

# THE CRANIAL VASCULAR SYSTEM IN TAENIOLABIDOID MULTITUBERCULATE MAMMALS

BY ZOFIA KIELAN-JAWOROWSKA<sup>1</sup>†, R. PRESLEY<sup>2</sup>  
AND CECILE POPLIN<sup>1</sup>

<sup>1</sup> Institut de Paléontologie, 8 rue de Buffon, 75005 Paris, France

<sup>2</sup> Department of Anatomy, University College, P.O. Box 78, Cardiff CF1 1XL, U.K.

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† Present address: Zakład Paleobiologii, Polska Akademia Nauk, 02-089 Warszawa, al Zwirki i Wigury 93, Poland.

Two skulls of Late Cretaceous multituberculates from Mongolia, *Nemegtbaatar gobiensis* and *Chulsanbaatar vulgaris*, were serially sectioned on a Jung microtome at thicknesses respectively of 25 and 20  $\mu\text{m}$ . A wax model of the endocranial cavity, with casts of certain vessels and nerves, was made for *Nemegtbaatar*. On the basis of the sections, model, various entire skulls from Mongolia and isolated Late Cretaceous multituberculate petrosals from Montana, U.S.A., a reconstruction of the vascular system was made. The internal carotid artery entered the pituitary fossa laterally at the junction of petrosal, basisphenoid and probably alisphenoid and pterygoid. A stapedia artery was present, possibly with a meningeal branch entering the skull through the 'hiatus Fallopii'. In some genera a canal ran from the facial sulcus to open in front of the mandibular nerve foramina outside the semilunar fossa, possibly transmitting the maxillary artery. In addition to undoubted arteries two other systems of cranial vessels were apparent: a dural sinus system and an orbito-temporal system. The dural sinus system included: sagittal sinus, transverse sinus, sigmoid sinus, prootic sinus, tentorial sinus; it received a tributary glenoprootic vein, which passed medially through a canal to join the ventral part of the prootic vein. The primary head vein passed from the cavum epiptericum through a post-trigeminal canal into the facial sulcus, received the prootic vein here and probably left the sulcus as the stylomastoid vein before joining the jugular system. The orbito-temporal system consisted of vessels that ran from the post-temporal fossa, through an ascending canal running between the anterior lamina of the petrosal and the squamosal, to enter the cranial cavity. Then it passed across the prootic sinus and bifurcated at the postorbital process with an intracranial branch running anteriorly and an extracranial branch running in the postorbital groove to the ethmoid foramen. In forms with a large post-temporal fossa the vessels entered the post-temporal recess of the subarcuate fossa to run to the ascending canal. In forms with a small post-temporal fossa the vessels ran to the ascending canal without entering the subarcuate fossa, and had a major communication with either the stylomastoid or the postglenoid foramen. This route shows considerable similarity to that of the arteria diploetica magna of *Tachyglossus*, and examination of the embryos of monotremes, marsupials and placentals suggests that an artery, not a vein, should be considered as the major vessel primarily associated with this orbitotemporal system, although the presence of companion veins can be expected. Because a very similar system occurs also in triconodonts, tritylodonts and cynodonts, although with larger portions extracranial, the attention of students of those groups is called to the possibility that this orbitotemporal or 'sinus canal' system may be primarily arterial rather than, as hitherto accepted, venous. The cavum epiptericum was completely floored and was separated from the cranial cavity by a bony wall consisting of the orbitosphenoid with a persistent pila antotica. The optic foramen may have pierced this medial wall. The semilunar ganglion was very large, the mandibular nerve leaving the skull by two main foramina, though a small foramen piercing the anterior part of the anterior lamina may have been for a deep temporal branch of the nerve. The sphenorbital fissure is hardly visible in lateral view, forming the anterior opening of a large cavum epiptericum lying between the anterior lamina and the posterior part of the orbitosphenoid. It is suggested that the bone previously referred to as tabular may be the mastoid part of the petrosal because it included the semicircular canal. In some genera the occipital condyles are hollow, the cavity probably acting as an accessory tympanic air sinus. The endocranial cast of *Nemegtbaatar* reconstructed here differs in proportions from the previously known endocast of *Chulsanbaatar*, and is characterized by large olfactory bulbs, shallow telencephalon with cerebral hemispheres extensive in dorsal aspect and concave latero-ventrally, deep rhombencephalon, no midbrain exposure on the dorsal surface, large central lobe of cerebellum, no obvious cerebellar hemispheres and relatively very large paraflocculi. The pons is situated caudal to the emergence of the trigeminal nerve, as in monotremes. A glossary is given of the osteological, vascular and neuroanatomical terms used in this paper.

## INTRODUCTION

This paper is a part of a study on multituberculate cranial anatomy investigated by the method of serial sectioning of undecalcified material on a Jung microtome, described by Poplin & de Ricqlès (1970) and Poplin (1977). In palaeontology this method has so far only been used in studies on the cranial anatomy of Carboniferous fish (Poplin 1974, 1984). This is the first time that it has been adopted for the study of the cranial anatomy of fossil mammals. The classical serial-section method, based on serially grinding the fossils, introduced by Sollas (1904) and referred to by him and subsequent authors as 'serial sectioning' differs from the method used here in that it destroys the specimens, whereas the present method preserves each section (which may be as thin as teens of micrometres). Although the grinding method has been used widely in studies on various groups of lower vertebrates, to our knowledge it has only twice been adopted in research on the cranial structure of fossil mammals. Simpson (1936) used it in studies on the Eocene notoungulate *Oldfieldthomasia* sp., making parasagittal sections at intervals of 0.4 mm of one half of the cranium, and Whitmore (1953) used it for studies on the Oligocene artiodactyl *Merycoiodon culbertsonii*, making transverse sections of a nearly entire skull at 2 mm intervals in the anterior part, and at 0.5 mm intervals posterior to the region of the foramen ovale.

Multituberculates are the longest-represented order of mammals, their remnants being found in all well-sampled Jurassic, Cretaceous and Palaeocene localities with continental deposits in the Northern Hemisphere. However, multituberculate cranial anatomy and, in particular, some details of braincase structure are still incompletely known. Gidley (1909) was the first to describe and figure a nearly complete multituberculate skull belonging to the Palaeocene *Ptilodus*. Broom (1914) made reconstructions of the skulls of the Palaeocene *Taeniolabis* (referred to as *Polymastodon*) and of *Ptilodus*. Simpson (1937) provided emended reconstructions of the skulls of both genera and described the basicranial region, previously unknown, of multituberculates, on the basis of *Ptilodus*. Hahn (1969) described a crushed skull of the Upper Jurassic (Kimmeridgian) *Paulchoffatia* and a rostrum of *Kuehneodon*, and made a tentative reconstruction of the skull of the former. Subsequently Hahn (1977, 1981) described new paulchoffatiid cranial fragments including *Pseudobolodon*. The skull of *Paulchoffatia* as reconstructed by Hahn differs from those of known Late Cretaceous and Palaeocene multituberculates in having a much longer snout and, in detail, elsewhere.

Kielan-Jaworowska (1970, 1971, 1974) described a rich collection of Late Cretaceous multituberculate skulls from Mongolia. She provided detailed reconstructions of *Kamptobaatar* and *Sloanbaatar* skulls (1971) and described the choanal region, the lateral wall of the braincase and the occipital plate, all previously unknown in multituberculates. Subsequently Kielan-Jaworowska (1974) emended some details of these reconstructions. Her interpretation of the lateral wall of the multituberculate braincase differs from that of Simpson (1937). Kielan-Jaworowska & Sloan (1978) reconstructed the skull of the Late Cretaceous *Catopsalis*, and Kielan-Jaworowska & Dashzeveg (1978) reconstructed the skulls of the Late Cretaceous *Kryptobaatar* and *Tugrigbaatar*, all on the basis of material from Mongolia.

Summaries of all known data on multituberculate skull structure have been published by Hahn (1978) and by Clemens & Kielan-Jaworowska (1979). After these publications Sloan (1979) published a reconstruction of the skull of the Palaeocene *Ectypodus* differing in osteological pattern from those given by Simpson (1937) and Kielan-Jaworowska (1971, 1974).

However, Sloan did not discuss these differences or describe the skull of *Ectypodus*. Kielan-Jaworowska (1983) reconstructed the multituberculate endocranial cast, mostly on the basis of the natural endocast of the Late Cretaceous *Chulsanbaatar vulgaris*.

The present paper is based mostly on the study of two serially sectioned skulls from the Late Cretaceous of Mongolia. A preliminary report of some of the results has been published (Kielan-Jaworowska *et al.* 1984). The sectioned skulls belong to *Nemegtbaatar gobiensis* Kielan-Jaworowska, 1974 and *Chulsanbaatar vulgaris* Kielan-Jaworowska, 1974. The sectioned skull of *Nemegtbaatar* derives from the Barun Goyot Formation, that of *Chulsanbaatar* from the red beds of Khermeen Tsav, which are the stratigraphic equivalent of the Barun Goyot Formation. The age of the formation and beds is disputable (Kielan-Jaworowska 1982). In the present paper we follow Gradzinski *et al.* (1977), accepting that they are of ?middle Campanian age (while the older Djadokhta Formation, also yielding multituberculates, is of ?late Santonian or early Campanian age).

Other skulls of *N. gobiensis* and *Ch. vulgaris* from the Barun Goyot Formation and the red beds of Khermeen Tsav, skulls of *Catopsalis catopsaloides* (Kielan-Jaworowska, 1974) from the red beds of Khermeen Tsav, skulls of *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970, *Kamptobaatar kuczynskii* Kielan-Jaworowska, 1970, and *Sloanbaatar mirabilis* Kielan-Jaworowska, 1970 from the Djadokhta Formation were studied for comparison. All these Asian Late Cretaceous multituberculates belong to the suborder Taeniolabidoidea, representatives of the Ptilodontoidea being absent from Asia (Kielan-Jaworowska 1980).

In addition to this Asian material we also studied isolated multituberculate petrosals from the Late Cretaceous Hell Creek Formation (Lancian), Bug Creek locality of Montana, in the collections of the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, and the Museum of Comparative Zoology, Harvard University. One of these is referred to ?*Catopsalis joyneri* Sloan & Van Valen, 1965; the others cannot be identified even at a subordinal level and are here referred to as the 'unidentified Hell Creek petrosals'.

Apart from *Catopsalis* all the genera studied here are monotypic. For this reason, for brevity, in the succeeding account we shall often use only the generic name for the monotypic genera.

From an initial study of the sections it soon appeared that much new information was available, especially on vascular markings. This provided insights that would otherwise have been unavailable. With these insights, entire specimens could be used and reinterpreted to provide a reasonable picture of the vascular system. Reconstructions of the cranial vascular system of fossils may be based on: grooves on the surface of bones; intramural canals; and endocasts of the vessels. Our interpretation of the latter two categories was considerably enhanced by the study of the sections. Vascular reconstructions in palaeontology are always a matter of speculation and interpretation. We have therefore chosen to place our account of the 'hard evidence' largely in a section describing the osteology and endocasts, followed by the more tentative account of the vasculature.

One difficulty encountered by us in writing this paper concerned the terminology used in describing the vascular system of mammals (and vertebrates in general). This varies from group to group and from author to author. It is, moreover, often difficult to find agreement on the homology of particular vessels, especially veins, in various groups of mammals. For Mesozoic mammals the cranial vascular system has been reconstructed only for *Morganucodon* (Kermack *et al.* 1981). Their terminology follows that of Shindo (1915). We found this terminology likely

to lead to confusion in some cases. For example, Shindo (1915) calls the vein transmitted by the prootic canal the *vena cerebialis media*. In human anatomy (Warwick & Williams 1973) two middle cerebral veins are recognized (*vena cerebialis media superficialis* and *vena cerebialis media profunda*), neither of which corresponds to Shindo's vein. The work of Padget (1957) and H. Butler (1957, 1967) has shown that the studies of Shindo (1915) lacked many developmental stages of mammalian embryos. This was confirmed by the examination of developmental series of mammals and other vertebrates in the collection of the Department of Anatomy, University College, Cardiff (for details see Presley 1978, 1984), information from which was used extensively in our vascular reconstruction. We found some of Shindo's (1915) conclusions on the similarity of mammalian and reptilian veins, upon which he based his terminology, very doubtful. Where possible we have employed the terminology of Padget's (1957) extremely thorough account.

There are also great differences in usage in the previous literature in both osteological and neuroanatomical terminology. We have therefore thought it useful to append to this paper a glossary defining our own usage and relating it to that of others, for osteological, vascular and neurological terms.

#### ABBREVIATIONS

ZPAL: the collection of the Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

MCZ: the collection of the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

#### OSTEOLOGY AND ENDOCASTS

##### *Description*

##### (a) *General*

The sections and other specimens showed that the pattern of the vascular system related to the petrosal was central to the understanding of the rest of the cranial vascular system. Because many of the essential features of petrosal vascular anatomy are very well shown by the isolated petrosals of *Catopsalis* and the unidentified Hell Creek forms, we describe these first.

##### (b) *Catopsalis*

(i) *Material*. The isolated left petrosal MCZ 19176 from the Hell Creek Formation, Bug Creek, Montana, is here referred to as ?*Catopsalis joyneri* Sloan & Van Valen, 1965. Our reasons are: it is so designated in the MCZ catalogue, and although it was not associated with other identifiable elements, its size is consistent with a skull length of *ca.* 80 mm. This would conform to the tooth size given by Sloan & Van Valen (1965). The promontorium is roughly rectangular as in *C. catopsaloides*, and *C. joyneri* is the only species of *Catopsalis* found in the Hell Creek Formation.

Two skulls of *Catopsalis catopsaloides* (Kielan-Jaworowska, 1974), ZPAL MgM-I/78 and ZPAL MgMI/79, are from the red beds of Khermeen Tsav I, Gobi Desert, Mongolia. Both skulls were figured by Kielan-Jaworowska (1974) and parts of their braincases relevant to this study are refigured in the present paper.

(ii) *Anatomy*

?*Catopsalis joyneri* (figures 1, 4 and 33)

?*Catopsalis joyneri*, MCZ 19176, is a robust and well-preserved petrosal with partial breakage of the semilunar fossa. A part of the anterior lamina is missing in front. The petrosal is broken along the sutures with the absent squamosal, basioccipital and supraoccipital. Because the bone is durable this specimen is nearly intact and the semicircular canals are not exposed.

Occipital aspect (figure 1 *a*, A)

In occipital aspect the petrosal is smooth-surfaced and roughly triangular, narrowing dorsally, slightly convex outwards, with its lateral margin (along the suture with the squamosal) running obliquely dorso-medially. No ridges corresponding to the posterior and lateral semicircular canals (very prominent in small forms such as *Kamptobaatar* and *Chulsanbaatar*) are visible in MCZ 19176 because of the great thickness of the bone. The occipital surface is prolonged antero-ventrally at an angle of about 120° to the dorsal part to form a sharply pointed triangular paroccipital process. The occipital surface of this is slightly concave and pierced by randomly distributed vascular foramina. The bone is damaged in its dorso-lateral part and reveals a fine cancellous structure. Midway up the occipital surface near the suture with the squamosal is a trace of a small post-temporal fossa with only its medial margin preserved. This fossa leads to a short post-temporal canal (preserved as a groove), which runs upwards and laterally to join the ascending canal (also preserved as a groove), which is of about the same width. A tiny canal runs antero-medially from the post-temporal canal into the subarcuate fossa. The squamosal being absent, the ascending canal is exposed as a groove on occipital and lateral aspects. The dorsal part of the ascending canal turns forward and enters the cranial cavity close to and above the groove for the transverse sinus.

Lateral aspect (figure 1 *b*, B)

The lateral aspect shows the large, roughly triangular surface of the anterior lamina of the petrosal, bounded posteriorly and dorsally by the ascending canal. Ventrally this canal opens at the postglenoid foramen, in the suture between the anterior lamina and the squamosal. The foramen is partly missing, only its anterior margin being preserved. The interglenoid canal from the supraglenoid foramen also opens at the postglenoid foramen. This canal, in contrast to all the other genera studied (in which it is transverse to the long axis of the skull) is arranged longitudinally in *Catopsalis*, running along the ventral margin of the anterior lamina. In consequence, the supraglenoid foramen is situated in front of the postglenoid foramen (not dorsal to it as in the other genera), very close to, posterior, lateral and dorsal to the foramina ovale inferium and masticatorium, which are incompletely preserved. The supraglenoid foramen is also connected with the prootic canal through a very short glenoprootic canal. On the outer surface of the anterior lamina three short grooves, probably for tributary veins, lead from the supraglenoid foramen: the largest runs antero-dorsally, the next largest postero-ventrally and the smallest and shortest anteriorly.

Ventral aspect (figure 1 *c*, C)

Ventrally the petrosal is more triangular than oval, in contrast to the other genera and *C. catopsaloides*, because of the relatively small size of the ventral part of the anterior lamina (see

Kielan-Jaworowska 1971, p. 12). The promontorium is relatively large and moderately convex in its lateral part, with a shallow longitudinal groove parallel to the broken medial margin, along the suture with the basisphenoid. Its antero-medial corner is broken off.

A shallow groove extends transversely across the posterior part of the promontorium in front of its swollen hinder edge. The surface of the promontorium is uneven. There is a distinct groove which extends antero-medially along the lateral wall of the promontorium from the vicinity of the fenestra vestibuli. This is tentatively identified as for the stapedia artery. Behind the notch designated 'hiatus Fallopii' (see below), the groove becomes less clear and it is possible that it bifurcates, a lateral branch leading to the 'hiatus'. A distinct but narrow groove leads forwards from the 'hiatus' along the lateral border of the promontorium to its anterior limit. The swollen posterior edge of the promontorium overhangs ventrally both the fenestra cochleae and the relatively wide groove of the aquaeductus cochleae, which leads to the incomplete jugular fossa. There is also another groove, of unknown function, extending postero-medially from the fenestra vestibuli.

A distinct rounded recess postero-lateral to the fenestra cochleae is identified as a pit for the levator hyoidei or digastric muscle (abbreviated in figures as 'hyoid muscle pit'). The fenestra vestibuli is large; a short groove, which may be an artefact, leads from it towards the facial sulcus. Behind the fenestra vestibuli there is a deep, rounded fossa muscularis minor, covered in direct ventral view by the prominent paroccipital process.

Most of the lateral flange and of the epitympanic recess are broken off, only the most anterior part of the recess being preserved. Because of this damage the lateral part of the facial sulcus, normally obscured by the roof of the epitympanic recess, has been exposed. On the lateral wall of the promontorium antero-medially to the fenestra vestibuli and antero-lateral to the groove for the stapedia artery is a large fossa muscularis major. Postero-laterally to it there is a large foramen, which is the tympanic opening of the prootic canal (designated 'prootic canal foramen' in the figures). In front of this is another large foramen, not visible in direct ventral view as it is obscured by the anterior part of the roof of the epitympanic recess. This foramen leads to a short canal, the post-trigeminal canal, joining the facial sulcus to the semilunar fossa. There are several grooves in the exposed roof of the facial sulcus. One of them, tentatively designated as for the maxillary artery, extends antero-medially, ventral to the tympanic foramen of the facial canal, to open (because of the breakage of this specimen) into the semilunar fossa. However, in the well-preserved Hell Creek petrosals (figures 8 and 9) a similar groove and canal open outside the semilunar fossa as a foramen (which we suggest is for the maxillary artery) in front of and between the foramen ovale inferium and the foramen masticatorium. We therefore suppose that, when intact, this foramen was similarly placed in *Catopsalis*. Another groove extends postero-laterally from the vicinity of the tympanic foramen of the facial canal. A third, wider groove extends posteriorly from the tympanic foramen of the prootic canal. Lateral to this groove are two broken stumps of bone, the posterior the larger, separated by a narrow groove. Behind the rear stump lies a wider groove extending laterally for a short distance in front of the lateral part of the paroccipital process. We regard this groove as the postero-lateral part of the facial sulcus. It ends abruptly at the place where the squamosal (not preserved) lay beneath the petrosal. Although a stylomastoid foramen is not present in *Catopsalis*, it is possible to visualize a facial nerve housed in the postero-lateral part of the facial sulcus (rather than in a canal as in the unidentified Hell Creek petrosals) and then turning away from the skull at the outer end of the sulcus. The anterior margin of the facial sulcus

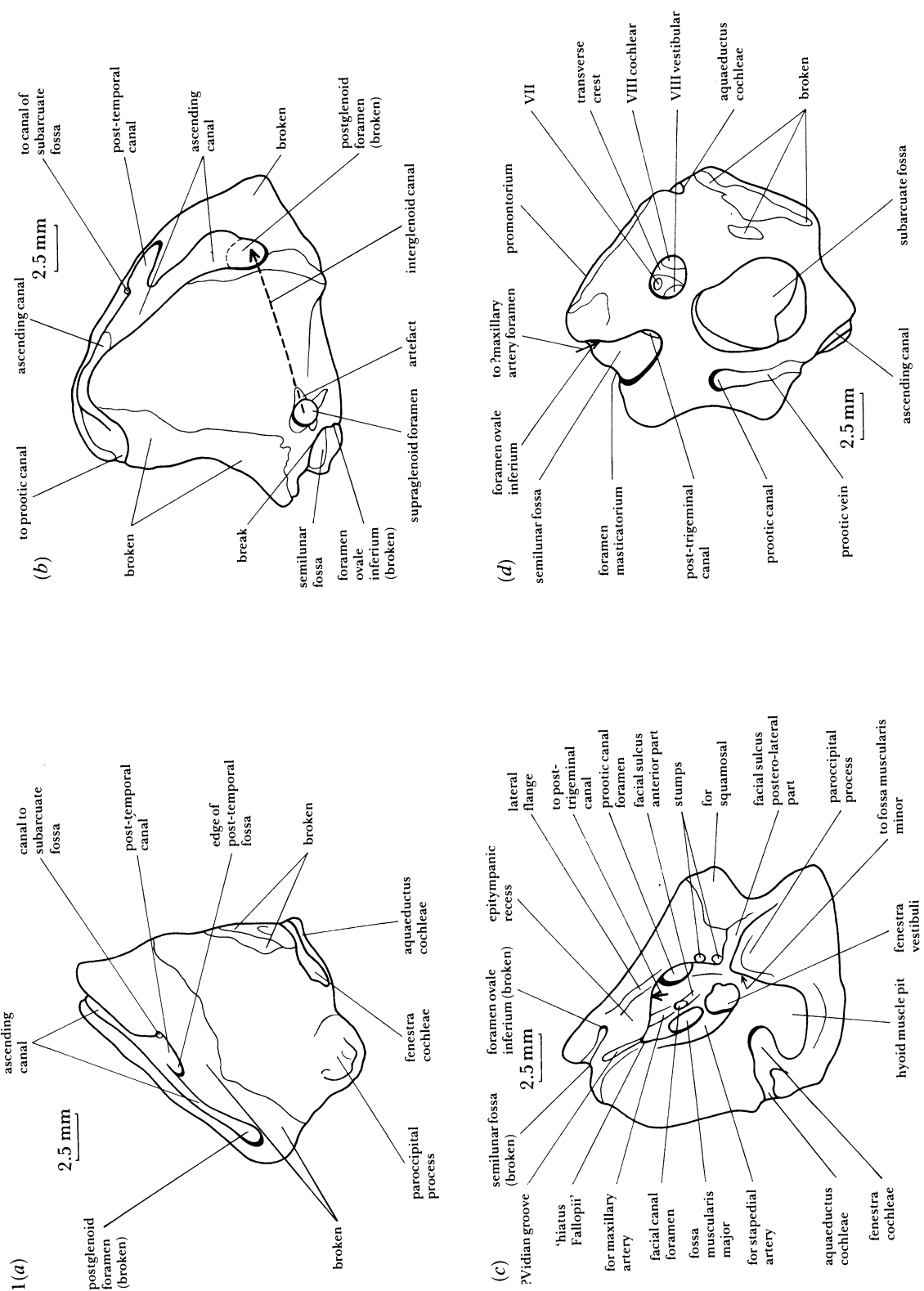
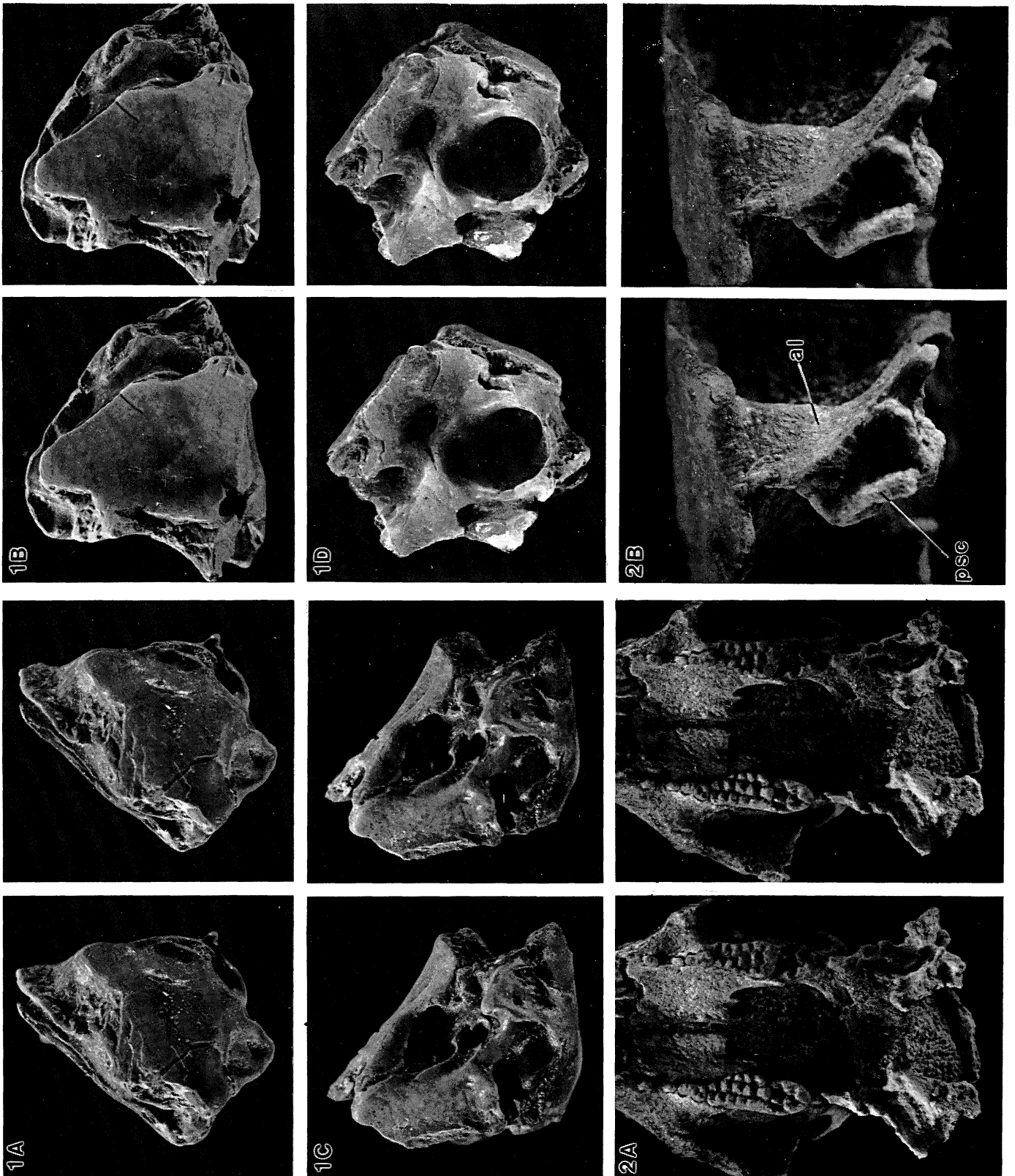


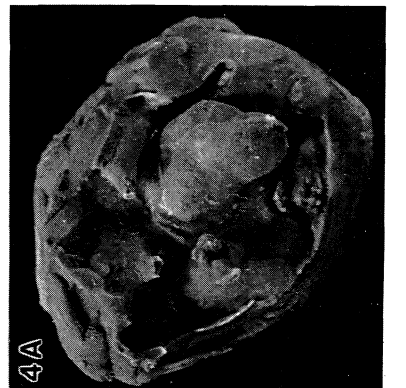
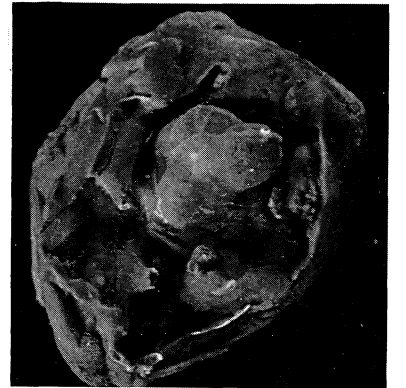
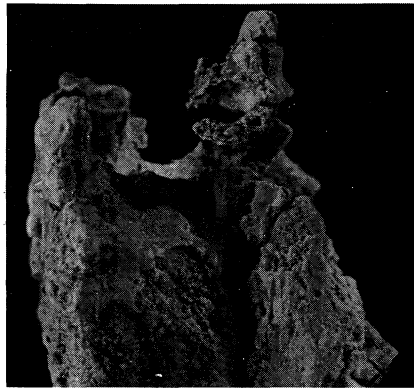
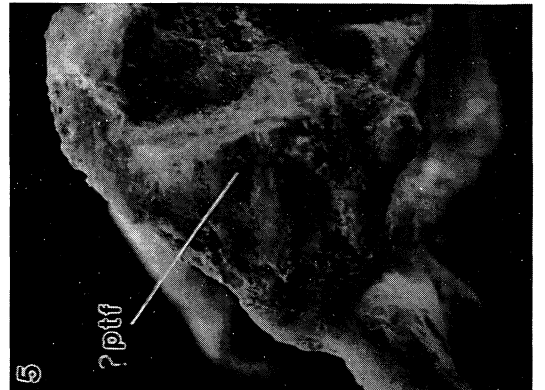
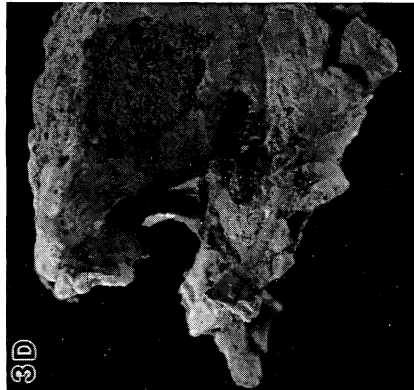
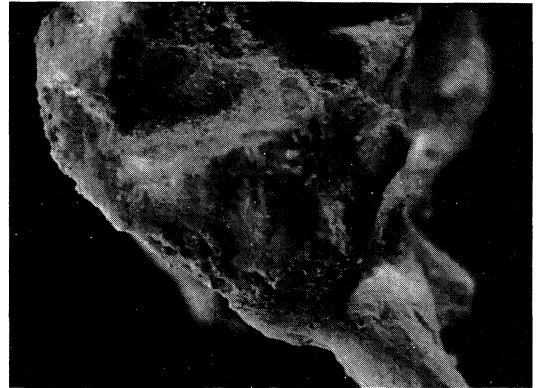
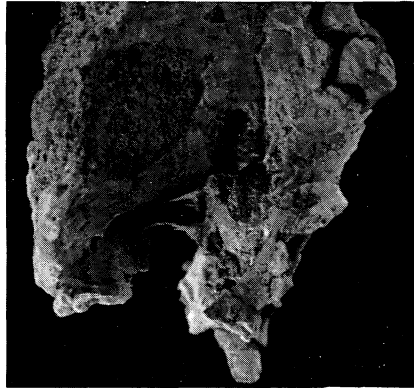
FIGURE 1. *Catopsalis joyneri*. MCZ 19176. Stereophotographs, magn.  $\times 3$ . Isolated left petrosal. (a, A) Posterior view. (b, B) Lateral view. (c, C) Ventral view. (d, D) Antero-medial view.

