crescents.

The occipital bones. The occipital condyles are prominent, extending to two thirds of the height of the foramen magnum. Dorsally they are bounded by a wide, roughly horizontal furrow. There are some indistinct protuberances of the exoccipitals (or supraoccipital) above the occipital condyles. The suture between the supraoccipital and exoccipital is not discernible. The suture between the exoccipital and mastoid is distinguishable only in the lower part of the occiput, extending parallel to the condyle, some distance lateral to it. The surface of the exoccipital between the condyle and the mastoid is relatively wider than in *Asioryctes*, but as in *Asioryctes* the paroccipital process is not developed.

The mastoid is large, roughly triangular, strongly convex posteriorly, especially in the ventromedial part. The mastoid differs in shape from that in *Asioryctes*, where it is more rectangular than triangular. The foramina on the mastoid are also different. In *Kennalestes* only

one mastoid foramen is recognized, situated half way along the bone, close to the suture with squamosal. It is called the mastoid foramen. The lower mastoid foramen, characteristic of *Asioryctes* is absent in *Kennalestes*.

In addition two small foramina are present on the occipital bone, close to and opposite the upper part of the mastoid. The mastoid sends two processes ventrally. The lateral, small mastoid process, which is not inflated and abuts against the posttympanic process of the squamosal, and the medial, very prominent tympanic process of the petromastoid. The latter is roll-like, with rounded tip, strongly protruding ventrally and anteriorly in lateral view and slightly incurved lateroventrally in posterior view. It is very well preserved in no. 44 (pl. 17: 2a and fig. 7) and present also on the left side of no. 1, although in the latter specimen it is somewhat compressed against the promontorium.

Temporal fossa (fig. 4). — This is badly damaged in all the specimens. In no. 1 it has been preserved on both sides of the skull, but is badly crushed and the dorsal part is missing; in nos. 2 and 3 the orbitosphenoid is preserved on both sides and there appear to be four foramina piercing it on the right side of no. 3 and less clearly on the right side of no. 2; in no. 44 a fragment of the right temporal fossa has been preserved.

The orbitosphenoid is comparatively small, elongated in the posteroventral-anterodorsal direction. As in *Asioryctes* the anterior margin of the alisphenoid and the ventral margin of the frontal somewhat overlap the orbitosphenoid. The surface of the orbitosphenoid, as preserved in no. 1 is whiter than that of the other bones, which indicates that in life at least the posterior part of the orbitosphenoid was probably covered by the alisphenoid, as in *Asioryctes*. Extending parallel to the orbitosphenoid-alisphenoid suture and close to it, is a distinct ridge on the orbitosphenoid.

The following foramina are distinguishable in the orbitosphenoid, similarly arranged as in *Asioryctes*: the ethmoidal foramen, placed at the anterodorsal corner, the larger foramen of the sinus canal, posterior to it, the optic foramen at the anteroventral corner and the sphenorbital fissure united with the foramen rotundum, at the posteroventral corner, at the boundary with the alisphenoid. The optic foramen is situated very low as seen from the side.

On *the palatine bone*, in front of the optic foramen there is a large recess, as in *Asioryctes*.

The alisphenoid is more extensive than the orbitosphenoid, and probably similar in shape to that of *Asioryctes*. Along its ventral border a prominent pterygoid ridge, as in *Asioryctes*, extends from the sphenorbital fissure towards the medial margin of the postglenoid process. The foramen ovale cannot be recognized with any certainty. In no. 1 it is obscured by the ectotympanics, which on both sides moved somewhat forward. In no. 44 there is a notch (fig. 7) in front of the medial margin of the glenoid fossa. In this part of the skull in *Asioryctes* there is a foramen below the pterygoid ridge which I identify as a foramen ovale (see figs. 1 and 3); it rather suggests that the notch described in no. 44 might be a foramen ovale.

Choanae and basicranium (figs. 6 and 7). — The choanal region has been described earlier, on the basis of specimens no. 2 and no. 3 (KIELAN-JAWOROWSKA 1969). In no. 1, which is a juvenile specimen, the posterior part of the hard palate has not yet developed (the last tooth is M²). On the lateral wall of the choanal channel, made by the palatine, there is a round notch (or foramen), well preserved on both sides of the specimen, of unknown function. In no. 1 in the middle of the choanal channel there is a fragment of longitudinal bone, which might be the vomer (fig. 6). The bones which form the lateral walls of the choanal channels, and protrude ventrally as distinct ridges are identified as pterygoids. They are preserved only in no. 1, where on the left side of the specimen there is a suture within the anterior part of the temporal fossa separating the pterygoid from the palatine. On the right side this suture is less clear. There are no definite sutures within the choanal channels, separating the pterygoids from the palatines.

The presphenoid. The interpretation of the anterior part of the basicranial region is very difficult due to the crushing and distortion of specimen no. 1. In other specimens this region is only fragmentarily preserved. The fragment of the presphenoid has been preserved in no. 2, where a suture between the palatine and presphenoid is clearly identifiable. It extends transversely, opposite the optic foramen.

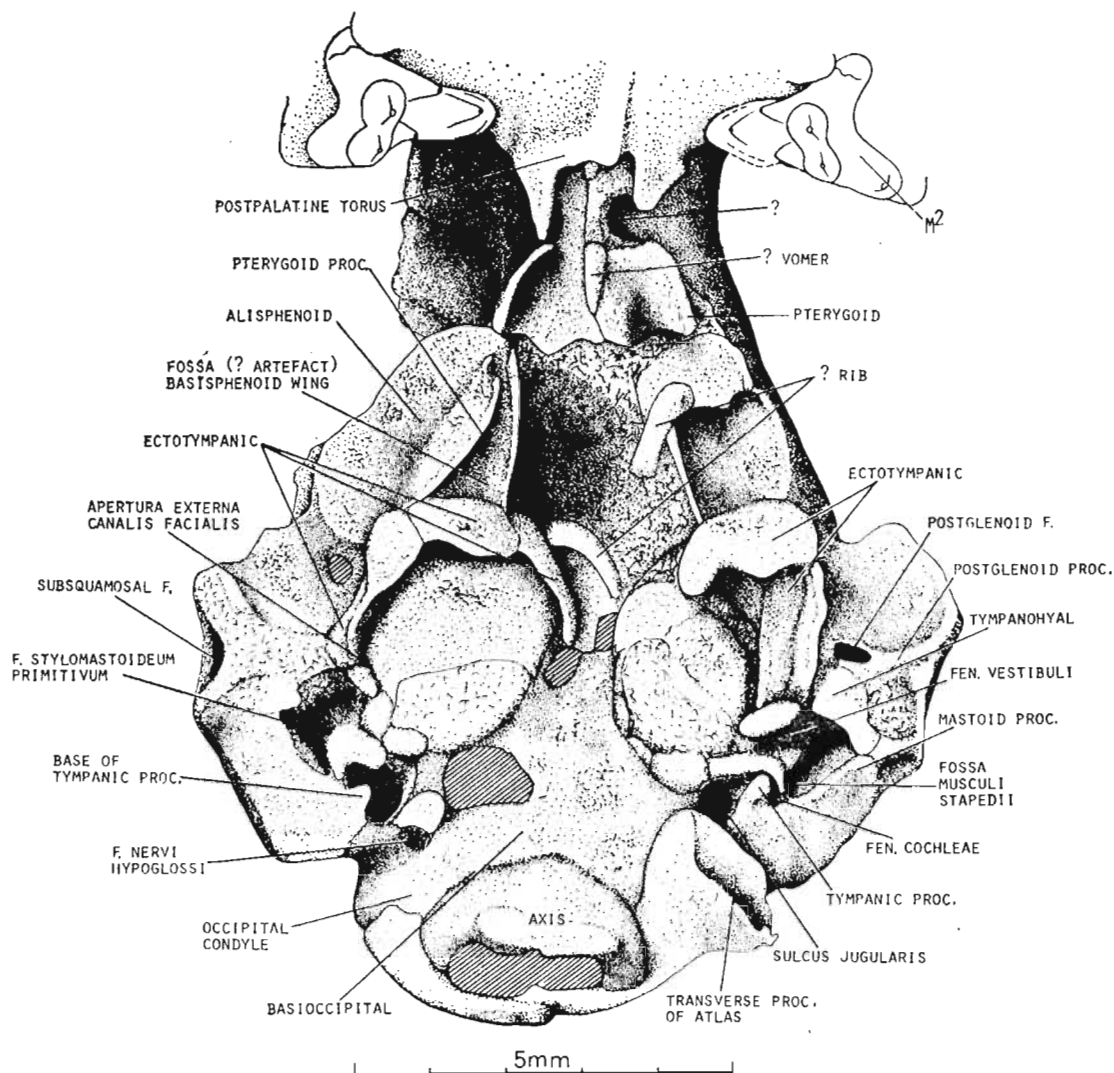


Fig. 6

Kennalestes gobiensis KIELAN-JAWOROWSKA, ZPAL MgM-I/1, ventral view of the braincase.

The basisphenoid has not been preserved in any specimen. In no. 1 the middle part of the skull is badly damaged and filled with matrix. The anterior part of the basicranial region, as preserved in no. 1, appears at first glance very different from that in *Asioryctes*. In this specimen, in front of the petrosal and surrounded by the ectotympanic there is a fossa, preserved on both sides of the specimen. However, I regard this fossa as an artefact due to distortion. It does not occur in nos. 2, 3 and 44, in which small fragments of this region are preserved. Also in *Asioryctes* which is very closely related to *Kennalestes* this fossa does not occur. The apparent ridge, which surrounds the fossa medially in no. 1 is probably an upturned medial corner of the basisphenoid wing. In *Asioryctes* the basisphenoid wing is somewhat concave. One can visualize that if the structure of this region was in *Kennalestes* similar to that in *Asio-*

ryctes, the basisphenoid wings on both sides of the skull of no. 1 become displaced and compressed laterally, creating the apparent fossae. The outer ridge which borders the fossa is probably a homologue of the pterygoid process of *Asioryctes*¹. As in *Asioryctes* it extends anteromedially along the medial edge of the glenoid fossa and partly supports the ectotympanic. As in *Asioryctes* the most posterior part of the ridge is probably formed by the squamosal, the middle by the alisphenoid and the basisphenoid and the most anterior by the pterygoid. However, the sutures between the particular bones in this region cannot be identified. Part of the pterygoid process is preserved in no. 44, but in the middle of its course the process is broken off; a fragment of it is also present on the right side of no. 3. In no. 1 (where the ridge is preserved on both sides of the specimen) the left side, which is less distorted than the right, is not very prominent and is similar to that in *Asioryctes*. It cannot be excluded that the basisphenoid wing was in *Kennalestes* arranged more horizontally than in *Asioryctes*, recalling the condition in *Leptictis* — (see p. 62–63).

The basioccipital is badly damaged in no. 1. The foramen nervi hypoglossi is visible only on the right side of the skull, as on the left side it is concealed by the processus transversus of the atlas. The occipital condyles have been described on p. 41.

The squamosal. The glenoid fossa is lateral to the anterior half of the promontorium; is moderately concave, bounded posteriorly, and partly posterolaterally by the postglenoid process, which has the shape of a rounded ridge. In no. 44 and on the left side of no. 1, in the medial prolongation of the postglenoid process there is a break, which represents the postglenoid foramen. On the right side of no. 1 this part is badly damaged.

The tympanohyal appears to be a triangular process, with a wide base. It is relatively smaller than in *Asioryctes* and differently shaped (rectangular in *Asioryctes*). Ventrally the tympanohyal conceals the lateral part of the fossa musculi stapedii and its tip abuts against the bent part of the ectotympanic. It is preserved on the left side of no. 1, on the right side of the same specimen it is partly broken off and reconstructed in fig. 6; its base is also preserved in no. 44.

Ear region (figs. 6, 7 and 8). — *The ectotympanic* is preserved only in no. 1, on both sides of the skull. As the angular process of the lower jaw is broken off, the relation of the ectotympanic to the posterior part of the lower jaw cannot be described in detail. Judging from the preserved parts (see photograph taken before the separation of the lower jaws, pl. 12:1b) the ectotympanic was partly concealed by the posterior part of the dentary, and situated probably even more anteriorly with regard to the dentary than it is in *Asioryctes*. The ectotympanic is a large, semicircular bone, broken into four parts on the right side of no. 1 and into three parts on the left side. By comparison with the ectotympanic of *Asioryctes* one can presume that the free margin of the ectotympanic is on both sides of no. 1 missing and that the medial edge of the ectotympanic probably formed 3/4 of a ring, which is open posterolaterally, widened anteriorly and elongated into a tip at its anteromedial edge. On the left side, the preserved part of the ectotympanic is shifted anterolaterally with regard to its original position, whereas on the right side it occupies more or less its original position.

The promontorium and the mastoid. The promontorium is very large (as in *Asioryctes*); it is strongly convex in both the longitudinal and transverse profiles, but not as high in the posteromedial part as in *Asioryctes*. Judging from the preserved part in no. 44 the rostral end was probably pointed. The fenestra vestibuli is a large, oval opening in the lateral face of the promontorium, 0.7 mm long in no. 2 and 0.5 mm long and 0.25 mm wide in no. 44. The fenestra cochleae, at the posterior end of the promontorium, lies in the anterior part of a large,

¹ A fossa-like cavity occurs in front of the promontorium in the Erinaceidae. BUTLER (1948) called the ridges which border it the internal and external pterygoid ridges. But, as I think that only one ridge was present in the skull of *Kennalestes*, and it is doubtful whether this structure is homologous to the external pterygoid ridge of the Erinaceidae, I call the ridge in question a pterygoid ridge.

ovoid, funnel-like recessus fenestrae cochleae. The recess appears larger than in *Asioryctes*. The fenestra cochleae occupies more than half of the total length of the recess. In no. 2 the length of the recessus fenestrae cochleae is 0.88 mm and the length of the fenestra vestibuli is 0.8 mm. In no. 44, the two fenestrae are respectively 0.53 mm and 0.5 mm long. It is, however, possible that in both described specimens the fenestrae have been somewhat enlarged by preservation or by preparation, particularly so in no. 2. The measurements of the fenestra vestibuli, fenestra cochleae and recessus cochleae in no. 1 cannot be given, as the openings cannot be fully cleaned because of their positions. The posterior part of the recess for the fenestra cochleae has a rounded floor vising to vertical walls. It is separated at its posterolateral end by a narrow wall of bone from the fossa musculi stapedii. This wall of bone is really the base of a strut-like support for the prominent processus tympanicus, which rises to a rounded tip just behind the fenestra cochleae from a relatively stout base. The recessus fenestrae cochleae is probably, therefore, nothing but a pocket formed by the growth of this basal strut, correlated with the large size of the tympanic process and ultimately with the large ectotympanic bone. It is nevertheless a diagnostic character in the ear region of *Kennalestes* and is not seen in the Bug Creek petrosals (MACINTYRE 1972).

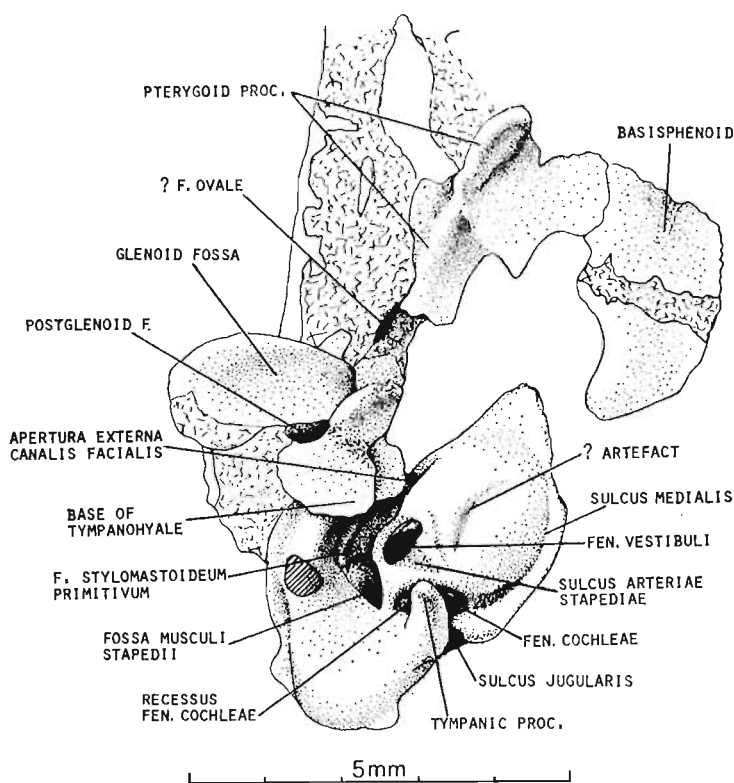


Fig. 7

Kennalestes gobiensis KIELAN-JAWOROWSKA, ZPAL MgM-1/44, fragment of the posterior part of the braincase with right petrosal, in ventral view.

In ventral view the tympanic process is preserved in no. 44 and on the left side of no. 1. In the latter specimen it is less stout than in no. 44 and (due to post-mortem distortion) is sharply bent, and now lies over the recess for the fenestra cochleae. The sulcus jugularis is a shallow, nearly vertical notch, located between the base of the tympanic process and the posterior end of the promontorium. The sulcus jugularis is clearly visible in no. 44. On the right side of no. 1,

as a result of damage, the sulcus jugularis is confluent with the fenestra cochleae. Extending posterolaterally from the sulcus jugularis is a more or less irregular area, where the exoccipital bone was in contact with the mastoid portion of the petrosal. Extending anteromedially along the medial edge of the promontorium, the prominent crista promontorii medio-ventralis is clearly visible in no. 44. It indicates the area that was in contact with basioccipital bone. In no. 1 the contact of both petrosals with the basioccipital is well preserved, but as the posterior part of the promontorium is preserved on both sides only as a matrix endocast of the cochlea, both cristae promontorii were lost from this specimen.

The apertura externa canalis facialis petrosi is preserved in no. 44 as a small, rounded opening, situated dorsal to the fenestra vestibuli, somewhat in front of the most anterior part of it (fig. 7). In no. 2 it is somewhat damaged, while in no. 1, it is hardly recognizable on the right side of the specimen, just in front and inside of the bent posterior part of the ectotympanic bone. Behind the apertura externa, there is a clearly defined sulcus facialis for the main (hyoid) trunk of the facial nerve. The sulcus facialis is well preserved only in no. 44, and in this specimen, there is a narrow, thread-like, slit in the bottom of the sulcus which disappears in the neighbourhood of the tympanohyal. However, the slit seems to be too narrow to house the facial nerve and is probably due to post-mortem damage. The lateral side of the petrosal is damaged in both no. 2 and no. 44, while in no. 1 it is concealed by the ectotympanic, and the hiatus fallopii is not visible as a separate opening.

The foramen stylo-mastoideum primitivum is not actually developed as a definite foramen, but rather as a sulcus defined by the tympanohyal. It appears as a shallow, smooth, notch dorsal and posterior to the base of the tympanohyal, at the point where the sulcus facialis widens, turns off and passes into the fossa musculi stapedii. The fossa musculi stapedii is arranged at an angle of about 110° with regard to the sulcus facialis and forms a common depression with the sulcus, but is distinguishable from it by being deeper. The fossa musculi stapedii is large and has a tear-drop shape, the rounded end in the direction of the sulcus facialis and the pointed end towards the tympanic process. This fossa is deep and clearly separated from the fenestra vestibuli and the recessus fenestrae cochleae by the basal strut on the tympanic process described above, which has a sharp anterior edge on the side toward the fossa musculi stapedii.

The crista promontorii medio-ventralis is strongly developed. This crest, which along its medial edge normally delimits the sulcus sini petrosi inferior, seems to be slightly broken in no. 2 and no. 44 and therefore the groove for the inferior petrosal vein cannot be identified with any certainty. In ventral view the bulge of the promontorium is surrounded by a shallow sulcus medialis, for the medial internal carotid artery. This sulcus separates the bulge from the flat medioanterior rim, which forms the ventral wall of the crista promontorii.