FIGURE 2. *Catopsalis catopsaloides*, ZPAL MgM-I/78. Stereophotographs. (A) Skull in occusal view, magn.  $\times 1.5$ . (B) The same, posterior part, right lateral view showing anterior lamina (al) and posterior semicircular canal (dsc), magn.  $\times 3$ .

DESCRIPTION OF FIGURE 1 AND PLATE 1







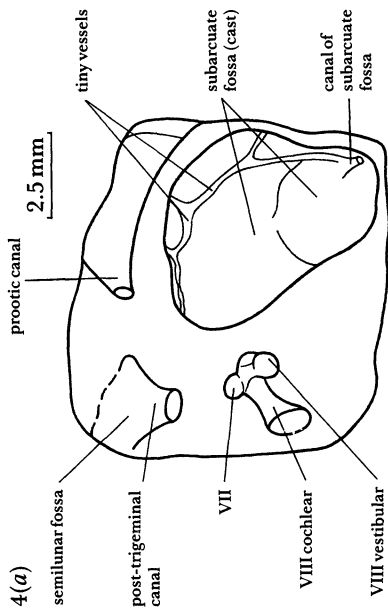


FIGURE 4. (a, A) ?*Catopsalis joyneri*, MCZ 19176. Endocranial cast. Stereophotograph, magn.  $\times 4.5$ .

DESCRIPTION OF PLATE 2

FIGURE 3. *Catopsalis catopsaloides*, ZPAL MgM-1/79. Stereophotographs. (A) Posterior part of skull, dorsal view. Margins of pituitary fossa (pf) on left, magn.  $\times 2$ . (B) The same, posterior view. Note sharply converging orbitosphenoids and ventral keel of basisphenoid, magn.  $\times 1.5$ . (C) The same, left lateral view. Note medial wall of cavum epiptericum, magn.  $\times 2$ . (D) The same, right lateral view, magn.  $\times 2$ .

FIGURE 5. Undescribed eucosmodontid genus, ZPAL MgM-1/50. Left side of occipital plate showing small post-temporal fossa (?ptf). Stereophotograph, magn.  $\times 8$ .

forms a distinct notch in front of the fossa muscularis major, at the lateral margin of the promontorium. In *Chulsanbaatar*, *Sloanbaatar* and *Kamptobaatar* this is developed as a foramen. Kielan-Jaworowska (1971) called this foramen in the latter two genera the hiatus Fallopii, and we refer to it as 'hiatus Fallopii' for reasons discussed in the Glossary. A notch or foramen is present here in all the petrosals studied by us, and may have transmitted the superficial petrosal branch of the facial nerve from the semilunar fossa. However, in *Chulsanbaatar* (figures 6 and 14) and *Kamptobaatar* there is a short groove extending posteriorly from this foramen over the surface of the promontorium. In *Catopsalis joyneri* there is a groove in front of the notch, extending anteriorly along the lateral margin of the promontorium, as well as the indication of a connection with the distinct groove for the stapedia artery mentioned above. We tentatively identify this as both vascular and nervous, supposing that it might house both the superficial petrosal nerve (anterior to the 'hiatus') and companion vessels, the artery possibly a branch of the stapedia. We therefore abbreviate this, conceptually, as the ?Vidian groove, and because of findings in *Nemegtbaatar* we tentatively reconstruct meningeal branches of the vessels passing through the 'hiatus Fallopii'.

The ventral part of the anterior lamina runs latero-dorsally for a short distance lateral to the epitympanic recess and then turns dorsally to form the large ascending part of the anterior lamina.

#### Antero-medial aspect (figure 1d,D)

The petrosal is concave in the aspect presented to the cranial cavity, with a very large subarcuate fossa and a much smaller internal auditory meatus. The deep groove for the prootic sinus extends obliquely antero-ventrally along the surface of the anterior lamina and leads directly to the prootic canal. The internal auditory meatus is very deep and, as usual, divided by the transverse crest into a postero-lateral, smaller, pit for the cochlear nerve (VIII), and, antero-medially, a small medial foramen for the vestibular nerve (VIII) and a larger, anterior one for the facial nerve (VII), which can be traced through to its tympanic opening. The semilunar fossa is very deep and lies in the antero-lateral corner of the endocranial surface. The fossa is defective ventrally and only parts of the margins of the foramina ovale inferium and masticatorium are preserved. The post-trigeminal and maxillary arterial canals leading from the lateral groove to the semilunar fossa are clearly seen in this view.

The cast of the subarcuate fossa (figure 4) is roughly pear-shaped, the proximal part being larger and the distal narrower, with a cast of the minute canal of the subarcuate fossa visible as the 'stalk' of the 'pear'. Tiny vascular markings are visible on the surface of the cast.

#### *Catopsalis catopsaloides* (figures 2 and 3)

In *Catopsalis catopsaloides*, ZPAL MgM-I/78, part of the basicranial region, with the promontoria and parts of the anterior laminae of both sides, is preserved. In front of the fenestra cochleae the promontorium is roughly rectangular with a swollen, rounded and slightly pointed anterior margin. The ventral part of the anterior lamina, although incomplete on both sides, is proportionately wider than in *C. joyneri*. The state of preservation of the bone is poor, and the ridge between ventral and ascending parts of the anterior lamina is partly broken off: the supraglenoid and postglenoid foramina are not preserved. The posterior aspect of the right side shows casts of the posterior and lateral semicircular canals. The occipital surface of the petrosal

is missing, but from the preserved parts it seems that the area between the posterior semicircular canal and the squamosal was very small, indicating that, as in ?*C. joyneri*, the post-temporal fossa must have been relatively small.

In ZPAL MgM-I/79 the ascending part of the anterior lamina is missing but the posterior part of the orbitosphenoid, which builds part of the medial wall of the cavum epiptericum, is preserved. This is directed obliquely postero-medially, resulting in a considerable narrowing of the cranial cavity, giving a V-shaped cross section in the region in front of the pituitary fossa. Posteriorly the orbitosphenoid turns abruptly outwards through about a right-angle and continues postero-laterally. Anterior to this flexure is a large, elongated, fissure-like foramen. Above it are two smaller foramina, close to the cranial roof. It cannot be excluded that these are artefacts of distortion. The posterior part of the medial wall of the cavum epiptericum is broken off. Opposite this missing portion of the orbitosphenoid part of the basisphenoid with the pituitary fossa is preserved and may be examined from above. On the ventral surface of the preserved part of the basisphenoid, below the pituitary fossa, there is a median keel, indicating the presence of sphenoidal air-sinuses in this region.

The postero-medially directed part of the orbitosphenoid has a longitudinal vascular groove on its ventral border that extends back to the semilunar fossa. This could be a continuation of the groove seen in *Kamptobaatar* (Kielan-Jaworowska 1971), extending posteriorly in the exposed part of the orbit from the sphenopalatine foramen along the ventral part of the orbitosphenoid. If so, it is very broad and shallow, barely visible in either specimen of *C. catopsaloides*.

(c) *Unidentified Hell Creek petrosals (figures 8 and 9)*

(i) *Material.* Two isolated petrosals, evidently conspecific, were used: MCZ 19177 and ZPAL MK-1, from the Hell Creek Formation, Bug Creek, Montana, ZPAL MK-1 is more complete, measuring about 7.5 mm from the anterior border of the semilunar fossa to the posterior broken margin of the subarcuate fossa, and about 7.2 mm maximum width perpendicular to the length. These petrosals belong to a species of about 35–45 mm estimated skull length.

(ii) *Anatomy.* The ascending part of the anterior lamina is partly broken off in both petrosals. The occipital part is completely lost in MCZ 19177, and only a small fragment of it is preserved in ZPAL MK-1. Cross sections of the semicircular canals are exposed in the broken walls of the subarcuate fossa. In MCZ 19177 the anterior wall and part of the floor of the semilunar fossa are missing. We describe these two petrosals only in ventral and antero-medial aspects because of their incomplete preservation and because the anterior lamina, being dorso-laterally directed (unlike the dorso-medial direction in *Catopsalis* and in other taeniolabidoid genera), is extensively exposed from ventral aspect.

Ventral aspect (figures 8a, A and 9a, A)

The outline of the petrosal is roughly circular, unlike the more triangular outline in ?*Catopsalis joyneri*, because of the different inclination of the anterior lamina. The promontorium is irregularly shaped, its medial margin convex medially, forming a bow, but in both specimens it appears that the antero-medial part of the promontorium is partly broken off, exposing fine

cancellous bone. Posteriorly the promontorium thins to a very narrow bridge between the fenestrae vestibuli and cochleae. A prominent medial ridge, broken anteriorly, disappears posteriorly at the level of the latter two fenestrae. Between this ridge and the lateral groove the surface of the promontorium is uneven, with one or two almost longitudinal ridges parallel to the lateral groove and a short oblique ridge in front of the fenestra vestibuli. The two specimens show individual variations in the detail of the promontorial surface. It cannot be excluded that one of the longitudinal grooves, which extend antero-medially from the vicinity of the fenestra vestibuli, is for the stapedial artery as in *Catopsalis*. However, as the detail of these grooves is less distinct than in the isolated petrosal of *Catopsalis* we have not specifically indicated the groove for the stapedial artery in figure 8a.

The fenestrae cochleae and vestibuli are about equal in size. A short groove for the cochlear aqueduct runs medially from the cochlear fenestra to the jugular notch. In both specimens the bone surface is damaged behind the cochlear fenestra and thus the hyoid muscular pit, present in *Catopsalis* (figure 1c), is not discernible here. In both, only a small part of the roof of the fossa muscularis minor, shallower than in ?*C. joyneri*, is preserved. The loss of the posterior part of this roof has exposed the cavity of the paroccipital process as a large hollow space. This is bounded posteriorly by the lateral semicircular canal, preserved in both specimens. The paroccipital process is lost in both, with only the medial part of its base preserved in ZPAL MK-1.

The exposure ventrally of the facial sulcus is very narrow and its anterior part is intact in MCZ 19177, delimited outside by the lateral flange. In the most anterior corner of it, at the lateral margin of the promontorium, there is the distinct notch of the 'hiatus Fallopii'. The related promontorial groove cannot be recognized with any certainty. Posterior to the notch, on the lateral wall of the promontorium, there is a deep fossa muscularis major, well seen in MCZ 19177. At this level, in both specimens, the lateral flange with a part of the epitympanic recess is broken off and the facial sulcus thus appears artificially broadened. Lateral to the fossa muscularis major is the tympanic foramen of the facial canal (designated 'facial canal foramen' in the figures) and, antero-laterally to that, the large orifice of the post-trigeminal canal leading to the semilunar fossa. Antero-medial to the orifice of the post-trigeminal canal is another foramen in the facial sulcus leading to the canal of the ?maxillary artery, which opens externally in front of and between the foramina ovale and masticatorium.

A small vertical stump bounds the lateral part of the facial sulcus posteriorly, and at this level the medial part of the sulcus turns laterally and the equivalent of the postero-lateral part of the sulcus is completely floored ventrally to form a bony cavity. The tympanic foramen of the prootic canal (designated 'prootic canal foramen' in the figures) opens into the most medial part of this. More laterally the cavity opens by two foramina. The more anterior is the supraglenoid foramen, the more posterior the stylomastoid foramen (which, however, is regarded as sharing the function of the postglenoid foramen of other forms, as discussed under Comparisons). The posterolateral border of the stylomastoid foramen is broken and a distinct groove extends dorsally from it. This forms a part of the wall of the ascending canal. Because of breakage the more dorsal part of the canal is not preserved but it seems clear that it led upwards as in *Catopsalis*.

The cavity enclosing the postero-lateral part of the facial sulcus would allow free communication of any vessels passing into it. However, the more anterior part of this cavity, between the supraglenoid foramen and the tympanic foramen of the prootic canal may be equated with

the gleno-prootic canal of *Nemegtbaatar* and *Catopsalis*, while the space between the supraglenoid and stylomastoid foramina may represent the interglenoid canal. The ventral surface of the flooring bone of this chamber shows a fine cancellous structure. It is presumed that this part corresponds to the area of contact with the squamosal, which covers this region ventrally in other multituberculates.

The epitympanic recess is relatively narrow, bounded medially by the lateral flange and laterally by a rounded ridge which extends postero-laterally from the foramen ovale inferium. The foramen masticatorium lies postero-dorsal to it and faces slightly more laterally. The ascending part of the anterior lamina is seen well in this view. It slopes gently dorso-laterally from the ridge bounding the outside of the epitympanic recess. Several almost parallel ripples extend obliquely dorso-laterally on the surface of the anterior lamina, and a minute nutrient foramen is present mid-way along its lower half, with another of similar size anterodorsal to it.

#### Antero-medial aspect (figures 8*b*, B and 9*b*, B)

The petrosal, as in the ventral aspect, appears roughly circular in outline. The postero-lateral walls of the subarcuate fossa are broken off in both specimens. From the preserved parts of the fossa it appears that the paraflocculus was irregularly spherical, with probably a large post-temporal recess as in *Nemegtbaatar*. No statement is possible about the post-temporal fossa communicating with the subarcuate fossa. In both specimens a cross section of the anterior semicircular canal is visible in the broken wall of the fossa. It lies posterior, lateral and dorsal to the cranial foramen of the prootic canal. In front of the cross section of the anterior semicircular canal several larger cavities are exposed in the broken wall of the fossa. In the posterior wall of the subarcuate fossa, in ZPAL MK-1, a cross section of the posterior semicircular canal is exposed. The canal is visible as a small rounded ridge on the outer surface of the residual fragment of the mastoid. The ridge ends ventrally on the broken base of the paroccipital process. Lateral to it on the occipital surface are several small nutrient foramina. The build of this small preserved fragment of the occipital part of the petrosal is similar to that of numerous Asian Taeniolabidoidea, e.g. *Kamptobaatar* (Kielan-Jaworowska 1971). In the broken medial wall of the subarcuate fossa a cross section of the crus commune is preserved in both specimens.

As the anterior lamina is partly broken only the most anterior part of the groove for the prootic vein, immediately behind its endocranial foramen, is preserved. A minute nutrient foramen in the anterior lamina lies in front of the latter foramen. The internal auditory meatus is arranged roughly transversely, with a relatively shallow foramen for the cochlear nerve, and a more deeply situated foramen for the vestibular and facial nerves separated from the former by a wide transverse crest. A bristle placed through this foramen into the facial nerve canal may be seen easily both through the facial sulcus and through the semilunar fossa.

The semilunar fossa is completely preserved in ZPAL MK-1. A thin bony wall separates it from the more anterior part of the cavum epiptericum. The two foramina for the mandibular nerve, described above, are well seen in this aspect, but the large foramen leading to the post-trigeminal canal is obscured by the vertical medial wall of the fossa. The foramen for the maxillary artery is also hardly discernible, being obscured by the oblique antero-medial wall of the fossa.

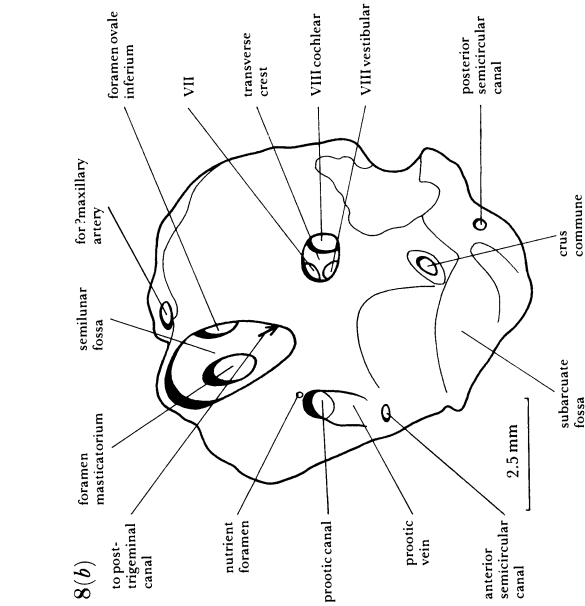


FIGURE 8

DESCRIPTION OF PLATE 3

FIGURE 8. Unidentified Hell Creek left petrosal. ZPAL MK-1. Stereophotographs, magn.  $\times 6$ . (a, A) Ventral view. (b, B) antero-medial view.

FIGURE 9. Unidentified Hell Creek left petrosal, MCZ 19177. Stereophotographs, magn.  $\times 6$ . (A) Ventral view. (B) antero-medial, view.

FIGURE 10. (a, A) *Chulsanbaatar vulgaris*, ZPAL MgM-I/89. Posterior part of skull, left lateral view, partial endocranial cast with vascular casts. Stereophotograph, magn.  $\times 4.5$ .

FIGURE 11. *Chulsanbaatar vulgaris* ZPAL MgM-I/168. Occipital plate, damaged, left side. Note cross section of condylar cavity (cc), and cast of subarcuate fossa dorso-laterally. Stereophotograph, magn.  $\times 8$ .

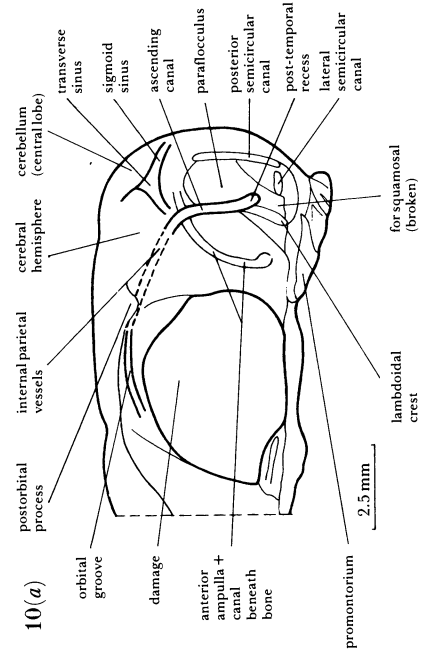
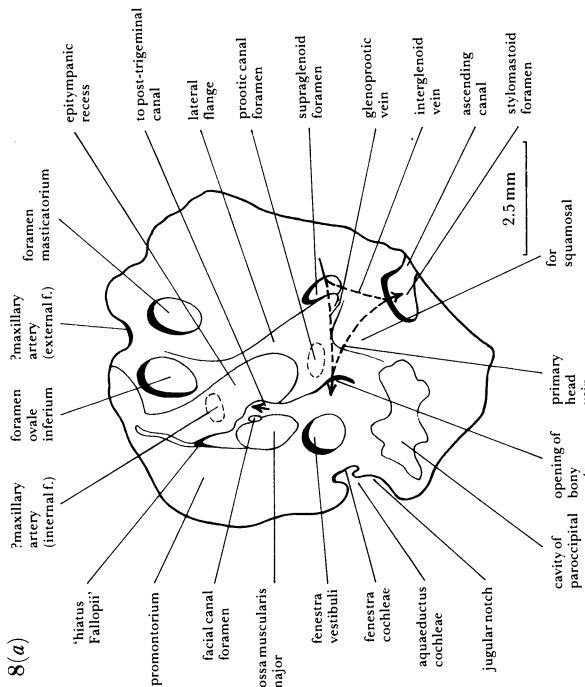


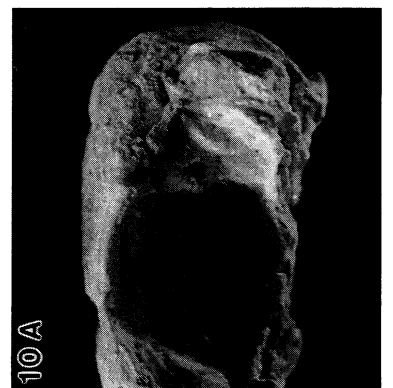
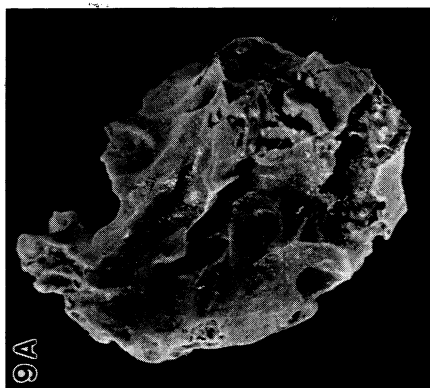
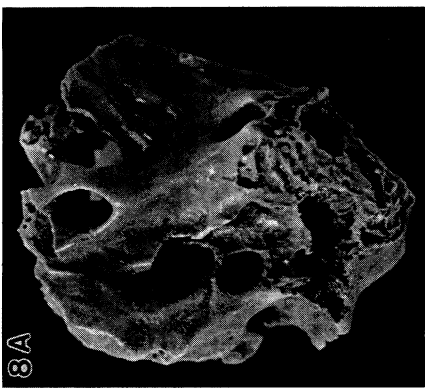
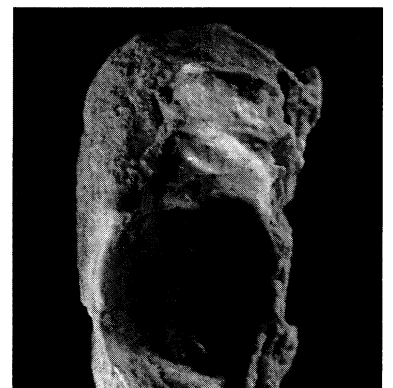
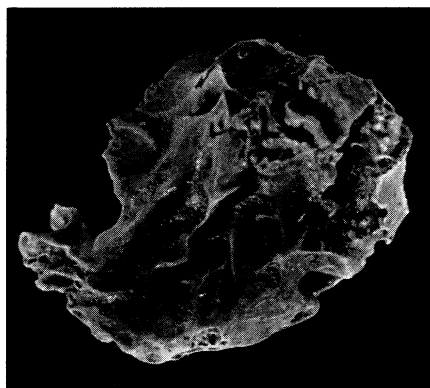
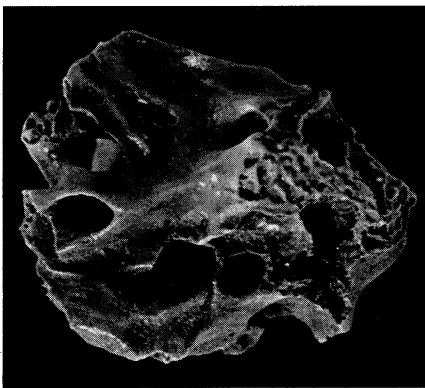
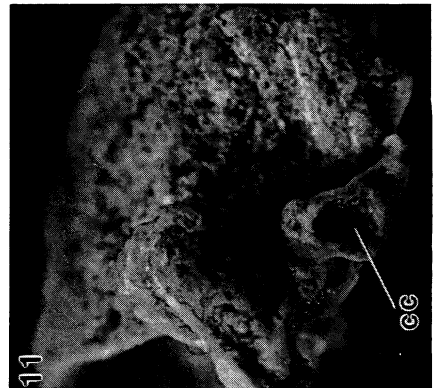
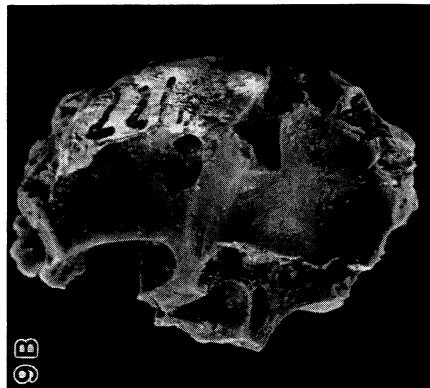
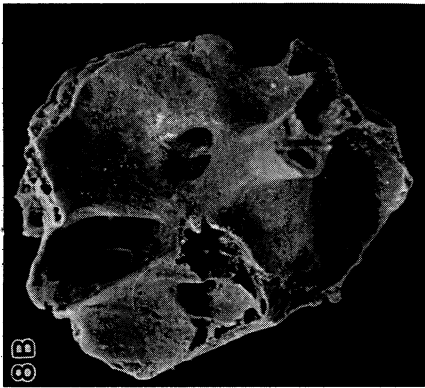
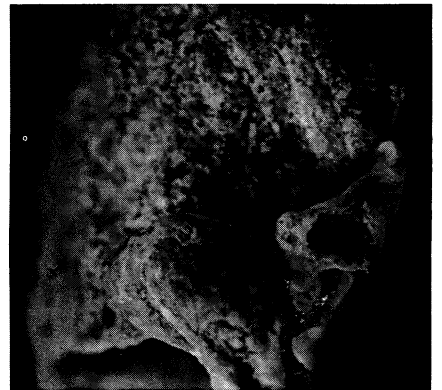
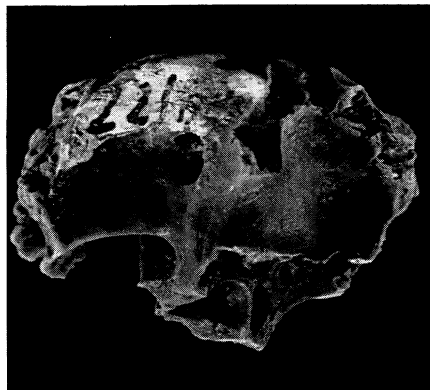
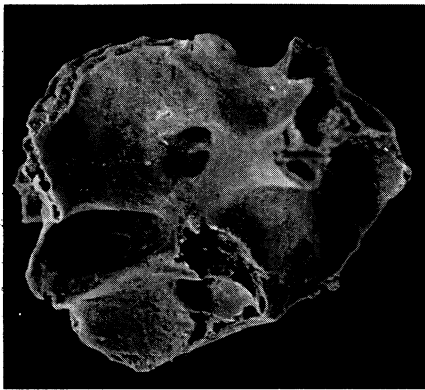
FIGURE 10 a

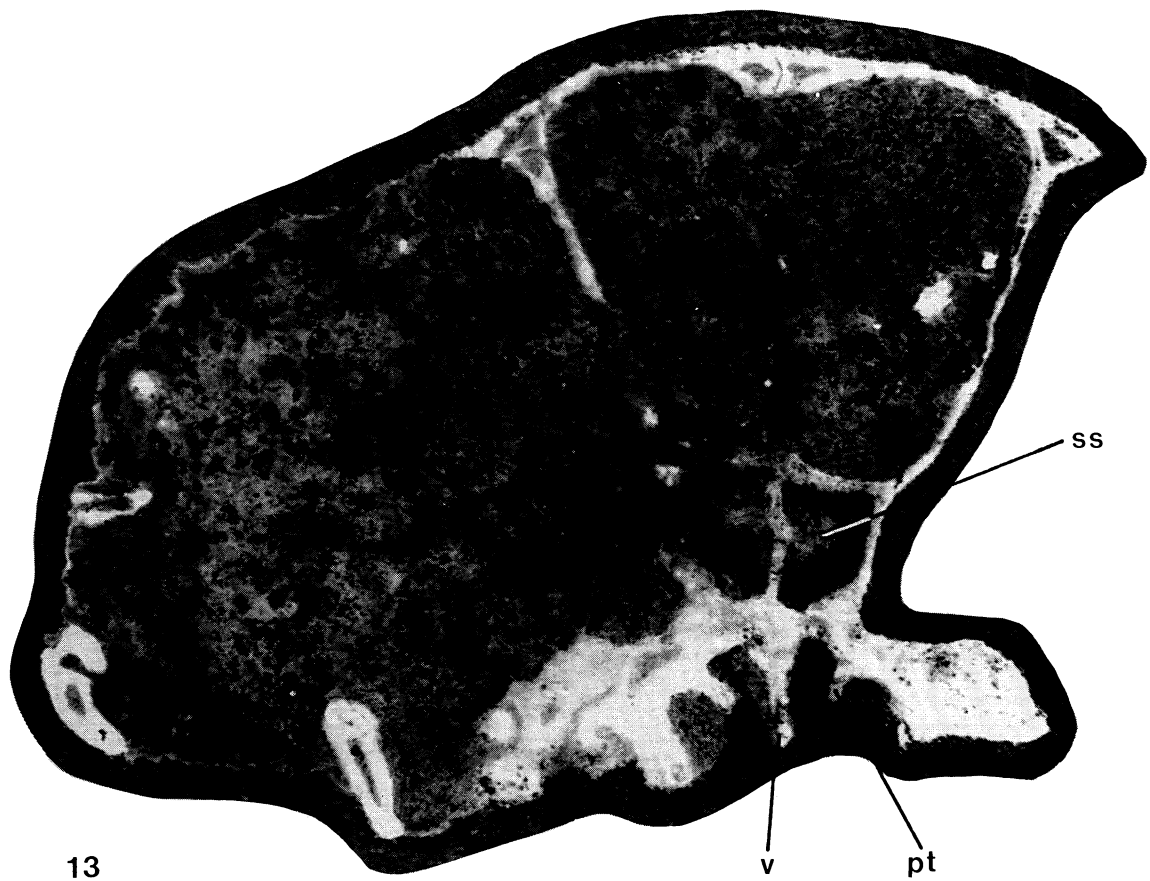
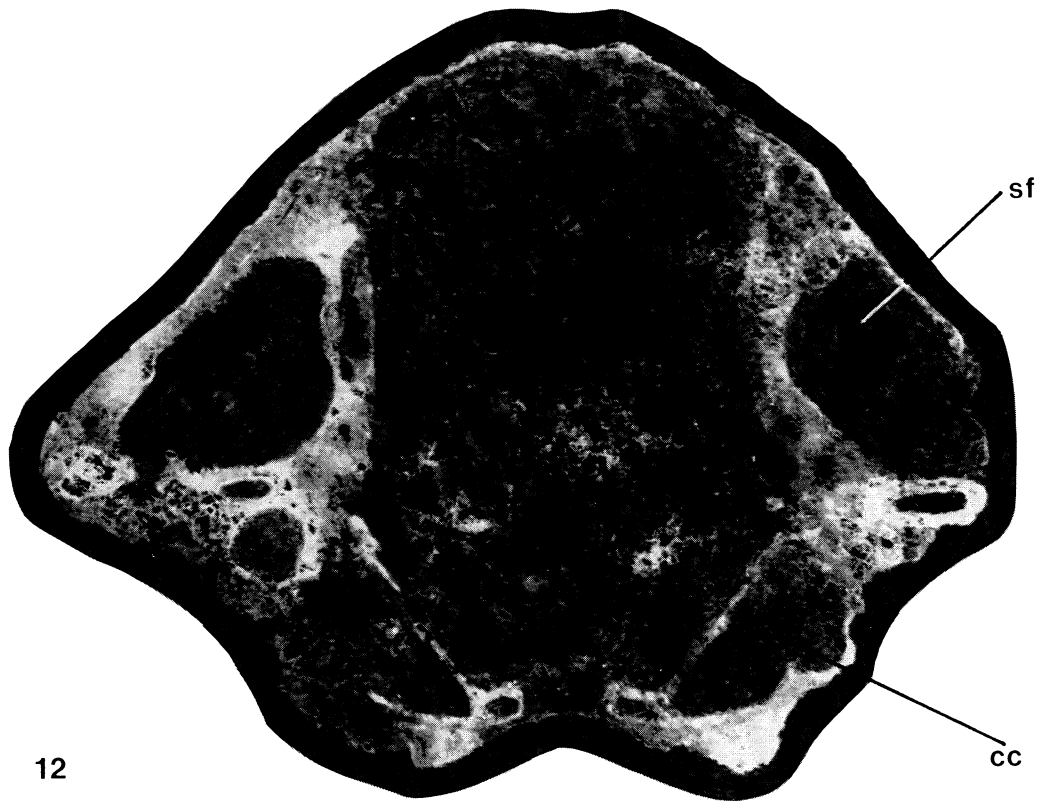
DESCRIPTION OF PLATE 4

FIGURE 12. *Chulsanbaatar vulgaris* ZPAL MgM-I/84. Transverse section 100 (level of occipital condyles), magn.  $\times 20$ . cc, Condylar cavity; sf, subarcuate fossa.

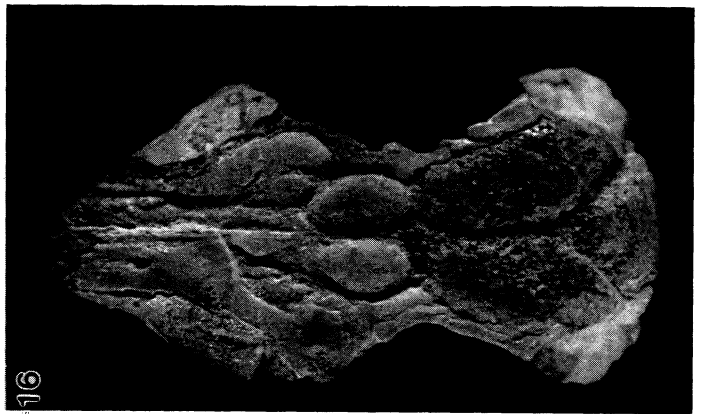
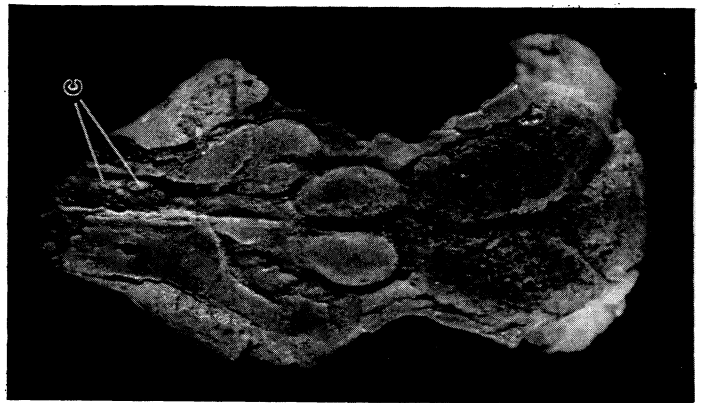
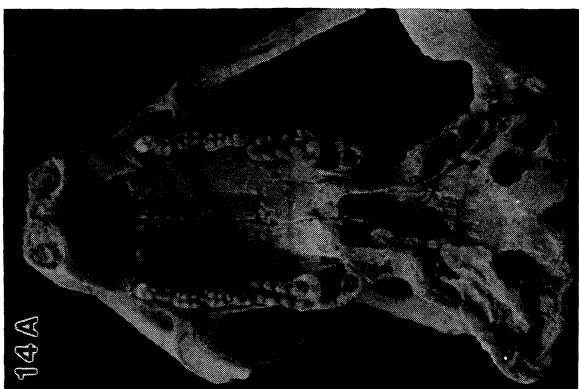
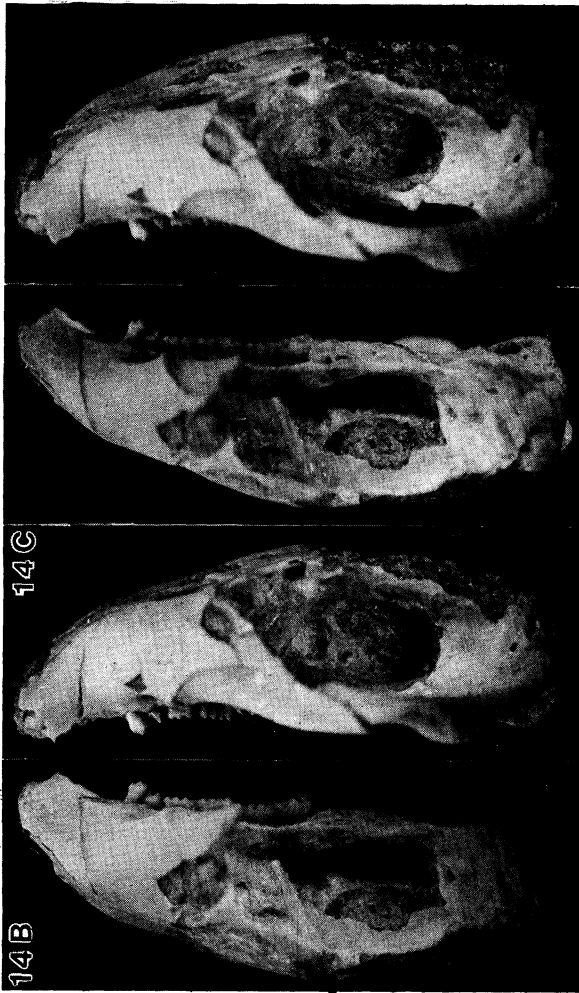
FIGURE 13. The same. Section 400 (level of choanae), magn.  $\times 20$ . pt, pterygoid bone; ss, sphenoid air sinus;



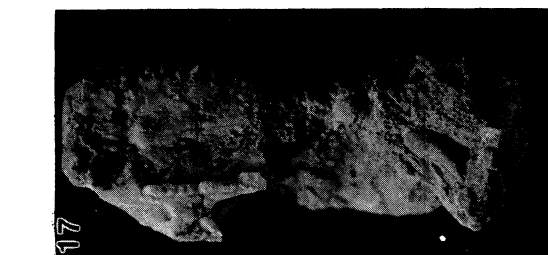
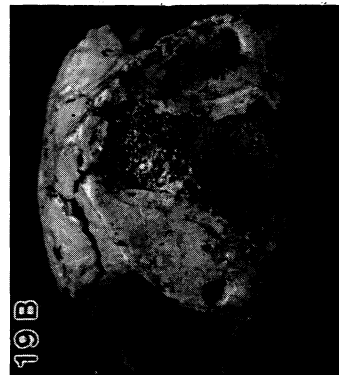
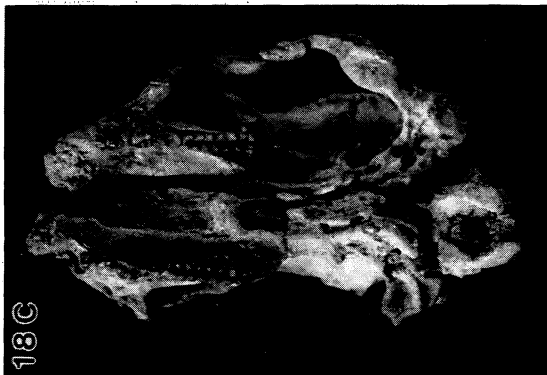
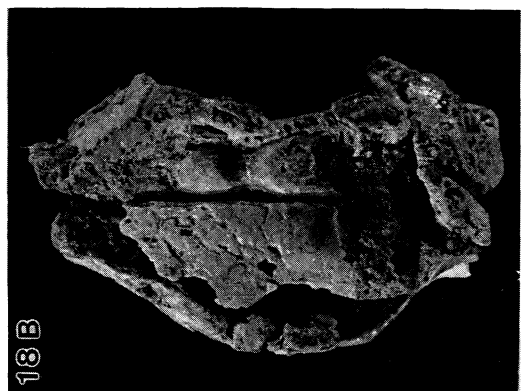
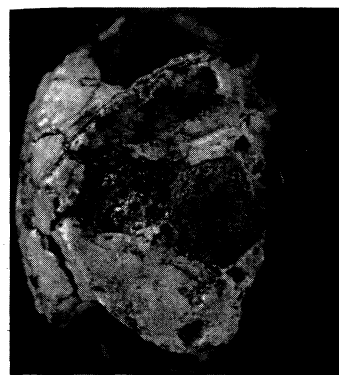
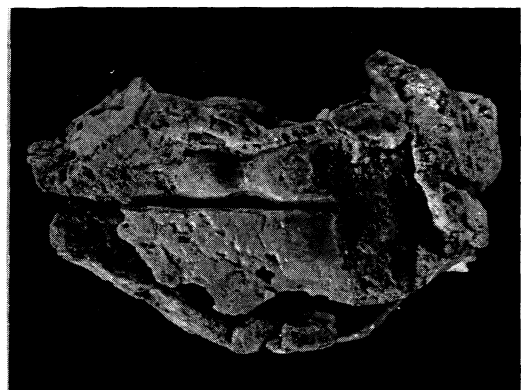




FIGURES 12 AND 13. For description see p. 538



FIGURES 14-16. For description see p. 539.



FIGURES 17-19. For description see opposite.

(d) *Chulsanbaatar* (figures 6 (page 541), 7 (page 542), 10–17)

(i) *Material*. *Chulsanbaatar* is a monotypic genus represented by *Ch. vulgaris* Kielan-Jaworowska, 1974, from the Khulsan locality of the ?Middle Campanian Barun Goyot Formation or its stratigraphic equivalent, the red beds of Khermeen Tsav, in the Gobi Desert, Mongolia. *Ch. vulgaris* is a small species, the length of the skull varying between 17 and 21 mm. Kielan-Jaworowska (1974) diagnosed it and described its natural endocranial cast (1983). In the two papers, six skulls were figured. The skull of *Chulsanbaatar* does not differ essentially in general morphology from those of *Kamptobaatar* and *Sloanbaatar* (Kielan-Jaworowska 1971; Clemens & Kielan-Jaworowska 1979). Therefore in the present paper the description is confined to new detail provided mostly from ZPAL MgM-I/58, ZPAL MgM-I/89 and ZPAL MgM-I/168, all prepared since the above papers were written, and the sectioned skull, ZPAL, MgM-I/84. The latter, its preserved part 17.7 mm long, has not been figured previously. From it 885 sections 20 µm thick were obtained. Every fifth section was photographed in ultraviolet light and prints, enlarged ×20, were made. The skull proved to be badly damaged: the left side, embedded in the matrix, particularly so. For the time being this specimen has not been modelled.

(ii) *Anatomy*

Occipital bone (figures 11, 12 and 15B)

The basioccipital, exoccipital and supraoccipital are completely fused, as is usual in multituberculates. In *Kamptobaatar* (Kielan-Jaworowska 1971, p. 14) the basioccipital–basisphenoid suture was tentatively recognized at a level medial to the foramen ovale inferium. In ZPAL MgM-I/168 the suture at this site is well preserved, the skull being slightly dislocated along it. Simpson (1938) reconstructed the basioccipital–basisphenoid suture further back in *Ptilodus*, but clearly in these Asian genera it is as described here.

The jugular fossa is relatively very large (as in *Kamptobaatar* and *Sloanbaatar*) and appears postero-laterally prolonged, possibly owing to distortion, so that that part of its roof is formed

#### DESCRIPTION OF PLATE 5

FIGURE 14. *Chulsanbaatar vulgaris* ZPAL MgM-I/168. Stereophotographs, magn. ×4. (A) Occlusal view. (B) Right lateral view. (C) Left lateral view. (See figure 6.)

FIGURE 15. *Chulsanbaatar vulgaris* ZPAL MgM-I/89. Stereophotographs, magn. ×4.5. (A) Posterior part of skull with partial endocranial cast, right lateral view. (B) Same, posterior view. asc, Anterior semicircular canal; cc, condylar cavity (broken); psc, posterior semicircular canal.

FIGURE 16. Same skull as figure 15. Dorsal view. Note partial endocranial cast and cast of nasal cavity. c, Casts associated with 'vascular foramina'. Stereophotograph, magn. ×4.

#### DESCRIPTION OF PLATE 6

FIGURE 17. *Chulsanbaatar vulgaris* ZPAL MgM-I/58. Ventral view. magn. ×3. Note cast of cochlea, and round anteriorly placed 'vascular cast' (see text).

FIGURE 18. *Nemegtbaatar gobiensis* ZPAL MgM-I/82. Skull and atlas of juvenile with partial endocast. Stereophotographs, magn. ×2. (A) Right lateral view. (B) Dorsal view. (C) Ventral view.

FIGURE 19. *Nemegtbaatar gobiensis* ZPAL MgM-I/76. The sectioned skull. Stereophotographs, magn. ×2.5. (A) Ventral view (portion drawn enlarged in figure 31). (B) Occipital view.

by the petrosal. The medial part of the fossa forms a cul-de-sac overhung medially by the basioccipital. The anterior part of the basioccipital lies horizontally, the posterior part slopes postero-ventrally. The ventral surface is pierced by numerous small foramina, and symmetrical shallow grooves run parallel to the suture with the petrosal.

The condyles are not prominent ventrally and are not separated from the anterior part of the occipital except for a postero-ventrally sloping and insignificant expansion of the bone in this region. In posterior aspect the condyles are more prominent, but are poorly preserved in *Chulsanbaatar* skulls.

The condyles protrude towards the cranial cavity ventrally, each forming a large, well-expanded structure, hollow inside, here designated the condylar cavity. The cavity is roughly triangular in cross section with a wide floor and tapering dorsally and anteriorly. In ZPAL MgM-I/168 it is about 2.5 mm long in a skull about 18.5 mm long. Its ventral wall forms the postero-lateral part of the basicranium, medial to the jugular fossa. The inner wall, lying obliquely medio-ventrally, separates the condylar cavity from the cranial cavity. The lateral wall forms the medial wall of the jugular fossa, and the posterior wall, part of the occipital plate, is roughly triangular, narrows dorsally, and lies at the lateroventral border of the foramen magnum in contact with the petrosal laterally and the supraoccipital dorsally. Ventrolaterally the condylar cavity abuts on the smaller cavity of the paroccipital process, separated from it by a bony partition. In the sectioned skull ZPAL MgM-I/84 the inner wall of the cavity appears to be penetrated by minute foramina, but it is possible that these are artefacts of distortion. If not, they raise the possibility that the condylar cavity communicated with both the cranial cavity and the jugular fossa. The bone surrounding the cavity is thin, and often becomes deformed, with the internal wall moving medially and the ventral wall being flattened. Such distortion in *Kryptobaatar* specimens induced Kielan-Jaworowska & Dashzeveg (1978) to call this configuration the 'basioccipital box'. This is now recognized to be an artefact (figures 12 and 15).

#### Petrosal bone

Ventral aspect (figures 6 and 14a,A). The alisphenoid-petrosal suture is unrecognizable with any certainty, as is usual in Asian Late Cretaceous multituberculates. In ZPAL MgM-I/168 it is tentatively identified in ventral aspect on both sides of the skull, extending transversely in front of the foramen masticatorium. Seen from ventrally the petrosal is roughly oval and the ascending part of the anterior lamina is not visible. The foramen for the internal carotid artery is indistinct, probably situated in front of the promontorium at the boundary between petrosal, basisphenoid, pterygoid and alisphenoid. The ventral surface of the promontorium is undulating. It may be divided into three zones: the anterior widest; the middle, opposite the jugular fossa, narrower; and the posterior, inserted between the fenestrae vestibuli and cochleae, very narrow. The fenestra cochleae faces almost directly posteriorly into the jugular fossa.

The facial sulcus is relatively short, lying opposite the middle part of the promontorium. On the lateral margin of the promontorium, antero-medial to the facial sulcus is the 'hiatus Fallopii', here a foramen as in *Kamptobaatar* and *Sloanbaatar*. A groove extends anteromedially from the 'hiatus' along the lateral margin of the promontorium towards the carotid foramen. The anterior part of the facial sulcus, lying along the lateral margin of the promontorium, is bounded posteriorly by a short bridge that joins the lateral flange to the part of the

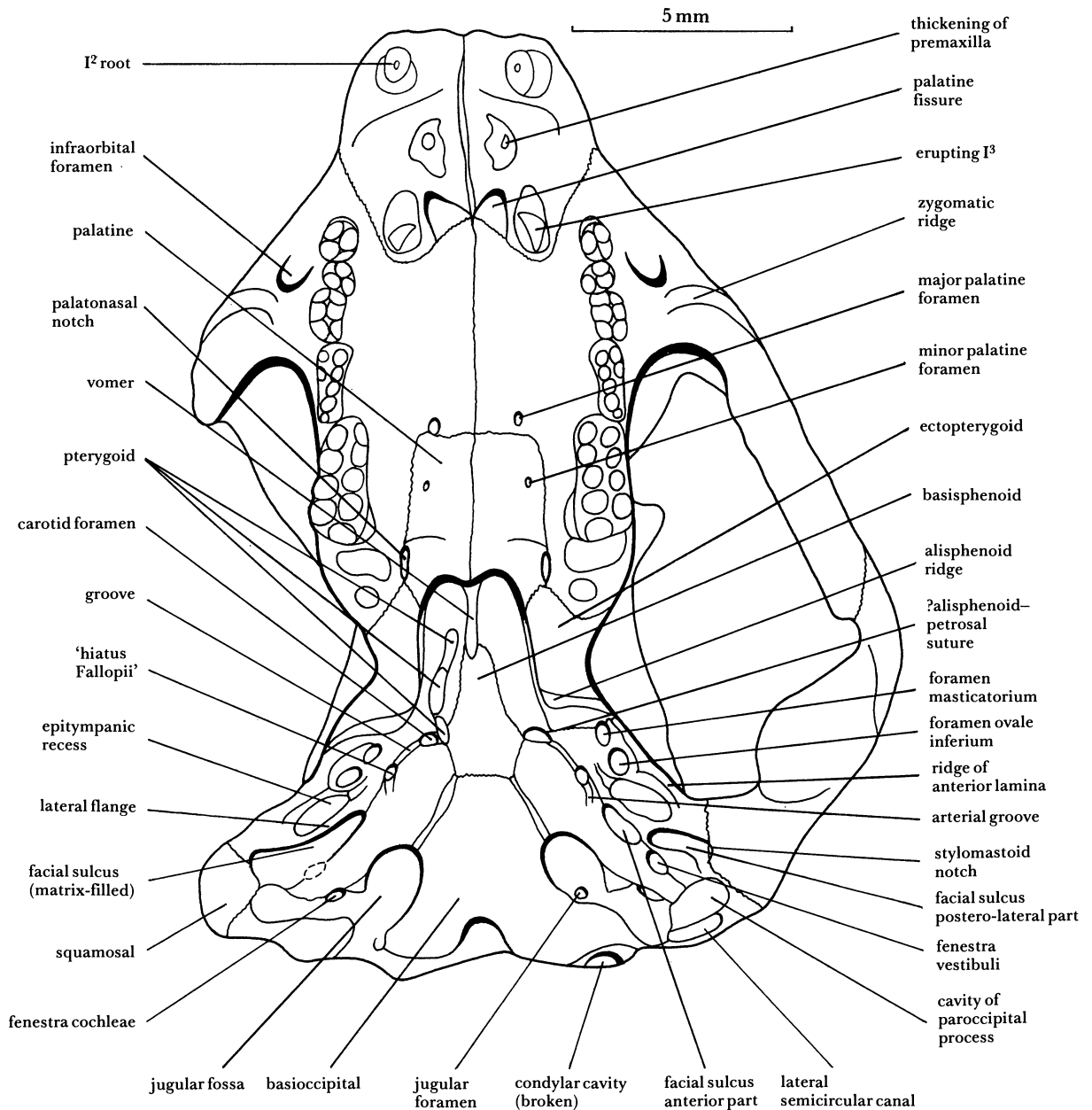


FIGURE 6. *Chulsanbaatar vulgaris*. ZPAL MgM-I/168. Schematic drawing, occlusal view. (See figure 14 A.)

promontorium forming the anterior margin of the fenestra vestibuli. Postero-lateral to this bridge the sulcus turns and continues transversely as an open groove, here called the postero-lateral part of the sulcus. Laterally this ends as a notch in the squamosal, which we identify as a stylomastoid notch, homologous with the stylomastoid foramen of the unidentified Hell Creek petrosals.