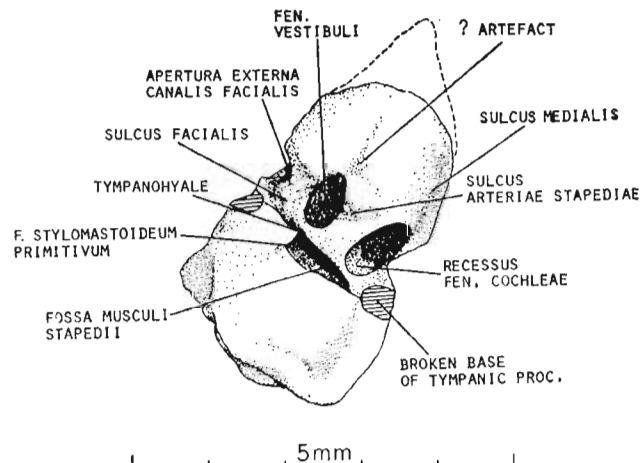


Fig. 8

Kennalestes gobiensis KIELAN-JAWOROWSKA, ZPAL MgM-1/2, right petrosal in ventral view.

The sulcus for the stapedia artery is definitely recognized in nos. 2 and 44; in no. 1, due to the state of preservation (endocast), it cannot be seen. The sulcus arteriae stapediae extends in no. 44 (fig. 7) medially from the posterior part of fenestra vestibuli; it is deep and wide near the fenestra and becomes shallower and narrower medially. In no. 2 (fig. 8) the sulcus extends from opposite the middle part of the fenestra and has the same course as in no. 44. In Bug Creek petrosals (MACINTYRE 1972) the lateral margin of the sulcus extends along the whole length of the fenestra vestibuli, whereas in two specimens of *Kennalestes* it extends only about half the length of the fenestra. This may be due to the fact that in the described specimens the fenestra has been enlarged by preparation or by preservation, and the original length of the fenestra possibly corresponded to the length of the lateral margin of the sulcus arteriae stapediae.

The sulcus arteriae promontorii appears to be absent. In no. 1 it is undistinguishable, although the bone is preserved in this area. In nos. 2 and 44 the surface of the lateral part of the promontorium wall is uneven and some indistinct grooves are present, differing, however, in their shape and position. In no. 2 there is a very faint groove bent at almost a right angle, which is an impossible course for an artery, placed in front of the fenestra vestibuli. In no. 44 there is a similar groove, less sharply bent and situated more medially, about half way between the fenestrae vestibuli and cochleae. In addition there is another transverse furrow between the above described groove and the sulcus arteriae stapediae. I am of the opinion that these grooves are artefacts.

Cerebellar side of the basicranium (fig. 9). — The cerebellar side of the basicranium is well exposed in no. 1, but the anterior part of the region is covered with matrix and broken bones of the cranial roof, and only the two petrosals, the basioccipital and part of the squamosal may be examined. The cerebellar side may be examined in two other available petrosals (no. 2 and no. 44). Of four studied petrosals the cerebellar side is best preserved on the left side of no. 1, the right petrosals of the same specimen being broken in two places and somewhat distorted. In no. 44 it is well preserved, but because the cranial roof is in the way it may be seen only in oblique view from the medial side. In no. 2 this side is badly damaged.

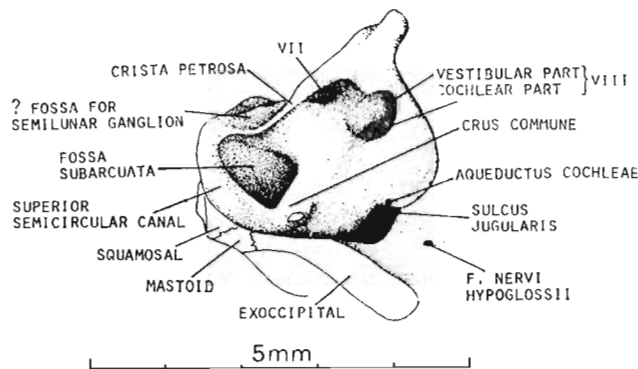


Fig. 9

Kennalestes gobiensis KIELAN-JAWOROWSKA, ZPAL MgM-I/1, endocranial view of the right side of the braincase, showing the details of the petrosal.

The mastoid portion of the cerebellar side of the petrosal is occupied by a very large, deep, roughly circular subarcuate fossa, encircled laterally and dorsally by the superior semicircular canal, and medially by the crus commune. A very sharp and prominent crest (crista petrosa) starts from the lateral margin of the subarcuate fossa and becomes less sharp and more rounded anteromedially towards the rostral apex. The crista petrosa divides the petrosal into cerebellar and squamosal sides. On the petrous portion of the cerebellar side there are two foramina. The first one, smaller, situated just under the crista petrosa, and partly delimited by the crista

dorsolaterally, is for the cranial nerve VII and continues in the petrosal ventrolaterally as the canalis facialis. Below this foramen and towards the midline there is another, larger foramen of nerve VIII subdivided into two parts: vestibular and cochlear, the latter situated dorso-laterally with regard to the vestibular part. The foramen for nerve VII and the foramina of VIII are situated together in a common big fossa of the internal auditory meatus. These details are clearly visible on both sides of no. 1 and partly visible in no. 44; but in this specimen the division of the foramen for VIII into two parts cannot be distinguished and the crista petrosa is not entirely prepared. In no. 2 the posterior and medial walls of the fossa subarcuata are broken so that the external gyri of the semicircular canals and crus commune are visible because the sheet of bone connecting them is missing. The crista petrosa and the upper part of the facial nerve canal is also broken off, so the foramen for VII appears to be a sulcus in this specimen. The bone between the two parts of the foramina for VIII is missing in this specimen. A small rounded opening situated ventromedially with regard to the foramen for VIII, is an artefact.

The medioventral margin of the petrosal is strongly incurved opposite the boundary between the fossa subarcuata and internal auditory meatus. This incurvature is the sulcus jugularis, which passes ventrally. In the anterodorsal corner of the sulcus jugularis in both petrosals of no. 1 and in no. 44 there is a minute foramen; this is the apertura externa aqueductus cochleae (ductus perilymphaticus). In all the available petrosals, there is a small but distinct node on the crus commune, about half way up. Near it, perhaps in the depression at the top of this node, one should expect to find an apertura externa aqueductus vestibuli for the ductus endolymphaticus. However, this opening is normally very minute and cannot be positively identified in these bones. Medial to the sulcus jugularis, on both sides on no. 1, there is a distinct, small round foramen in the exoccipital, which is a foramen nervi hypoglossi. The exoccipital is completely fused to the basioccipital. On the squamosal side of the petrosal, just below the crista petrosa near the junction of the mastoid and petrous portions, the bone is slightly concave. As a result of this concavity, the lateral margin of the petrous portion is slightly incurved at the boundary with the squamosal just behind the rostral apex. The semilunar ganglion of the fifth trigeminal nerve (V) may have been located in this area, but there is no clearly defined fossa.

LOWER JAW

ASIORYCTES

(Fig. 10 and pls. 4:2, 5:2 and 2*b*, 6, 7:1 and 2, 8:1*b-1g*, 9:1 and 2, 10:1*d-1f* and 2, 11:1*b-1g*)

Complete lower jaws are preserved in nos. 56 and 98, but are incomplete or fragmentary in nos. 73, 74, 87, 134, 144, 148.

The lower jaw consists of a slender body and a large ramus. The body strongly tapers anteriorly and narrows somewhat posteriorly being at its highest below M_1 . The alveolar border is nearly straight anteriorly and convex upwards between P_3 - M_3 . The tooth row is about 65% of the total length of the dentary. The lower margin is convex opposite the alveolar border and concave below the masseteric fossa. The coronoid process slopes steeply upwards; it is high and has a nearly transverse upper margin. As the coronoid process passes dorsally it curves medially. The masseteric crest starts from the middle of the height of the body and is very stout and prominent particularly at the base. The coronoid fossa is deep, sharply limited by the masseteric crest and a less prominent ridge below. There is also a very faint ridge which extends along the upper margin of the fossa; this is best seen on the left side of no. 98, which is somewhat larger than the other specimens. The masseteric fossa is deepest at the anteroventral corner. The angular process when seen from the side is roughly rectangular, directed posteroventrally; in dorsal and ventral views it may be seen to be inflected inwards.

The posterior margin forms two concavities, separated from each other by the condyle, which is situated high above the level of the teeth, on a distinct neck; the condyle appears pear-shaped when viewed from the side. In top view the condyle is roughly trapezoidal and widens posteriorly.

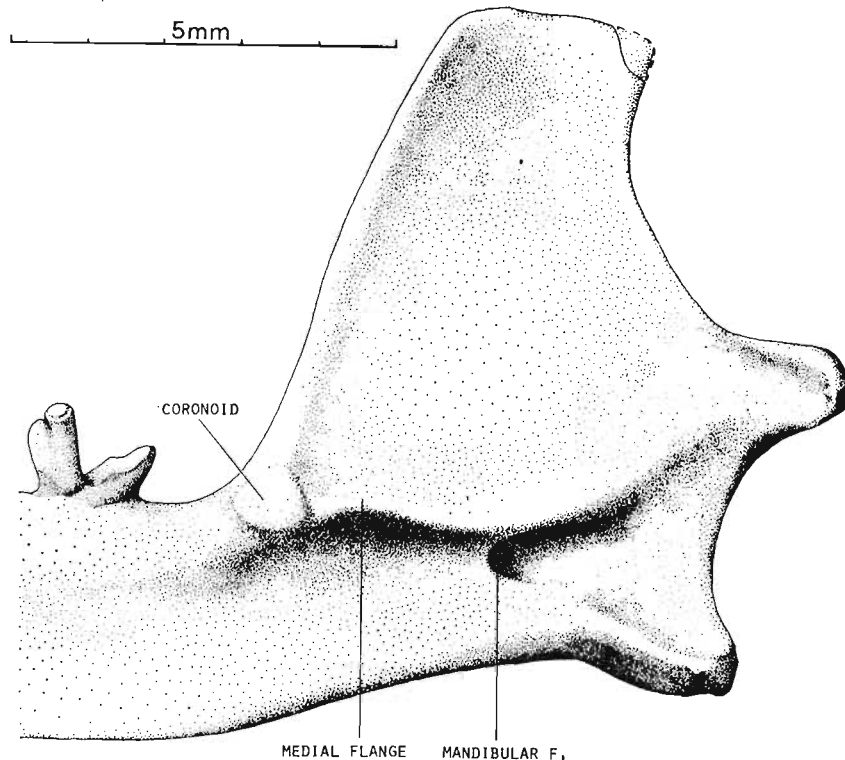


Fig. 10

Asioryctes nemegetensis KIELAN-JAWOROWSKA, ZPAL MgM-I/56, posterior part of the lower jaw in inner view.

The number of mental foramina varies from 3 in no. 98 to 4 in the left jaw of no. 56, and 6 in the right jaw of the same specimen. In other specimens because of the state of preservation or the incompleteness of the material the number of foramina cannot be ascertained.

The symphysis forms a large, crescent-shaped area, which reaches back as far as P_2 . The symphyseal surface is strongly rugose; it is bounded from above by the symphyseal ridge, which extends from the front of the jaw as far back as P_1 . The ridge is bounded from below and from above by distinct thread-like grooves. Otherwise the mandibular ramus is completely smooth and there is no trace of any internal mandibular groove. The coronoid process is in medial view gently concave, the concavity being deepest at the antero-ventral corner. Immediately in front of this deepest part there is a distinct, rounded swelling at the base of the ascending ramus of the coronoid process. I regard this swelling as a remnant of the coronoid bone, fused with the dentary. In no. 56 the diameter of the remnant coronoid is ca. 1 mm, in no. 134 ca. 0.8 mm. In both jaws of no. 56 the coronoid is surrounded by a very faint furrow, visible only under high magnification. In the left jaw of no. 134 the coronoid has a somewhat different colour than the surrounding bone and is separated from it by a very faint suture-like line. It seems that in no. 134 the coronoid has a somewhat different shape than in no. 56, being provided with an anterior spine-like projection.

Behind and below the remnant coronoid there is a ridge (medial flange of KERMACK *et. al.* 1973) which extends posteriorly and disappears some 1.6 mm in front of the posterior margin. In the middle of its course the medial flange is slightly bent, convex below. The mandibular

foramen is large, situated in no. 56 ca. 4.5 mm behind the last molar. Running posteriorly from the mandibular foramen is an oval-shaped fossa sharply delimited from above by a medial flange. The fossa is smooth, not divided by ridges.

The angular process is prominent, roughly rectangular in shape, strongly bent medially. The lower boundary of the angular process forms a ridge, which extends for ca. 2 mm from the end of the process and then continues anterodorsally along the mandibular ramus. The ridge divides the angular process into a large, concave dorsal side and a small ventral side, a part of which is visible in medial view below the anterior part of the ridge.

KENNALESTES

(Fig. 11 and pls. 7:3, 12:1a and 1b, 13:1a and 1b, 17:3)

The lower jaw of *Kennalestes* has been described and figured by KIELAN-JAWOROWSKA (1969). In this paper I would like to mention only some features of the structure of the posterior part of the dentary, not discussed previously. The coronoid process has been broken in all the specimens except the right lower jaw of no. 3, where, however, it is badly damaged and the posterodorsal part is missing. In contrast to *Asioryctes*, in the left lower jaw of no. 3 the coronoid bone appears to be completely fused with the dentary. The dentary here is distinctly swollen, but no trace of a suture can be recognized. In the left lower jaw of no. 3, which is less complete, one can trace under high magnification a small coronoid (ca. 0.6–0.7 mm of a diameter) surrounded by an indistinct suture. The mandibular foramen, preserved only in the right lower jaw of no. 3 is situated ca. 5.3 mm behind the last molar; thus it is further back than in *Asioryctes*, for, though the lower jaw of *Asioryctes* is larger, the foramen is placed only 4.5 mm behind the last molar. The medial flange is less prominent in *Kennalestes* than in *Asioryctes*. The fossa behind the mandibular foramen is incompletely preserved in *Kennalestes*, but the preserved fragment shows that its structure is similar to that of *Asioryctes*. A weak trace of the meckelian groove is present in front of the mandibular foramen, and has the shape

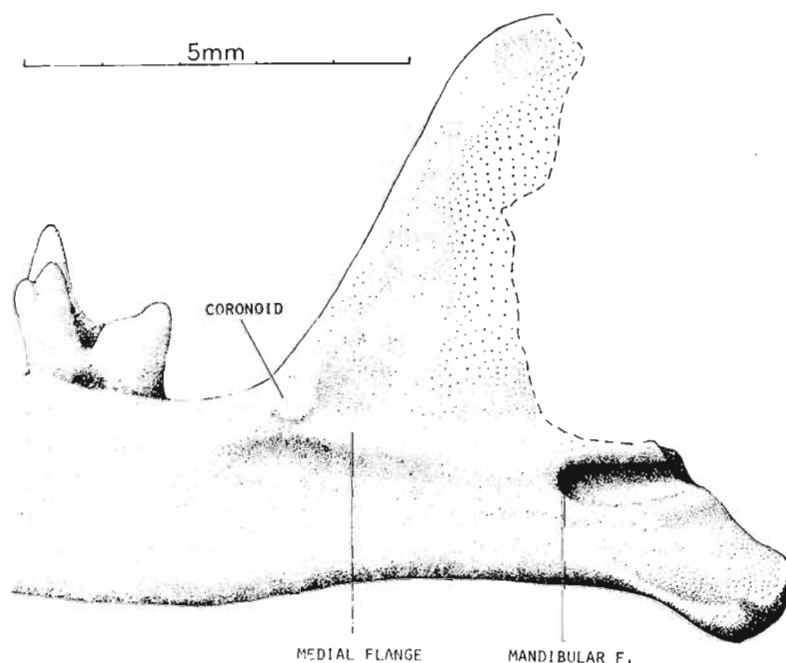


Fig. 11

Kennalestes gobiensis KIELAN-JAWOROWSKA, ZPAL MgM-I/3, posterior part of the lower jaw in inner view.

of a very faint shallow furrow, parallel to the medial flange, whereas there is no trace of such a furrow in *Asioryctes*. The angular process is incomplete in *Kennalestes* and the preserved part does not differ from that in *Asioryctes*.

DENTITION

ASIORYCTES

(Fig. 12; pls. 3, 4: 1*a* and 2, 5: 1 and 2*b*, 6, 7: 1 and 2, 8-11, 18 and 19)

Dental formula: $\frac{5 \ 1 \ 4 \ 3}{4 \ 1 \ 4 \ 3}$

Measurements. — See Table 1.

Upper teeth. — The upper incisors have been preserved only in no. 98. The incisor row is antero-posterior rather than transverse. The first four incisors are placed in the premaxilla, the fifth in the premaxillary-maxillary suture. I¹ and I² are peg-like, I³ triangular with a narrow base, I⁴ triangular, short, with a wide base, I⁵ narrow, peg-like.

The upper canine is a strong tooth, double-rooted, directed downwards, bent somewhat backwards, situated to the rear of the premaxillary-maxillary suture.

P¹ is a compressed tooth, situated 0.5 mm behind C, (all the measurements given in this section are of no. 56) with a strong main cusp and much smaller, but distinct posterior basal cusp. P² situated 0.6 mm behind P¹, is shorter than P¹, with a posterior basal cusp more prominent than in P¹. There is a diastema of 0.2–0.3 mm between P² and P³. P³ is a three-rooted tooth, subtriangular in lateral view, highest of all the cheek teeth, of about the same height as the

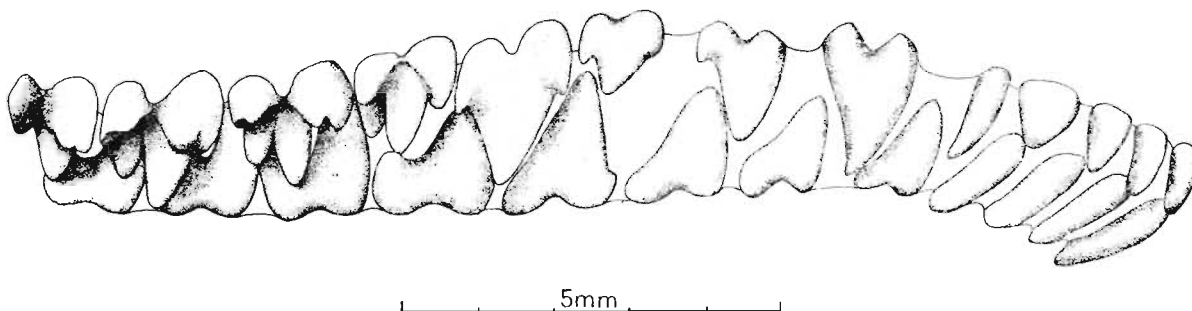


Fig. 12

Asioryctes nemegetensis KIELAN-JAWOROWSKA, reconstruction of the upper and lower dentition in occlusion, in lateral view, based upon ZPAL MgM-I/98, ZPAL MgM-I/56 and ZPAL MgM-I/166.

canine. There is no cingulum or styler shelf. The main labial cusp (paracone) is placed entirely labially, in the middle of the tooth length. In addition there are two smaller labial cusps, anterior and posterior. P³ has a well developed protocone and differs in this respect from *Kennalestes*, in which P³ is also three-rooted, but much shorter transversally and without a protocone. In occlusal view P³ is only roughly triangular, as it has a distinctly concave anterior margin and insignificantly concave posterior one. P⁴ is similar in structure to the molars, however, without a metacone. It is not as wide transversally as M¹ and in lateral view it is distinctly shorter than P³ and M¹. The styler shelf is wide laterally and very narrow in the middle, because of the strong ectoflexus. There is a prominent parastyle; the stylocone is unrecognizable (possibly absent). The metastyle is less prominent than the stylocone. The protocone is lower than the paracone; the profossa is very narrow, the postprotocrista is situated lower than the preprotocrista. The conules are not discernible. The precingulum and postcingulum are absent.

Table 1

Asioryctes nemegetensis KIELAN-JAWOROWSKA
Measurements of the dentition in mm.

ZPAL cat. nos.	MgM-I/56 (Holotype)		MgM-I/70		MgM-I/73		MgM-I/74		MgM-I/87		MgM-I/134		MgM-I/148	MgM-I/166
	right	left	right	left	right	left	right	left	right	left	right	left		
Upper C ant.-post. ext.	1.60	1.62											1.20	
P ¹ ant.-post. ext.	1.25	1.26												
P ² ant.-post. ext.		1.25											1.10	1.00
P ³ ant.-post. ext.	1.72	1.70							1.62				1.78	1.63
P ³ tr.	1.69	1.67							1.64				1.40	1.60
P ⁴ ant.-post. ext.	1.43	1.70	1.74						1.73				1.68	1.50
P ⁴ tr.	2.23	2.25	2.40										2.15	2.00
M ¹ ant.-post. ext.	1.70	1.72	1.82		1.90				1.78				1.78	1.64
M ¹ tr.	2.53	2.27	2.68		2.94				2.44				2.51	2.42
M ² ant.-post. ext.	1.62	1.83	1.72		1.60				1.76				2.01	2.13
M ² tr.	2.58	2.57	2.72		3.10				2.70				2.62	2.64
M ³ ant.-post. ext.		1.20	1.76		1.23								1.34	1.65
M ³ tr.		2.73	2.80		2.64								2.32	2.55
Lower C ant.-post. ext.	1.00	1.06												1.20
P ₁ ant.-post. ext.	0.90	1.02												1.21
P ₂ ant.-post. ext.	1.30	1.36												1.41
P ₃ ant.-post. ext.	1.72	1.86					1.03	1.60	2.00	1.92			1.68	
P ₃ tr.	0.80	0.71					0.56	0.90	0.82	0.94			0.72	
P ₄ ant.-post. ext.	1.33	1.70	1.61	1.70			(d P ₄)	1.62	1.62	2.76			1.48	
P ₄ tr.	0.96	0.91	1.20	1.12			1.40	0.96	0.84	0.83			0.80	
M ₁ ant.-post. ext.	1.70	1.48	1.68	1.76			(d P ₄)	1.52	1.82	1.76			1.52	
M ₁ tr. (trigonid)	1.21	1.48		1.24			0.80	1.09	1.24	1.44			1.21	
M ₂ ant.-post. ext.	1.60	1.66	1.60		1.88		1.75	1.80	1.72	1.63			1.52	
M ₂ tr. (trigonid)	1.40	1.49	1.63		1.20		1.09	1.30	1.40	1.40			1.38	
M ₃ ant.-post. ext.	1.77	1.75	1.60		1.84		1.78	1.72	1.79	1.73			1.76	
M ₃ tr. (trigonid)	1.40	1.31	1.50		1.34		1.28	1.25	1.25	1.31			1.28	

Explanation. — The poorly preserved specimens, or the specimens in which the lower jaws were left in occlusion, have not been measured. In the specimen no. ZPAL MgM-I/70 the mean values of the measurements of right and left sides are given.

M¹ and M² have a similar structure and will be described together (see also scanning electron micrographs of M¹–M³ on pl. III in KIELAN-JAWOROWSKA 1975a and p. 261 and fig. 6 in CROMPTON and KIELAN-JAWOROWSKA 1978). The ectoflexus is very deep, especially in M². The styler shelf is very wide at the corners, almost disappearing in the middle. The parastylar area forms a very large lobe, with a prominent parastyle and stylocone. The metastylar area is much reduced, with an indistinct mesostyle and metastyle, visible only in lateral view. The paracone is very large and high, situated centrally, the much smaller metacone is situated posterolabially in relation to the paracone. The protocone is comparatively low, the protofossa very narrow. The paraconule is distinct, the metaconule not discernible in any available specimen; the postprotocrista is placed lower than the preprotocrista. The precingulum and postcingulum are absent. M³ differs from M¹ and M² in being smaller and in the lack of metastylar area.

Lower teeth. — Incisor row is antero-posterior rather than transverse. Four lower incisors have been preserved only on both sides on no. 98; all are peg-like. I₁, situated in the prolongation of the lower edge of the jaw is very strongly procumbent. I₂–I₄ are gradually less procumbent; I₂ and I₃ are insignificantly longer than I₄ in contrast to my previous recon-

struction (KIELAN-JAWOROWSKA 1975a, fig. 1B). All lower teeth behind I_4 , including the canine are double-rooted. The canine is placed immediately behind I_4 . It is relatively smaller than in *Kennalestes*, slightly procumbent, roughly triangular, but with a small basal cusp on the posterior margin.

There is a diastema of 0.4 mm between the canine and P_1 , which is smaller than the canine, subtriangular, compressed, with a main cusp and small posterior basal cusp. P_2 placed 0.3 mm behind P_1 is distinctly larger than P_1 , with a main cusp and two basal cusps: anterior and posterior. There is a diastema of 0.6 mm between P_2 and P_3 . P_3 is a strong tooth, higher than the canine, with high main cusp and two basal cusps, the posterior one more prominent than the anterior. P_4 is similar to P_3 and differs from it in having a somewhat more prominent posterior basal cusp, which forms an unbasined talonid. It is not molariform.

In no. 74 (see pls. 18:2 and 19:2), which belongs to a young individual (M_3 is just erupting) dP_4 has been preserved. This differs from P_4 (see e.g. no. 148, pl. 18: 3b and 3e and pl. 19: 3b) in being molariform. Three trigonid cusps are well developed; the talonid is much smaller than on the molars, but is basined (pl. 18: 2a) and 3 incipient cusps are recognizable.

The molars have a relatively small trigonid, strongly compressed antero-posteriorly, with a very short and small paraconid; the protoconid and metaconid are high, subequal. The talonid is very large with three cusps (hypoconid, hypoconulid and entoconid) situated rather far posteriorly. The hypoconulid is the highest of the talonid cusps; the entocristid is very low. M_3 is somewhat smaller than M_1 and M_2 and has a talonid more strongly elongated antero-posteriorly. In M_3 the hypoconulid remains very high even in heavily worn specimens. (See also p. 261 and fig. 6 in CROMPTON and KIELAN-JAWOROWSKA 1978, and scanning electron micrographs of M_2 - M_3 on pl. IV in KIELAN-JAWOROWSKA 1975a).

KENNALESTES

(Pls. 7: 3, 12: 1a and 1b, 13: 1a, 1b and 1d, 14: 1a, 15, 17: 3)

Dental formula: $\frac{4 \ 1 \ 4 \ 3}{3 \ 1 \ 4 \ 3}$

The dentition of adult individuals has been described by KIELAN-JAWOROWSKA (1969), and the structure and the shearing surfaces of the molars by CROMPTON and KIELAN-JAWOROWSKA (1978). In this paper I make only comments on the dentition of a juvenile specimen (no. 1) the skull of which is here described, in which both deciduous and permanent teeth are preserved.

Upper teeth. — Three left upper incisors are preserved (right are missing). These are possibly I^3 , dI^4 and erupting I^4 . I^3 is placed in the premaxilla, dI^4 and I^4 in the premaxillary-maxillary suture. Left canine is missing; on the right side the canine is erupting and only its tip is visible. This is situated to the rear of the premaxillary-maxillary suture as in adult individuals. Immediately behind the erupting canine there is a deciduous canine, which in contrast to the permanent one is single-rooted.

Behind dC there are five right upper premolars but only four left. The right upper premolars are interpreted as: P^1 , P^2 , P^x , P^3 , dP^4 , the left ones as: P^1 , P^2 , P^3 , dP^4 . The P^x is a supernumerary premolar. P^3 on both sides are erupting. The last premolars on both sides are interpreted as deciduous, as they are whiter than the molars and than the erupting P^3 and differ from P^4 preserved in specimens nos. 2, 3 and 5. DP^4 differs from P^4 in being shorter transversely, in having a narrower styler shelf and styles that are less incurved in the middle and possibly less prominent. Five upper premolars are characteristic only of juvenile *Kennalestes*; in adult skulls there are four.

M^1 and M^2 on both sides are very well preserved, unworn, with high conules. M^3 have

not erupted. Scanning electron micrographs of left M^2 of the described specimen have been figured by CROMPTON and KIELAN-JAWOROWSKA (1978, fig. 12 A-B).

Lower teeth. — On the left side broken off dI_3 and erupting I_3 are present. On the right side there is an alveolus possibly for I_2 , in front of which the jaw is broken off and it seems that there was room for one more tooth. To the rear of the alveolus is a large peg-like incisor, possibly dI_3 , behind which, as on the left side, an incipient I_3 is erupting. The deciduous single-rooted canines are preserved on both sides, broken off on the left and nearly complete on the right. The permanent lower canines (see KIELAN-JAWOROWSKA 1969 and 1975a) are double-rooted.

Behind the canine, double-rooted small P_1 and P_2 are preserved on both sides, right P_2 badly damaged. It is impossible to state whether these are permanent or deciduous teeth. Permanent P_3 are erupting on both sides and only the tips of strong protoconids are visible. Immediately behind the protoconid of P_3 on both sides the remnants of strongly worn dP_3 are preserved. DP_4 are in place on both sides. DP_4 in contrast to P_4 is completely molariform, with three trigonid cusps, similar to those in the molars and with an anterior cingulum, more prominent than in the molars. When describing the dentition of no. 3 and no. 5 (KIELAN-JAWOROWSKA 1969) I stated that the structure of P_4 was different on the right and left sides of no. 3 and referred to the right one of no. 3 as P_4 and to the left as well as the right and left in no. 5 as dP_4 . A re-examination of these specimens and a comparison with the dentition in a juvenile (no. 1) indicate that all P_4 preserved in nos. 3 and 5 are permanent, the left one in no. 3 having the protoconid broken off and glued back in the opposite direction, which caused it to appear different from the right tooth. It follows that the permanent P_4 of *Kennalestes* is a tooth figured by KIELAN-JAWOROWSKA (1969) in pl. 23, figs. 1f, 1g, 2a-d, and not in figs 1d and 1e, and text-figs. 2 and 3. Also in text-fig. 1A (KIELAN-JAWOROWSKA 1975a) P_4 has been wrongly reconstructed.

M_1 and M_2 are completely erupted and there is a place behind M_2 for unerupted M_3 . Scanning electron micrographs of M_1 and M_2 of the described specimen were published by CROMPTON and KIELAN-JAWOROWSKA (1978, fig. 12C).

DISCUSSION

SYNOPSIS OF *ASIORYCTES* AND *KENNALESTES* CHARACTERS

The foregoing descriptions show that the skulls of *Kennalestes* and *Asioryctes* differ in proportions and in details, but part of these differences may be caused by a difference in age of the individual specimens. The best preserved skull of *Kennalestes* (ZPAL MgM-1/1) belongs to a young individual, whereas all the skulls of *Asioryctes* are of adults. Some of the apparent differences may be effects of the state of preservation.

At first sight the skulls of *Kennalestes* (ZPAL MgM-1/1) and *Asioryctes* (ZPAL MgM-1/56) differ in proportions, the mesocranial region being relatively shorter in *Kennalestes*. In *Asioryctes* the length of the mesocranial region is 0.3 of the skull length, whereas in *Kennalestes* it is only 0.24. However, there are differences in proportions between young and adult skulls of *Kennalestes*; in ZPAL MgM-1/3 and ZPAL MgM-1/44, the preserved mesocranial region was relatively longer than in the juvenile skull, but because the material is incomplete meaningful measurements cannot be given. In Recent *Tenrec ecaudatus* the mesocranial region is also very long in the adult skull and relatively shorter in younger individuals; in ZPAL Mw/2 which is 67 mm long, the mesocranial region measures 0.27 of the skull length, whereas in MCZ 44988 which is 93 mm long, it measures 0.33 of the length. One can assume that the mesocranial region was relatively longer in adult *Kennalestes* than in juvenile individuals, the general skull proportions being similar in *Asioryctes* and *Kennalestes*.

Another difference between *Kennalestes* and *Asioryctes*, appearing from study of the juvenile skull of *Kennalestes* is the presence of what appear to be fossae in front of the promontoria. But, as demonstrated above, the fossae preserved in ZPAL MgM-I/1 are probably due to distortion, and the bone of which the fossae are built, is a basisphenoid wing. It is possible that the basisphenoid wing was more horizontal and more concave in *Kennalestes* than in *Asioryctes*, but I presume that the mesocranial region was of similar structure in the two genera.

The main differences between *Kennalestes* and *Asioryctes* (see Table 2) concern the structure of the jugal, of the zygomatic arch and the mastoid, the shape of the tympanohyal, the presence or absence of the sulcus arteriae stapediae, the shape of the coronoid process and some details in the structure of the posterior part of the lower jaw. In addition the two genera differ markedly in the dentition (see KIELAN-JAWOROWSKA 1969 and 1975a, CROMPTON and KIELAN-JAWOROWSKA 1978).

Table 2

Differences between the skulls of *Kennalestes* and *Asioryctes*

Characters	<i>Kennalestes</i>	<i>Asioryctes</i>
Suture between jugal and maxilla	straight	sigmoid
Jugal contribution to the structure of the snout	relatively small	extensive
Zygomatic arch	moderately deep	deep
Promontorium	moderately high in posteromedial part	extremely high in posteromedial part
Sulcus arteriae stapediae	present, distinct	absent, an uncertain tube present
Tympanohyal	poorly known, relatively small, triangular	very large, rectangular, but medial part that might be pointed is missing
Mastoid (seen from behind)	roughly triangular	roughly rectangular
Lower mastoid foramen	absent	present
Lateral mastoid flange	very prominent, crescent shaped when seen from behind	moderately prominent
Occipital condyles	known only in a juvenile skull, extending for two thirds of the height of the foramen magnum	extending for half the height of the foramen magnum
Coronoid process of the lower jaw	moderately large, with rounded upper margin	large, with straight (transversal) upper margin
Mandibular foramen	placed at the posterior part of the mandibular ramus	placed at mid-length of the mandibular ramus
Remnant of the meckelian groove	very weak	absent

SEGALL (1970) showed that the round outline of the stapes plate (or fenestra vestibuli) may be regarded as the primitive condition, and the elliptical as the specialized one. According to him the stapedia ratio (*l. c.* fig. 26) is 1.0 in *Tachyglossus*, 1.1–2.1 in marsupials and 1.8–2.9 in insectivores (*sensu lato*, including e.g. the Leptictidae and *Tupaia*). The stapedia ratio is 2.0 in *Kennalestes* (ZPAL MgM-I/44) but only 1.4 in *Asioryctes* (ZPAL MgM-I/56). If these measurements are correct, *Asioryctes* would have the lowest stapedia ratio of any eutherian mammals. However, in both specimens the fenestra vestibuli may have been enlarged in one or other direction by preparation (as has clearly happened in ZPAL MgM-I/2). So the above measurements must be regarded as tentative.

Common characters of *Kennalestes* and *Asioryctes* skulls

Skull small, elongated, anterior part of the snout widening opposite P³, infraorbital foramen large, situated above the anterior part of P³. Nasals expanded posteriorly in contact with lacrimals. Lacrimal with facial wing, lacrimal foramen opens into the orbit. Orbit confluent with temporal fossa. Distinct groove in the floor of the orbit, extending posteriorly from the maxillary foramen to a notch at the posterior margin of the maxilla. Large recess at the posteroventral corner of the palatine, possibly for a sphenorbital foramen. Zygomatic arch made exclusively by jugal, which overlaps maxilla anteriorly and extends back to the glenoid fossa; glenoid fossa situated far posteriorly, opposite anterior half of promontorium; postglenoid process moderately prominent. Subsquamosal foramen large, three to four postsquamosal foramina, single postparietal foramen. Parietals extensive, sagittal crest weak, lambdoidal crests present, passing downwards into prominent lateral mastoid flanges. Mesocranial region strongly elongated, narrow. Pterygoid bones poorly known, hamulus large. Presphenoid moderately long, basisphenoid extensive, consisting of a horizontal medial part and basisphenoid wings arranged ventrolaterally. Orbitosphenoid roughly trapezoidal in lateral view, probably partly covered in life by the alisphenoid, pierced by four foramina: optic, ethmoidal, sinus canal foramen and sphenorbital fissure. Alisphenoid extensive, roughly triangular in lateral view. Foramen rotundum absent, foramen ovale at the posteroventral corner of the alisphenoid, at the boundary with the squamosal. Alisphenoid canal absent, but a groove present. Quadrangle ramus of the alisphenoid and lateral flange of the petrosal are fused, forming a characteristic flange, which, when viewed from below extends anteromedially as a prolongation of the postglenoid process, continues as a pterygoid ridge of the basisphenoid and alisphenoid and passes anteriorly into the pterygoid bone. Ectotympanic large, forming three quarters of a ring, open in posterolateral-dorsal part, arranged obliquely (about 45°) to the horizontal plane. Promontorium very large, sulcus arteriae promontorii absent, sulcus arteriae stapediae present in *Kennalestes*, absent in *Asioryctes*, but uncertain tube for stapedial artery present. Foramen for internal carotid artery tentatively recognized, situated medially to the dorsal apex of promontorium. Fenestra cochleae situated in a recess, fenestra vestibuli large. Crista promontorii prominent, but sulcus for inferior petrosal vein not preserved. Tympanic process of pteromastoid large, fossa muscoli stapedii tear-shaped, tympanohyal large. Occipital plate arranged at an angle of about 75° to the plane of the teeth. Mastoid large, roughly triangular or rectangular, pierced by foramina that are differently distributed in *Kennalestes* and *Asioryctes*. Paroccipital process absent, mastoid process poorly developed. Lower jaw slender with large coronoid process. Angular process inflected medially. Rudimentary coronoid presumably present, fused with the dentary.

INTERNAL CAROTID CIRCULATION AND PRIMITIVE EUTHERIAN MORPHOTYPE

It is generally accepted in current paleontological literature that possession of two main vessels of internal carotid, usually referred to as medial internal carotid and promontory arteries, is characteristic of a primitive eutherian morphotype (MCDOWELL 1958, MCKENNA 1966, VAN VALEN 1966, MACINTYRE 1972, SZALAY 1975, ARCHIBALD 1977 and others). This hypothesis has been recently challenged by PRESLEY (1979) on embryological evidence. PRESLEY (1979: 240) stated: "The present findings indicate that in all recent mammals, as in other vertebrates, the internal carotid artery at the level of auditory capsule is a single vessel, homologous through the development, and derived from the dorsal aorta. There is no vertebrate so far recorded, in which the dorsal aorta divides here into developmentally equivalent branches, and the hypothesis that it did so in some ancestral mammal requires to be supported by substantial evidence".

According to PRESLEY the internal carotid artery may move medially or laterally during the growth of promontorium and may be placed either along its medial border, or cross the middle or lateral side of the promontorium and lie within the wall of the tympanic cavity.

In recent therian mammals the medial position of internal carotid is retained among others in marsupials. If we accept PRESLEY's idea, we may say that the internal carotid artery never moved laterally in marsupials. The stapedia artery is found in embryo of marsupials, but is generally lost in adults (TANDLER 1899, ARCHER 1976, PRESLEY 1979). In Cretaceous marsupials (CLEMENS 1966, ARCHIBALD 1976) the grooves for the stapedia and promontory arteries are absent.

The medial position of the internal carotid artery is also characteristic of various recent eutherian mammals, e.g. rodents (GUTHRIE 1974), lagomorphs (BUGGE 1974) and ungulates (PRESLEY 1979). The lateral position of the internal carotid artery, usually referred to as promontory artery, is characteristic of insectivores, bats and primates (BUGGE 1974, CARTMILL 1975, PRESLEY 1979). The internal carotid artery of carnivores may also be a promontory artery, although medially placed in spite of HUNT's (1974) statement that in a number of carnivores both medial and promontory arteries coexist (see PRESLEY 1979:242 for discussion).

If PRESLEY is right, there is no single case in which the coexistence of medial and promontory arteries has been unequivocally demonstrated in recent mammals.

Let us discuss now late Cretaceous and early Tertiary eutherian mammals in which the basicranial region has been preserved.

The oldest known skulls of this type are those of *Kennalestes* and *Asioryctes*, described in the present paper. It follows from the foregoing descriptions that no trace of a groove for promontory artery has been encountered in *Asioryctes*, whereas the apparent grooves on the lateral side of the promontorium in *Kennalestes* are probably artefacts, and cannot be interpreted as having housed the promontory artery. Thus in oldest known eutherian skulls only one main vessel, the internal carotid artery existed. In addition the stapedia artery was present in *Kennalestes*, and less certainly in *Asioryctes*, where it probably was encased in a tube. A vidian foramen is recognized in *Asioryctes*; according to VAN VALEN (1966), ARCHIBALD (1977) and others, the vidian artery is a branch of a promontory artery. But in various mammals e.g. in *Rattus* (GUTHRIE 1974), vidian artery is a branch of stapedia artery, and this was probably the case in *Asioryctes*.