The bridge separating anterior and postero-lateral parts of the facial sulcus is well preserved on the left of ZPAL MgM-I/168 (figures 6 and 14) and on the right of ZPAL MgM-I/108 (Kielan-Jaworowska 1974, plate XIV, figure 1A). A similar bridge was described in *Ptilodus*

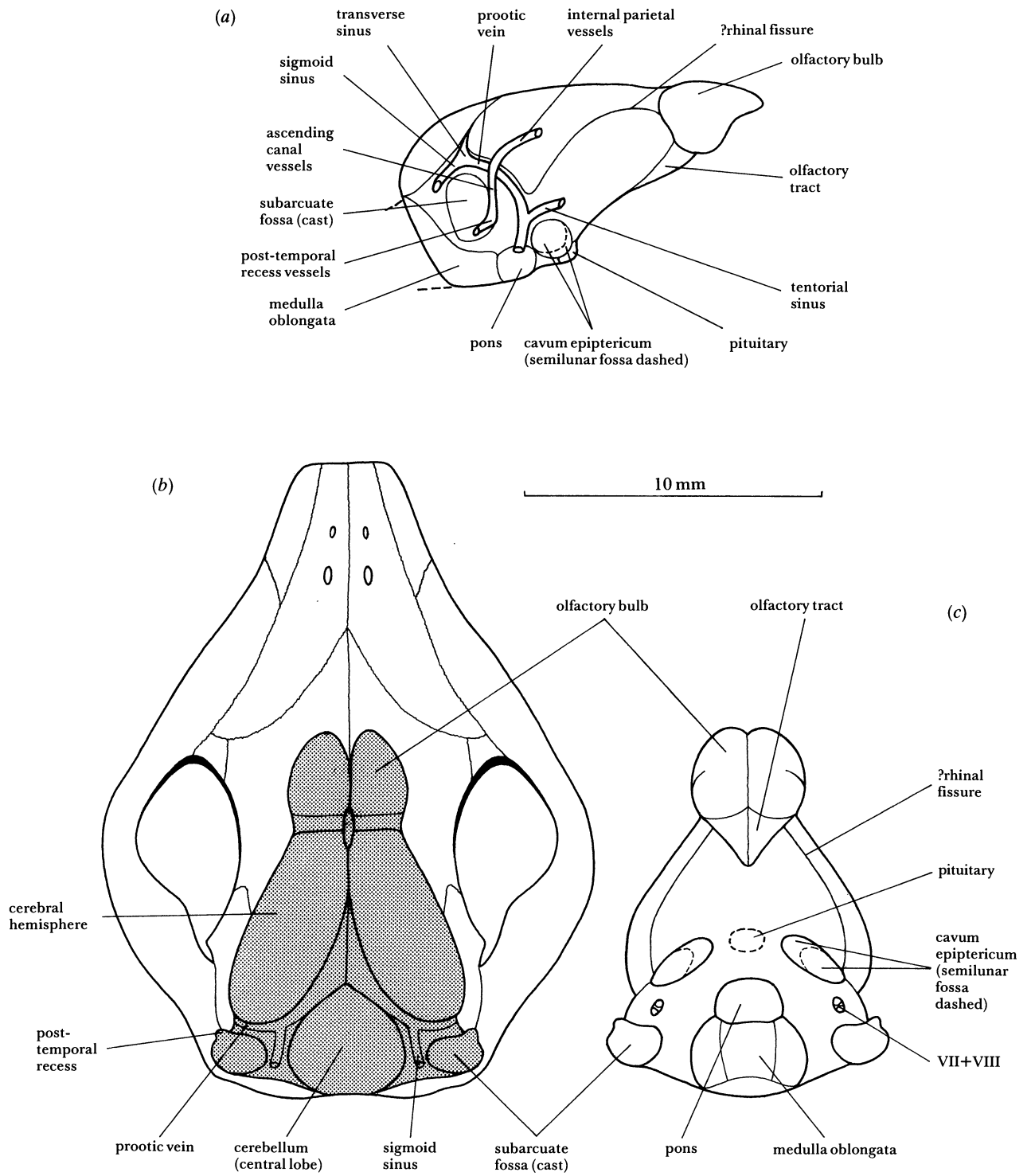


FIGURE 7. *Chulsanbaatar vulgaris*. Reconstructions. (a) Endocast, lateral view. (b) Skull and endocast (hatched), dorsal view. (c) Endocast, ventral view. After Kielan-Jaworowska (1983), emended.



by Simpson (1937) between his 'dehiscencia canalis facialis' and his 'apertura tympanica canalis facialis'. Here we re-interpret this bridge as separating the two descriptive parts of the facial sulcus. Re-examination of the *Kamptobaatar* skull ZPAL MgM-I/33 shows that this bridge was possibly originally present but now broken in this specimen. It seems probable that it was also present in other genera, but being a very delicate structure it could be easily destroyed either by preparation or during fossilization in small specimens.

Because of the small size of *Chulsanbaatar* skulls and difficulties in preparation, it proved impossible to recognize other details of the structure of the facial sulcus comparable with those well preserved in *Catopsalis* and the unidentified Hell Creek petrosals. For example the tympanic opening of the prootic canal cannot be located with any certainty, nor can the supraglenoid and postglenoid foramina.

The fossa muscularis minor is partly destroyed in all specimens. No hyoid muscular pit has been found. The paroccipital process is preserved in ZPAL MgM-I/108 (Kielan-Jaworowska 1974, plate XIV, figures 1a and 1a) while in ZPAL MgM-I/168 it is broken off on the left side to expose the cavity of the paroccipital process, bounded posteriorly by the lateral semicircular canal. The epitympanic recess is relatively wide, prolonged anteriorly as a groove extending between the foramen ovale inferium and the 'hiatus Fallopii'. The lateral flange bounding the epitympanic recess medially and posteriorly is not very prominent. Laterally the recess is bounded by a prominent ridge that protrudes ventrally, separating the ascending part of the anterior lamina from the rest of the petrosal. This ridge is tentatively regarded as a support for the tympanic bone, which has not been preserved. The foramen ovale inferium is larger than the foramen masticatorium, which is anterior, rather than lateral, to it. Both foramina face ventrally and are bounded laterally by the ridge overhanging the ventral aspect of the basicranium.

Posterior aspect (figures 11 and 15B). The ridges corresponding to the posterior and lateral semicircular canals, and the relatively large post-temporal fossa, are well preserved in several specimens (figure 15; see also Kielan-Jaworowska 1974, 1983).

Lateral aspect (figures 10A, 14B,C and 15A). The anterior lamina is large and the ridge corresponding to the anterior semicircular canal and ampulla is very prominent, extending obliquely postero-dorsally in the posterior part of the lamina. On both sides of ZPAL MgM-I/168 a distinct rounded foramen, the dorsal foramen of the lamina, is well preserved.

Basisphenoid-presphenoid complex (figures 6, 13 and 14A). The ventral part of the basisphenoid-presphenoid complex is well shown in ZPAL MgM-I/168, forming a large part of the choanal roof. The exposed bone in front of the suture with the basioccipital widens anteriorly, medial to the petrosal and then tapers forwards to reach the broken posterior end of the vomer, which covers it ventrally. The boundary between basisphenoid and presphenoid cannot be identified with certainty. The sectioned skull shows that, as is usual in mammals, the sphenoid contained large air-sinuses (figure 13). The suture between alisphenoid and petrosal was described above; the suture between alisphenoid and ectopterygoid is barely discernible but is possibly as described for *Kamptobaatar* (Kielan-Jaworowska 1971). In ZPAL MgM-I/168 the alisphenoid is well exposed in lateral aspect and the specimen confirms

that it is a small ventral element that contributes to the floor of the posterior part of the orbit as in *Kamptobaatar*. The orbitosphenoid is less well preserved than in the latter but appears to have been of a similar shape. A shallow groove, here designated the sphenopalatine groove extends from the sphenopalatine foramen posteriorly along the ventral part of the orbitosphenoid towards the cavum epiptericum.

The shape and size of the sphenorbital fissure, reconstructed by Kielan-Jaworowska (1971), possibly because of distortion, as a large opening in the orbitosphenoid, in fact can hardly be seen in lateral aspect. It forms the anterior opening of the cavum epiptericum and can be seen, by looking backwards into the posterior prolongation of the temporal fossa, on both sides of ZPAL MgM-I/168, as a space between the two walls of the cavum. It proved impossible to photograph this view. The lower part of the orbitosphenoid, a very thin bone, is partly missing in all the specimens studied. A small groove, here designated the orbital groove, extends along the upper part of the orbitosphenoid. It extends posteriorly on the parietal towards the post-orbital process, where it disappears. The sectioned skull shows that here the post-orbital process was pierced by the post-orbital foramen leading to a short canal. Anteriorly the post-orbital groove turns ventrally and reaches the ethmoid foramen. A wide, shallow groove extends postero-ventrally from the ethmoid foramen (as in *Kamptobaatar*) to meet the sphenopalatine groove.

#### Frontal bone

The frontal bone has a large orbital exposure, as in *Kamptobaatar*. The orbital ridge (figure 14B, C) extends antero-ventrally along the posterior part of this, being more prominent than in *Kamptobaatar*. It supports the cranial roof overhanging the orbit. The anterior part of the orbital groove and the ethmoid foramen are situated just behind the orbital ridge. In front of it in the cranial roof is a large rounded recess, as in *Kamptobaatar*, here designated the orbitonasal fossa.

#### Nasal bone

The so-called 'vascular foramina' on the nasal bones (Simpson 1937), but which might transmit the lateral ethmoid nerve (Kielan-Jaworowska 1971), show great variation in their distribution. In most specimens (but not in the type specimen (Kielan-Jaworowska 1974, plate XI, figure 1a)) there is a symmetrical pair of larger foramina and another pair of tiny ones in front. In ZPAL MgM-I/89 (figure 16) in which the right nasal bone has been intentionally removed, casts of two canals are preserved, the larger leading from the nasal cavity to the more posterior foramen, the smaller to the anterior.

#### Premaxilla

In the middle of the palatal part of the premaxilla are conspicuous irregular thickenings of the bone, which do not occur in *Kamptobaatar*, but which are also present, though less distinct, in *Nemegtbaatar*. Otherwise the skull of *Chulsanbaatar* does not differ essentially from that of *Kamptobaatar*.

#### Endocranial cast (figures 7, 16 and 17)

An endocranial cast of *Chulsanbaatar* was reconstructed (Kielan-Jaworowska 1983) on the basis of a natural endocast prepared from ZPAL MgM-I/88. Subsequently the specimen was

prepared slightly more and the anterior part of the left promontorium was removed. It appears that the pituitary fossa was smaller than as reconstructed (there incorrectly labelled 'pons' in figure 1, corrected to 'hypophysis' in the Addendum). The present reconstruction (figure 7) of the size of the fossa is only tentative. It seems possible that the lateral part of the large trapezoidal 'hypophysis' corresponds to a cast of the anterior part of the cavum epiptericum, because on the left side of the above specimen this structure is connected with the cast of the semilunar fossa. In the sectioned skull ZPAL MgM-I/84 the medial wall of the cavum epiptericum is extremely thin and thus might easily be destroyed, causing the narrow part of the cranial cavity above the pituitary fossa to become confluent with the cast of the cavum epiptericum. Kielan-Jaworowska (1983, figure 1) called 'hypophysis' a structure some way in front of the 'pons', based on ZPAL MgM-I/58, here illustrated (figure 17). This structure is placed too far anteriorly to be a cast of the optic chiasma, and it is presumed that it may be a cast of part of the cerebral venous system. If this reconstruction (figure 7c) is true, the pons in *Chulsanbaatar* was situated caudal to the emergence of the trigeminal nerve.

On the antero-lateral part of the subarcuate fossa cast in ZPAL MgM-I/88 (Kielan-Jaworowska 1983, text figure 1, plate 1, figures 1e and 1g) there is an oval cuspule that evidently corresponds to the recess here designated the post-temporal recess. On several casts of *Chulsanbaatar* (figure 16) the furrow housing the superior sagittal sinus bifurcates posteriorly, as is usual in mammals, in front of the central lobe of the cerebellum, to extend postero-laterally as the transverse sinuses, casts of which are often well preserved. The cast of the sigmoid sinus departs from the transverse sinus and extends between paraflocculus and central lobe of the cerebellum postero-ventrally and then ventrally (well shown on the right of ZPAL MgM-I/88, medial to the cast of the crus commune, Kielan-Jaworowska 1983, plate 1, figure 1d). Any more ventral part of the sigmoid sinus is not visible. The cast of the transverse sinus continues laterally as the prootic sinus to become the vertical segment of the prootic canal. This begins dorsal to the upper margin of the cast of the semilunar fossa. On the right side of the same specimen there is a cast of another vessel extending above the cast of the semilunar fossa and entering the prootic canal from anterior. This may represent the tentorial sinus. To the rear of the semilunar ganglion the prootic canal turns postero-ventrally. The gleno-prootic canal present in other genera is not preserved. Because of the small size of *Chulsanbaatar* skulls the existence of supraglenoid and postglenoid foramina cannot be established.

In ZPAL MgM-I/88 and 89 another vascular cast extends from the post-orbital process posteriorly along the dorso-lateral border of the cerebral hemisphere. This corresponds to the orbito-temporal vessels. On the left side of ZPAL MgM-I/89 (figure 10) this cast passes posteriorly above the transverse sinus and then turns postero-ventrally, entering the subarcuate fossa to be seen on the cast, its prolongation forming the cast of the post-temporal recess.

(e) *Nemegtbaatar* (figures 18–32)

(i) *Material*. The monotypic genus *Nemegtbaatar* is represented by *N. gobiensis* Kielan-Jaworowska, 1974 from the Khulsan locality of the Barun Goyot Formation or the stratigraphically equivalent red beds of Khermeen Tsav (locality of Khermeen Tsav II). The type specimen ZPAL MgM-I/81 and the skull ZPAL MgM-I/76, which was sectioned for this study, were described and illustrated, with the diagnosis, by Kielan-Jaworowska (1974).

The length of the adult skull of *Nemegtbaatar* is estimated to be about 40–45 mm. The skull that was sectioned, lacking the anterior part of the snout and a fragment of the occipital plate,

was 36 mm long (figure 19). It was previously figured by Kielan-Jaworowska (1974, plates IX and X). From this skull 1370 sections, 25 µm thick, were obtained, and were numbered consecutively from back to front. Every fifth section was photographed in ultraviolet light, and prints at ×16 enlargement were made. On the basis of these photographs, drawings and two wax models were made at the same scale. The models were one of the endocranial cavity with casts of nerves and blood vessels where possible, and a second of the posterior part of the endocranial cavity, without the paraflocculi but with the osseous labyrinths.

Two other skulls from Khermeen Tsav II in the ZPAL collection: MgM-I/82 and 57, were also examined. The former is illustrated here (figure 18). As with *Chulsanbaatar* we confine our account to previously undescribed structures, or to those in which *Nemegtbaatar* differs from *Chulsanbaatar* or *Kamptobaatar* (Kielan-Jaworowska 1971).

(ii) *Anatomy*

Occipital bone (figure 19B)

The basioccipital–basisphenoid junction is at the level of the foramen ovale inferium as in *Chulsanbaatar*. In contrast to that genus and *Kamptobaatar* the occipital condyles protrude well ventrally, forming crescent-shaped scrolls directed postero-laterally, each with its concavity forming the medial wall of a relatively shallow jugular fossa. There appears to be a very small condylar cavity, with its inner wall concave towards the cranial cavity rather than bulging into the latter as in *Chulsanbaatar*-like forms. A jugular foramen is present in the roof of the left jugular fossa in ZPAL MgM-I/82. Antero-laterally to the condyle is a rounded recess in the basioccipital, 1.2 mm in diameter in the above specimen, included in an anterior prolongation of the jugular fossa not seen in other genera. Also unique to *Nemegtbaatar*, though seen clearly only in this specimen, is a median ridge on the basioccipital. In ZPAL MgM-I/81 the supraoccipital is preserved and shows keels that converge ventrally towards a relatively small foramen magnum, which may have been partly diminished by distortion (Kielan-Jaworowska 1974, plate VII, figure 1c).

Petrosal bone

Ventral aspect (figures 18C, 19A and 20c). In ventral aspect the petrosal is roughly oval and the anterior lamina is not visible. The alisphenoid–petrosal suture is not distinguishable. The anterior part of the promontorium runs posteriorly and then postero-laterally. It has an irregular surface and a distinct uncinat process at its mid-length. It narrows rapidly at the rear between the fenestrae vestibuli and cochleae. On its medial margin is a narrow groove, well-preserved in ZPAL MgM-I/82. The facial sulcus is relatively short. Anteriorly it narrows and ends as a notch, which we identify as the ‘hiatus Fallopii’, as in *Catopsalis* and the unidentified Hell Creek petrosals, and similarly we reconstruct both the emerging petrosal branch of the facial nerve and meningeal vessels passing through it. A groove extends antero-medially from the ‘hiatus Fallopii’ along the lateral edge of the promontorium towards the carotid foramen. In the entire skull specimens no foramina are discernible in the facial sulcus, and their distribution in figures 20 and 31 is based on the examination of sections of ZPAL MgM-I/76. The fenestra vestibuli and cochleae are, as is usual, situated opposite one another and are of comparable, relatively large, size. The groove for the aquaeductus cochleae, well preserved in ZPAL MgM-I/82, runs medially from the fenestra cochleae towards the jugular fossa. It cannot be excluded that the anterior part of the facial sulcus was delimited

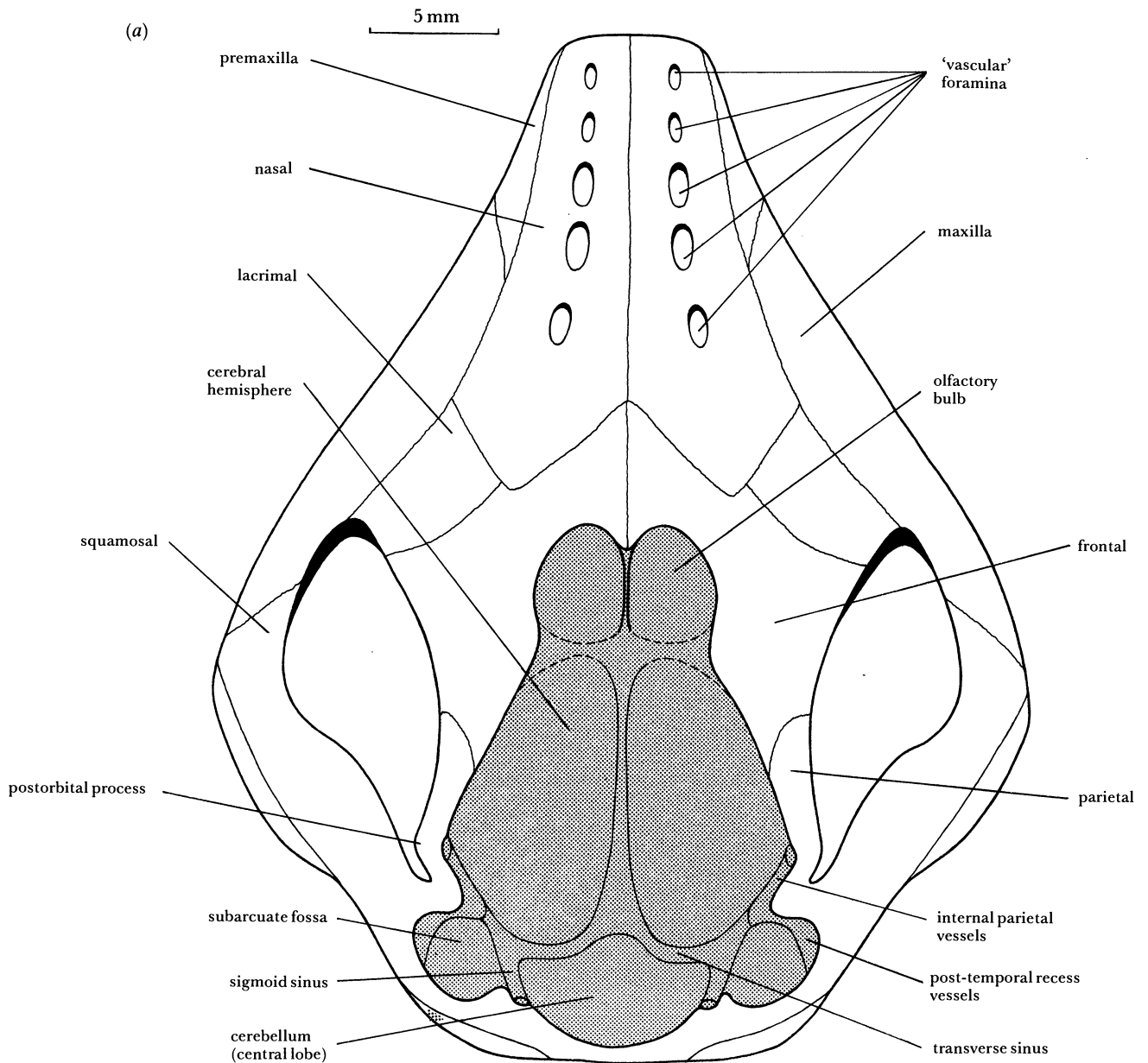


FIGURE 20*a*. *Nemegtbaatar gobiensis*, Dorsal view, endocast hatched.

posteriorly by a bridge, now broken, as in *Chulsanbaatar*. The postero-lateral part of the sulcus, a groove between the lateral flange and the paroccipital process, is relatively shorter in *Nemegtbaatar* than in *Chulsanbaatar* and *Kamptobaatar*, and is developed rather as a rounded fossa, the postero-medial part of which includes a shallow fossa muscularis minor. Laterally it ends as a stylomastoid notch on the squamosal, which in this region overlaps the petrosal ventrally. The paroccipital process is prominent and pointed. Owing to damage, no specimen shows whether the pit for levator hyoidei or digastric musculature was present. Medial to the base of the process in ZPAL MgM-I/82 is a small pit or foramen in the ventral extension of the

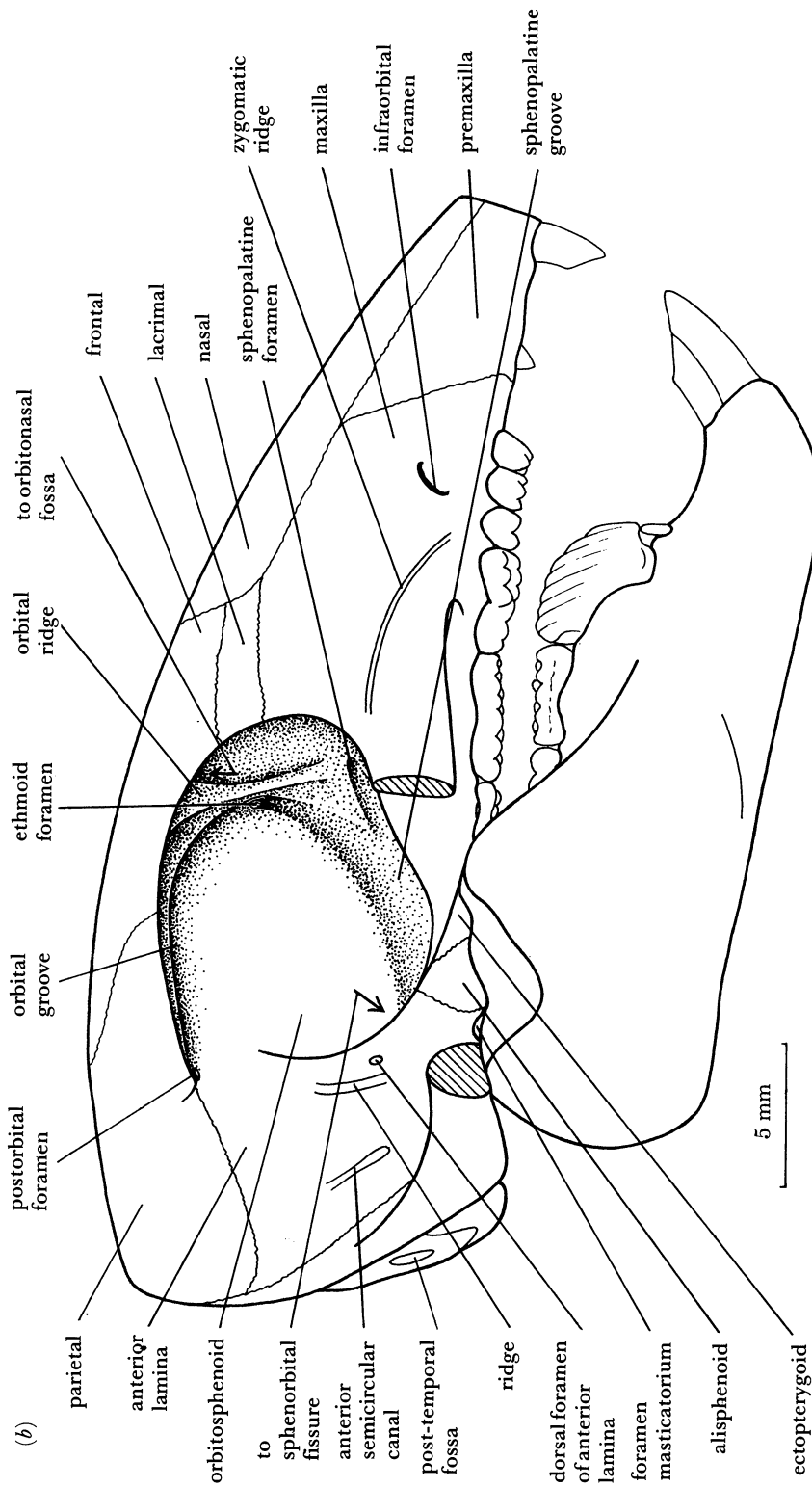


FIGURE 20 b. For description see opposite.