The only other described Cretaceous eutherian basicrania are the isolated petrosals from Hell Creek Formation, Bug Creek locality of Montana (MACINTYRE 1972), referred to in this paper as Bug Creek petrosals. MACINTYRE recognized among Bug Creek petrosals the ferungulate and unguiculate types and reconstructed basicrania in both groups. In my opinion, both types of MACINTYRE recall the petrosals of the Leptictidae and that is why I shall discuss both groups together.

The representatives of the Leptictidae are known from the Paleocene, Eocene and Oligocene rocks. Unfortunately, no basicranial region of a Paleocene or Eocene leptictid has been described. The skull of Lower Paleocene *Paleoictops biscupis* assigned by MATTHEW and GRANGER (1918) to *Diacodon* has been reconstructed from fragments and the basicranial region is missing. In contrast, the Oligocene genus *Leptictis* is known from numerous, well preserved skulls with basicranial region preserved (LEIDY 1869, COPE 1883, DOUGLASS 1905, GREGORY 1910, SCOTT and JEPSEN 1936, and BUTLER 1956).

The basicranial region of *Leptictis* has been described in detail by BUTLER (1956). In this genus (referred by BUTLER to *Ictops*, which is a junior synonym of *Leptictis*, see VAN VALEN 1967), there is a very distinct groove for stapedia artery, which bifurcates, giving rise to an anterior branch — the promontory artery. In all the well preserved skulls of *Leptictis*, including the two specimens housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich, which I have examined and which are figured in this paper (pl. 17:1 and 2), the deep open grooves indicate the presence of stapedia and promontory

arteries. However, the presence of a medial branch of the internal carotid artery is less certain. BUTLER stated that the groove on the medial side of the tympanic wing of the petrosal (1956:461): "...evidently corresponds to the canal which in *Tupaia* and other insectivores carries the inferior petrosal vein (SABAN 1956). It also closely resembles the carotid canal in *Didelphis*, *Thylacinus* and *Caenolestes* (GREGORY 1910) and may have carried a medial branch of the carotid artery in addition to vein". An examination of well preserved skulls of *Leptictis* and a comparison with various marsupial and rodent genera in which the groove for the medial internal carotid artery is present, led me to the conclusion that it is doubtful if the medial groove in *Leptictis* indeed carried the medial branch of the internal carotid. Thus in my opinion the coexistence of two branches of the internal carotid artery cannot be unequivocally demonstrated in the Leptictidae.

The same situation is encountered in both types of Bug Creek petrosals (MACINTYRE 1972). We have here distinct grooves for the stapedia and promontory arteries, similarly placed as in the Leptictidae, and a shallow groove — sulcus medialis, which according to MACINTYRE housed the medial internal carotid. The situation is less clear than in the Leptictidae, as medially to the sulcus medialis MACINTYRE recognized a sulcus sini petrosi inferior. Not having examined the Bug Creek petrosals myself, I cannot venture an opinion as to what, if anything, could have lain in the sulcus medialis.

The next group of primitive early Tertiary mammals to be discussed are the Palaeoryctidae. A poorly preserved basicranium of Eocene *Didelphodus altidens* — USNM 18369, was described by VAN VALEN (1966), who recognized on the promontorium grooves for the internal carotid and promontory arteries. The latter is sharply bent at almost a right angle, which is an impossible course for an artery. VAN VALEN (1966:45) stated: "There is no trace of a groove from the fenestra rotunda to the fenestra ovalis, but a stapedia branch of the internal carotid artery may, nevertheless, have been present there". Because of the poor state of preservation of this specimen and its ambiguity, I shall not discuss it further.

The only described palaeoryctine skull in which the basicranial region has been preserved, is that of *Palaeoryctes puercensis* — AMNH 15923 (MATTHEW 1913, McDOWELL 1958 and VAN VALEN 1966). In this specimen, as stated by two latter authors, there are no grooves on the promontorium that can be assigned with confidence to branches of the internal carotid artery. In spite of this VAN VALEN (1966:55) stated that: "There is, however, a good evidence for the presence of complete number of branches of the internal carotid". He based this conclusion upon an examination of poorly preserved foramina in the basicranium.

In an undescribed new species of *Palaeoryctes* (or *Pararyctes*) from the Eocene of Wyoming, studied by Prof. M. C. MCKENNA (personal information) there is no groove for the medial branch of the internal carotid artery: the stapedia artery was encased in a tube and this was probably also the case with the promontory artery.

In the Middle Eocene representative of the Miacidae *Viverravus* and related genera MATTHEW (1909) found three grooves, which he interpreted as carrying medial internal carotid, promontory and stapedia arteries. On this basis the primitive eutherian morphotype was established. The three grooves are reasonably well seen on the photograph of *Viverravus* published by MATTHEW (1909 pl. 43:1), and there is no doubt that the stapedia and promontory arteries were present in this genus. The occurrence of the medial branch of the internal carotid is disputable, as e.g. in case of Bug Creek petrosals discussed above, but as this branch was absent in the Palaeoryctidae and Leptictidae and is absent in modern carnivores, it seems more probable that it was absent in *Viverravus* as well.

Summing up, one can state that in the oldest known skulls of eutherian mammals *Kennalestes* and *Asioryctes* only one main internal carotid vessel existed, as characteristic of marsupials: the difference from marsupials being the presence of the stapedia artery, which in marsupials is generally lost in adults. The age of beds yielding *Kennalestes* is ?late Santonian and/or early Campanian, those of *Asioryctes* ?middle Campanian. By latest Maastrichtian (Bug Creek

petrosals) at least in two eutherian lines the medial internal carotid moved laterally, to the side of promontorium, being known as the promontory artery. The view presented here assumes that in Bug Creek petrosals the sulcus medialis did not house the medial internal carotid artery. The two lines occurring in Bug Creek, within which MACINTYRE (1972) recognized the unguiculate and ferungulate types, could give rise to the Leptictidae and Palaeoryctidae, in both of which the medial branch of the internal carotid appears to have been absent. The subsequent evolution in leptictid lineage involved the deepening of the grooves for stapedial and promontory arteries, whereas in the palaeoryctid lineage it involved the closing of the grooves for the arteries, which at least in one Eocene member of the family are enclosed in tubes.

The pattern characteristic of the Bug Creek ancestors of the Palaeoryctidae was in one case retained in the Miacidae (providing that the internal groove in *Viverravus* did not house an artery), and in another case in recent carnivores.

The rodents, lagomorphs, ungulates and other modern mammals in which only the medial branch of the internal carotid artery is preserved, may derive from generalized forms, similar to *Kennalestes*, but not from forms the petrosals of which have been encountered at Bug Creek. The latter may have given rise to the insectivores, primates and carnivores.

If the authors mentioned on p. 63 had not been influenced by MATTHEW's morphotype, they would probably have presented a different interpretation of the internal carotid pattern in the basicrania studied than they did. On the other hand, my interpretation has been influenced by PRESLEY's hypothesis, and so cannot be regarded as entirely objective either. However, I agree with PRESLEY that the currently accepted morphotype is a poor one (PRESLEY 1979:242): "...being in possession of an advanced feature of development found neither in their ancestors nor in their descendants". The morphotype accepted in this paper (in which only one main vessel — medial internal carotid was present in earliest eutherian mammals), appears to concur better with current knowledge on the anatomy and embryology of both fossil and recent therian mammals.

OSTEOLOGICAL COMPARISONS

Comparison with cynodonts

The skulls of *Asioryctes* and *Kennalestes* are essentially of eutherian pattern, but they display some characters intermediate between Cynodontia and modern Theria.

PARRINGTON and WESTOLL (1940) pointed out that the mammalian braincase lies relatively closer to the snout than in cynodonts. The effective shortening of the mammalian skull (PARRINGTON and WESTOLL, *l. c.*: 347): "...must be regarded as confined between the posterior end of the snout and the region of basiptyergoid processes..." The authors argued that the close approximation of the optic foramen, sphenorbital fissure, foramen rotundum and foramen ovale implies that the mammalian basis cranii has been moved forwards, towards the snout. The skull of *Asioryctes* (and possibly also *Kennalestes*) does not display the shortening of the snout characteristic of eutherian mammals; the mesocranial region is very long here, as characteristic of cynodonts and the Triassic triconodont *Morganucodon*.

Another cynodont feature of *Kennalestes* and *Asioryctes* skulls is the position of the occipital plate, which (see PARRINGTON and WESTOLL 1940) in cynodonts slopes upwards and forwards from the condyles, whereas in mammals it slopes upwards and backwards. In *Kennalestes* and *Asioryctes* the occiput retains a cynodont slope, which may at least in part, be due to the fact that the base of the cranium has not yet begun to move forward.

In cynodonts the lower jaw suspensorium is placed at the very end of the skull, opposite the periotic. It is situated lateral to the promontorium also in various groups of non-therian

mammals: in triconodonts, multituberculates and monotremes (KIELAN-JAWOROWSKA 1971). In therian mammals, the glenoid fossa moved forward in association with the posterior expansion of the braincase and is situated half way along the braincase and in front of the promontorium. In *Kennalestes* and *Asioryctes* the glenoid fossa is situated opposite the anterior half of the promontorium, and thus occupies an intermediate position between the cynodont and therian conditions.

The basisphenoid in *Asioryctes* with its large basisphenoid wing is unusual for mammals, and also different from cynodonts. But it may be argued that the basisphenoid wing is homologous to the reptilian basipterygoid process. In cynodonts the basipterygoid process is a projection of the anterior part of the basisphenoid which joins the pterygoid and epipterygoid. The lateral margin of the posterior part of the basisphenoid to the rear of the basipterygoid process remains free. In mammals, because of the incorporation of the cavum epiptericum into the braincase, the expanded alisphenoid forms a large part of the lateral wall of the braincase. It is possible that in therian mammals the basipterygoid process has moved backwards to fill the gap between the basisphenoid and alisphenoid. If this is so, the basisphenoid wing of *Asioryctes* would be a homologue of the reptilian basipterygoid process.

The next feature present in *Asioryctes* and *Kennalestes* skulls but not found in modern therian mammals is a flange which extends anteromedially in a prolongation of the postglenoid process. This is interpreted as homologous to the posterior part of the quadrate ramus of the alisphenoid and lateral flange of the petrosal which are characteristic of cynodont and triconodont skulls (PARRINGTON 1946, KERMAK 1963).

Comparison with triconodonts, docodonts, and eupantotheres

Complete or fragmentary skulls, or isolated skull bones of Triconodonta (SIMPSON 1925, 1928, PATTERSON and OLSON 1961, RIGNEY 1963, KERMAK 1963, KERMAK and KIELAN-JAWOROWSKA 1971, PARRINGTON 1971, CROMPTON 1964, CROMPTON and JENKINS 1979), Docodonta (KRUSAT 1973) and Eupantotheria (HENKEL and KREBS 1977) have been found. But as the descriptions that have so far been published are mostly partial or preliminary they do not provide sufficient information on the skull structure of these Mesozoic mammals to allow a close comparison with the skulls of *Asioryctes* and *Kennalestes*. For this reason the comparison that follows concerns only the lower jaw.

The lower jaws of *Asioryctes* and *Kennalestes* are of essentially therian pattern, but they retain certain primitive features, not present in modern Theria. Prime among these is the presumed presence of a rudimentary coronoid bone, which has been found in *Asioryctes* and less certainly in *Kennalestes*. In both genera the coronoid appears to be fused to the dentary, but the trace of a suture is discernible in all the specimens of *Asioryctes* in which this region is preserved and in one left lower jaw of *Kennalestes* (in the right jaw of the same specimen the suture has disappeared).

Dr. D. DASHZEVEG kindly informed me that in the collection of Early Cretaceous mammals from Guchin Us locality in the Gobi Desert, housed in the Museum of the Geological Institute (Section of Stratigraphy and Paleontology) of the Academy of Sciences of the Mongolian People's Republic in Ulan Bator, there is a fragmentary lower jaw of a eutherian "*Prokennalestes*" (which has been named but not described by TROFIMOV in BELIAJEVA *et al.* 1974 and is cited here as a *nomen nudum*). In this specimen (GISPS 10-6 PST) a rudimentary, but distinct coronoid has been preserved, fused with the dentary, but delimited from it by an indistinct suture.

Among other Mesozoic mammals the coronoid has been found in triconodonts (PARRINGTON 1971, KERMAK *et al.* 1973), in docodonts (KRUSAT 1973), in multituberculates (HAHN 1977) and in eupantotheres (KREBS 1969). In all these cases, except the multituberculates, the coronoid has not been preserved, but there is a distinct articular surface for it at the anterior

corner of the coronoid process, exactly where the coronoid bone, fused with the dentary, is placed in "*Prokennalestes*", *Asioryctes* and less certainly in *Kennalestes*. If this interpretation is correct one can conclude that whereas in triconodonts, docodonts, multituberculates and eupantotheres the coronoid bone was free, in Early and Late Cretaceous eutherian mammals, it became fused to the dentary.

Another primitive feature of the lower jaw in triconodonts, docodonts and eupantotheres is the presence of the meckelian groove for the persistent MECKEL'S cartilage. In "*Prokennalestes*" (personal information from Dr. D. DASHZEVEG) the meckelian groove is still present, although it is very weak and narrow. It is absent from *Asioryctes*, but a presumable remnant (see description) is preserved in *Kennalestes*.

In triconodonts (see KERMACK *et al.* 1973) the mandibular foramen is situated below the last molar. Extending posteriorly from the foramen is relatively large trough of the dentary for the accessory jaw bones, which is divided by a diagonal ridge into two parts. In *Kennalestes* and *Asioryctes* the mandibular foramen is placed posteriorly (more so in *Kennalestes* than in *Asioryctes*) and the fossa to the rear of it is relatively small and smooth; it cannot have housed the accessory bones. However, the fossa, being the remnant of the trough of the dentary is better defined in *Kennalestes* and *Asioryctes* than in contemporary therian mammals.

In *Kennalestes* and *Asioryctes* the angular process is situated far posteriorly, more or less below the condyle, as is characteristic of eupantotheres (where e.g. in *Crusafontia* it is placed to the rear of the condyle, see KREBS 1971) and of modern therian mammals. In this respect *Kennalestes* and *Asioryctes* differ from triconodonts (KERMACK *et al.* 1973) and docodonts (KRUSAT 1973) in which the angular process is placed about the midlength of the mandibular ramus.

Comparison with marsupials

The skulls of *Kennalestes* and *Asioryctes* are of eutherian pattern, however, they retain a few features that are characteristic of marsupials.

The marsupial characters are:

— incisor number, which is 5/4 in *Asioryctes* (typical marsupial formula) and 4/3 in *Kennalestes* (more upper incisors than in modern eutherians);

— a very long jugal, reaching back to the glenoid fossa (marsupial feature, occurring also in some modern eutherians — see MARSHALL 1979);

— a subsquamosal foramen (marsupial feature, which among the eutherian mammals occurs also in the Leptictidae — see BUTLER 1956);

— a comparatively large alisphenoid, much larger in *Asioryctes* than in modern eutherian mammals and approaching more the marsupial condition, although relatively larger than in modern marsupials;

— a medial inflection of the angular process of the dentary — marsupial character, present among eutherians in *Barunlestes* — see KIELAN-JAWOROWSKA (1975a), (possibly also in *Zalambdalestes* in which the angular process has not been preserved), in *Gypsonictops* — see LILLEGRAVEN (1969) and in the Didymoconidae — see MELLETT and SZALAY (1968).

The characteristic feature of the marsupial basicranium is the alisphenoid bulla. In *Asioryctes* a strongly inflated quadrate ramus of the alisphenoid occupies the same position as the alisphenoid bulla in marsupials and is probably homologous to it. It seems that the marsupial alisphenoid bulla originated from the enlarged quadrate ramus of the alisphenoid of early therians. SEGALL stated (1970 : 169): "in the insectivores the tympanic process of the basisphenoid takes the place of the tympanic process of the alisphenoid of the marsupials". It seems, however, that the two processes cannot be regarded as analogous structures as they occupy different positions in the basicranial region. The tympanic process of the basisphenoid in the insectivores (see Section "Comparison with the Tenrecidae") is medial to the promontorium

and the ectotympanic, whereas the tympanic wing of the alisphenoid in marsupials lies anterolaterally to them.

Since the skulls of *Asioryctes* and *Kennalestes* exhibit few marsupial characters, it would appear that most of the eutherian characters were acquired by the eutherian lineage as long ago as the Late Cretaceous.

Comparison with Bug Creek petrosals (see also p. 57–59)

MACINTYRE (1972) described isolated eutherian petrosals from the Hell Creek Formation (Lancian, equivalent of Upper Maastrichtian, see CLEMENS *et al.* 1979) from Bug Creek, Montana, and recognized among them the ferungulate and unguiculate types. He follows the idea of MCKENNA (1969) and LILLEGRAVEN (1969) that there are two lines of Late Cretaceous eutherian mammals: the palaeoryctid and leptictid groupings. MACINTYRE's ferungulate petrosal type should correspond to the palaeoryctid lineage, and the unguiculate type to the leptictid lineage (in spite of the fact that SIMPSON 1945, originally assigned the Palaeoryctidae to the cohort Unguiculata).

It is not clear on which basis MACINTYRE recognized the ferungulate and unguiculate types, because, as shown under "Internal carotid circulation" in all his specimens the distinct sulci arteriae stapediae and promontorii are present, as characteristic of the Leptictidae.

The basicranium of *Asioryctes* differs from both the ferungulate and unguiculate types (*sensu* MACINTYRE 1972) in having a very large tympanohyal superimposed on the squamosal in the region of the external auditory meatus and touching the mastoid with its posterior border; in the ferungulate type it is very small and lies far back on the ridge of the mastoid; in the unguiculate type it approaches the condition in *Asioryctes*, but is smaller than in *Asioryctes* and situated further back. In addition the petrosal of *Asioryctes* approaches the unguiculate type in having a petromastoid with large tympanic process. The process has been described by MACINTYRE as vestigial in the ferungulate type.

The petrosal of *Kennalestes* differs from both the ferungulate types in more anterior position of the tympanohyal, which approaches more the unguiculate than the ferungulate condition. In addition it differs from the ferungulate type in having a large process of the petromastoid.

The length of the facial canal bridge, which distinguishes the ferungulate and unguiculate from the unguiculate types, is not known in either *Kennalestes* or *Asioryctes*.

MACINTYRE reconstructed both ferungulate and unguiculate basicrania with paroccipital processes. These do not occur in *Kennalestes* and *Asioryctes*. In addition the distance between right and left promontoria is relatively smaller in *Kennalestes* and *Asioryctes*, but this may be due in part to distortion.

Comparison with the Leptictidae (see also p. 57).

The postpalatine torus is more prominent in *Leptictis* (see pl. 17:1 and 2) than in *Kennalestes* or *Asioryctes*, the posterior palatine foramina are large, oval in *Leptictis* and there is only a notch in *Kennalestes* and *Asioryctes*.

The promontorium in both *Leptictis* and *Kennalestes* is moderately high, much less so than in *Asioryctes* and the Palaeoryctidae.

The mesocranial region is relatively shorter in *Leptictis* than in *Kennalestes*, but is relatively longer in the Paleocene *Prodiacodon* (see MATTHEW and GRANGER, 1918, fig. 5).

The tympanic wing of the basisphenoid, characteristic of most insectivore families is absent in the Leptictidae, *Asioryctes* and *Kennalestes*. The basisphenoid has a similar structure in the Leptictidae and the two Cretaceous genera. The basisphenoid in *Leptictis* (as in *Kennalestes* and *Asioryctes*) consists of the medial and lateral parts, the latter being called in *Asioryctes*

the basisphenoid wings. The basisphenoid wing has a somewhat different structure in *Leptictis* from *Asioryctes*. In *Asioryctes* it is oblique and ventro-lateral; in *Leptictis* (see pl. 17:1, 2) it consists of two parts: an anterior, roughly triangular part, placed horizontally and more ventral than the medial part, and a concave posterior part, which contributes to the structure of the inner ear roof. The anterior triangular part has a sharp posterior edge, that receives the tympanic bone. The anterior part of the basisphenoid wing in *Leptictis* appears to be homologous to the basisphenoid wing in *Asioryctes* and *Kennalestes*, and the posterior part is not developed in these genera because of the more anterior position of the promontorium. The basisphenoid wing is poorly known in *Kennalestes*, being preserved only in a juvenile specimen ZPAL MgM-1/1; on both sides it is concave, due to the distortion. The comparison suggests that the basisphenoid wing in *Kennalestes* might originally have been similar to that in *Leptictis*, being placed more horizontally than in *Asioryctes*.