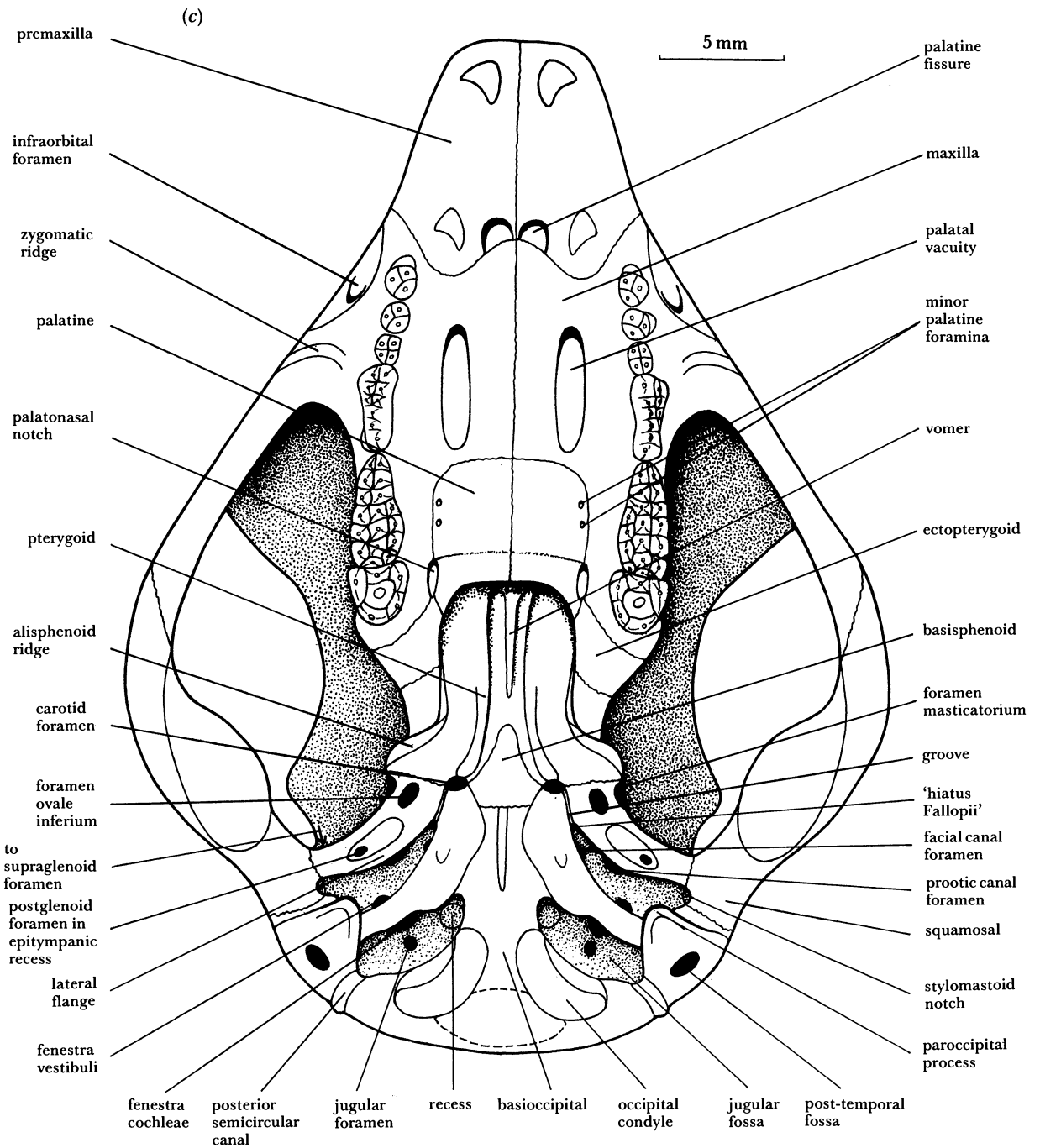
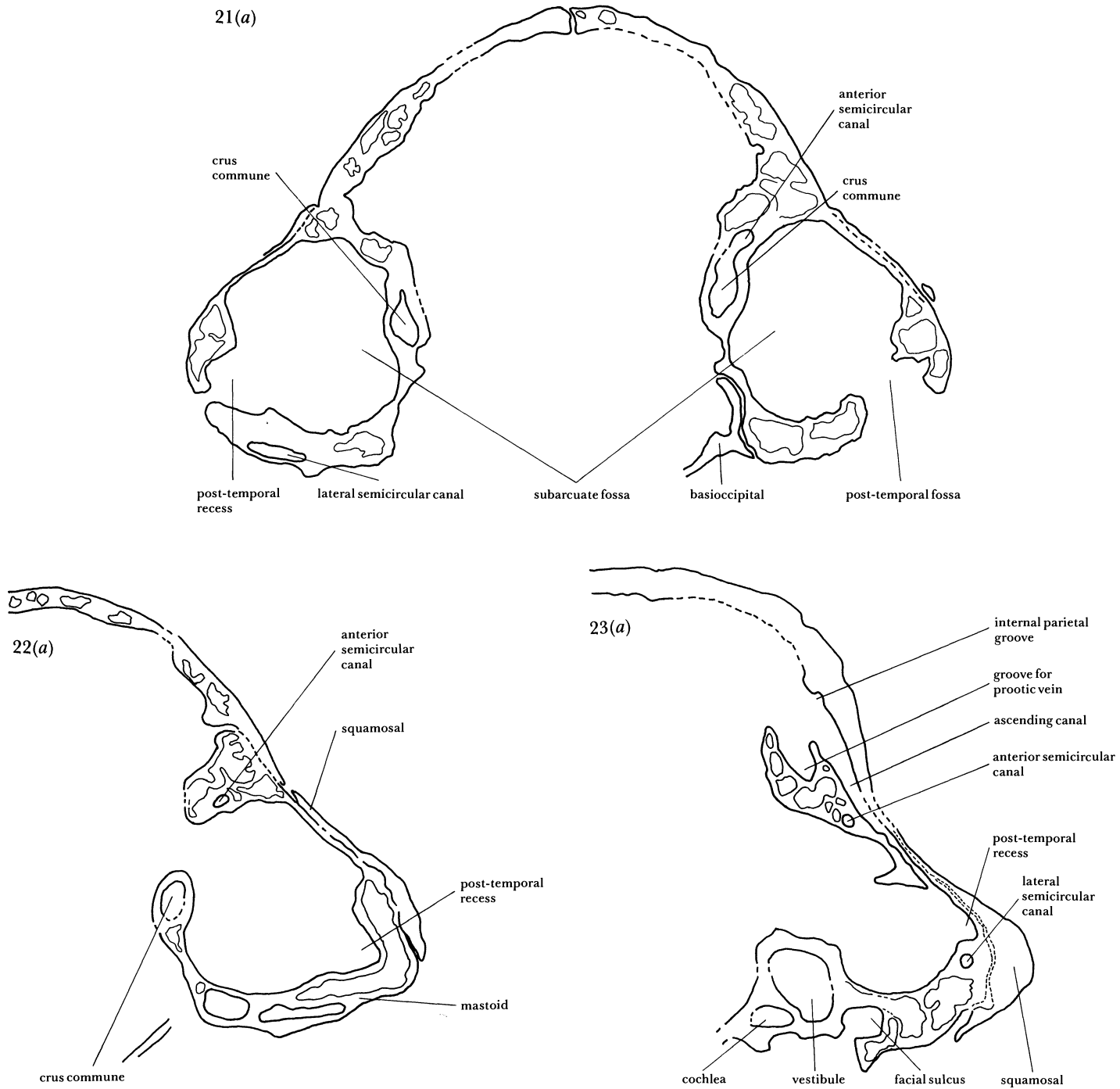


FIGURE 20. *Nemegtbaatar gobiensis*. Composite reconstructions, position of some sutures tentative. (a) See page 547. (b) Lateral view. (c) Occlusal view.

ridge overlying the posterior semicircular canal. The epitympanic recess is very deep, relatively narrow, and bounded by the lateral flange and a prominent ridge which, separating the ventral aspect of the petrosal from the anterior lamina, continues forward lateral to the foramen masticatorium.



DESCRIPTION OF FIGURES 21-23

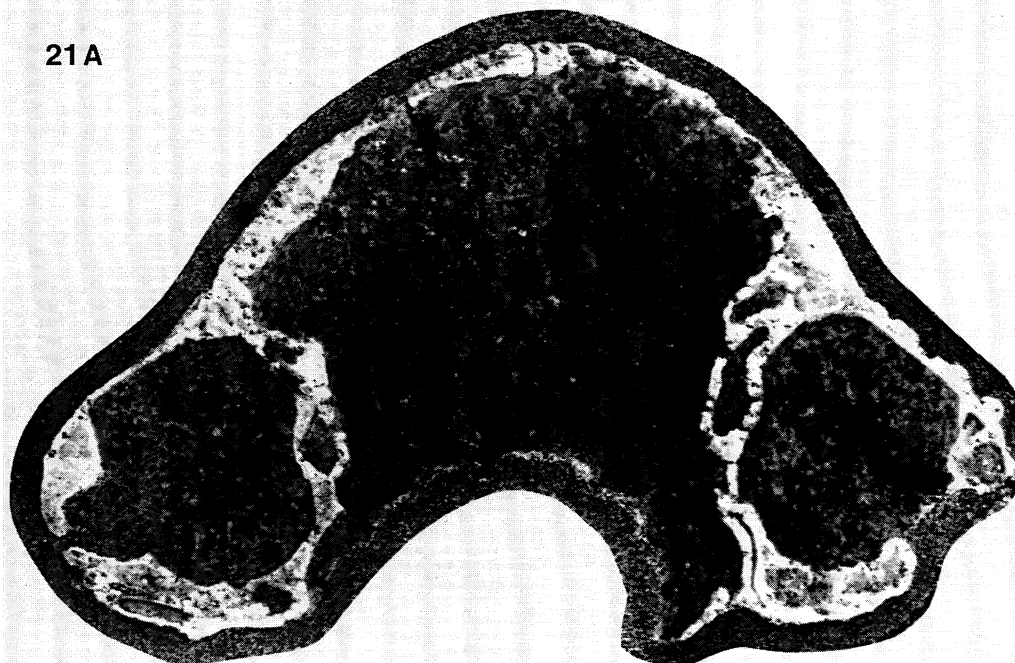
FIGURE 21 (a, A). *Nemegtbaatar gobiensis* ZPAL MgM-I/76. Transverse section 90 (sections numbered from rear). Photo magn.  $\times 8$ .

FIGURE 22 (a, A). The same. Right half of section 105. Photo magn.  $\times 8$ .

FIGURE 23 (a, A). The same. Right half of section 110. Photo magn.  $\times 8$ .



21 A



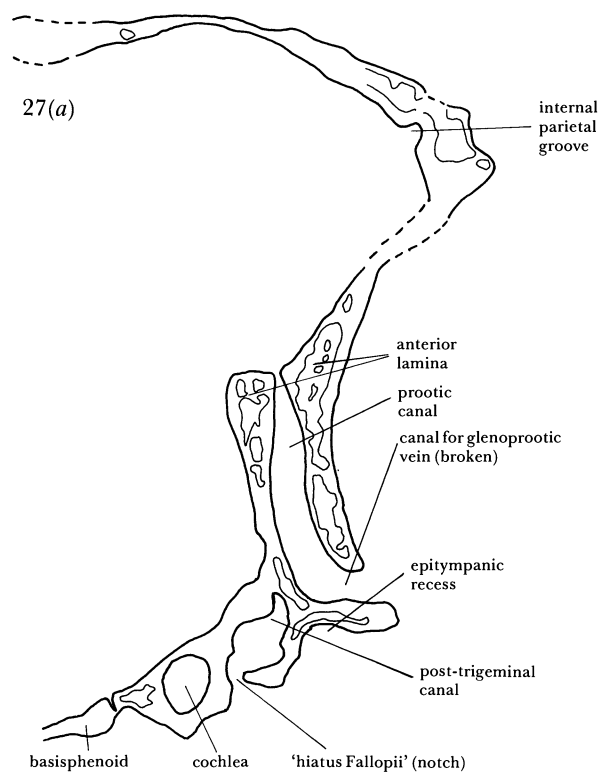
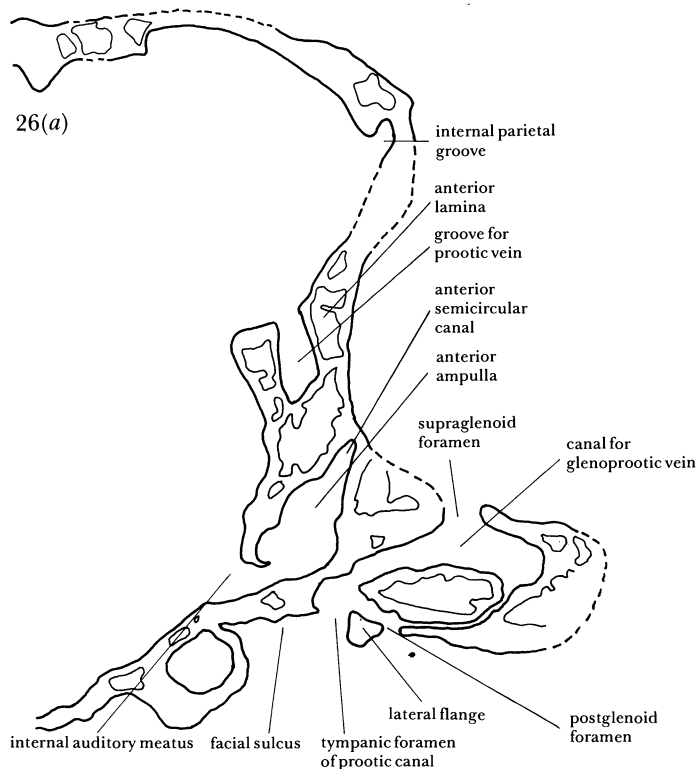
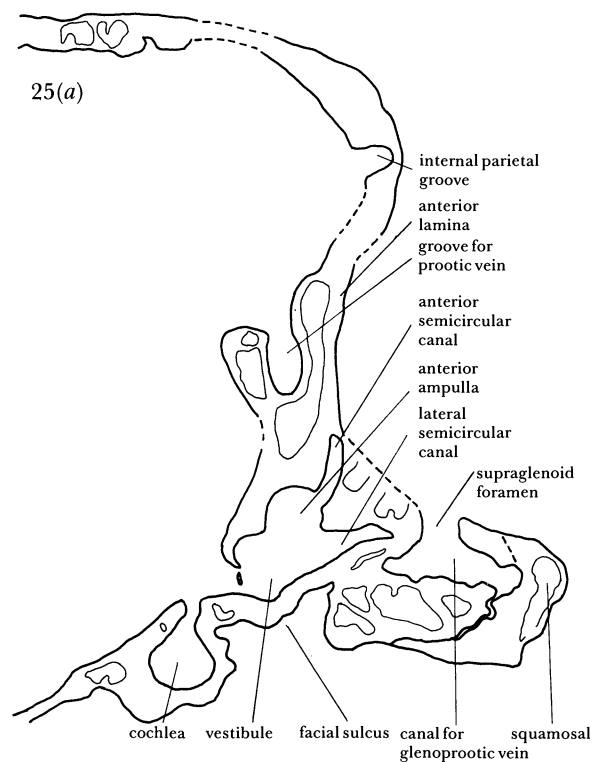
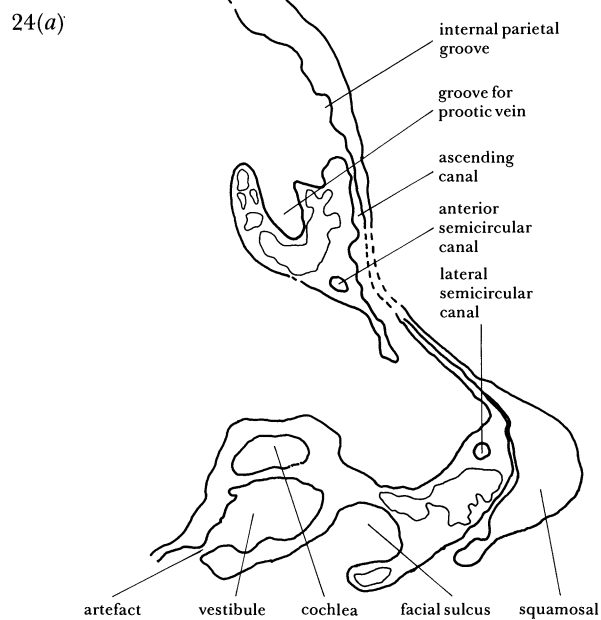
22 A



23 A



FIGURES 21 A, 22 A AND 23 A. For description see opposite.



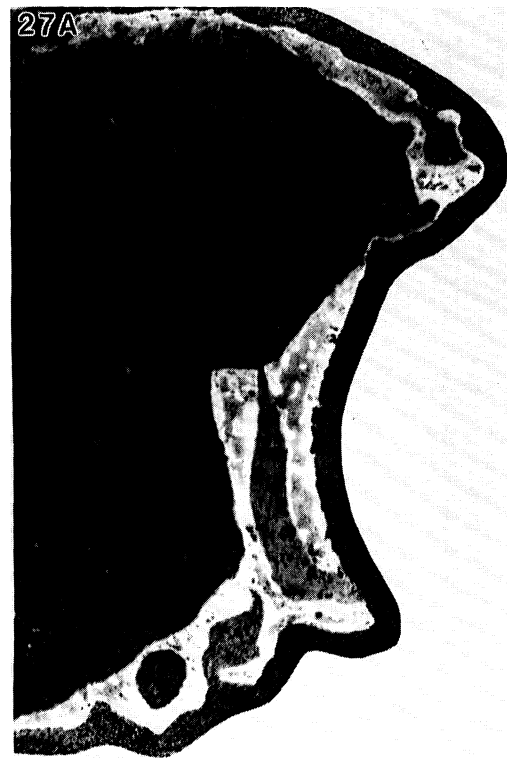
#### DESCRIPTION OF FIGURES 24–27

FIGURE 24 (a, A). *Nemegtbaatar gobiensis* ZPAL MgM-I/76. Right-half of section 170. Photo magn.  $\times 8$ .

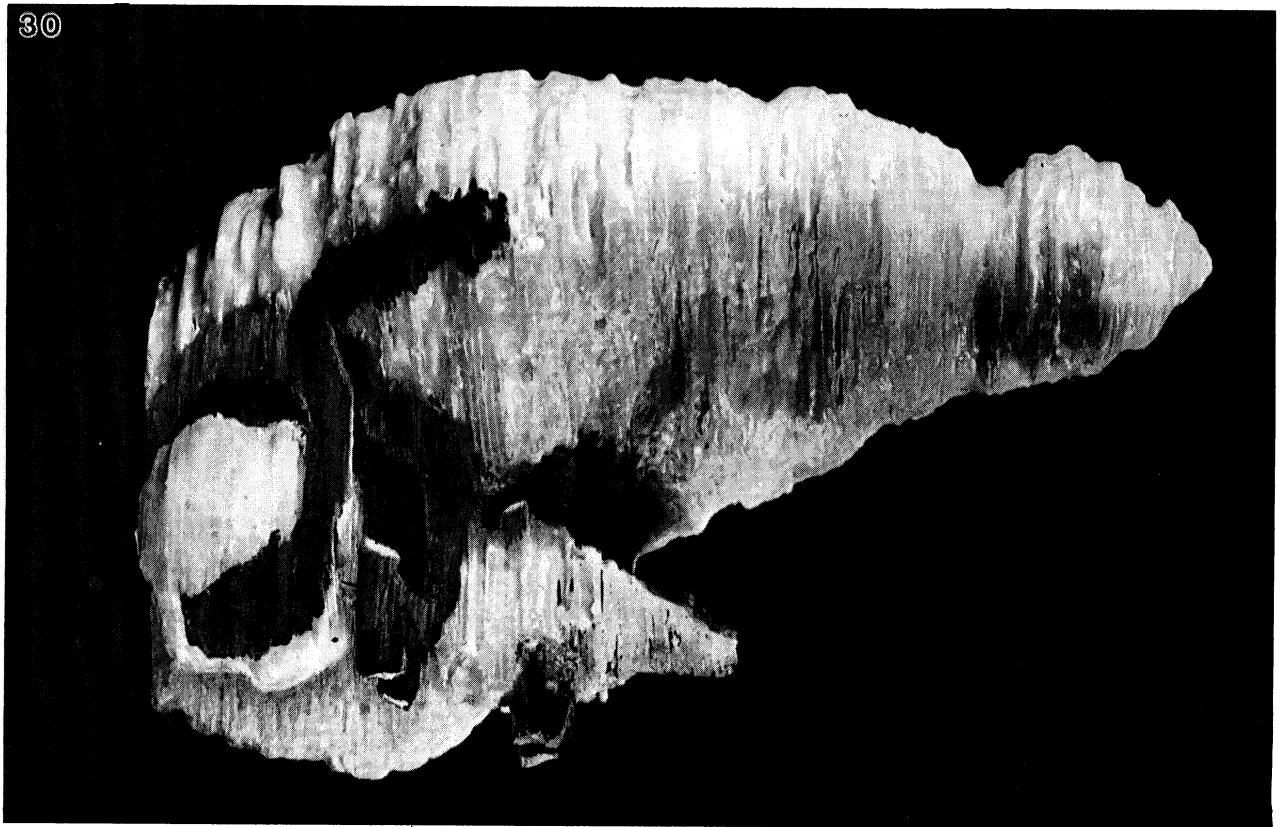
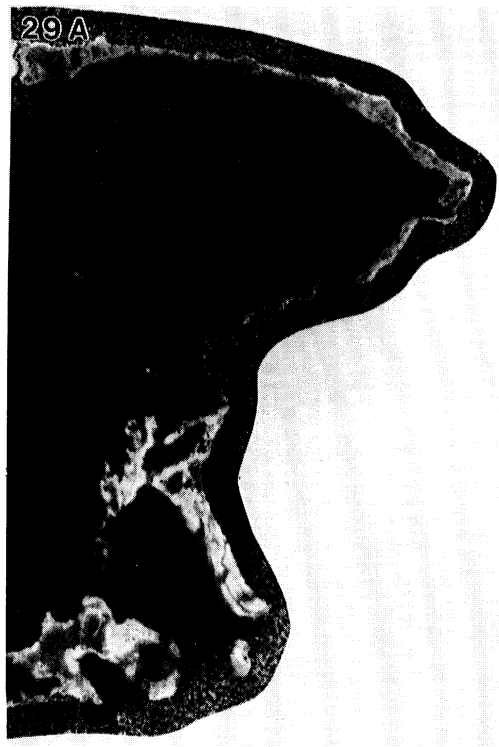
FIGURE 25 (a, A). The same. Right half of section 210. Photo magn.  $\times 8$ .

FIGURE 26 (a, A). The same. Right half of section 215. Photo magn.  $\times 8$ .

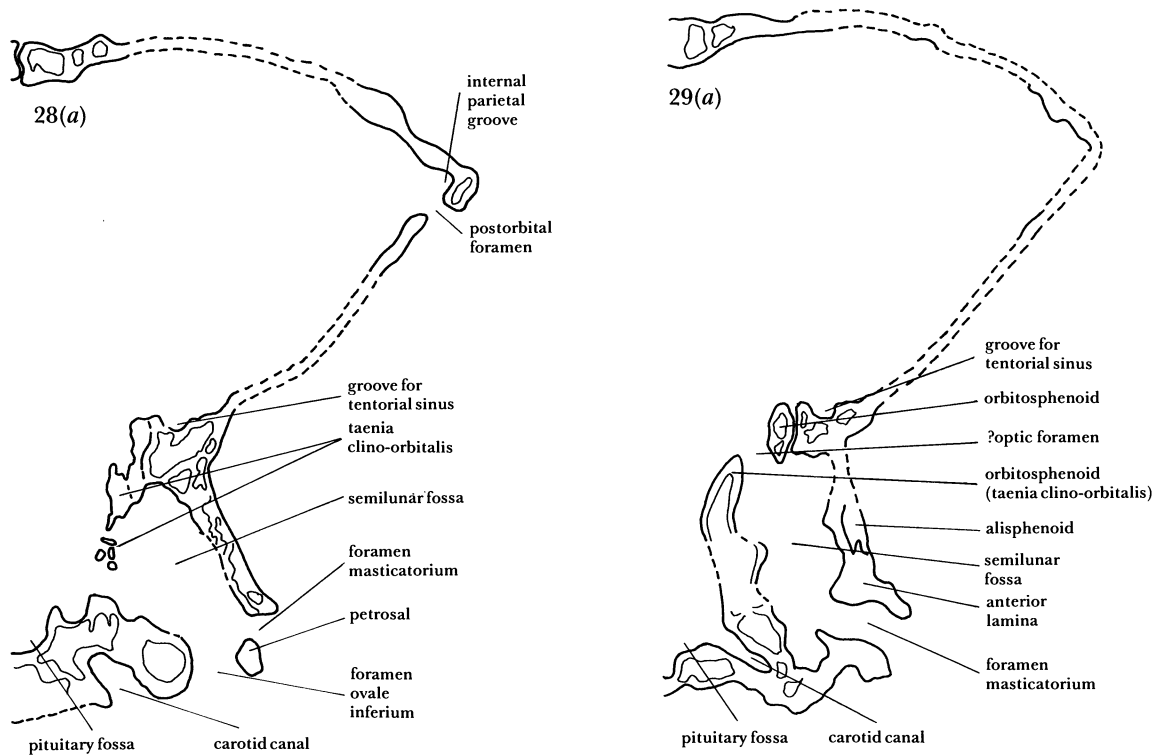
FIGURE 27 (a, A). The same. Right half of section 245. Photo magn.  $\times 8$ .



FIGURES 24A, 25A, 26A AND 27A. For description see opposite.



FIGURES 28A, 29A AND 30. For description see opposite.



FIGURES 28a AND 29a. For description see below.

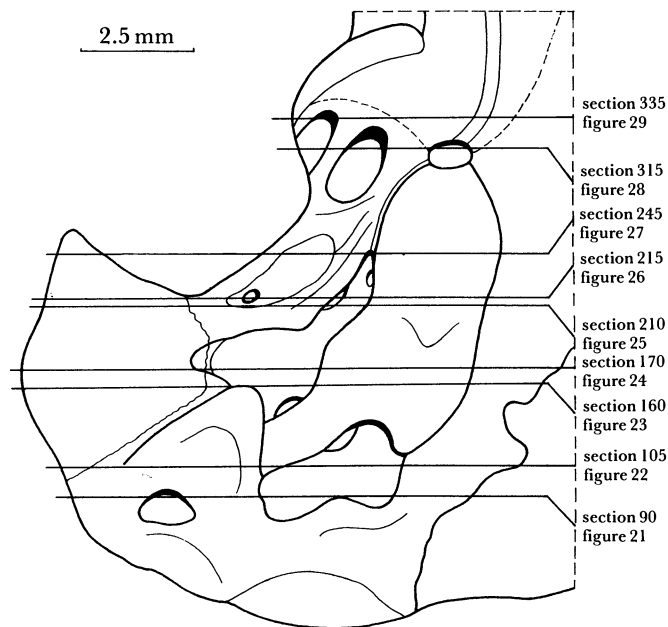


FIGURE 31. *Nemegtbaatar gobiensis* ZPAL MgM-I/76. Enlargement of part of figure 19A to show levels of sections in figures 21–29.

DESCRIPTION OF FIGURES 28–30

FIGURE 28 (a, A). *Nemegtbaatar gobiensis* ZPAL MgM-I/76. Right half of section 315. Photo magn  $\times 8$ .

FIGURE 29 (a, A). The same. Right half of section 335. Photo magn.  $\times 8$ .

FIGURE 30. *Nemegtbaatar gobiensis* ZPAL MgM-I/76. Wax model of endocast reconstructed from sections. Plate magnification *ca.*  $\times 8$  natural size,  $\times 0.5$  size of model.

The positions of the supraglenoid and postglenoid foramina are unusual. In ZPAL MgM-I/82 (figure 18C) the poorly preserved postglenoid foramen is situated within the postero-lateral part of the epitympanic recess, not outside it as in for example *Ptilodus* and *Kamptobaatar*. The supraglenoid foramen is situated more dorsally than in other genera, in the postero-ventral corner of the anterior lamina near the base of the zygomatic arch, and so is not visible from ventrally. The nature and positions of the foramina are confirmed in the sectioned skull (figure 26), although damage is present here.

The foramen ovale inferium is large, directed and opening ventrally in an antero-medial prolongation of the epitympanic recess. The foramen masticatorium is more lateral to it, not directly in front of it as in *Chulsanbaatar*, and is directed and opens latero-ventrally. The two foramina are separated by a prominent lateral flange. The sectioned skull confirms that the foramen for the maxillary artery, present in *Catopsalis* and the unidentified Hell Creek petrosals, is not present in *Nemegtbaatar*.

The carotid canals lie immediately in front of the promontorium. The section series (figures 28, 29) clearly shows them to lie within the basisphenoid–petrosal suture, and probably near the junction of the pterygoid and alisphenoid, though here the sutures cannot be traced with certainty. The canals run upwards, forwards and medially to open into the pituitary fossa just medial to the base of the taenia clino-orbitalis.

Posterior aspect (figure 19B). The ridges corresponding to the posterior and lateral semicircular canals are distinct, though less prominent than in *Chulsanbaatar*. A large post-temporal fossa is present.

Lateral aspect (figures 18A and 20b). The anterior lamina is large, as is usual. The postglenoid foramen and the dorsal foramen of the anterior lamina are well seen in both ZPAL MgM-I/82 (Figure 18) and the sectioned skull (reconstructed in figures 20, 32). The oblique, antero-ventrally directed ridge over the anterior semicircular canal and ampulla lies on the posterior part of the lamina. It is less distinct than in smaller genera such as *Chulsanbaatar* and *Kamptobaatar*. In the middle of the lamina, below the post-orbital process, is a short robust ridge, its ventral part more prominent. Posterior to the dorsal foramen a small wrinkle is present on the lamina.

#### Parietal bone

The whole cranial roof posteriorly is, as usual, formed by the paired parietal bones. The internal parietal groove runs postero-ventrally along its ventral surface, extending from the postorbital process (pierced by the postorbital foramen). The internal parietal groove also runs forward from the postorbital foramen, though this portion is less distinct than the posterior part. Parallel to it on the outer surface the postorbital groove runs forward from the foramen, beneath the cranial roof, and extends onto the orbitosphenoid.

#### Sphenoid bone

In the skulls studied the basisphenoid–parasphenoid complex was poorly exposed, and even in the sectioned series many of the sutures can only be very tentatively placed. In it the basal part of the complex appears to be pneumatized, as is usual in mammals, by large sphenoidal

sinuses. Little information can be obtained from these specimens on the structure of the alisphenoid. The orbitosphenoid, though poorly preserved, appears to have the fan-shape of those of *Kamptobaatar* and *Chulsanbaatar*, with an orbital groove having run forward over the parietal from the postorbital foramen onto it, then turning ventrally to reach the ethmoid foramen (figure 20*b*). A wide, shallow groove extends from the ethmoid foramen postero-ventrally to join the sphenopalatine groove which extends from the sphenorbital foramen along the ventral part of the orbitosphenoid to the cavum epiptericum.