There is a subsquamosal foramen in Leptictidae, *Kennalestes* and *Asioryctes*. The paroccipital process is absent in *Kennalestes*, *Asioryctes* and *Leptictis*, in spite of BUTLER's statements (1956, fig. 3), naming the small inflation on the mastoid (close to the suture with the exoccipital) a paroccipital process. However, the paroccipital (= jugular = paramastoid) process in mammals is a process of the exoccipital and not the mastoid (MATTHEW 1901, GREGORY 1910, SISSON and GROSSMAN 1953, ANSON 1966, NICKEL *et al.* 1968 and others), and such a process is obviously not present in *Kennalestes* and *Asioryctes* and in the skulls of *Leptictis* available to me.

There are differences in the structure of the lateral wall of the braincases between *Leptictis* and *Asioryctes-Kennalestes*. The alisphenoid canal present in *Leptictis* is absent from *Asioryctes* (and possibly also from *Kennalestes*). The alisphenoid is relatively longer in *Asioryctes* (and probably also in *Kennalestes*) than in *Leptictis*, but is roughly similar in shape; the arrangement of the foramen ovale, sphenorbital fissure, posterior opening of the sinus canal and sphenopalatine foramen is the same in *Leptictis* and the two Cretaceous genera. The optic foramen in *Asioryctes* and *Kennalestes* is more ventral and situated further forward than it is in *Leptictis* and the ethmoidal foramen pierces the frontal in *Leptictis* but the orbitosphenoid in *Asioryctes* and *Kennalestes*.

Comparison with the Paleoryctinae⁷ (see also p. 68)

The basicranium of *Palaeoryctes puercensis* MATTHEW, AMNH 15923, which is the only palaeoryctine skull in which the basicranial region has been preserved (see MATTHEW 1913, MCDOWELL 1958 and VAN VALEN 1966) is poorly preserved, but as far as can be judged it is more like *Asioryctes* than *Kennalestes*. In both *Asioryctes* and *P. puercensis* the postpalatine torus is weak and the promontorium is very high in the posteromedial part. So long as the grooves in the process which borders the glenoid fossa posteriorly are not artefacts in the two specimens, then the entoglenoid process would be characteristic of both genera and the chorda tympani would follow a similar course.

MCDOWELL (1958) recognized the fragmentary ring, preserved on the left side of the skull of *P. puercensis* as entotympanic, while VAN VALEN (1966: 53) stated: "I do know whether the fragment of bulla present is entotympanic, as proposed by MCDOWELL, or tympanic as claimed by MATTHEW". The comparison of the position of this bone and its shape with the ectotympanic in *Asioryctes*, shows that the bone in question in *P. puercensis* is an ectotympanic and not entotympanic.

The characteristic feature of *Asioryctes* basicranium is the presence of a flange which prolongs the postglenoid process anteromedially (see: "Descriptions"). A similar flange, may be found in *P. puercensis*, although it is less conspicuous and directed first medially and then anteriorly, rather than anteromedially as in *Asioryctes*. Because the flange has a different course,

the basisphenoid appears relatively narrower in *P. puercensis*. The basisphenoid wing, characteristic of *Asioryctes*, cannot be distinguished with any certainty in *Palaeoryctes*, but this may be partly due to the state of preservation.

The tympanohyal is in both compared specimens large, placed in front of the fossa musculi stapedii, and lateral to the fenestra vestibuli; it is relatively larger in *Asioryctes* than in *P. puercensis*. Because the glenoid is further back in *Asioryctes*, the tympanohyal is relatively further forward, immediately behind the postglenoid foramen, whereas in *P. puercensis* the postglenoid foramen and the tympanohyal are far apart.

The promontorium is relatively larger in *Asioryctes*, and right and left promontoria are relatively closer to each other than in *P. puercensis*. It seems, however, that they have been pushed slightly inwards in ZPAL MgM-1/56 and tilted medially. This is why the fenestra vestibuli faces downwards in this specimen, rather than laterally as in *P. puercensis*. Probably, in the undistorted condition, the position of promontorium and fenestra vestibuli was alike in both genera.

It is not known whether the paroccipital process, which is absent in *Asioryctes*, was present in *P. puercensis*. The posterior palatine foramen is present in *P. puercensis* and developed as a notch in *Asioryctes*; the alisphenoid canal is present in *P. puercensis*, but only a groove for the internal maxillary artery is present in *Asioryctes*.

It can be seen from the above that there are many similarities in the structure of the basicranial region of *Asioryctes* and *P. puercensis*. They are sufficiently important to suggest that *Asioryctes* has palaeoryctine affinities.

Comparison with the Tenrecidae

The skull of *Asioryctes* resembles that of *Tenrec* (but not other tenrecid genera) in having a very long mesocranial region. However, the shape of this region is very different in the two genera: in *Asioryctes* the skull when viewed from below widens gradually from the end of the palate towards the glenoid fossae, but in *Tenrec* this part of the skull is cylindrical, and the basicranial region abruptly widens at the level of the glenoid fossae. In *Asioryctes* the alisphenoid is very long, extending for about half of the mesocranium, but in *Tenrec* it is the maxilla, palatine and orbitosphenoid that form most of the lateral wall of the braincase in this region, the alisphenoid extending for less than 0.3 of the length. The skulls of *Asioryctes* and the Tenrecidae are alike in lacking a foramen rotundum, the presence of the postglenoid process and postglenoid foramen, and the structure of the alisphenoid, which in both groups partly overlaps the orbitosphenoid. In the Tenrecidae the anterior opening of the sinus canal opens into the sphenorbital fissure; in *Asioryctes* it opens above it, but it is possible that the free edge of the alisphenoid covered the opening of the sinus canal in life and that this was confluent with the sphenorbital fissure.

In *Asioryctes* and *Kennalestes* there is a basisphenoid wing, but in the Tenrecidae the posterior part of the basisphenoid is provided with a tympanic wing, directed obliquely downwards and projecting posteriorly (DOBSON 1882, PARKER 1886, McDOWELL 1958). Because of the different proportions of the skulls of *Asioryctes* and the Tenrecidae, the tympanic and basisphenoid wings occupy different positions. The basisphenoid wing is situated in front of the foramen ovale and anterolateral to the promontorium, which in *Asioryctes* is very large; the posterior part of the basisphenoid wing supports the anterior margin of the ectotympanic. In the Tenrecidae, however, the tympanic wing is situated to the rear of the foramen ovale and borders the very small promontorium and ectotympanic medially, partly covering the ectotympanic from below. It follows that although both the basisphenoid and tympanic wings are lateral projections of the medial part of the basisphenoid, they are probably not homologous structures.

The alisphenoid canal is absent in *Asioryctes* and probably also in *Kennalestes*, but present

in the Tenrecidae; the optic foramen in the Tenrecidae is confluent with the sphenorbital fissure but separate in *Asioryctes*. The flange that extends anteromedially from the glenoid process and is characteristic of the *Asioryctes* skull, is lacking in the Tenrecidae, but the remnant of the inflated quadrate ramus of the alisphenoid is present. A large paroccipital process is present in the Tenrecidae and absent in *Asioryctes*, the occiput in *Asioryctes* retains the primitive, cynodont slope whereas in the Tenrecidae it has a typical mammalian slope.

From this it can be seen that the basicranial regions of *Asioryctes* (and *Kennalestes*) and the Tenrecidae are in many ways dissimilar. The elongation of the mesocranial region, which is a primitive feature in *Asioryctes*, is probably a secondary specialization in *Tenrec*, for in *Tenrec* the bones contributing to the structure of the anterior part of this region are different from those in cynodonts, the elongation is not correlated with the primitive slope of the occiput and does not occur in all the members of the family. Of the features that the *Asioryctes-Kennalestes* and Tenrecidae skulls have in common, the overlapping of the orbitosphenoideum by alisphenoideum is probably a plesiomorphous character, whereas the postglenoid process and postglenoid foramen are also characteristic of many other mammals.

PHYLOGENETIC AND SYSTEMATIC CONCLUSIONS

The comparisons with cynodonts, marsupials and various groups of primitive eutherian mammals discussed above allow a synopsis to be made of features that may be regarded as primitive for Theria. Those structures that *Asioryctes-Kennalestes* share with cynodonts, Mesozoic mammals, and those that they share with the Tertiary and modern marsupials (skulls of Cretaceous marsupials are not known) can be referred to as symplesiomorphous therian character states. These are:

- inclination of the occipital plate upwards and forwards from the condyles;
- long mesocranial region, associated with a large alisphenoid;
- a basisphenoid wing, possibly homologous with the basiptyergoid process of cynodonts;
- foramen rotundum confluent with sphenorbital fissure;
- no alisphenoid canal;
- posterior position of foramen ovale, the posterior margin of which touches the suture with the squamosal;
- medial position of internal carotid artery, no promontory artery;
- no entotympanic, ectotympanic forming 3/4 of a ring, inclined to the horizontal;
- postglenoid process prolonged into a flange extending anteromedially, built from the posterior part of the inflated quadrate ramus of the alisphenoid, possibly fused with the lateral flange of the petrosal;
- glenoid fossa placed relatively far back opposite the anterior half of the promontorium;
- no paroccipital process;
- long jugal, reaching back to the glenoid fossa;
- subsquamosal foramen;
- medial inflection of the angular process of the dentary;
- rudimentary coronoid fused with the dentary.

One of the genera described (*Asioryctes*) has a marsupial incisor count, however, there is not sufficient evidence to conclude that the 5/4 incisor formula was a plesiomorphous therian character. A juvenile specimen of *Kennalestes* has 5 premolars and it is probable (see also MCKENNA 1975) that the primitive Theria had eight postcanine teeth.

In recent years numerous papers have been published which discuss the problem of the relationships of early eutherian mammals (e.g. BUTLER 1956, 1972, MCDOWELL 1958, VAN VALEN 1966, 1971, SZALAY 1968, 1977, MCKENNA 1969, 1975, NOVACEK 1977 and others) and numerous authors have pointed out how difficult it is to classify early Eutheria (e.g. ROMER 1968, BUTLER 1972). MCKENNA (1969), and independently LILLEGRAVEN (1969), have shown that by the Late Cretaceous two distinct lineages of eutherian mammals may be recognized: the leptictid grouping which gave rise to lipotyphlous insectivores, primates and rodents and the palaeoryctid grouping which gave rise to the creodonts, carnivores and ungulates². The conclusions of these authors were based almost exclusively upon dentition, as at that time no skull of Cretaceous leptictid or palaeoryctid was known. The present studies confirm the existence of a palaeoryctid lineage (*Asioryctes*) in the Late Cretaceous of Asia, whereas *Kennalestes* may be tentatively regarded as close to the ancestors of the Leptictidae, although it differs from the leptictids in having a more primitive internal carotid circulation pattern. On the other hand, as emphasized throughout the description, *Kennalestes* and *Asioryctes* are closely related to each other and may be derived from a common ancestor (see also KIELAN-JAWOROWSKA 1975a and 1975b).

As postulated by MCKENNA (1975) "*Prokennalestes*" TROFIMOV from the Early Cretaceous of Mongolia (cited here as a *nomen nudum*) is a possible candidate.

Although the two genera described here, were incompletely known until now they have served as a basis for creating higher rank taxa. SZALAY (1977) erected the family Asioryctidae and placed it in Eutheria *incertae sedis* but has not diagnosed the family, has not discussed its range and not designated the type genus (though presumably it is *Asioryctes*).

Up till 1974, according to the International Code of Zoological Nomenclature (1964, article 16 (a)), it was permissible to propose a family name by "indication"; the word "indication" applies among others (I.C.Z.N., 1964 Article 16(a), clause (IV)) to: "the formation of a new family-group name from the stem of the name of a genus, which thus becomes the type genus". But the "Amendments to the International Code of the Zoological Nomenclature" 1974 rule against this practice (p. 79): "Article 13. Names published after 1930. — (c) Exclusions. — After 1930, the name proposed only by "indication" under any of the methods listed in Article 16(a), clauses (II), (IV), (V), (VI), (VII), and (VIII) is not available". It follows that the family name Asioryctidae SZALAY 1977, proposed only by indication, is not available.

Despite the strong palaeoryctine affinities of *Asioryctes* (described and discussed above) it cannot be placed in the subfamily Palaeoryctinae (for differences with *Palaeoryctes* see "Comparisons with Palaeoryctinae"). I therefore here allocate it to the subfamily Asioryctinae nov., within the family Palaeoryctidae WINGE, 1917.

MCKENNA (1975) erected the superorder Kennalestida in the magnorder Ernotheria MCKENNA, 1975, in the cohort Epitheria MCKENNA, 1975. To the magnorder Ernotheria in addition to the Kennalestida he assigned the superorder Leptictida MCKENNA, 1975. MCKENNA (1975:32) referred to Ernotheria: *Asioryctes*, paleoryctines, *Kennalestes*, *Gypsonictops*, leptictids, didymoconids, macroselidids, anagalids, pseudictopids, zalambdalestids, eurymylids, ochotonids and leporids. The range of the superorder Kennalestida has not been unequivocally defined, but it may appear from fig. 3 of MCKENNA (1975) that he assigned to the Kennalestida: *Kennalestes*, *Asioryctes* and paleoryctines.

I do not agree with MCKENNA's (1975) concept of the magnorder Ernotheria, (see also KIELAN-JAWOROWSKA 1979). The results of the present studies concur better with the idea of NOVACEK (1977) who, following BUTLER (1972), allocated the families: Leptictidae, Panto-

² It appears from the unpublished studies of Prof. M. C. MCKENNA on the new *Palaeoryctes* species from Wyoming that the Palaeoryctidae are probably more allied to the lipotyphlous insectivores than to any other grouping of primitive eutherians. The discussion of this problem is, however, beyond the scope of the present paper and will be discussed by Prof. MCKENNA in the forthcoming publication.

lestidae, Ptolemaiidae, Apatemyidae and Palaeoryctidae to the order Proteutheria ROMER, 1966. To this list I add the family Kennalestidae nov. which I regard as the most primitive family within the order.

DIAGNOSES OF NEW TAXA

Order PROTEUTHERIA Romer, 1966

Family KENNALESTIDAE nov.

Type genus. — *Kennalestes* KIELAN-JAWOROWSKA, 1969

Diagnosis. — Small proteutherian mammals with 3 or more upper incisors, 4–5 premolars, transverse upper molars with or without pre- and postcingula, conules present, wide embrasures; P⁴ molariform but without true metacone, P₄ not molariform. Nasals expanded posteriorly, lacrimal with facial wing, orbit confluent with temporal fossa, posterior palatine foramen developed as a notch. Zygomatic arch made exclusively by jugal, subsquamosal foramen present. Basisphenoid consisting of a horizontal medial part and basisphenoid wings. Alisphenoid extensive, alisphenoid canal absent. Glenoid fossa situated opposite anterior half of the promontorium. Entotympanic absent, ectotympanic horse-shoe shaped, promontorium moderately convex, sulcus medialis shallow, sulcus arteriae stapediae distinct, sulcus arteriae promontorii absent. Tympanic process of petromastoid very large, paroccipital process absent. Lower jaw slender with angular process inflected medially. Transverse foramen in atlas absent.

Stratigraphical and geographical range. — ?Lower and Upper Cretaceous of Asia.

Discussion. — *Kennalestes* which is a type genus of the new family is relatively well known from its complete dentition, almost complete skulls and an atlas. The attribution of other genera to this family is tentative. It seems probable that "*Prokennalestes*" TROFIMOV, 1974, from the ?Aptian of ?Albian of Mongolia which has been named but not described by TROFIMOV (in BELLAJEVA *et al.* 1974) and is cited here as a *nomen nudum*, and the poorly known *Endotherium* SHIKAMA 1947 from the ?Albian of Manchuria (see PATTERSON 1956 and KERMACK *et al.* 1965) belong also to this family.

The closest relative of the Kennalestidae is probably the Late Cretaceous North American genus *Gypsonictops*. FOX (1977) demonstrated that *Kennalestes* itself cannot be regarded as an ancestor of *Gypsonictops*, which appears convincing. Traditionally *Gypsonictops* was assigned to the Leptictidae (see SIMPSON 1927 and CLEMENS 1973). NOVACEK (1977), however, concluded that although *Gypsonictops* is a member of the superfamily Lepticoidea, it has many characters more advanced than typical Cenozoic leptictids (e.g. *Prodiacodon*, *Leptictis*) and should be excluded from this family. NOVACEK (1977) in assigning *Gypsonictops* suggested that Gypsonictopinae Van Valen 1967, be elevated to family rank. The Kennalestidae differ from *Gypsonictops* in not having a molariform P₄ and an incompletely molariform P⁴, only 4 premolars in adult stage and in having the nasals expanded posteriorly. Unfortunately the braincase of *Gypsonictops* is not known and further comparisons cannot be made. For comparisons with the Leptictidae see p. 62, and with the Asioryctinae see below, p. 54–56 and Table 2.

Family PALAEORYCTIDAE WINGE, 1917

Subfamily Asioryctinae nov.

Remark. — For the reasons discussed on p. 66, the family Asioryctidae SZALAY, 1977 is not available.

Type genus. — *Asioryctes* KIELAN-JAWOROWSKA, 1975, the only genus in this family.

Diagnosis. — Small palaeoryctids with 5/4 incisor count, double rooted upper and lower canine, P¹ submolariform (without metacone), P₁ not molariform, upper molars strongly elongated transversely with comparatively narrow styler shelves, nasals expanded posteriorly, lacrimal with facial wing, orbit confluent with temporal fossa, posterior palatine foramen developed as a notch. Zygomatic arch made exclusively by jugal, subsquamosal foramen present. Mesocranial region very long; basisphenoid consisting of medial part and basisphenoid wings arranged obliquely downwards. Characteristic feature of the mesocranial region is a flange extending anteromedially prolonging the postglenoid process. Glenoid fossa situated opposite anterior half of the promontorium. Entotympanic absent, ectotympanic horse-shoe shaped, arranged obliquely to the horizontal, promontorium strongly convex, sulcus arteriae promontorii absent, an uncertain tube for arteria stapedia present, sulcus medialis shallow. Tympanohyal very large, paroccipital process absent. Angular process in the lower jaw inflected medially. Transverse foramen in atlas absent. Pollex and hallux not opposable. Astragalus only incipiently superimposed on the calcaneus; tibial trochlea on astragalus not developed, astragalo-cuboid contact present.

Stratigraphical and geographical range. — Upper Cretaceous of Asia.

Discussion. — The closest relatives of the Asioryctinae are the Kennalestidae and the Palaeoryctinae. Asioryctinae share plesiomorphous characters with the Kennalestidae indicating that they had only recently separated from a common ancestor, but differ distinctly in the structure of the dentition and in details of skull structure (see Table 2).

The Asioryctinae are similar to the Palaeoryctinae (especially to Late Cretaceous North American genera such as *Cimolestes*, *Procerberus* and *Batodon*) in structure of their dentition. As the braincase structure of the Late Cretaceous North American palaeoryctines is not known, relevant comparisons may be made only with Tertiary palaeoryctines. The Asioryctinae differ from them in having a more elongated mesocranial region, the glenoid fossa further back and in lacking a posterior palatine foramen (see also discussion on p. 63).

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EXPLANATION OF THE PLATES 3-19

PLATE 3

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Nemegt (Southern Monadnocks),
Gobi Desert, Mongolia, ZPAL MgM-I/56 — holotype

- 1a. The skull in right lateral view.
- 1b. The same in left lateral view.

Both stereo-photographs $\times 5$
(See also text-fig. 1 and plates 4-7)

Photo: E. Wyrzykowska

PLATE 4

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Nemegt (Southern Monadnocks),
Gobi Desert, Mongolia, ZPAL MgM-I/56 — holotype

- 1a. Stereo-photograph of the skull in ventral view.
- 1b. Stereo-photograph of the same in occipital view.

(See also text-fig. 2 and plates 3 and 5-7)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin,
Gobi Desert, Mongolia, ZPAL MgM-I/148

- 2a. Stereo-photograph of the left lower jaw in medial view.
- 2b. The same in outer view.