The sphenorbital fissure is visible in the sectioned series and on the left side of ZPAL MgM-I/81. As in *Chulsanbaatar*, its lateral wall is the anterior, crescentic margin of the anterior lamina, and its medial wall is the orbitosphenoid, sloping downwards and inwards. The fissure is thus a triangular-sectioned communication between the orbit and the front of the cavum. In the sectioned skull there is a foramen in the orbitosphenoid close to the upper edge of the taenia clino-orbitalis (figures 28 and 29). This leads from the cranial cavity downwards, forwards and outwards into the upper part of the cavum. If the optic chiasma were close to the anterior clinoid processes, as in modern mammals, the optic foramen would be found here, with the optic nerve joining the contents of the cavum to pass forwards into the orbit. But in all the specimens there is partial damage; the shape and size of other foramina in the orbitosphenoid are impossible to reconstruct. Therefore our identification of this as the optic foramen is extremely tentative.

#### Frontal bone

The frontal bone has its usual large exposure in the orbit with the orbital ridge very prominent in its posterior part. Because of damage to the ventral part in all specimens the orbitonasal recess is hardly discernible.

#### Nasal bone

There are five symmetrically arranged 'vascular foramina' (Simpson 1937) on the nasal, the medial being the largest (figure 20*a*).

#### Endocranial cast (figures 20*a*, 30 and 32)

A small part of the dorsal aspect of the endocranial cast, including the right olfactory bulb and the anterior part of the right cerebral hemisphere, is preserved in ZPAL MgM-I/82 (figure 18), and in ZPAL MgM-I/57 the posterior part of the endocranial cast is shown, badly damaged and laterally compressed. Most of the following description is based on the wax model (figure 30) of the endocranial cast.

The greatest width of the endocranial cast is across the paraflocculi, and the greatest depth is in the region of the medulla oblongata. The ventral extent of the medulla is uncertain because of the damage to the sectioned specimen. The cast differs from that of *Chulsanbaatar* (Kielan-Jaworowska 1983) in size and proportions. The olfactory bulbs, as preserved in the natural endocast of ZPAL MgM-I/82 (figure 18), are about 5 mm long, including the furrow that delimits them from the cerebral hemispheres. In the sectioned skull they were possibly only slightly longer; they are proportionately shorter than those of *Chulsanbaatar*. The transverse furrow in the posterior part of the dorsum of the olfactory bulbs, found in *Chulsanbaatar*, is absent, as is the single median fusiform structure between the posterior part of the bulbs and

the anterior part of the hemispheres. Seen from the side, the olfactory bulb is very tall at the rear and slopes off sharply towards the front, as in *Chulsanbaatar*. In the sectioned skull the bulbs appeared too short in the model (figure 30), probably because of the poor preservation of this part of the skull. In figures 20*a* and 32 a more probable length is drawn, based on ZPAL MgM-I/82. However, the nasal septum was well preserved, permitting a confident reconstruction of the ventral aspect of the bulbs, which are widely separated ventrally. The olfactory tracts could not be reconstructed.

The cerebral hemispheres broadened posteriorly to about the level of the postorbital foramen, behind which their postero-lateral margins converged on the central lobe of the cerebellum at angles of about 45°. In cross section they show a typical convex dorso-lateral part, with very slightly concave sides converging ventrally on a short horizontal ventral margin. The roughly similar cross section in *Chulsanbaatar* was tentatively interpreted (Kielan-Jaworowska 1983) as indicating an expanded, concave, lissencephalic neocortex dorsally and ventrally a less expanded palaeocortex. However, in neither genus is the rhinal fissure preserved, and only the line of change of curvature can be used as a guide. The region of the pyriform lobe appears moderately convex.

As in *Chulsanbaatar* and *Ptilodus* the midbrain is not exposed dorsally. The central lobe of the cerebellum is inserted somewhat less deeply between the cerebral hemispheres and is relatively shorter and wider. As is usual in multituberculates, there is no indication of cerebellar hemispheres. The subarcuate fossa cast differs from that of *Chulsanbaatar* in being spherical rather than oval, with a very large cuspule corresponding to the post-temporal recess ventrally on the cast, on its lateral and antero-lateral aspect. The sections clearly demonstrate the connection of this recess to post-temporal fossa in the rear and ascending canal in front (figures 21–23).

The cast of the pituitary fossa is not very clearly delineated from the rest of the endocranial cast, which narrows markedly here between the prominent casts of the semilunar fossae (figures 30 and 32). The casts of the semilunar fossae are relatively enormous, and are separated antero-medially from the rest of the cranial cavity by the taenia clino-orbitalis. Two nerves are directed from each, the anterior ramus of the mandibular nerve running ventro-laterally and the posterior running ventrally. If correctly reconstructed, the pons lay posterior to the emergence of the trigeminal nerve, as in *Chulsanbaatar* and in monotremes.

Anteriorly the semilunar casts merge with the cast of the front part of the cavum epiptericum, which communicates with the cranial cavity through the optic foramen. A structure, possibly a deep temporal nerve, runs dorsally from the anterior part of the semilunar ganglion and passes through the dorsal foramen of the anterior lamina of the petrosal.

The rhombencephalon is very deep and relatively very long, as in *Chulsanbaatar*, and protrudes strongly ventrally. Details of pons, corpus trapezoideum and pyramid cannot be discerned.

#### Casts of vascular canals

The course of sagittal, transverse and sigmoid sinuses is as in *Chulsanbaatar* (figure 20*a*). Placed antero-dorsally on the internal surface of the anterior lamina of the petrosal, the very deep groove for the prootic sinus leads directly to the prootic canal (figures 24–27). The tentorial sinus is recognizable as a distinct groove (figures 28 and 29) for a short distance along the internal part of the dorsal surface of the anterior lamina in the region in front of the semilunar fossa. The prootic canal bends slightly, convex anteriorly. In its ventral part it is entered laterally by the glenoprootic canal. This commences at the supraglenoid foramen and



runs horizontally to reach the prootic canal, and presumably carried the glenoprootic vein. As may be seen from the sections (figures 25 and 26) the walls of the glenoprootic canal are irregular, presumably reflecting the opening of numerous medullary spaces from the fine cancellous bone present in this region. After the junction with the glenoprootic canal, the prootic canal leaves the skull by two foramina, separated by the lateral flange. These are the tympanic foramen of the prootic canal opening into the facial sulcus and the smaller, more lateral, equivalent of the postglenoid foramen situated in the posterior part of the epitympanic recess.

The sections show the carotid canals entering the pituitary fossa from the side (figures 28 and 29). On the model of the endocranial cavity (figure 30), reconstructed in figures 20*a* and 32, the orbito-temporal vessels are clearly seen as a cast, corresponding to the groove on the internal aspect of the parietal. Further back they pass above the prootic sinus. They turn abruptly downwards and continue as the vessels of the ascending canal to reach the post-temporal recess in the subarcuate fossa.

#### *Comparisons*

A comparison of the skulls of Asian Taeniolabidoidea with the isolated petrosals from the Hell Creek Formation suggests that two types of braincase structure may be recognized. In all of the former the anterior lamina of the petrosal, directed dorsally or dorso-medially, is not seen in ventral aspect. The larger the size, the more the dorso-medial slope. Thus, although exact measurement is meaningless, the anterior lamina is more medially inclined in *Catopsalis catopsaloides* (figure 2) than it is in *Kamptobaatar kuczynskii* or *Chulsanbaatar vulgaris*. Still greater medial inclination of the anterior lamina is found in the isolated petrosal of ?*Catopsalis joyneri* (figure 1), which is larger than *Catopsalis catopsaloides*, and in the Palaeocene *Taeniolabis taoensis* (Granger & Simpson 1929), which by multituberculate standards is gigantic. We conclude that the antero-medial inclination of the anterior lamina of the petrosal may be related to a specialization of the jaw muscles in these large forms, in which the fourth premolars tend to be reduced and the main cutting action, probably gnawing, was done by the very enlarged, self-sharpening, incisors, a similar pattern to that of rodents.

The unidentified Hell Creek petrosals, belonging to a species of 35–45 mm in skull length, show a different structure. The anterior lamina is well seen from ventrally, since it is dorso-laterally, rather than dorso-medially, directed. Presumably the braincase in these forms was more expanded laterally, perhaps in association with less specialized jaw muscles. The taxon to which these distinctive petrosals belong cannot be identified with certainty. Should the suspicion be confirmed that they belong to the Ptilodontoidea (although there is to our knowledge no common ptilodontoid of appropriate size in the Hell Creek Formation), this would establish a difference in the build of the braincase between these and the Taeniolabidoidea, possibly reflecting the differences in musculature and dentition suggested above.

In addition to the differences discussed above, the genera studied here differ in other details of petrosal structure which reflect differences in vascular pattern and the course of the facial nerve trunk. The main difference concerns the post-temporal fossa, which is large in *Nemegtbaatar*, *Chulsanbaatar*, *Kamptobaatar* and *Sloanbaatar* but very small in *Catopsalis* and in an unidentified Late Cretaceous eucosmodontid figured here (figure 5). This difference is associated with the two different patterns of the ascending canal and its connections, discussed in detail later.

The unidentified Hell Creek petrosals (figures 8 and 9) differ from all other multituberculates

known to us in having the postero-lateral part of the facial sulcus developed, not in the form of an open groove (as in *Chulsanbaatar* and *Kamptobaatar*), or an open fossa (as in *Nemegtbaatar* and *Catopsalis*), but with a ventral floor completing a bony chamber. In consequence the facial nerve leaves the bone in these Hell Creek petrosals by a well-defined stylomastoid foramen, while in the other genera there is only a stylomastoid notch (by which the postero-lateral part of the facial sulcus ends near the boundary with the squamosal). This difference is further emphasized because the bone floors not only the postero-lateral part of the facial sulcus but also incorporates an extension into the chamber forward to the supraglenoid foramen. The tympanic foramen of the prootic canal opens into the antero-medial part of this chamber. Thus the transverse anterior part of the chamber corresponds to the glenoprootic canal of *Nemegtbaatar* and *Catopsalis*. The roughly parasagittal part of this chamber joining the supraglenoid foramen to the stylomastoid foramen corresponds to the interglenoid canal. Therefore the stylomastoid foramen has assimilated the function of the postglenoid foramen, which is separate in the other genera. Those other genera show no direct connection of the glenoid canal system to the stylomastoid notch, although this is visualized as transmitting the primary head vein, which becomes the stylomastoid vein, as well as the facial nerve. The unidentified Hell Creek petrosals have in effect lost the postglenoid foramen by incorporation within the chamber, leaving the stylomastoid foramen as the effective communication to the exterior.

In *Nemegtbaatar* (and possibly also in *Kamptobaatar* and *Chulsanbaatar*) the glenoprootic canal appears to lie more deeply within the prootic than in the unidentified Hell Creek petrosals. This is associated with a dorsal position of the supraglenoid foramen in *Nemegtbaatar*, where the glenoprootic vein has to cross the full thickness of the petrosal, while in the unidentified Hell Creek forms, because the supraglenoid foramen is more ventrally placed, the glenoproitic vein was also ventrally and superficially placed.

In *Catopsalis* yet another situation is found, related to allometric differences in skull structure. Because of the anterior position of the supraglenoid foramen the glenoproitic canal is very short, whereas the interglenoid canal is very long, extending along the whole ventral margin of the anterior lamina. The postglenoid foramen also communicates strongly and directly with the ascending canal. In the unidentified Hell Creek petrosals the stylomastoid foramen similarly communicates strongly with the ascending canal, emphasizing how it has taken on the functions of the postglenoid foramen. This suggests that there was a vascular connection here with arteries or veins in the stylomastoid or postglenoid region in these forms. No evidence for this is seen in *Nemegtbaatar* and its allies. *Catopsalis* differs from the unidentified Hell Creek petrosals in having a stylomastoid notch rather than a foramen, and it must be assumed that this, as in *Nemegtbaatar*, transmitted a stylomastoid vein as well as the facial nerve.

Another difference between the petrosals is the presence or absence of the canal for the ?maxillary artery, running from the anterior part of the facial sulcus to the foramen on the outer surface of the petrosal between and in front of the foramina ovale inferium and masticatorium. This canal is found in *Catopsalis* and the unidentified Hell Creek petrosals, but no trace can be found in the entire or sectioned skulls of *Nemegtbaatar*, or in *Chulsanbaatar*. However, it cannot be excluded that one of the five foramina (some of which may be due to distortion) described in *Kamptobaatar* (Kielan-Jaworowska 1971) may be for the maxillary artery.

The features discussed above demonstrate great individual variation at the generic level in petrosal structure, and especially in the associated vascular pattern. In the present state of

knowledge it is impossible to attribute characteristics of higher taxonomic rank to such features. There seems, indeed, to be some random admixture of characters among the genera studied. In *Catopsalis* and the Hell Creek petrosals, for example, the ascending canal enters the postglenoid foramen or its functional equivalent, and both types have a canal for the ?maxillary artery. On the other hand, *Catopsalis* resembles *Nemegtbaatar* in having an open postero-lateral part of the facial sulcus, with a stylomastoid notch distinct from the postglenoid foramen, and in the dorso-medial inclination of the anterior lamina, features not seen in the unidentified Hell Creek petrosals.

In *Chulsanbaatar* the ventral border of the anterior lamina protrudes strongly ventrally to form a lateral wall or ridge screening the epitympanic recess on its lateral side. A similar wall is present in *Kamptobaatar*, *Sloanbaatar*, *Nemegtbaatar* and possibly in other genera, but it is very thin and may easily be broken. We regard this wall as the analogue, but not the homologue, of the alisphenoid bulla of marsupials, and it may have played some role in the support of the tympanic bone.

Kielan-Jaworowska (1981) demonstrated that in the Late Cretaceous eutherian *Asioryctes* the tympanic bone was arranged obliquely with respect to the basicranium, parallel with the posterior part of the mandible, and argued that this orientation was primitive for mammals, reflecting the position in which it was 'released' from the therapsid jaw. It must be recognized that this 'release' took place very early in multituberculates, possibly during the Triassic, because the Kimmeridgian (Hahn 1969) and Purbeckian (Simpson 1928) multituberculate mandibles show no trace of the groove for accessory jaw bones. A rudimentary coronoid is present in the Kimmeridgian *Kuehneodon* (Hahn 1977), but this is the longest surviving of the accessory bones in the mammalian mandible, and its traces have been found even in Late Cretaceous eutherian mammals (Kielan-Jaworowska 1981).

It seems reasonable to presume that the angular (tympanic) when released from the mandible of the multituberculate ancestor was similarly arranged obliquely, parallel with the posterior part of the lower jaw. However, by the Late Cretaceous, and possibly much earlier, a more horizontal position may have been achieved. If the tympanic had a ring-shaped profile in multituberculates and lay horizontally, as in monotremes, the tympanic cavity must have been relatively small. It should be stressed, however, that accessory air-spaces existed, such as the condylar cavity and the cavity of the paroccipital process, comparable with the expanded mastoid cavity of the Palaeocene *Lambdopsalis* (Chow & Qi 1978; see also Kielan-Jaworowska & Sloan 1979). The existence of large air-sinuses in the middle ear of multituberculates may be compared with analogous adaptations in modern mammals (Lay 1972). There is no recognizable trace of an external auditory meatus in our material, suggesting that, as in monotremes, it may have bent away from the skull as it approached the tympanic cavity.

In all the Late Cretaceous multituberculates studied the internal auditory meatus has a structure typical of therian mammals, with two foramina for the auditory-vestibular nerve and one for the facial placed in a common pit. In this respect they differ from the Jurassic *Paulchoffatia* (Hahn 1969), in which the foramina, though placed close together, are not included in a common pit. In triconodonts, by contrast, both in *Morganucodon* (Kermack *et al.* 1981) and *Trioracodon* (Kermack 1963), the foramen for the facial nerve is placed well away from that for the auditory-vestibular, close to the semilunar fossa. It is interesting to note that the tritylodonts (e.g. *Oligokyphus* (Kühne 1956)) attained by the Liassic the more advanced condition of the common pit for the internal auditory meatus.

In Cretaceous multituberculates the internal carotid foramen is placed in the junction

between basisphenoid, petrosal, and probably the alisphenoid and pterygoid, with the carotid canal entering the pituitary fossa from laterally. However, in the Jurassic *Pseudobolodon* (Hahn 1981) the internal carotid foramen pierced the basisphenoid and the carotid canal entered the pituitary fossa directly from below as in *Morganucodon* (Kermack *et al.* 1981). Again, interestingly, in the tritylodonts (Kühne 1956; Kemp 1983) the carotid canal entered the pituitary fossa from laterally, as in therians.

These examples show an interesting parallel development of some anatomical features in mammals and tritylodonts. In some respects the tritylodonts achieved advances in the Liassic that multituberculates and therians are known to have achieved only in the Late Cretaceous.

## THE VASCULAR SYSTEM

### *Description*

#### (a) *General comments*

There is great variation in terminology employed for the veins of mammals, and for vertebrates in general (Grosser 1907; Shindo 1915; O'Donoghue 1920; Padget 1957; H. Butler 1957, 1967). Where possible we employ here the nomenclature of Padget (1957).

For descriptive purposes we employ the term 'intracranial' for vessels that are seen in endocranial casts or in grooves on the endocranial surface; 'intramural' for vessels in canals within the bones of the skull; and 'paracranial' for vessels that are extracranial but close enough to the outer surface of the skull to leave a marking. We also divide the vessels into arteries, veins of the dural venous sinus system, where these are readily identified, and the orbito-temporal vessels, whose nature we find more problematical, though we suggest a primary arterial component. Undoubted arteries, however, are represented only as disconnected markings on the ventral aspect of the cranium, and their interpretation is left until the reconstruction.

#### (b) *Veins of the dural sinus system*

(i) *Superior sagittal sinus.* The superior sagittal sinus lies beneath the sagittal suture, as in other mammals and other vertebrates. No distinct hollow impression is present on the endocranial aspect of the bones. Although a distinct groove is present on the endocranial cast of *Chulsanbaatar*, probably representing adjacent meningeal attachments, in no specimen is a filled cast of the venous sinus visible. It is considered reasonable, however, to include this vessel in reconstructions because of its known incidence in other animals and because of the pattern of the transverse sinuses and their distributaries. It is not possible to say whether both superior and inferior sagittal sinuses were present, as in modern mammals with a deep falx cerebri. No tributaries are discernible, which is to be expected if, as in modern mammals, the tributaries were cerebral veins passing across the subarachnoid space rather than lying between dura mater and the cranial vault.

(ii) *Transverse sinus.* Imprints of the line of the transverse sinuses and their surrounding meninges are visible as grooves on the endocranial cast of *Chulsanbaatar*, and appropriately placed projections of the parietal are present on the sectioned skull. In the sectioned skull of *Nemegtbaatar* much shallower grooves are preserved, hardly discernible on the damaged parietal,

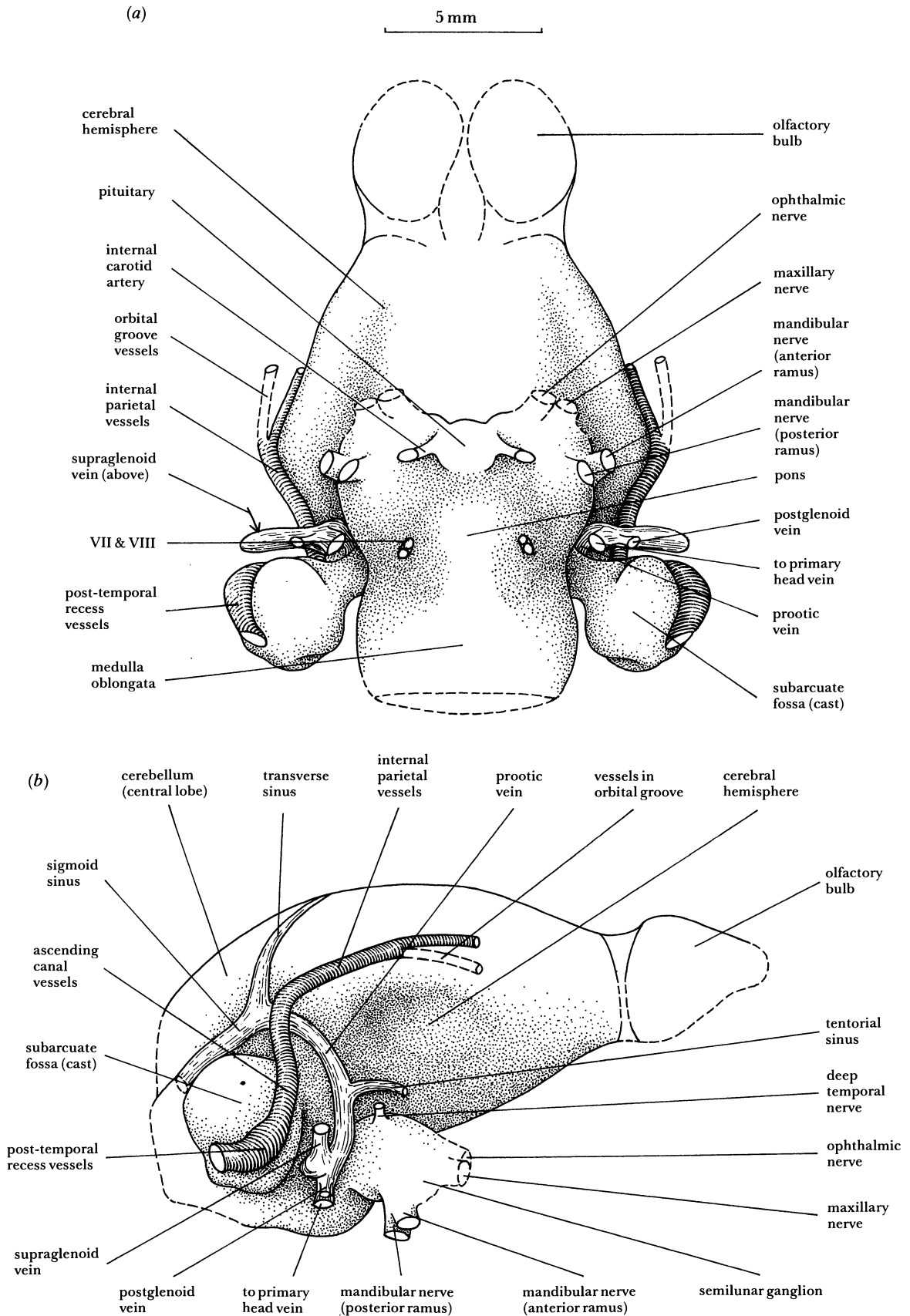


FIGURE 32. *Nemegtbaatar gobiensis*. Reconstructions of endocranium and vascular system based on sections. (a) Ventral view. (b) Lateral view.

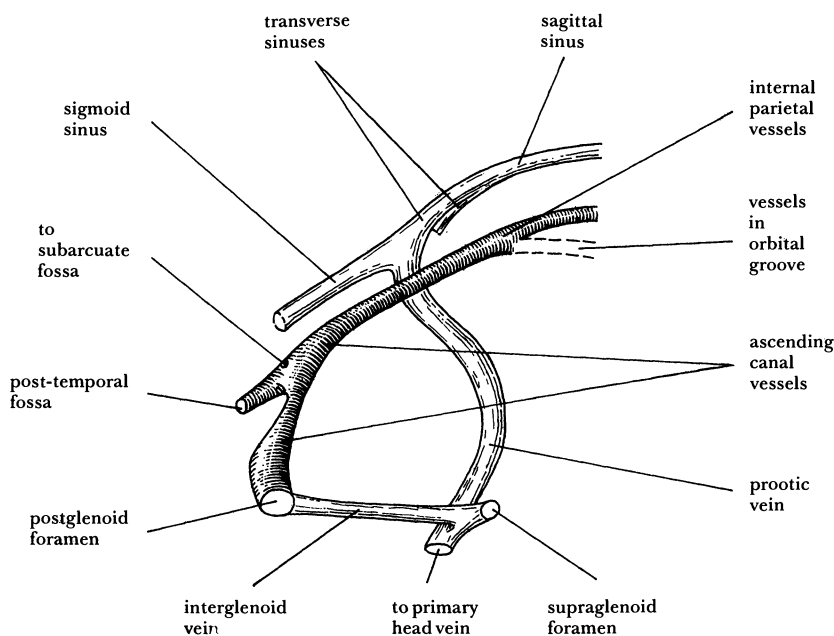


FIGURE 33. *Catopsalis*. Reconstruction of vascular system based mainly on isolated petrosal of ?*Catopsalis joyneri* and partly on skulls of *C. catopsaloides*. Not to scale.

and in a poorly preserved endocranial cast (ZPAL MgM-I/57) the markings are also much shallower than in *Chulsanbaatar*. They lie between the postero-medial border of the cerebral hemisphere and the central lobe of the cerebellum on each side (figures 7, 16, 20a and 32). Dorsally the sinuses meet at the sagittal sinus. Each diverges posteriorly, curving progressively more ventrally, parallel with the endocranial surface, to reach the posterior corner of the central lobe of the cerebellum close to the suture between the anterior lamina of the petrosal and the parietal, where each branches. The posteriorly directed branch is the upper segment of the sigmoid sinus. The other branch is the prootic sinus.

(iii) *Sigmoid sinus*. Casts of the sigmoid sinus are well preserved on several specimens of *Chulsanbaatar*, especially on the right of ZPAL MgM-I/88 (Kielan-Jaworowska 1983, figure 1d), where it is seen to lie in a groove medial to the crus commune. This region is not preserved in the sectioned skull.

The upper segment of the sinus runs backwards and slightly downwards towards the region of the foramen magnum. No specimen shows any more ventral segment of the sinus able to make a substantial connection with the region of the jugular foramen.

(iv) *Prootic vein*. The prootic vein is defined here as commencing intracranially at the bifurcation of the transverse sinus into sigmoid and prootic sinus. From this point it runs forwards and, by virtue of its marked curvature, rapidly more vertically, above the subarcuate fossa and in a deep groove on the endocranial surface of the petrosal, to enter the foramen of the prootic canal. This is well seen on the endocranial casts of *Chulsanbaatar*, in the isolated petrosal of ?*Catopsalis joyneri* and on the sectioned skull of *Nemegtbaatar*, where a deepening notch is incised into the anterior lamina of the petrosal, leading to the prootic canal.

On the endocranial cast of *Chulsanbaatar* ZPAL MgM-I/88 (figure 7) the vertical part of the

vein is joined by a vein passing dorsal to the semilunar fossa, here identified with the tentorial sinus of Padget (1957), the equivalent of the posterior rhinencephalic vein of Hofmann (1901). In *Nemegtbaatar* a groove for this sinus is seen anteriorly (figures 28 and 29) but its junction with the prootic sinus is indeterminate.

At the ventral end of the prootic canal the prootic vein is joined from laterally at an angle of about  $95^\circ$  by the glenoprootic canal which is entered dorsally at its lateral end by the supraglenoid foramen of Simpson (1937). Two foramina open ventrally from this complex of canals. Outside the lateral flange, the more lateral opening is equated with the very variably positioned postglenoid foramen of other multituberculates (in this case in the posterior part of the epitympanic recess). The more medial opening, medial to the lateral flange, is the tympanic foramen of the prootic canal, where this joins the facial sulcus.

In *Nemegtbaatar* the tympanic foramen is much larger than the postglenoid foramen. Simpson (1937) regarded the postglenoid foramen as 'the principal external opening of the prootic canal' in *Ptilodus*. There may be a generic difference here, as indeed may be expected from the very considerable variations in size of venous apertures found in modern mammals.

In *Catopsalis* the main ventral opening of the prootic canal is into the facial sulcus but there is here also a connection with the supraglenoid foramen, whose tributary deep temporal veins groove the external surface of the anterior lamina. In the unidentified Hell Creek Formation petrosals the prootic sinus opens into the most medial part of the chamber (figure 8), behind the epitympanic recess. In this form of petrosal, the junction of the prootic sinus and primary head vein was relatively far back in the facial sulcus, at the level of the fenestra vestibuli, and the supraglenoid veins joined the major veins within the chamber.

(v) *Primary head vein.* In *Catopsalis*, in the unidentified Hell Creek petrosals and in the sectioned skull of *Nemegtbaatar* there is a substantial post-trigeminal canal connecting the facial sulcus and the cavum epiptericum. Considering its size, and following the accounts of Padget (1957) and H. Butler (1967) of the structure of the early embryo, we suppose that a large vein lay here, representing the post-trigeminal and vena capitis lateralis (lateral head vein) segments of the primary head vein.

Just behind the level of the fenestra vestibuli in front of the paroccipital process the lateral head vein turned more laterally into the postero-lateral part of the facial sulcus. In the monotreme, marsupial and placental embryos available to us showing this portion of the lateral head vein, the facial nerve crosses its ventral aspect to emerge anterior to it; we therefore reconstruct a similar arrangement in multituberculates, with the facial nerve leaving the tympanic cavity through the stylomastoid notch and the vena capitis lateralis, now called the stylomastoid vein, leaving posterior to it.

(vi) *Petrosal sinus.* No trace exists in the available specimens of either an inferior or a superior petrosal sinus.

(c) *Orbito-temporal vessels*

In numerous skulls of Asian multituberculates there is a distinct shallow orbital groove, dorsally placed in the orbit, first on the orbitosphenoid and then on the parietal. This commences at the ethmoid foramen and runs back just below the part of the cranial roof that

overhangs the orbit. It disappears at the postorbital foramen, which is visible in many skulls and present in both sectioned skulls, beneath the postorbital process.

In *Chulsanbaatar*, where the postorbital process is relatively broad, the foramen leads into a canal that enters the cranial cavity by running through its ventral part. The endocranial course backwards from this point may be traced on endocranial casts of *Chulsanbaatar*, in both ZPAL MgM-I/88 and ZPAL MgM-I/89 (figures 7 and 10). In the latter it is seen running posteriorly and then postero-ventrally towards a position corresponding to that of the postorbital process, and then above the prootic sinus in front of the paraflocculus and longitudinally above the anterior semicircular canal.

In the section series of *Nemegtbaatar* (figures 23–28) this part is marked by the internal parietal groove of semicircular profile. At the rear it starts from the suture between the parietal and anterior lamina of the petrosal, just above the thickened ridge of the lamina. It lies about 0.4 mm dorso-lateral to the opening of the prootic canal, and behind this it approaches the groove for the prootic sinus more closely, but no clear evidence is provided for a major communication between the prootic sinus and the orbito-temporal vessels marking the bone on which they lie. Anteriorly the internal parietal groove rises more dorsally onto the parietal. In this course it passes immediately medial to the postorbital process. It then disappears as a distinct marking further forwards where the parietal and then the frontal become thicker.

Thus there is evidence that anterior to the postorbital foramen a paracranial and an intracranial vessel lay in parallel, the former joining the latter through the foramen. Further back the combined vessels lay intracranially and passed to the vicinity of the prootic vein.

On both sides of the sectioned skull of *Nemegtbaatar* (figures 21 and 22) it is possible to trace the course of a vascular canal from the post-temporal fossa (which was large) into the subarcuate fossa, and forward through this along the post-temporal recess. On the endocranial cast of *Chulsanbaatar* ZPAL MgM-I/88 (figure 7) this is marked by a small cuspule on the anteroventral aspect of the subarcuate fossa cast. The horizontally placed groove in the sectioned skull reaches the antero-lateral wall of the fossa and then turns dorsally as an ascending canal enlarging the suture between the squamosal laterally and the anterior lamina of the petrosal medially. This opens close to, and slightly lateral to, the opening of the prootic canal and appears to communicate directly with the internal parietal groove (figures 23 and 24).

In the sectioned series, on both sides, the bone of the squamosal covering the ascending canal is very thin and defective in the mid-part of the canal. However, in no well-preserved skull in the ZPAL collection does an external foramen appear in this position, so that it may confidently be asserted that the canal was normally intramural in eucosmodontid multituberculates.

In *Catopsalis* (figures 1 and 4) the evidence is of a smaller post-temporal fossa, and only a short, minute, vessel appears to have entered the subarcuate fossa. The ascending canal vessel extends up the posterior margin of the anterior lamina of the petrosal, within its suture with the squamosal, and then along the dorsal margin of the anterior lamina to open directly into the lateral wall of the groove of the prootic sinus. Below the junction between the post-temporal canal and the ascending canal the groove continues to the postglenoid foramen where it joins the interglenoid canal.

In the unidentified Hell Creek petrosals, damage has removed the dorsal part of the ascending canal system. However, the stylomastoid foramen shows a substantial groove leading



postero-dorsally from it, very similar in appearance to the ascending canal of ?*Catopsalis* leading from the postglenoid foramen. We therefore assume that the rest of the ascending canal was present in the unidentified Hell Creek forms, although we can know nothing of its connections either within the skull or with the post-temporal canal.

*Reconstruction: arteries*

(a) *Internal carotid artery*

From the sectioned skull of *Nemegtbaatar* it is clear that in this form, and therefore probably in all Taeniolabidoidea, the internal carotid artery ran from ventro-lateral to dorso-medial in a short carotid canal to enter the pituitary fossa. The external opening of this lies more laterally than has been indicated in previous accounts. Thus in *Kamptobaatar* it was tentatively and incorrectly interpreted as the ventral opening of the cavum epiptericum (Kielan-Jaworowska 1971). In *Nemegtbaatar* the foramen lies clearly within the junction of basisphenoid with petrosal, and probably that of alisphenoid with pterygoid. Simpson (1937) described the foramen as piercing the basisphenoid in *Ptilodus*, but the sutures in his specimen were not preserved, and since this foramen lies quite laterally it is possible that it was as in *Nemegtbaatar*. Hahn (1981) described the internal carotid foramen as piercing the basisphenoid in the plagioulacoid *Pseudobolodon*.

(b) *Other arteries*

(i) *General*. The variability of the mammalian cephalic arterial tree is well known (Tandler 1899, 1901; Bugge 1972). In the present study we see, only on occasions, isolated pieces of evidence for the tree, not always present together, and in some but not all species.

(ii) *Stapedial artery*. A distinct groove in ?*Catopsalis joyneri* can reasonably only be interpreted as being for a stapedial artery running from the internal carotid artery postero-laterally over the promontorium to the fenestra vestibuli. It may be conjectured that after crossing the fenestra, the artery, as in many modern mammals, turned forward in the medial part of the facial sulcus, giving rise to a large maxillary branch, among others.

(iii) *Maxillary artery*. In both ?*Catopsalis joyneri* and the unidentified Hell Creek petrosals the canal ascribed to this artery passes medial to the emerging mandibular nerve rami and then curves to open on the outer surface of the anterior lamina. This is very similar to the course of the artery of the 'alisphenoid canal' in *Ornithorhynchus* (Watson 1915), and of the infraorbital or maxillary artery (whether or not enclosed in a bony alisphenoid canal, or a branch of the stapedial artery) of many modern mammals. It is of interest that in *Pseudobolodon*, Hahn (1981) described a canal running beneath the cavum epiptericum from the antero-medial margin of the foramen ovale inferium to the sphenorbital fissure. It is tempting to consider that this canal, though longer, might correspond to our canal of the maxillary artery.

(iv) *Vidian artery*. In many cases a groove is associated with the 'hiatus Fallopii', lying variably in front of, behind, or on both aspects of it. This may well represent vessels running forward to join and run with the superficial petrosal branch of the facial nerve, passing close to the internal carotid artery, and then on the lateral wall of the choana. Such vessels may

conveniently be called 'Vidian' since the neurovascular bundle approximates functionally to that of the Vidian (pterygoid) canal of modern mammals. The appearance of the grooves in *Catopsalis joyneri* and the unidentified Hell Creek petrosals suggests that the 'Vidian' artery may have branched from the stapedia artery on the promontorium, but because the internal carotid artery is related to the groove anteriorly the matter must be regarded as uncertain.

(v) *Meningeal branch of 'Vidian' artery.* The 'hiatus Fallopii', either a notch or a foramen, may be regarded quite reasonably as a nervous passage, with the superficial petrosal branch of the facial nerve leaving the semilunar fossa through it. However, it is always relatively large, and in the sectioned series of *Nemegtbaatar* there is an elongated notch opposite it in the anterior margin of the post-trigeminal canal, suggesting a route for meningeal vessels. We therefore tentatively suggest that such vessels may have been present in all animals possessing a 'hiatus Fallopii'. In modern mammals meningeal branches in this region may either be branches of the stapedia or external carotid vascular tree, or of that of the internal carotid. This may be relevant to the question of the origin of the 'Vidian' artery mentioned above.

*Reconstruction: the dural sinus system*

The system including sagittal, transverse, sigmoid and prootic sinuses, clearly present in multituberculates, (figures 7, 20a, 32 and 33) is found not only in them but also in *Morganucodon* (Kermack *et al.* 1981), *Ornithorhynchus* (Hochstetter 1896), *Didelphis* (Toeplitz 1920) and in embryos and adults of numerous placental mammals (Shindo 1915; Padget 1957, H. Butler 1967). In the multituberculates studied here the course of these vessels has been followed in detail in the sectioned skull of *Nemegtbaatar* and on the natural endocranial casts of *Chulsanbaatar*. The homology of these major venous dural sinuses with their homonyms in modern mammals seems clear. In modern mammals the transverse sinus joins the sigmoid sinus and this frequently (but by no means universally) drains to the internal jugular vein through the jugular foramen; this is the major venous pathway in man. The work of Padget (1957) and H. Butler (1957, 1967) shows that in modern mammals alternative major pathways of drainage are often found. The prootic sinus drains to the lateral head vein and then to the internal jugular vein in monotremes (and the embryos of other mammals). In later stages of the latter, various foramina in the supraglenoid, postglenoid, temporal and mastoid regions connect the prootic sinus with both internal and external jugular systems. The similarity of this system to that found in multituberculates will be discussed below.

The work of the above authors also shows that in many mammals only the upper segment of the sigmoid sinus becomes large, and from this there can be a substantial venous drainage through the foramen magnum to the vertebral and occipital veins. In *Nemegtbaatar* and *Chulsanbaatar* evidence for the upper part only of the sigmoid sinus has been found, and it is quite probable that drainage was from this through the foramen magnum, rather than through a hypothetical ventral segment, draining through the jugular foramen.

In *Chulsanbaatar* there is clear evidence for a vessel of considerable size extending above the trigeminal ganglion and joining the prootic vein. We tentatively equate this vessel with the tentorial sinus of Padget (1957), equivalent to the posterior rhinencephalic vein of Hofman (1901), because this is the only vein of considerable size found in this region in modern mammals. Significantly, the position of this vessel is shown by Padget (1957) to be very variable both during development and in adults, and this is consistent with the lack of a clear marking

of the junction in *Nemegtbaatar* despite the more anterior part of the tentorial sinus being clearly marked.

In the multituberculates studied here the prootic vein is in essence vertical, with a smooth-walled canal. It is joined by the glenoprootic vein (whose canal has irregular walls in the sectioned skulls, suggesting a reason for the more variable pattern of its tributaries, which were deep temporal veins from the posterior part of the temporal fossa, entering through the supraglenoid foramen). Two ventral 'exit' foramina were normally available for blood in the prootic and glenoprootic veins: the postglenoid foramen, and the tympanic foramen of the prootic canal opening into the facial sulcus. There is some similarity here with developmental stages of modern mammals (H. Butler 1967), and, if this comparison is valid, it is possible that the connection through the postglenoid foramen was with the external jugular system, while the 'lateral head vein' (perhaps better called, in terms of developmental morphology, the lateral segment of the primary head vein) was the vessel that was joined at the tympanic foramen of the prootic canal.

In early developmental stages of monotremes and modern therians the prootic sinus is a small tributary of the primary head vein at the junction of its post-trigeminal and lateral segments, and the principal flow of blood is from ophthalmic veins, via the medial segment of the primary head vein (cavernous sinus) to the more caudal segments (in the cranio-quadrate passage (Goodrich 1930)). The existence of a large foramen joining the semilunar fossa with the facial sulcus suggests that the post-trigeminal segment of the primary head vein may have been retained in adult multituberculates, running between cavum epiptericum and the sulcus. This is not so in any modern mammals, including monotremes, known to us.

The glenoprootic sinus is a striking feature of the multituberculates studied, and may be compared with the much shorter and often less horizontally inclined veins by which the prootic sinus of modern mammals, such as opossum, phalanger, ferret and hedgehog, turns laterally in front of the otic capsule to the more externally situated postglenoid foramen. The greater relative length of the glenoprootic channel in the multituberculate reflects the considerable out-turning of the rapidly widening braincase in this region. In modern mammals the braincase does not narrow so sharply in the temporal fossa, so that the prootic sinus emerges at much the same distance from the mid-line as the glenoid foramina.

From the present studies, and from previous descriptions of entire skulls (Simpson 1937; Kielan-Jaworowska 1971) it appears that the basic pattern described above was present not only in the Taeniolabidoidea but also in the Ptilodontoidea. However, there exists very great variation in the distribution of the exit foramina of the prootic vein and in the relative distances between them, possibly due at least in part to the different shapes and proportions of the braincase discussed in the osteology section.

The petrosal of ?*Catopsalis joyneri* and its foramina appear at first sight very different from those of *Nemegtbaatar* and *Chulsanbaatar*. However, there are also the very different proportions in the build of this region and the very different inclinations of the anterior lamina of the petrosal to be considered. The prootic vein in *Catopsalis*, as in *Nemegtbaatar*, leaves the skull through the tympanic foramen into the facial sulcus. Additionally, however, the prootic canal connects with the supraglenoid foramen, which is also connected to a probably large postglenoid foramen at the suture with the squamosal, at the postero-ventral corner of the anterior lamina. The interglenoid canal running through the anterior lamina to unite them would then correspond to that of other forms, though much longer and more horizontal. In

this interpretation the general pattern of venous drainage of homologous regions of the cranium would be very similar, despite the apparent differences in form. In each pattern the prootic vein drains into both the facial sulcus and the postglenoid foramen. In each the post-trigeminal segment of the primary head vein runs from semilunar fossa to facial sulcus. In each, deep temporal veins drain into the prootic vein through the supraglenoid foramen. The apparent difference between the two forms in respect of the course of the vessels of the ascending canal system may also be reconciled, as will be discussed below.

The unidentified Hell Creek petrosals described in this paper also appear at first sight to differ from the pattern of *Nemegtbaatar* and *Chulsanbaatar*. Here again this may be a matter of proportion, and of the more superficial position of the space housing the glenoprootic vein, the ventral wall of which appears in the Hell Creek forms as a ridge on the ventral surface of the petrosal. In these petrosals the opening of the prootic vein into the facial sulcus lies near the junction with the glenoprootic vein, and the distance between this junction and the postglenoid foramen is proportionately larger than in *Nemegtbaatar*. As in all other genera there is a large canal between the semilunar fossa and the facial sulcus, accommodating the post-trigeminal vein.

*Reconstruction: orbito-temporal vessels*

Evidence is presented in detail in the previous section, from the serially sectioned skulls, from endocranial casts and from the extracranial aspect of conventionally prepared skulls, for the existence of vessels whose course was part endocranial, part intramural and part paracranial, on a line from post-temporal fossa to orbit. It would be reasonable to suppose that vessels on this line, which includes the post-temporal canal, the ascending canal, the internal parietal groove and the orbito-temporal grooves, did not make a major communication with the dural sinus system, because their markings pass close to, but nevertheless distinctly lateral to, the groove for the prootic vein. Behind this point different courses are apparent when comparing *Catopsalis*, on the one hand, with *Nemegtbaatar* and *Chulsanbaatar* on the other. In analysing this it seems simplest to assume that this line was occupied by continuous vessels, extending from post-temporal fossa to orbit. Two problems then need consideration: the nature of the vessels and the occurrence in some forms of an intracranial course through the subarcuate fossa, apparently unique among mammals.

In the present paper, for reasons discussed in detail in the next section, we suggest that the primary occupants of this vascular line in multituberculates were arteries (though probably in company with venae comitantes). In *Nemegtbaatar* and *Chulsanbaatar* an artery entered the subarcuate fossa from the post-temporal fossa, lying in the post-temporal recess and then in the ascending canal, entering the main cranial cavity just above and lateral to the prootic vein (figures 7, 20*a* and 32). It continued in the internal parietal groove to the postorbital foramen, where it bifurcated, one branch continuing forward intracranially, the other entering the orbit and passing in the orbital groove to the ethmoid foramen through which it entered the nasal cavity, as well as presumably supplying orbital branches. It is reasonable to suppose that as they crossed the prootic vein, any venae comitantes may have communicated with the dural sinus system, but not sufficiently strongly to merge the markings of the two systems.

In *Catopsalis* (figure 33) and possibly in other genera with a small post-temporal fossa, only a relatively small vessel can have passed between fossa and ascending canal, the larger channel

from the latter being directed to the postglenoid or stylomastoid foramina. The ascending canal vessel in these forms did not pass through the subarcuate fossa, only a tiny branch of the post-temporal canal communicating with the fossa. On the basis of the skulls of *C. catopsaloides* it may be concluded that the anterior part of the orbito-temporal system did not differ essentially from those of *Nemegtbaatar* and *Chulsanbaatar*. However, one should perhaps think of occipital vessels in the latter two, and vessels in the stylomastoid or postglenoid regions in *Catopsalis*, as being the principal caudal connection.

Fenestration of the subarcuate fossa is rare in modern mammals, but we have found it in embryos of some bats and elephant-shrews. Through such fenestrae the dural sinuses, fed by cerebellar veins, pass to join paracranial veins associated with the mastoid emissary system. It seems reasonable to regard the tiny communication between the post-temporal canal and subarcuate fossa seen in *Catopsalis* as being quite similar, carrying either a small emissary vein or a minute meningeal artery branching from the main vascular line, which in this case remained intramural.

If fenestration occurs, it may be reasonable to homologize apparently paracranial or intramural vessels with endocranial vessels. Consider a vessel lying lateral to the cartilage of the developing petrosal. At a later stage the squamosal ossifies in membrane external to it. The vessel, previously paracranial, has thus become intramural. If later the petrosal does not ossify, but rather becomes fenestrated so that the cartilage internal to the vessel disappears, then the vessel will now appear to be endocranial, despite its not having migrated through any tissue plane during this morphogenetic change.

We suppose that in the development of *Nemegtbaatar* and *Chulsanbaatar* this process occurred, bringing the post-temporal canal vessel from an intramural to an apparently endocranial position. Thus the vessels of *Catopsalis*, on the one hand, and of *Nemegtbaatar* and *Chulsanbaatar*, on the other, could be homologous. The apparently unique intracranial course of a major vessel in the latter also becomes explicable in a manner that can be related to processes seen in modern mammals.

#### *General comparison*

As illustrated by the previous section the interpretation of the grooves and channels for some arteries and for veins of the dural sinus system is obvious in multituberculates. However, the orbito-temporal system poses difficulties, which will be discussed here.

Parker (1885) described the 'sinus canal' in about the same place as our postorbital and internal parietal vessels, in embryonic insectivores, and Watson (1911) equated it with the 'sinus canal' of cynodonts. Kermack *et al.* (1981) discussed this question, and stated (p. 90):

'Parker describes a sinus canal in a number of insectivores but this can have nothing whatsoever to do with the "sinus canal" of Watson. Parker's canal is a groove on the inside of the cranial wall, while Watson's "sinus canal" is a groove on the external surface of the bones. More important, the vein of Watson's "sinus canal" – our canal of vena temporo-orbitales – connects with the vena capitis lateralis while the sinus canal of Parker lodges the lateral sinus (Parker, 1885). This lateral sinus drains into the external jugular vein via the postglenoid foramen (Butler, 1948). The condition in which the external jugular vein becomes the main drainage path of the cranium is a specialization found in many mammals (Shindo, 1915). Watson (1911) was here incorrect in his homology.'

P. Butler (1948) followed Parker (1885) in calling the problematic sinus the 'lateral cerebral sinus', a term not recommended here (see Glossary). Of this vessel, P. Butler (1948, p. 457) stated:

'...[it] is large and lies in a groove on the inner surface of the side of the skull, re-emerging into the orbit through one of the two ethmoid foramina situated near the upper border of the orbitosphenoid. This vein is accompanied by an artery which enters the orbit usually by a separate foramen near to those which transmit the branches of the vein.'

To ascertain which vessel in modern insectivores might be equated with the orbito-temporal system of multituberculates we examined the anatomy of developmental series of various mammals, including insectivores (*Erinaceus*, *Sorex*, *Talpa* and *Potamogale*) and macroscelidids (*Elephantulus* and *Petrodromus*) in the collection of the Department of Anatomy, University College, Cardiff. In all cases the specimens included examples near to birth, comparable with those in which Parker (1885) originally described the 'lateral sinus'. In all cases the supraorbital ramus of the stapedia artery is present as a large vessel along the course attributed to the 'sinus canal'. It is accompanied by small veins, which join the postglenoid system posteriorly. Anteriorly the small veins with the artery are joined by large diploic veins from the marrow of the frontal and orbitosphenoid, often with several openings into the orbit. We suggest, contrary to Parker (1885) that it is the artery that is the constant feature of the 'sinus canal' of insectivores. In the absence of this artery we have found no significant continuous vein in this position in any of our specimens of modern mammals.

The intracranial part of this artery in foetal mammals lies just below the cartilage of the taenia marginalis. In insectivores it is a branch of the stapedia artery, passing through a foramen in the roof of the tympanic cavity. It supplies the orbital and nasal region anteriorly. But it is not always a branch of the stapedia artery in mammals. Thus in man the equivalent vessel is a branch of the middle meningeal branch of the maxillary (external carotid) artery, through its connection with the recurrent meningeal branch of the ophthalmic artery.

In *Tachyglossus* the equivalent vessel is the arteria diploetica magna (Kuhn 1971), a branch of the occipital branch of the external carotid artery which, with venae comitantes, runs into the post-temporal fossa, enters the cranial cavity above the petrosal, runs forward over parietal in a groove or canal, and enters the orbit through a foramen in the orbitosphenoid near to the exit foramina of a number of diploic veins. The artery supplies the orbit and also the nasal cavity through the ethmoidal foramina. The course described has striking similarities to that of the orbito-temporal vessels of multituberculates. We are therefore strongly inclined to base our interpretation of the orbito-temporal vascular system of multituberculates on a pattern like that seen in *Tachyglossus*. The principal difference is that in monotremes the post-temporal canal is external to the cranial cavity and consequently the arteria diploetica magna enters the cranial cavity more anteriorly in *Tachyglossus* than in multituberculates, and it does not pass through the subarcuate fossa as in some, but not all, multituberculates.

There is less similarity to the insectivore pattern, where it is the superior ramus of the stapedia artery, entering the cranial cavity anterior to the prootic vein, which then turns forward inside the cranial wall to give vessels that might correspond with the internal parietal and orbital grooves of multituberculates. There is no clear evidence for such a branch of the stapedia artery in multituberculates (though its presence cannot be excluded). As demonstrated by Bugge (1972, 1974), the arterial system is extremely variable in mammals, especially with

respect to anastomoses between principal arteries (i.e. common, internal and external carotids) and the distributaries supplying particular regions. In this connection, bearing in mind that multituberculates probably branched from the line leading to modern insectivores by the Early Jurassic (or the Late Triassic), such a dissimilarity is probably not important. Any detailed similarity to *Tachyglossus* may be equally insignificant taxonomically, since in *Ornithorhynchus* (personal observations) the equivalent regions of the head are supplied by a stylomastoid branch of the external carotid artery (often loosely called 'stapedial'). If the taxonomic use of such similarities were valid, then *Nemegtbaatar* would be regarded as *Tachyglossus*-like, with a principal connection with the occipital artery, while the unidentified Hell Creek petrosals would be *Ornithorhynchus*-like, with the principal connection with the stylomastoid artery. We would regard such ideas as very misleading. It is better simply to accept that extraordinary variability is possible here in mammals. Thus while recent mammals give strong indications of the arterial nature of this system, we do not regard the system as giving precise taxonomic information about the affinities of multituberculates.

We therefore recognize three reasons for regarding the orbito-temporal system of multituberculates as being principally arterial in its morphological significance. The first and simplest is the conspicuous similarity to the occipital artery and arteria diploetica magna of *Tachyglossus*. The second is that in many eutherians, if a vessel is present in a corresponding position to the anterior part of the system, it is most consistently an artery. The third reason is that in the modern mammals studied here such arteries and their venae comitantes pass beside, rather than join directly, the grooves or other impressions for dural sinuses, in a very similar way to that in which the multituberculate orbito-temporal system passes just lateral to the prootic vein. In modern mammals there may be minor venous interconnections between the two systems, but usually not sufficient to merge the markings.

In the light of this interpretation of the orbito-temporal system of multituberculates it is relevant to consider the vascular system of some therapsids and other non-therian mammals. Since the work of Watson (1911) it has been generally accepted by therapsid specialists that the 'sinus canal' primarily carried a vein. This was based on the comparison with Parker's (1885) account of a venous 'sinus canal', which we have now rejected in favour of a primary association with an artery.

The only non-therian fossil mammal in which the cranial vascular system has been reconstructed until now is *Morganucodon* (Kermack *et al.* 1981). The authors had at their disposal one entire skull and numerous isolated bones. Their reconstruction was based mostly on the interpretation of vascular grooves on isolated bones. They suggested a dual system of venous drainage in the posterior part of the cranial cavity, comparable with the dural sinus system and orbito-temporal system recognized by us in multituberculates (with the difference that we regard the orbito-temporal system as arterial). They argued that the 'sinus canal' of insectivores cannot be equated with that of therapsids since the former is intracranial and the latter extracranial. However, they themselves demonstrated that in *Morganucodon* the sinus canal (their vena temporo-orbitalis) becomes partly intracranial by being overlapped as it lies within a suture. Such a finding illustrates how homologous vessels may lie variably in an intracranial or an extracranial position.

The dural sinus system in *Morganucodon* seems to have been generally similar in pattern to that of multituberculates. There are two differences. The first is the apparent lack of the tentorial sinus in *Morganucodon*. This sinus is present in *Chulsanbaatar*, seen on endocranial casts.

It is present, though less completely marked (seen only on sections well in front of the prootic canal) in the sectioned skull of *Nemegtbaatar*. Its traces are difficult to identify on isolated petrosals or in the intact skull. The tentorial sinus is very variable in position in modern mammals (Padget 1957). Thus it cannot be excluded that *Morganucodon* had a tentorial sinus that left no trace. The second difference concerns the prootic vein. In *Morganucodon* the vein transmitted by the prootic canal (called by Kermack *et al.* the middle cerebral vein) opened by a single foramen into the facial sulcus (their lateral trough). In multituberculates the prootic vein left the skull by two foramina, the tympanic foramen into the facial sulcus and the postglenoid foramen (by way of the glenoprootic vein). The glenoprootic vein is not known to exist in *Morganucodon*.

The orbito-temporal vessels show important differences. In *Morganucodon*, interpreting grooves on the margins of the anterior lamina, the squamosal and the parietal, Kermack *et al.* (1981, figure 102) reconstructed the orbito-temporal vein as lying intracranially, within the suture, and leaving the cranial cavity at the posterior margin of the anterior lamina. They also reconstructed the vein of the post-temporal canal, entering a short canal from a relatively large post-temporal fossa. This canal in *Morganucodon* lies within the suture between squamosal and petrosal and is separated only by a very thin layer of bone from the subarcuate fossa. As in cynodonts and tritylodonts the post-temporal canal opens anteriorly, external to the braincase, in the suture between the squamosal and the petrosal. According to the reconstruction of Kermack *et al.* (1981) the vein it transmitted drained forwards to join the orbito-temporal vein and both, united, drained into the lateral head vein.

The direction of flow thus reconstructed above was hypothetical, based on similar reconstructions of flow in cynodonts and tritylodonts proposed by most previous authors (see below). It should be noted, however, that to the best of our knowledge there are no grooves on the relevant bones in *Morganucodon* that would house the united vessel or show unequivocally its connection to the lateral head vein.