(See also plate 7)
All $\times 5$

Photo: E. Wyrzykowska

PLATE 5

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II,
Gobi Desert, Mongolia, ZPAL MgM-I/98

1. Almost complete skull, strongly compressed laterally, with both lower jaws in occlusion; the posterior part of the right lower jaw and zygomatic arch have been removed to show the details of the lateral wall of the braincase.

Upper Cretaceous, Barun Goyot Formation, Nemegt (Southern Monadnocks),
Nemegt Basin, Gobi Desert, Mongolia, ZPAL MgM-I/56 — holotype

- 2a. Left lower jaw in ventral view.
- 2b. The same in occlusal view.
- 2c. The skull of the same in dorsal view.

(See also plates 3-4 and 6-7)
All $\times 5$

Photo: E. Wyrzykowska

PLATE 6

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Nemegt (Southern Monadnocks),
Gobi Desert, Mongolia, ZPAL MgM-I/56 — holotype

- a. Stereo-photograph of the right lower jaw in outer view.
- 1b. Stereo-photograph of the same in inner view.
- 1c. Left lower jaw of the same specimen in inner view.
- 1d. The same in outer view.

(See also text-fig. 10 and plates 3-5 and 7)
All $\times 5$

Photo: E. Wyrzykowska

PLATE 7

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Nemegt (Southern Monadnocks)
Nemegt Basin, Gobi Desert, Mongolia, ZPAL MgM-I/56-holotype

- 1a. Stereo-photograph of the right lower jaw in occlusal view.
- 1b. The same in ventral view.

(See also plates 3, 4:1, 5:2 and 6)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin
Gobi Desert, Mongolia, ZPAL MgM-I/148

- 2a. Stereo-photograph of the left lower jaw in occlusal view.
- 2b. The same in inner view.

(See also plate 4:2)
All $\times 5$

Kennalestes gobiensis KIELAN-JAWOROWSKA

Upper Cretaceous, Djadokhta Formation, Bayn Dzak (Main Field),
Gobi Desert, Mongolia, ZPAL MgM-I/1

3. Stereo-photograph of the right and left lower jaws of the juvenile specimen in occlusal view, $\times 7$.
(See also plates 12-15, 16:3 and 7:3)

Figs. 1a-1b and 2a-2b photo: E. Woźniak
Fig. 3 photo E. Wyrzykowska

PLATE 8

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin,
Gobi Desert, Mongolia, ZPAL MgM-I/70

- 1a. Stereo-photograph of the incomplete skull in ventral view with right and left P⁴-M³.
- 1b. Stereo-photograph of the incomplete right lower jaw with P⁴-M³ of the same specimen in inner view.
- 1c. Stereo-photograph of the same in outer view.
- 1d. Stereo-photograph of the same in occlusal view.
- 1e. Stereo-photograph of the left lower jaw with P⁴-M³ of the same specimen in occlusal view.
- 1f. Stereo-photograph of the same in outer view.
- 1g. Stereo-photograph of the same in inner view.

All × 5

Photo: E. Wyrzykowska

PLATE 9

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation. Khulsan, Nemegt Basin,
Gobi Desert, Mongolia, ZPAL MgM-I/71

1. Stereo-photograph of the anterior part of the face of a juvenile individual, with almost complete dentition and both lower jaws in occlusion, in left lateral view.

(See also plate 10:2)

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II,
Gobi Desert, Mongolia, ZPAL MgM-I/144

- 2a. Right and left damaged maxillae, each in occlusion with incomplete right and left lower jaws, with right P²-M⁰ and P₄-M₃ and left P³-M³ and C-M₃, before the separation, in left lateral view.
- 2b. The same in right lateral view.
- 2c. Left side of the same, after the separation from the right side in outer view.
- 2d. The same in inner view.

All × 5

Photo: E. Wyrzykowska

PLATE 10

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II,
Gobi Desert, Mongolia, ZPAL MgM-I/87

- 1a. Stereo-photograph of the incomplete left maxilla with P³-M³ in inner view.
- 1b. Stereo-photograph of the same in occlusal view.
- 1c. The same in outer view.
- 1d. Stereo-photograph of the incomplete left lower jaw of the same specimen, with P³-M³ in outer view.
- 1e. Stereo-photograph of the same in occlusal view.
- 1f. The same in inner view.

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin,
Gobi Desert, Mongolia, ZPAL MgM-I/71

- 2a. Stereo-photograph of the anterior part of the face of a young individual with almost complete dentition, with both lower jaws in occlusion, in ventral view.
2b. The same in right lateral view.

(See also plate 9:1)

All × 5

Photo: E. Wyrzykowska

PLATE 11

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Nemegt (Eastern Sayr),
Nemegt Basin, Gobi Desert, Mongolia, ZPAL MgM-I/134

- 1a. Stereo-photograph of the incomplete face, strongly compressed laterally with left P¹-M³ and right P²-M³.
1b. Stereo-photograph of the incomplete left lower jaw of the same specimen with P₃-M₃.
1c. Stereo-photograph of the same in inner view.
1d. Stereo-photograph of the same in outer view.
1e. Stereo-photograph of the right lower jaw of the same specimen with P₃-M₃ in inner view.
1f. Stereo-photograph of the same in occlusal view.
1g. Stereo-photograph of the same in outer view.

All × 5

Photo: E. Wyrzykowska

PLATE 12

Kennalestes gobiensis KIELAN-JAWOROWSKA

Upper Cretaceous, Djadokhta Formation, Bayn Dzak (Main Field),
Gobi Desert, Mongolia, ZPAL MgM-I/1

- 1a. Stereo-photograph of the skull of a juvenile individual with both lower jaws in occlusion, almost complete dentition, an atlas and fragment of axis, before preparation, in right lateral view.
1b. Stereo-photograph of the same in ventral view.
1c. The same in dorsal view.
1d. The same in dorsal view after partial preparation.

(See also pls. 7:3, 13-15, 16:3, 17:3)

All × 4.5

Photo: Ch. Tarka

PLATE 13

Kennalestes gobiensis KIELAN-JAWOROWSKA

Upper Cretaceous, Djadokhta Formation, Bayn Dzak (Main Field),
Gobi Desert, Mongolia, ZPAL MgM-I/1

- 1a. Stereo-photograph of the skull of a juvenile individual, with both lower jaws in occlusion, almost complete dentition, an atlas and fragment of axis, after partial preparation, in left lateral view.

- 1 b. The same after further preparation.
 1 c. The same in dorso-lateral view, further prepared than the stages figured on pl. 12:1 b and 1 c.
 1 d. Stereo-photograph of the same skull in ventral view, after the separation of lower jaws.
 All $\times 4.5$

Photo: Ch. Tarka

PLATE 14

Kennalestes gobiensis KIELAN-JAWOROWSKA

Upper Cretaceous, Djadokhta Formation, Bayn Dzak (Main Field),
 Gobi Desert, Mongolia, ZPAL MgM-I/1

- 1 a. Stereo-photograph of the skull of a juvenile individual, after the final preparation and separation of the lower jaws, in ventral view.
 1 b. The same in dorsal view, showing the inside of the braincase.
 (See also plates 7:3, 12, 13, 15, 16:3, 17:3
 Both $\times 7$

Photo: E. Wyrzykowska

PLATE 15

Kennalestes gobiensis KIELAN-JAWOROWSKA

Upper Cretaceous, Djadokhta Formation, Bayn Dzak (Main Field),
 Gobi Desert, Mongolia, ZPAL MgM-I/1

- 1 a. Stereo-photograph of the skull of a juvenile individual, after the final preparation and separation of the lower jaws, in right lateral view.
 1 b. Stereo-photograph of the same in left lateral view.
 (See also pls. 7:3, 12-14, 16:3 and 17:3)
 Both $\times 7$

Photo: E. Wyrzykowska

PLATE 16

Kennalestes gobiensis KIELAN-JAWOROWSKA

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

- 1 a. Stereo-photograph of the isolated, damaged right petrosal found in the same piece of rock as the incomplete skull. Ventral view, showing fenestra vestibuli, f. cochleae and fossa musculi stapediae (see also text-fig. 8), ZPAL MgM-I/2, $\times 8$.
 1 b. Stereo-photograph of the same in dorsal (endocranial) view, showing meatus acousticus internus; as the posterior and medial walls of fossa subarcuata are broken, the external gyri of the semicircular canals and crus commune are visible, $\times 8$.

- 1c. Stereo-photograph of the same in medial view, $\times 8$.
- 1d. The same in outer view, $\times 8$.
- 2a. Stereo-photograph of the posterior part of the cranial roof with incomplete occipital plate and right petrosal, in ventral view, ZPAL MgM-I/44, $\times 8$ (see also text-fig. 7).
- 2b. The same in dorsal view, $\times 4$.
- 2c. Stereo-photograph of the same in right lateral view, $\times 4$.
- 2d. Stereo-photograph of the same in occipital view, $\times 4$.
3. Stereo-photograph of the cerebellar side of the basicranium in oblique dorsolateral view, showing the left petrosal, ZPAL MgM-I/1, $\times 6$.

(See also pls. 7:3, 12-15, and 16:3)

Photo: M. Czarnocka

PLATE 17

Leptictis haydeni LEIDY

Oligocene, Oreodon Beds, Colorado Draw, South Dakota

1. Stereo-photograph of the skull, after the separation of the lower jaws, in ventral view, BSM 1897 x 2/1, $\times 2$.
2. The skull in ventral view, BSM 1897 x 2/2, $\times 2$.

Kennalestes gobiensis KIELAN-JAWOROWSKA

Upper Cretaceous, Djadokhta Formation, Bayn Dzak (Main Field),
Gobi Desert, Mongolia, ZPAL MgM-I/1

- 3a. Stereo-photograph of both lower jaws, after separation of the skull, in left lateral view, $\times 7$.
- 3b. The same in right lateral view, $\times 7$.

Figs. 1 and 2, photo: S. Woźniak
Figs. 3a and 3b, photo: E. Wyrzykowska

PLATE 18

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II,
Gobi Desert, Mongolia, ZPAL MgM-I/166

- 1a. Right P^3 in outer view.
- 1b. Right P^3 of the same in outer view.
- 1c. Right P^4 of the same in outer view.
- 1d. Right M^1 of the same in outer view.
- 1e. Right M^2 of the same in outer view.
- 1f. Right M^3 of the same in outer view.

(See also plate 19)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemeget
Basin, Gobi Desert, Mongolia, ZPAL MgM-I/74

- 2a. Left P_3 , dP_4 , M_1 and M_2 in inner view.
- 2b. The same in outer view.

(See also plate 19)

Same horizon and locality, ZPAL MgM-I/148

- 3a. Left C, P₁ and P₂ in outer view.
- 3b. Left P₃ and P₄ of the same in outer view.
- 3c. Left M₁, M₂ and M₃ of the same in outer view.
- 3d. Left C, P₁, P₂ of the same in inner view.
- 3e. Left P₃ and P₄ of the same in inner view.
- 3f. Left M₁, M₂ and M₃ of the same in inner view.

(See also plates 4:2, 7:2 and 19)

All SEM photographs × 15

Photo: W. Skarżyński

PLATE 19

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II,
Gobi Desert, Mongolia, ZPAL MgM-I/166

- 1a. Right P² in occlusal view
- 1b. Right P³ of the same in occlusal view.
- 1c. Right P⁴ of the same in occlusal view.
- 1d. Right M¹ of the same in occlusal view.
- 1e. Right M² of the same in occlusal view.
- 1f. Right M³ of the same in occlusal view.

(See also plate 18)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin,
Gobi Desert, Mongolia, ZPAL MgM-I/74

- 2a. Left P₃ and dP₄ in occlusal view.
- 2b. Left M₂ in occlusal view.
- 2c. Left M₂ in occlusal view.

(See also plate 18)

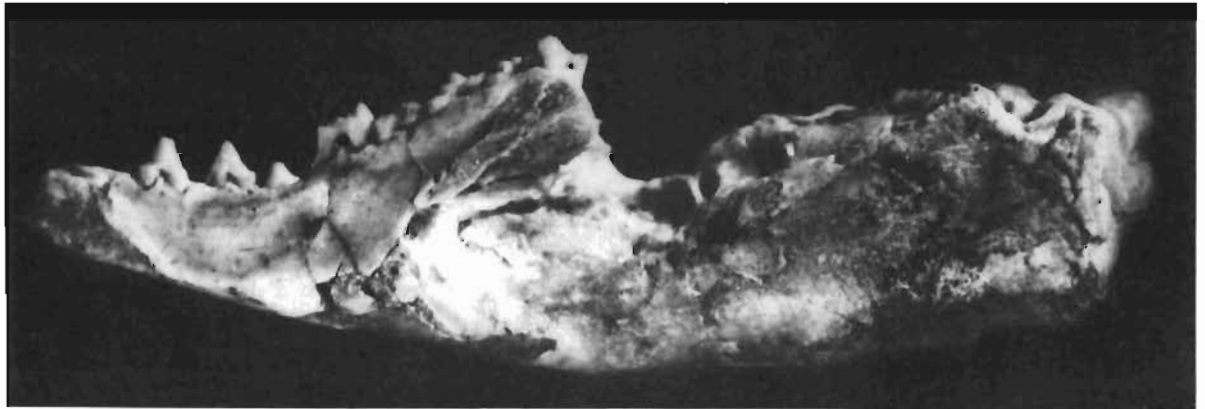
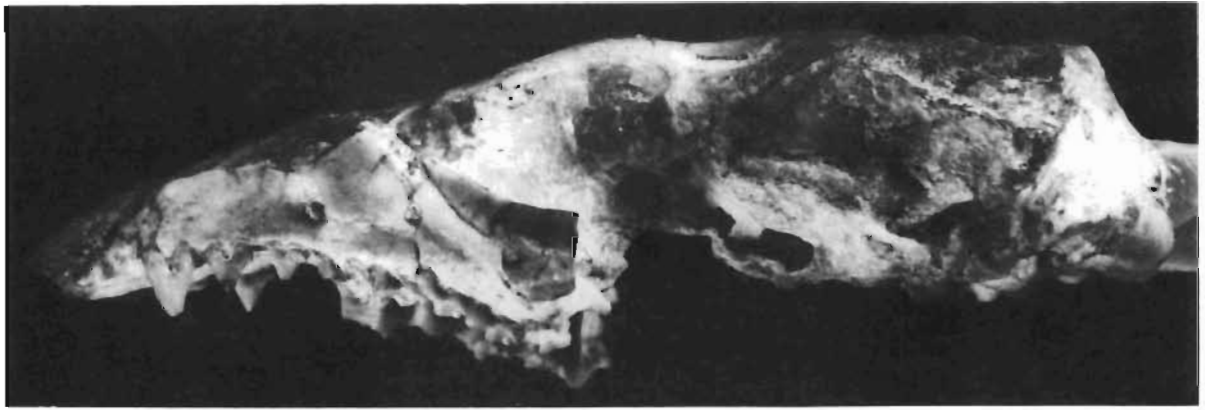
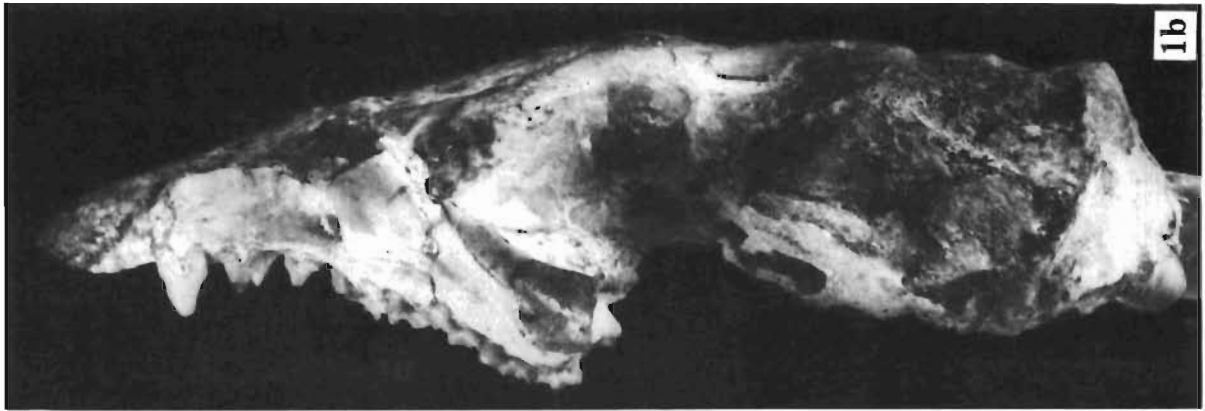
Same horizon and locality, ZPAL MgM-I/148

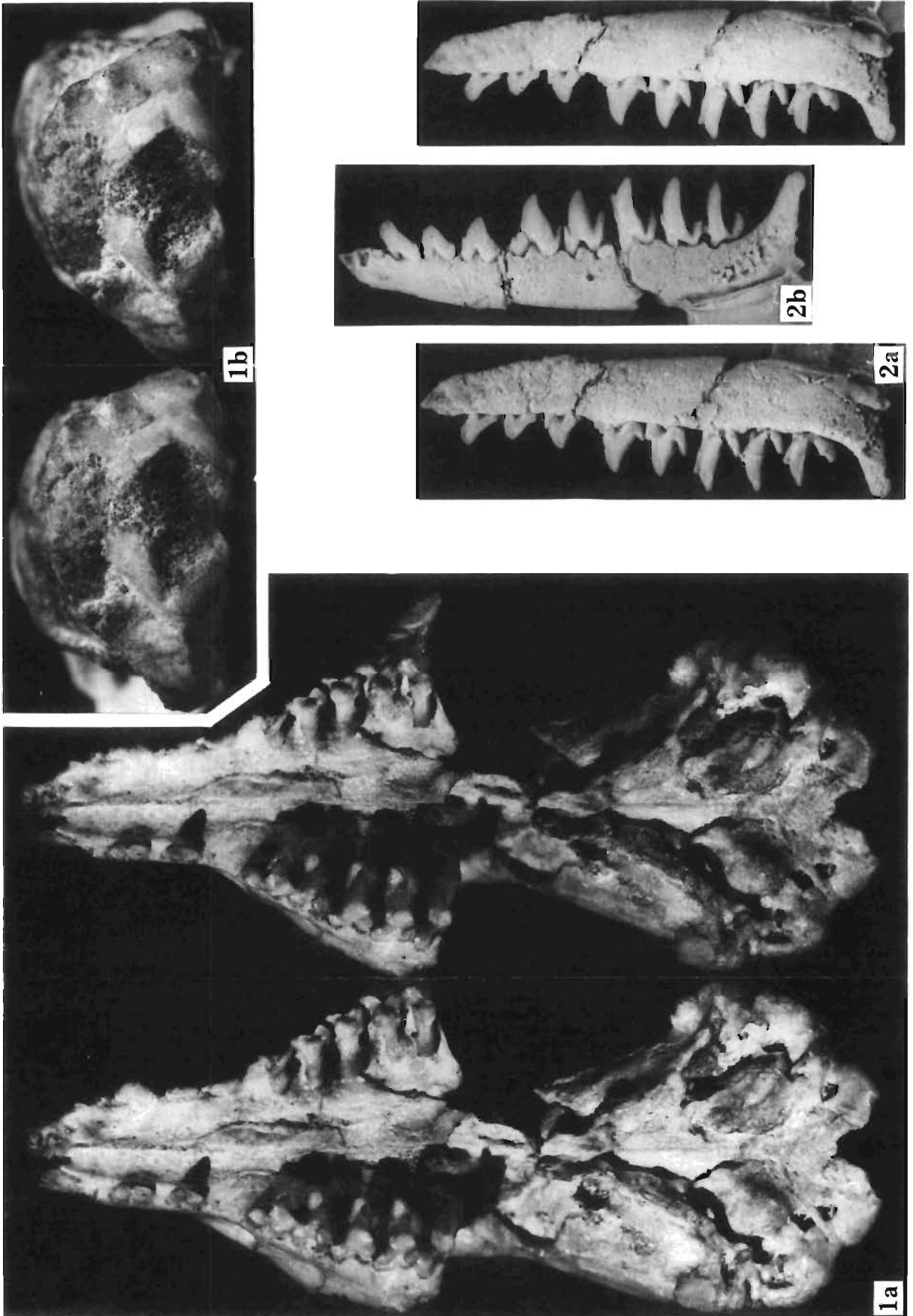
- 3a. Left P₃ in occlusal view.
- 3b. Left P₄ of the same in occlusal view.
- 3c. Left M₁ of the same in occlusal view.
- 3d. Left M₂ of the same in occlusal view.
- 3e. Left M₃ of the same in occlusal view.

(See also plates 4:2, 7:2 and 18)

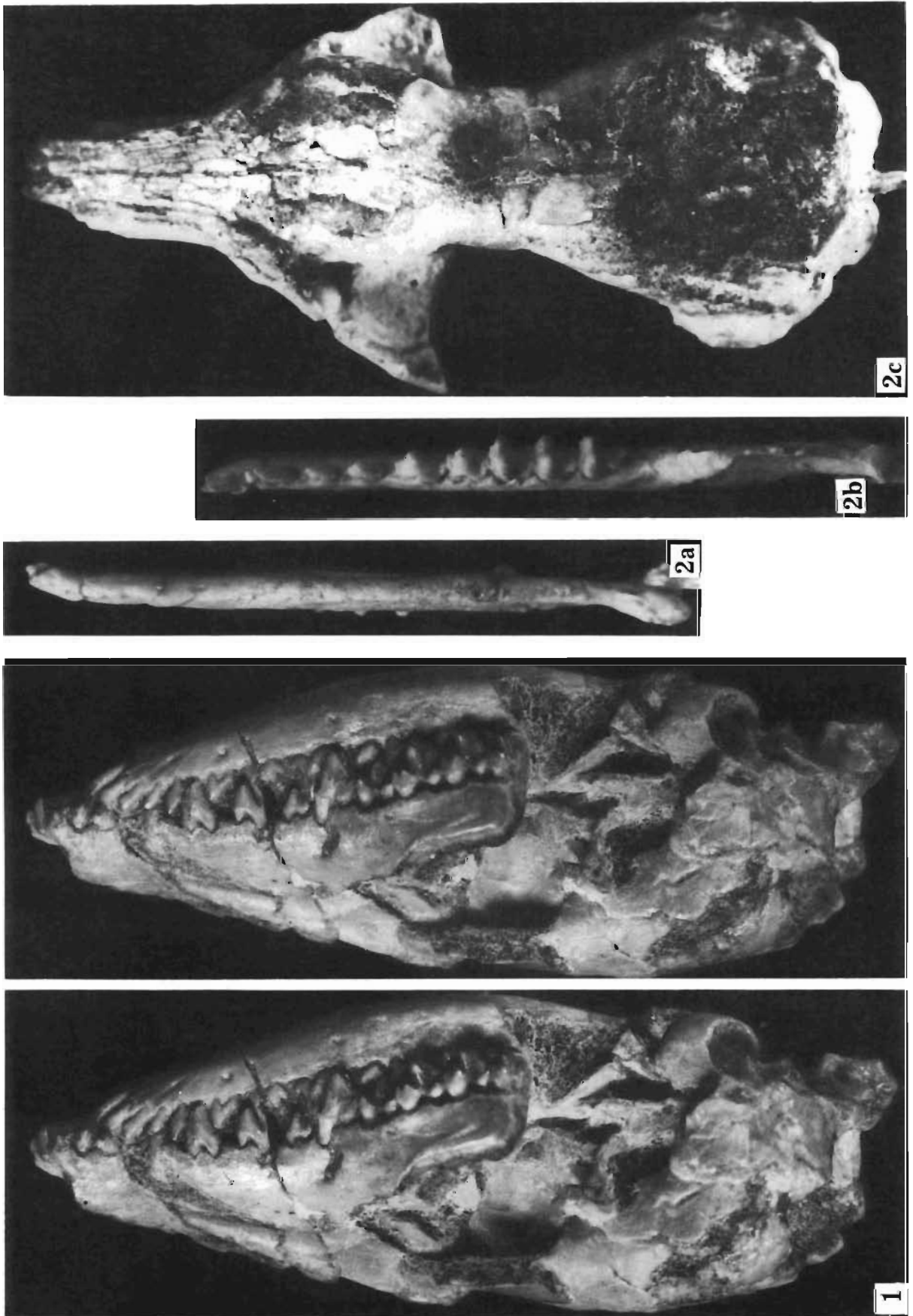
All SEM stereo-photographs × 15

Photo: W. Skarżyński

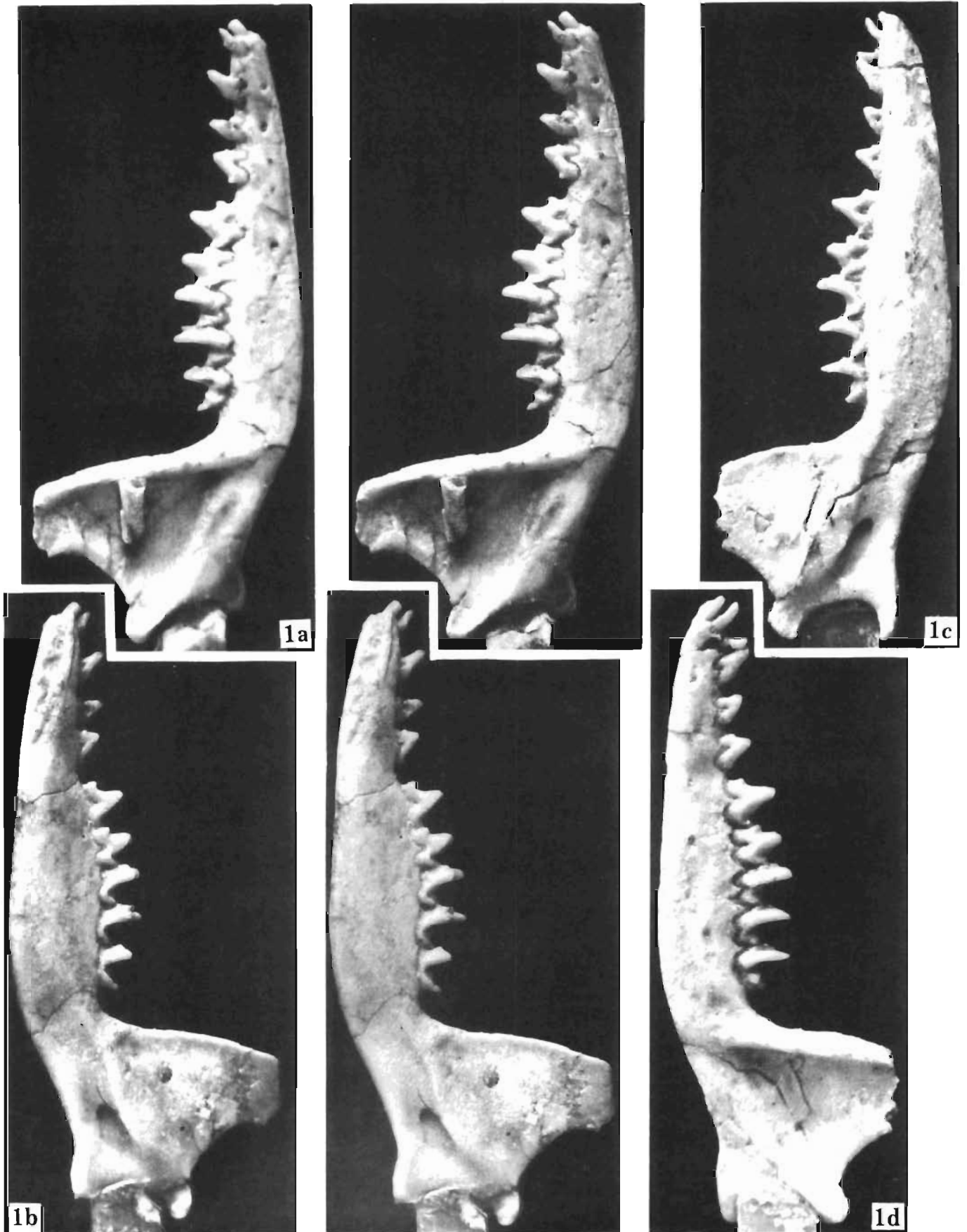


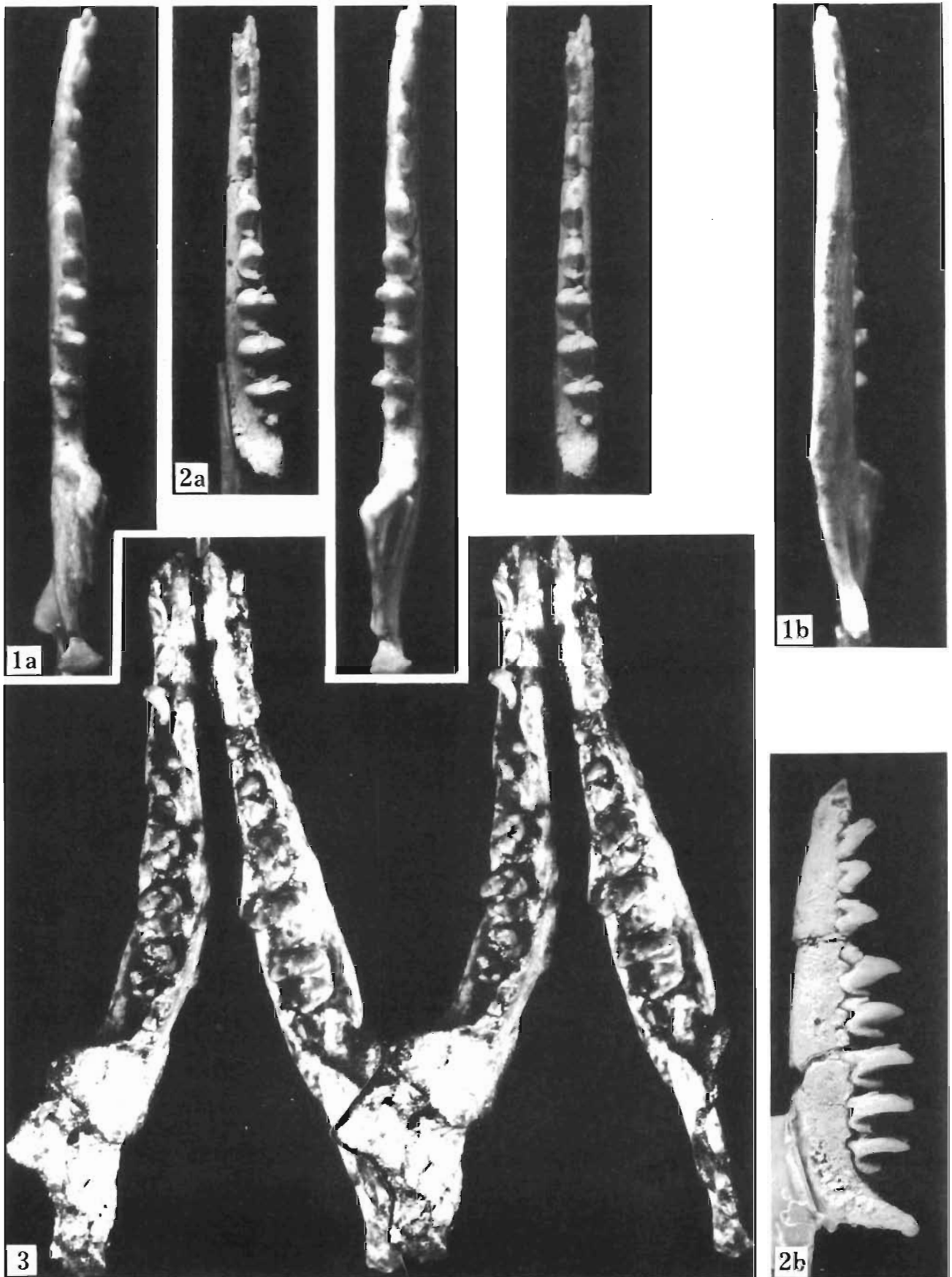


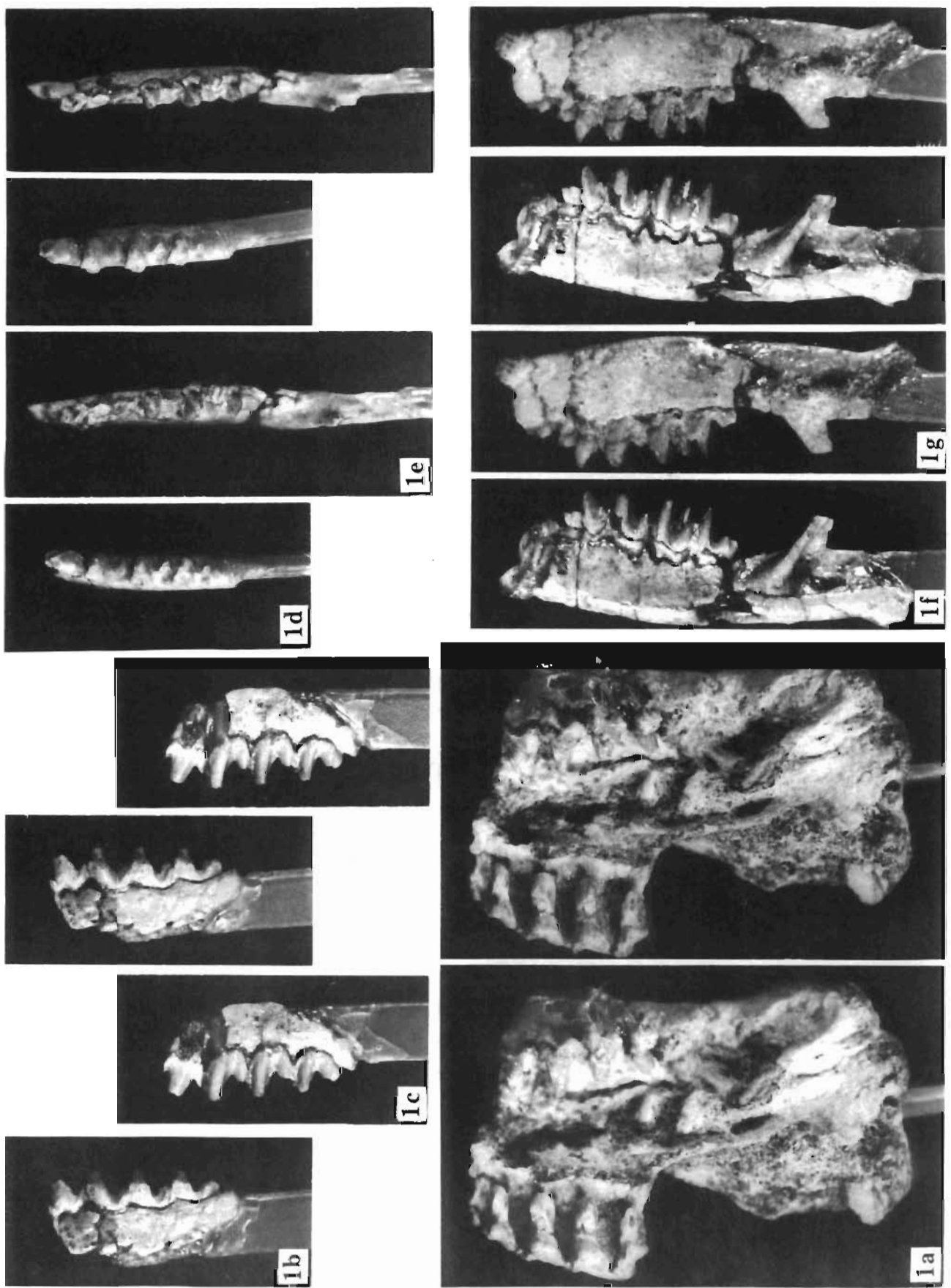
Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE IN *Kennalestes* AND *Asioryctes*



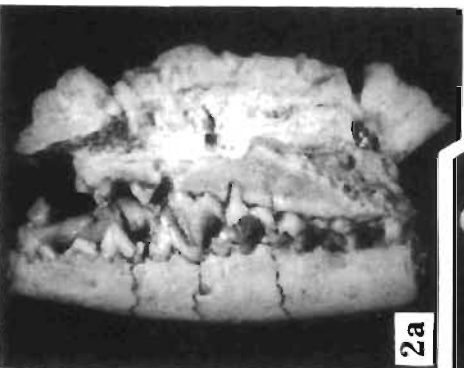
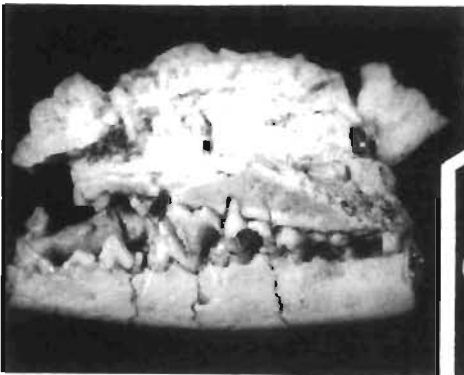
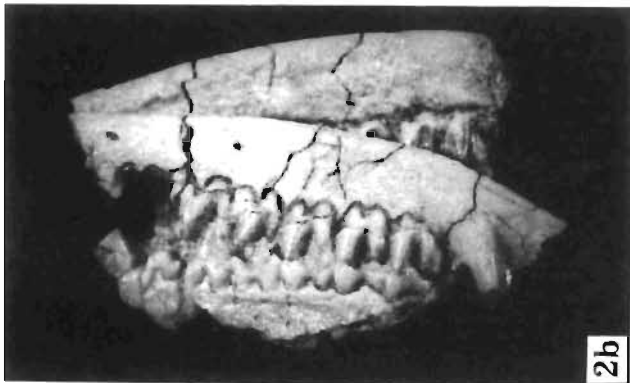
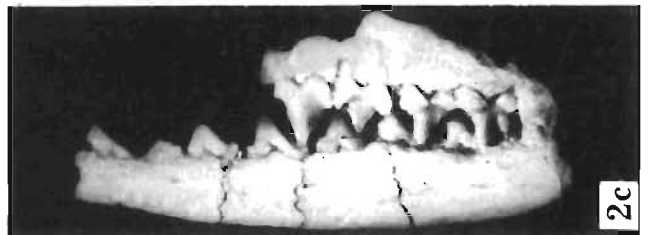
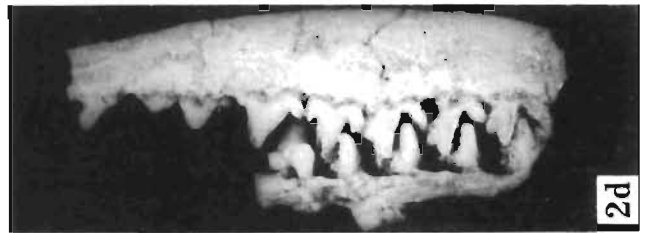
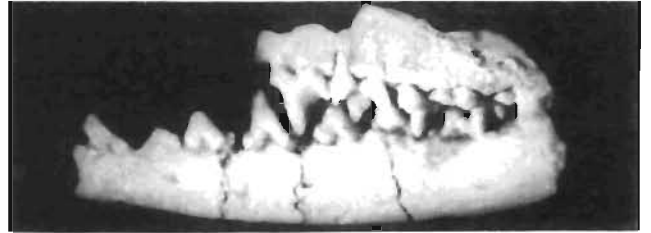
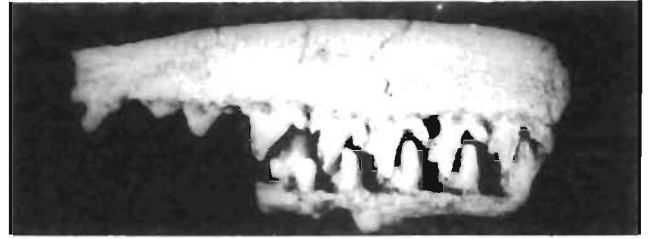
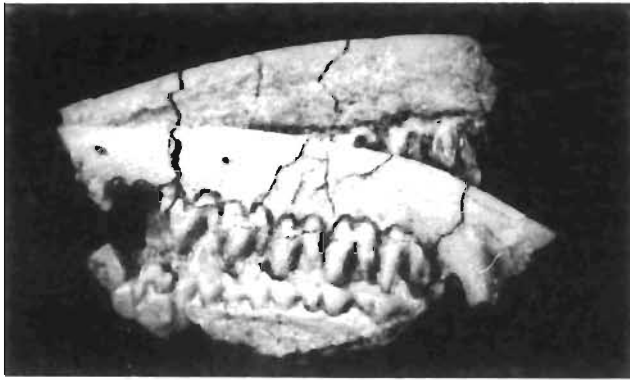
Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE IN *Kennalestes* AND *Asioryctes*

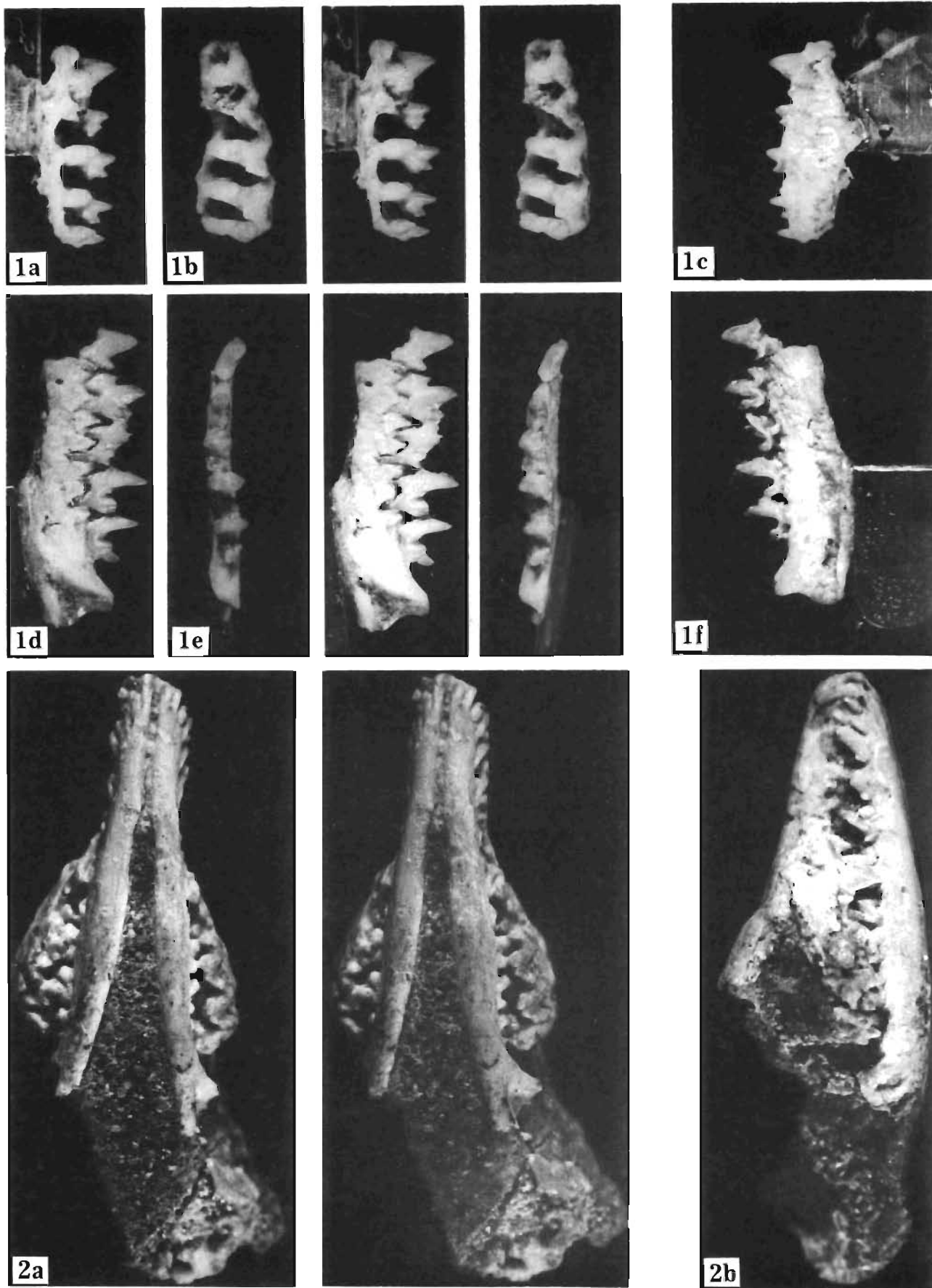




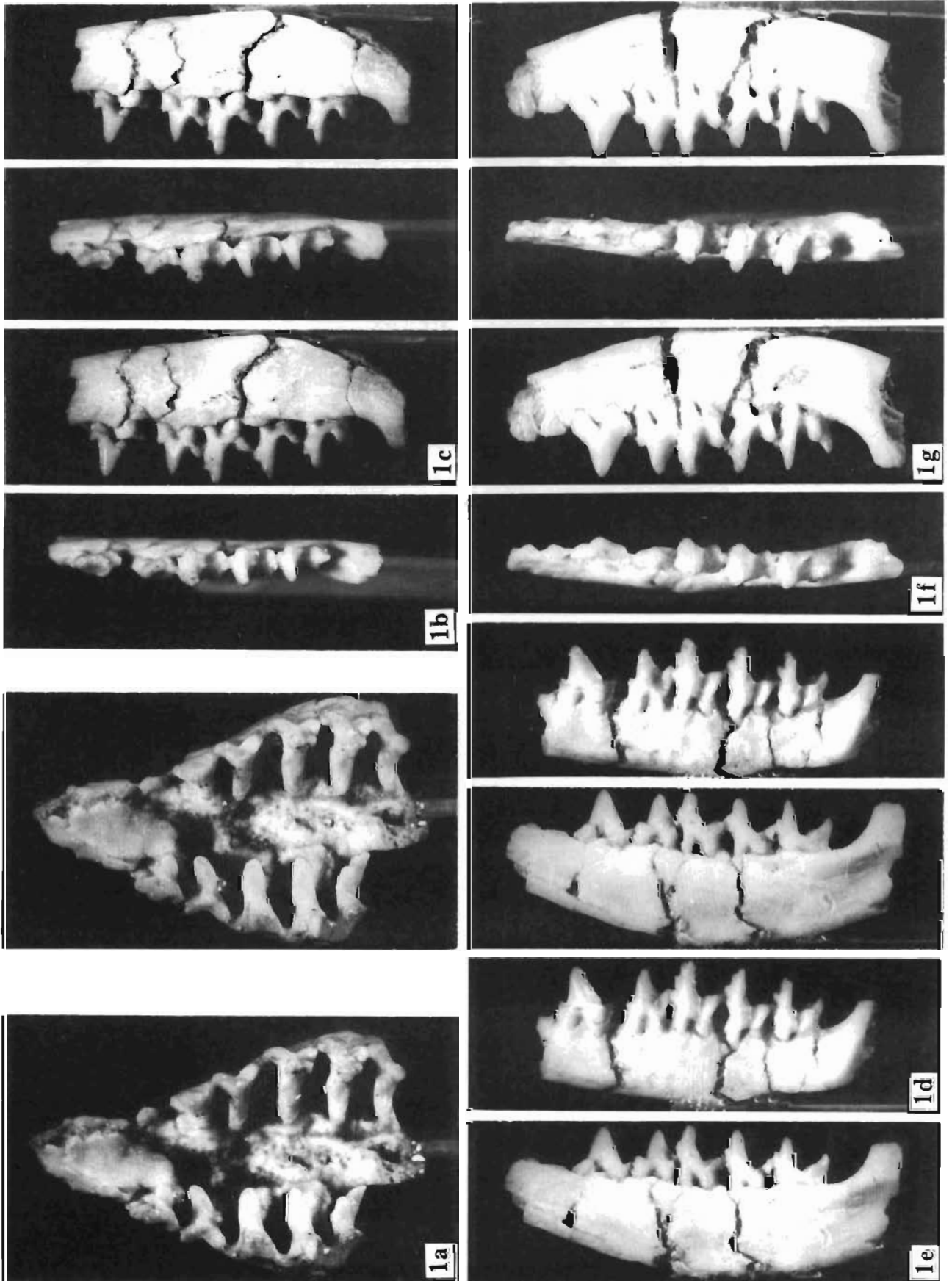


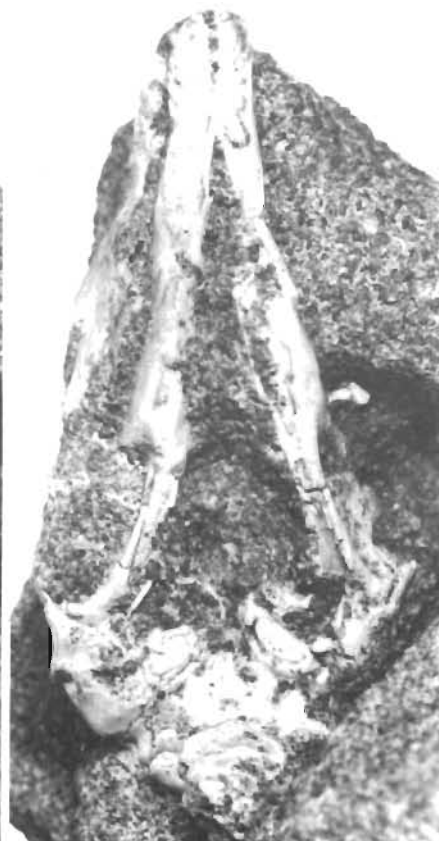
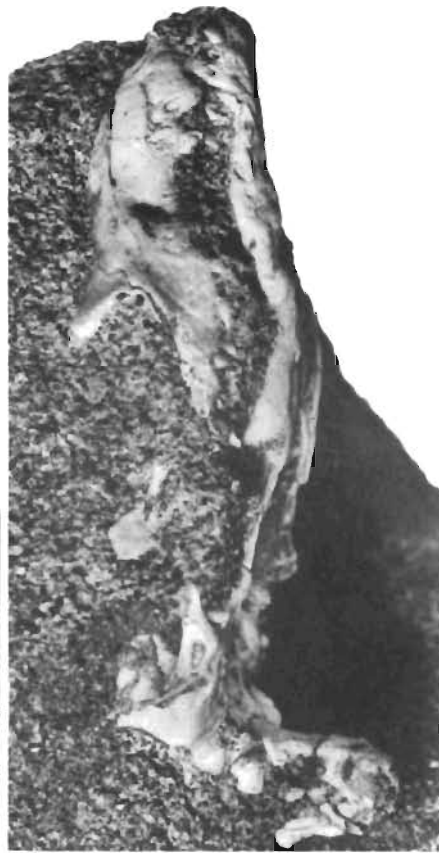
Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE IN *Kennalestes* AND *Asioryctes*





Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE IN *Kennalestes* AND *Asioryctes*







1a



1b

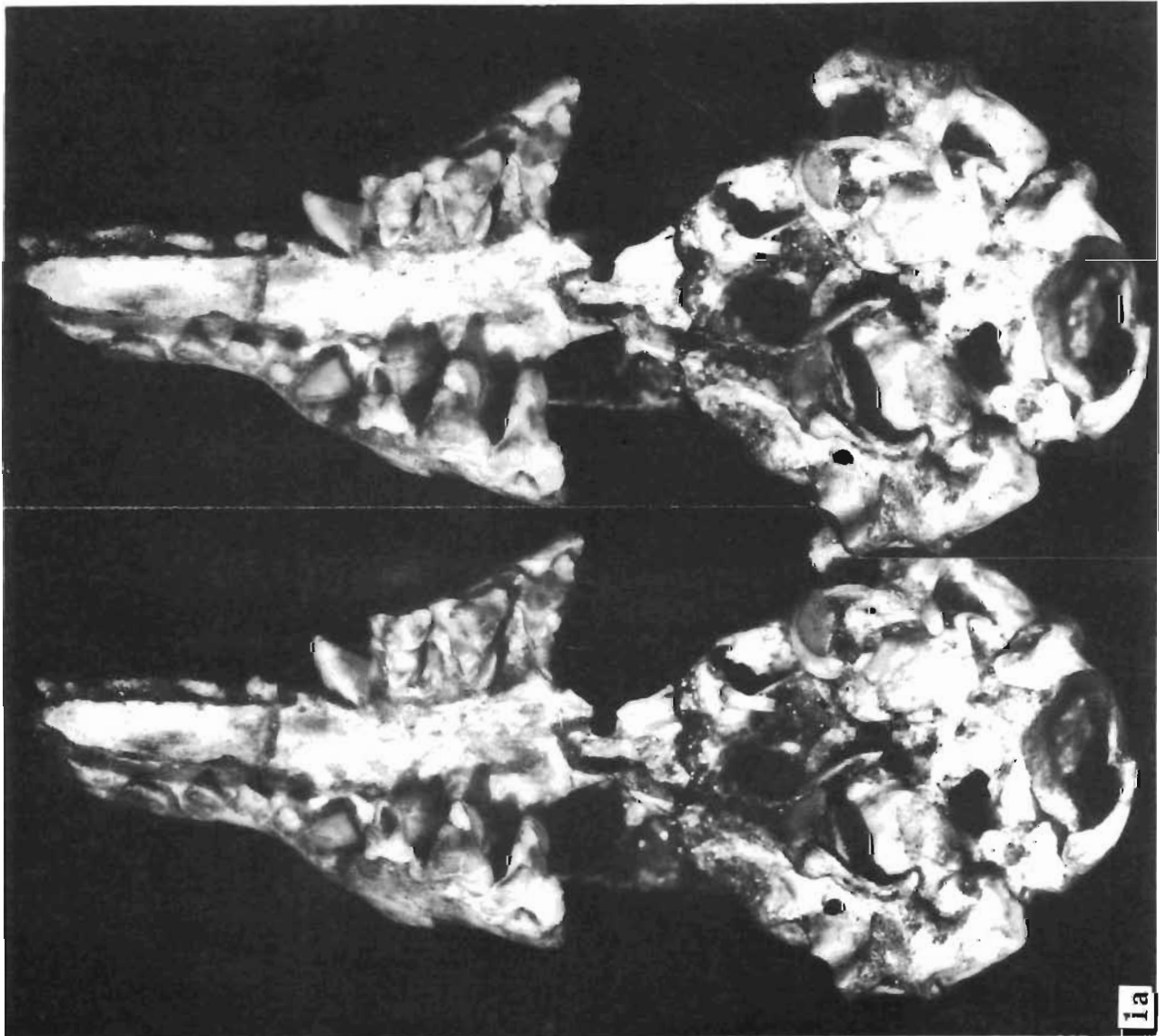
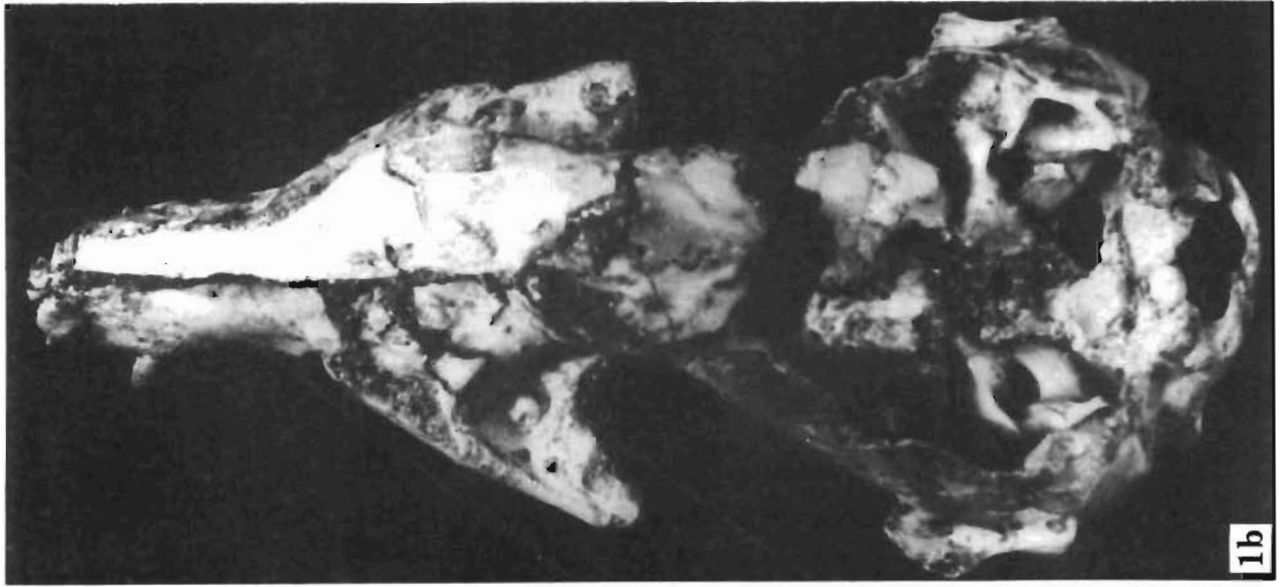


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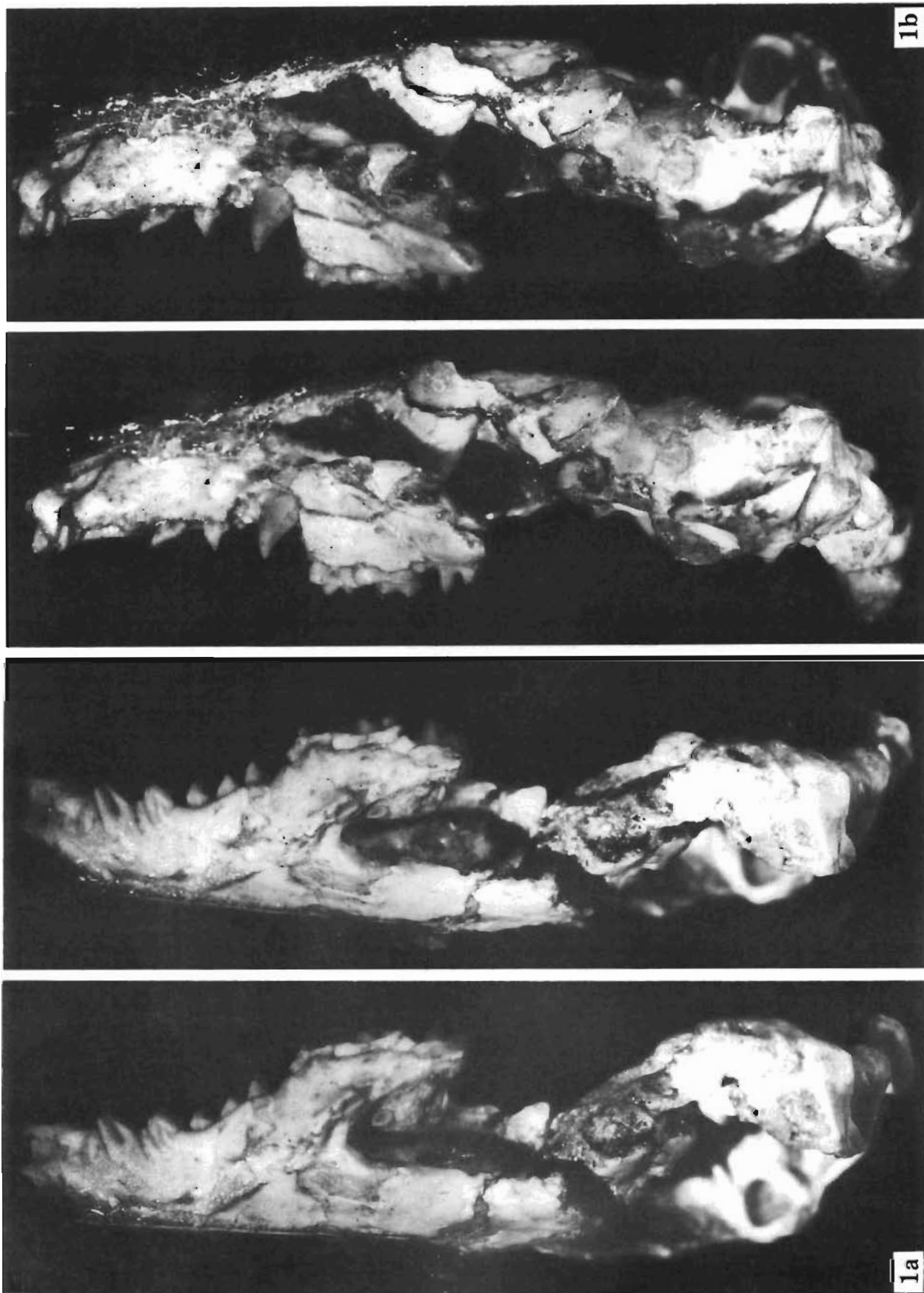


1d





Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE IN *Kennalestes* AND *Asioryctes*



Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE IN *Kennalestes* AND *Asioryctes*