Our analysis tempts us to propose a different interpretation of the orbito-temporal system of *Morganucodon*. We suggest that as in *Tachyglossus*, and as accepted by us for multituberculates, the principal vessels in this system were arteries. An artery may have entered the skull through the post-temporal fossa, passed by a short post-temporal canal and entered the cranial cavity at the boundary between the anterior lamina and the squamosal, continuing forwards intracranially as the orbito-temporal artery. Thus the only major difference would be the extracranial situation of the artery after leaving the post-temporal canal in *Morganucodon*, while this part was intramural or intracranial in multituberculates.

It is important to compare the vascular system of multituberculates and morganucodontids with that of tritylodonts. Kemp (1983) discussed the relationships of tritylodonts and morganucodontids, demonstrated a number of anatomical similarities and concluded that the tritylodonts form the sister group of all mammals. It is clear that a great deal of parallelism existed between the various groups of non-therian mammals and the tritylodonts. Here we shall point out some similarities between multituberculates and tritylodonts not discussed by Kemp. The vascular grooves and openings in tritylodonts have been discussed by numerous authors (Watson 1942; Ginsburg 1962; Kühne 1956; Hopson 1964; Crompton 1964). However, of these authors, only Kühne discussed the direction of flow in certain vessels. The dural sinus system, found in multituberculates and other mammals, was presumably present in tritylodonts, but no descriptions are available.



Hopson (1964) described the braincase of *Bienotherium* and although he did not reconstruct the vascular system in detail, it appears from his description and comparisons that he interpreted the cranial vascular system on the cynodont pattern. A canal, interpreted by him as being venous, was equated with the 'sinus canal' of cynodonts. This canal in *Bienotherium* is covered externally by a thin lappet of the parietal and opens just behind the anterior opening of the post-temporal canal. In accord with generally accepted reconstructions of cynodonts, the post-temporal and sinus canals unite at this point and the conjoint vein extends ventrally, extracranially, to pass through the pterygo-paroccipital foramen to enter the lateral head vein. In *Bienotherium* the post-temporal canal lies outside the subarcuate fossa, which is not penetrated by vascular foramina.

*Oligokyphus* shows a somewhat different structure in this region, characterized by Kühne (1956, p. 49) as follows:

'Above the paroccipital process is a vascular canal, perforating the cranial wall and emerging in the subarcuate fossa. Outside the cranial cavity this canal is joined by a groove from above, belonging to the vein of the sinus canal. Both structures leave the skull together through the post-temporal foramen. The course of the vein of the sinus canal is as follows: emerging from the canal presumably between the parietal and the periotic, it runs for a short distance in a groove horizontally backwards and turns vertically downward above the canal from the subarcuate fossa. After the two have joined, they proceed again horizontally towards and through the post-temporal foramen.'

The course reconstructed by Kühne for *Oligokyphus* is strikingly similar to that described by us for *Catopsalis*. The difference is that in the latter the canal of the subarcuate fossa is proportionately smaller than in *Oligokyphus*, but it should be remembered that a very large canal penetrates the subarcuate fossa in *Nemegtbaatar*. Another difference is that, as is usual in therapsids, the vessel of the 'sinus canal' (our orbito-temporal vessel) was extracranial. We suggest a different interpretation from that of Kühne (1956), namely that in common with *Tachyglossus*, and multituberculates and *Morganucodon* as interpreted here, these grooves in *Oligokyphus* may represent arteries entering the region through the post-temporal fossa.

Thus in multituberculates the artery was intramural or intracranial from post-temporal fossa to the post-orbital foramen, and then had an extracranial branch running in the orbital groove. It was much more completely paracranial in tritylodonts. In *Morganucodon* the homologous vessel was intracranial in its anterior part, but unlike multituberculates a part of it lay paracranially between the 'sinus canal' segment and the post-temporal fossa. This difference of position with respect to the bones of the skull parallels a similar variation found in the maxillary and supraorbital arteries of modern placental mammals, and suggests that such apparently major differences in position can be quite often attained by essentially homologous vessels.

The cranial vascular system in cynodonts has been described by Watson (1911), Fourie (1974), Kemp (1979, 1982) and others, and Cox (1959) considered the veins of dicynodonts. Although all these reconstructions differ in detail (see Kemp (1979) for a summary), all the authors accepted that all the grooves found in the posterior part of the cranial cavity contained veins rather than arteries. Thus veins are described entering the post-temporal canal from the occipital surface, flowing forwards, and joining the vein of the sinus canal. The combined trunk then passed ventrally through the pterygo-paroccipital foramen to join the primary head vein

(lateral head vein). Discussion of the various interpretations of the cynodont vascular system is outside the scope of the present paper, but in the light of the above analysis we call the attention of students of cynodonts to the possibility that the post-temporal and 'sinus' canals may have been arterial in their primary affinities.

#### CONCLUSIONS

The study of the two serially sectioned skulls of Late Cretaceous taeniolabidoid multituberculates has provided a continuity between endocranial, intramural and extracranial vascular markings. This has aided the interpretation of other entire skulls, endocasts and isolated petrosals, and together these studies have enabled a reconstruction of the vascular anatomy of multituberculates, which may be compared with that of other mammals and therapsids.

The venous system of multituberculates contained vessels clearly represented in all modern mammalian groups, including monotremes. These were, in the dural sinus system, the sagittal, transverse, dorsal part of the sigmoid, prootic and tentorial sinuses. Deep temporal veins draining into a supraglenoid vein, a connection between this and the postglenoid foramen and the connection of the prootic venous channel to the latter are also found in modern mammals. Drainage of the prootic sinus via the lateral head vein, with this then becoming a stylomastoid vein before entering the jugular system, is found in monotremes. Modern mammals also exist with no ventral part of the sigmoid sinus leading to the jugular foramen. It appears, therefore, that of the clearly recognizable veins in multituberculates, only the post-trigeminal segment linking medial and lateral segments of the primary head vein is without parallel in adult modern mammals. This apparent difference, however, must be considered while remembering that this post-trigeminal segment is present in the embryos of all modern mammals, and a similar venous channel has been frequently attributed to therapsids. The cranial venous system of these multituberculates can thus be considered to show a characteristically mammalian pattern, possibly indicating primitive features like the absence of a sigmoideo-jugular connection and the presence of a large post-trigeminal vein.

Of that portion of the arterial system related to the basicranium, the internal carotid artery within its canal, a stapedia artery running from it over the promontory to the fenestra ovalis, with probable maxillary, 'Vidian', and meningeal branches are indicated by very firm evidence. These arteries are also represented among modern mammals, and can reasonably be considered to be parts of a probable primitive pattern.

The orbito-temporal system consisted of vessels running from a paracranial situation in the post-temporal fossa, through an intramural ascending canal, then intracranially in the internal parietal groove to the postorbital foramen. Here an intracranial branch continued forward while an extracranial branch passed to and through the postorbital foramen and forwards through the orbit to the ethmoid foramen, with presumed further branches through that foramen into the nose. In modern mammals both veins and arteries can be found in portions of this course. We have argued in favour of the primary determinant of this line of blood vessels being an artery similar to the arteria diploetica magna of *Tachyglossus*. In multituberculates with a large post-temporal fossa the ascending canal was reached through a large post-temporal recess passing intracranially through the region of the subarcuate fossa. In these forms there is no clear evidence of a connection with vessels in the stylomastoid region. This would favour the concept of this artery's being a branch of the occipital artery, as in *Tachyglossus*. In genera with a small post-temporal fossa there is clear evidence of a somewhat larger connection with

the stylomastoid or postglenoid foramina, as well as a connection between ascending canal and post-temporal canal. This suggests that branches of the stapedia artery may have passed via these foramina to supply the orbito-temporal system. There is considerable variability in the pattern of this system at the generic level, and in the present state of knowledge it would be misleading to use such patterns as indicators of higher systematic rank.

Although the orbito-temporal system of multituberculates appears to have a close parallel in the arteria diploetica magna of *Tachyglossus*, and remnants may be found in the other modern mammals studied here, it must be concluded that to possess the system in its entirety is probably a primitive feature beyond which most modern mammals have since evolved. This is because the system occurs consistently in cynodonts, morganucodonts and tritylodonts, the anterior part being described as the vessel of the 'sinus canal' and the posterior part as the vessel of the post-temporal canal. In multituberculates a greater part of the course of these vessels is intracranial than in the other groups. We conclude that this part of the cranial vascular system is the most problematical of our reconstruction, and that this is because it represents a primitive pattern, very reduced in most modern mammals and therefore not sufficiently considered in the analyses of comparative anatomy. We commend to the attention both of mammalogists and of students of the above-mentioned fossil groups the possibility that this system was arterial, with companion veins, rather than entirely venous.

On the basis of our reconstruction of the vascular system we conclude that it is possible to recognize many similarities to the cranial vascular pattern of modern mammals (Padgett 1957; H. Butler 1967) in taeniolabidoid multituberculates. Conversely, there is no striking resemblance to the vascular pattern of modern reptiles (O'Donoghue 1920, Shindo 1915).

In the course of this study, new data have emerged on the structure of the multituberculate skull. There is a relatively large cavum epiptericum, completely floored ventrally, and separated from the body of the cranial cavity and from the pituitary fossa by a bony wall, the taenia clino-orbitalis, representing a persistent pila antotica co-ossified with the orbitosphenoid. The cavum epiptericum opens anteriorly into the orbit through a large sphenorbital fissure, walled laterally by the anterior lamina of the petrosal and a modestly sized alisphenoid and medially by the orbitosphenoid. This possibly transmitted the optic nerve, as well as the ophthalmic, maxillary and three eye-muscle motor nerves, with ophthalmic veins, because the sectioned skull of *Nemegtbaatar* shows a possible optic foramen opening into the cavum.

The taenia clino-orbitalis is proportionately thicker and broader than in cynodonts and tritylodonts. This is unlike modern mammals, where bone here is thin or absent, and it may be a derived character, related to the general robustness and thickness of the cranial bones in multituberculates when compared with modern mammals of comparable size. Nevertheless the presence of this taenia must be regarded as a primitive feature.

Although great detail has emerged about the structure of the ventral surface of the skull in the tympanic region, the tympanic bone has not been described in multituberculates. The epitympanic recess has been found in this study to be overhung laterally by a ridge of the anterior lamina of the petrosal, and it seems quite likely that this served as a support for a tympanic bone, whose orientation may have been relatively horizontal because there is no clear marking for an external auditory meatus close to the skull near the epitympanic recess. Evidence is found of air-spaces, possibly with a resonant function like the accessory tympanic sinuses of many modern mammals. These were present in the occipital condyles and in the paroccipital processes, with generic variation.

The bone described as the tabular bone in earlier papers has been shown by this study not

to be present. It has been found that this portion of the skull is continuous with the bone enclosing the semicircular canals, and it is therefore concluded that the posterior or mastoid portion of the petrosal is exposed on the cranial surface. This represents the removal of another primitive character previously attributed to multituberculates.

The endocranial casts show generic differences in proportion but an essentially similar structure. They suggest that the multituberculate brain had relatively large, shallow cerebral hemispheres with large olfactory bulbs. Although possibly with an extensive dorsally and laterally placed lissencephalic neocortex, a marked concavity on the latero-ventral surface is unique among mammals to multituberculates. The cerebellum lacked obvious lateral lobes but appears to have had relatively very large paraflocculi. The midbrain is concealed in dorsal aspect. The rhombencephalon was deep in comparison with other mammals and this, together with the large paraflocculi, is more similar to the proportions found in therapsids. The pons appears to have lain caudal to the emergence of the trigeminal nerve, as in monotremes.

In summary conclusion, it may be stated that although in many characters the multituberculate skull and vascular system show strikingly mammalian characteristics, a number of primitive features are retained, such as the taenia clino-orbitalis and the continuous orbito-temporal vessels. The study therefore supports the hypothesis that multituberculates diverged rather early from the line leading to the main mammalian radiation.

See notes added in proof on page 602.

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## GLOSSARY

*Pattern of entries*

The English form of each term is given, with the Latin equivalent (based on the *Nomina Anatomica* 1977) following in parentheses. If these are identical, this indicates a predominant usage of the Latin form in English vernacular. A brief indication is then given of the general morphological definition adopted in this paper, where this is felt to be needed because of confusion or ambiguous usage found by us in past literature. Except where otherwise indicated, our comparative anatomical summaries are based on the works of Goodrich (1930) and de Beer (1937), and the venous nomenclature on Padget (1957). The last part of the entry describes the conditions found in multituberculates.

*Abbreviations*

- Gen. where needed, a summary of the definition in terms of general vertebrate morphology employed in this paper.
- Multis. the definition or description as found in multituberculates. Figure references are to well-shown examples and are not exhaustive.
- Plag. the condition in Plagiaulacoidea.
- Ptil. the condition in Ptilodontoidea.
- s. *sive* precedes alternative Latin nomenclature.
- Taen. the condition in Taeniolabidoidea.
- \* a term introduced here, unique to multituberculates.
- more detail or explanation may be found under the cited entry.

Alisphenoid (*ala temporalis* (*s. major*) *ossis sphenoidalis*)

Gen: in mammals, greater wing of sphenoid bone, articulating medially with body of →sphenoid bone, generally accepted as being partly homologous with epipterygoid of reptiles and contributing to lateral wall of →cavum epiptericum, separating this from orbit and →temporal fossa.

Multis.: (figure 20) small element antero-ventral to →mandibular nerve foramina and →anterior lamina (which is the major component of the lateral wall of the cavum). Not pierced by foramina (*contra* Sloan 1979, who gives for *Ectypodus* a relatively large bone with foramina for individual maxillary and mandibular nerves).

Anterior lamina of the petrosal (*lamina anterior ossis petrosi*)

Gen.: in advanced therapsids, non-therian mammals, extension of →petrosal forward as lateral wall of →cavum epiptericum to form part of wall of temporal fossa.

Multis.: (figures 1, 8, 20*b* and 25–29) a large component of the lateral aspect of the braincase.

Aquaeductus cochleae (*aquaeductus cochleae*)

Gen.: passage leading from →fenestra cochleae medially towards cranial cavity through jugular foramen occupied by perilymphatic duct. Bony canaliculus in therians.

Multis.: (figures 1 and 8) often well marked on medial part of →promontorium.

\*Ascending canal (*canalis ascendens*)

Multis.: (figures 1, 8, 10, 23 and 24) intramural canal, probably vascular, within suture between posterior margin of anterior lamina of petrosal and squamosal. In forms with large →post-temporal fossa runs between cranial cavity and intracranial →post-temporal recess. In forms with small post-temporal fossa, communicates both with the latter and with →stylomastoid or →postglenoid foramina.

Basioccipital (*os basioccipitale*): →occipital bone

Basisphenoid (*os basisphenoidale*): →sphenoid bone

\*Canal of ?maxillary artery (*canalis arteriae maxillaris*)

Multis.: (figures 1 and 8) in *Catopsalis* and unidentified Hell Creek petrosals, canal leading from facial sulcus ventral and then lateral to →post-trigeminal canal to open at foramen of ?maxillary artery on external surface of anterior lamina. Here interpreted as for maxillary (infraorbital) branch of stapedia artery, and similar to alisphenoid canal of some modern mammals.

\*Canal of subarcuate fossa (*canalis fossae subarcuatae*)

Multis.: (figures 1 and 4) in *Catopsalis* a minute canal, probably vascular, branching from →post-temporal canal, running anteromedially to enter the posterolateral corner of the subarcuate fossa.

Carotid canal (*canalis caroticus*)

Gen.: passage through basicranium from carotid foramen to lateral aspect of →pituitary fossa. In mammals, prevailing view that it primitively passes through body of basisphenoid to enter fossa from below, as in monotremes and some marsupials, but in advanced forms, such as placentals and other marsupials, runs dorsomedially to reach fossa from more laterally placed carotid foramen. This usually anterior to →promontorium, between bones (foramen lacerum medium) lateral to body of sphenoid and medial to →alisphenoid unless canal secondarily elongated.



Multis.: (figures 28 and 29) in present work, shown to run as in advanced mammals in Late Cretaceous forms, though probably piercing basisphenoid in Jurassic forms (Hahn 1981).

Carotid foramen (*foramen caroticum*)

Gen.: →carotid canal.

Multis.: (figures 6 and 20c) in Late Cretaceous forms a relatively large opening, medial to →foramen ovale inferium, probably between same bones as →carotid canal. This foramen previously misidentified as opening in floor of cavum epiptericum in *Kamptobaatar* (Kielan-Jaworowska 1971).

Cavernous sinus (*sinus cavernosus*)

Gen.: in mammals, plexiform venous bed medial to →trigeminal (semilunar) ganglion in →cavum epiptericum and lateral to, but intercommunicating beneath, pituitary gland. Often intimately related to →internal carotid artery. Derived from medial segment of →primary head vein. Receives blood from →ophthalmic veins via →sphenorbital fissure, and various intracranial veins via pituitary fossa and fenestra post-optica. Drains variously through →inferior and superior petrosal sinuses, and peritrigeminal and pericarotid emissaries to →pterygoid and →pharyngeal plexuses. In embryos, major drainage pathway is by →post-trigeminal vein to rest of →primary head vein.

Multis.: not clearly delineated. Presumed to lie within capacious cavum epiptericum. Evidence is for persistence of post-trigeminal vein.

Cavum epiptericum (*cavum epiptericum*)

Gen.: space between palatoquadrate and neurocranium anterior to →post-trigeminal canal, containing →trigeminal ganglion in →semilunar fossa, and →primary head vein (→cavernous sinus). In mammals, →ophthalmic, oculomotor, trochlear and abducent nerves leave it anteriorly through →sphenorbital fissure, →maxillary nerve either with them or piercing its lateral wall in foramen rotundum, and →mandibular nerve piercing its lateral wall through →foramen ovale or equivalent passages. Separated from true cranial cavity medially by →pila antotica, which is usually fibrous in therians, but a partly ossified →taenia clino-orbitalis in monotremes. Walled laterally either by anterior lamina of →petrosal or by →alisphenoid or both.

Multis.: (figures 28 and 29) a large space, walled laterally by →anterior lamina and very small alisphenoid, medially by extensive ossified →taenia clino-orbitalis joining orbitosphenoid. Completely floored in post-Jurassic forms.

Cerebellum (*cerebellum*)

Multis.: (figures 7, 10, 16, 20a and 32) shown by endocranial casts to have central lobe, lateral lobes not obvious, and presumably large →paraflocculi within large →subarcuate fossae.

Cerebellar veins (*venae cerebelli*)

Gen.: veins with same meningeal relations as →cerebral veins but lying on anterior, posterior and dorsal aspects of cerebellum.

Cerebral veins (*venae cerebri*)

Gen.: this term restricted, following practice of *Nomina Anatomica* (1977) to veins lying in pia and arachnoid mater and only crossing subarachnoid space at discrete points to join dural sinuses. Modern mammals show great interspecific and intraspecific variation: such vessels not good palaeontological landmarks. In modern mammals, not homologous by development with 'anterior, middle, and posterior cerebral veins' of early embryos of vertebrates, which has caused considerable confusion in past literature (Padgett 1957).

Cerebrum (*cerebrum*)

Multis.: (figures 7, 16, 20a and 32) shown by endocranial casts to be major, bilobed portion of forebrain. Shallow, probably lissencephalic, with characteristic concavity on latero-ventral surface.

Choanae (*choanae*)

Gen.: internal nostrils. In forms with secondary palate, usually meaning posterior internal openings of nasopharyngeal ducts.

Multis.: divided by vomer and pterygoids into four grooves.

Cochlear nerve (*nervus cochleae*)

Multis.: this term used here as an abbreviation for the inferior division of the vestibulo-cochlear (VIII) cranial nerve, principally innervating the cochlea (lagena).

\*Condylar cavity (*cavitas condylaris*)

Multis.: (figures 11 and 12) cavity, probably air-sinus in →occipital condyle.

Condylar foramen (*foramen condylaris*): →hypoglossal foramen.

Condylar fossa (*fossa condylaris*): →hypoglossal foramen

Corpus trapezoideum (*corpus trapezoideum*)

Gen.: in mammals, transverse ridge visible ventrally, rostral to →medulla, containing auditory pathway fibres, visible in forms where ventral →pons does not extend to caudal limit of metencephalon.

Multis.: details obscured within cast of hindbrain and adnexae.

Cranio-quadrangle passage (*canalis cranioquadratus*)

Gen.: in description of vertebrate embryos (Goodrich 1930), compartment between (laterally) epipterygoid and dorsal process of quadrate, and (medially) true neurocranium including otic capsule. In early embryos, →primary head vein runs through full length of this passage, while trigeminal and facial nerves cross parts of it.

Multis.: size of →post-trigeminal canal suggests that →primary head vein ran through full length of passage in adults, unlike monotremes where only medial and lateral segments persist, and therians in which only medial segment persists (in both cases the passage is thus obscured in adult forms).

Cribriform plate (*lamina cribrosa*)

Gen.: in modern mammals, partition between olfactory bulbs and nasal cavity, with multiple fenestrations for fila olfactoria.

Multis.: not preserved entire in any skull. In sections of *Nemegtbaatar* matrix contains tiny bone remnants in the appropriate sections, suggesting that a cribriform plate was present.

Crista parotica (*crista parotica*)

Gen.: in embryos, ridge on otic capsule beneath lateral semicircular canal and lateral to →facial sulcus. In mammals, incus articulates anteriorly in →epitympanic recess, styloid articulates posteriorly. Posterior part is →mastoid.

Multis.: not used in adult terminology.

Crus commune (*crus commune*)

Gen.: conjoined limbs of anterior and posterior semicircular canals.

Deep temporal veins (*venae temporales profundae*)

Gen.: group of veins draining from deep part of temporal fossa, receiving blood from →pterygoid plexus and from orbit, draining usually in modern mammals to external jugular system. Often across region of zygomatic arch through supraglenoid foramen, with intramural course to postglenoid foramen (therians) or →lateral head vein (*Ornithorhynchus*).

Multis.: interpreted as entering →supraglenoid foramen.

Dehiscence of facial canal (*dehiscencia canalis facialis*)

Gen.: in mammals the site of branching of the →superficial petrosal branch from the trunk of the facial nerve, usually the site of the sensory (geniculate) ganglion.

Multis.: identified by Simpson (1937) in *Ptilodus*. Here the same aperture redesignated anterior part of →facial sulcus since →tympanic foramen of facial canal situated in anterior extremity of this sulcus in our material.

\*Dorsal foramen of anterior lamina of petrosal (*foramen dorsalis laminae anterioris ossis petrosi*)

Multis.: (figure 20*b*) present in several genera of Taen., directed dorsally from →semilunar fossa near anterior border of lamina. Possibly for deep temporal branch of →mandibular nerve.

Dural sinus (*sinus durae matris*)

Gen.: general descriptive term for veins enclosed in firm walls derived from the endocranium and dura mater. If wholly enclosed by dura, no marking on bone, e.g. →straight sinus. If one aspect of vessel intimately applied to bone, clear marking may be produced on endocranial aspect, e.g. →transverse sinus.

Ectopterygoid bone (*os ectopterygoideum*)

Gen.: membrane bone behind palatine and lateral to pterygoid in reptiles, forming anterior border of palatal opening of temporal fossa. Presence disputed in therians (Presley & Steel 1978) though possibly a discrete bone in monotremes.

Multis.: (figures 6 and 20*c*) suture with alisphenoid indistinct, other sutures preserved in

some specimens of Taen. Plate of bone situated ventrally, lateral to choana in front of →alisphenoid, tapering anteriorly at →palatonasal notch between palatine and maxilla.

Emissary vein (*vena emissaria*)

Gen.: term applied to minor veins passing through skull from →dural sinuses to exterior veins.

Ethmoid foramen (*foramen ethmoidale*)

Gen.: aperture permitting passage of nerve (→ophthalmic) and vessels between orbit and nasal cavity, usually initially leading to position on cerebral aspect of cribriform plate before passage contained through it.

Multis.: (figure 20*b*) piercing orbitosphenoid, with wide groove running posteroventrally from it to meet →sphenoplatine groove. →Orbital groove running back to →post-orbital foramen.

Ethmoidal vessels (*vasa ethmoidales*)

Gen.: arteries passing from orbit to nasal cavity, and veins returning, through →ethmoid foramina.

Epitympanic recess (*recessus epitympanicus*)

Gen.: found only in mammals, fossa in petrosal at front end of crista parotica, above dorsal margin of tympanic membrane and therefore a useful index of position of membrane, includes body of malleus and incus and houses articulation of dorsal process of latter.

Multis.: (figures 1, 6, 8 and 20*c*) fossa bounded medially by and impressed into →lateral flange and laterally by ridge on anterior lamina of →petrosal. →Postglenoid foramen opens in its posterior part in *Nemegtbaatar*.

Exoccipital bone (*os exoccipitale*): →occipital bone.

External auditory meatus (*meatus acusticus externus*)

Gen.: passage from surface of head to a deeply placed tympanic membrane. Found in mammals, in cynodonts groove on squamosal so interpreted. No clear osteological marking in monotremes, where cartilaginous meatus curves well away from skull.

Multis.: no clear marking visible.

External carotid artery (*arteria carotis externa*)

Gen.: Branch of common carotid artery arising at bifurcation in neck proximal to tympanic region, found in all groups. Branches supply variable parts of cranio-facial apparatus, thus →internal carotid artery restricted more to region of the forebrain. Complementary in distribution to →stapedial artery, hence absence of latter correlates with presence of external carotid artery with large territory.

Multis.: Evidence fragmentary, presence of large stapedial artery probable.

External jugular vein (*vena jugularis externa*)

Gen.: characteristically a major system of venous drainage in modern mammals: situation between cutaneous and deeper muscles provides force for venous return. Very variable system,

joined by →pterygoid, superficial temporal, →postglenoid and →occipital veins and plexuses, which can receive blood from 'emissary' veins such as those of foramen ovale, postglenoid foramen, temporal, spurious jugular, mastoid, stylomastoid and posterior condylar foramina.

Multis.: this system, being prevalent in all groups of modern mammals, may be assumed to be present in multituberculates.

#### Facial canal (*canalis facialis*)

Gen.: in therians →facial nerve enclosed in long bony canal (Fallopian canal or aqueduct). Proximal segment from internal auditory meatus to tympanic opening or dehiscence (when canal fully enclosed); intermediate segment (in embryos always →facial sulcus, later enclosed in some forms) over stapes to caudal margin of styloid attachment (site of →foramen stylomastoideum primitivum); distal segment between mastoid part of petrosal and squamosal, to →foramen stylomastoideum secundarium.

Multis.: only proximal part, then into →facial sulcus.

#### Facial nerve (*nervus facialis*)

Gen.: cranial nerve VII, so named from extensive supply of facial muscles in mammals. Ganglion (geniculate) lies in mammals at →tympanic opening of canal, and →superficial petrosal (palatine) branch runs forward from this, while main trunk continues backwards in →facial sulcus or →canal to emerge usually behind styloid process through →stylomastoid foramen, thence giving chorda tympani, auricular, facial and cervical branches.

Multis.: our reconstruction incorporates a facial nerve of this pattern.

#### Facial sulcus (*sulcus nervi facialis*)

Gen.: deep groove on petrosal above stapes, between cochlea and crista parotica, in which lie: main trunk of →facial nerve distal to its ganglion; →stapedial or equivalent artery; and lateral segment of →primary head vein. Enclosure in some therians gives intermediate segment of →facial canal.

Multis.: (figures 1, 6, 8, 20c and 23–26) distinct and deep, just medial to lateral flange (→crista parotica). Divided descriptively into anterior part and postero-lateral part, junction at about level of fenestra vestibuli. Anteriorly connected to →post-trigeminal canal. Postero-laterally terminates in stylomastoid notch or foramen. Postero-lateral part enclosed in bony chamber in unidentified Hell Creek petrosals. Sulcus bridged by delicate strand of bone in some Taen.

#### Falx cerebri (*falx cerebri*)

Gen.: sagittal fold of meninges between cerebral hemispheres in deep intercerebral fissure.

#### Fenestra cochleae (*fenestra cochleae*)

Gen.: site of secondary tympanic membrane and perilymphatic duct, in opening in cochlear capsule (→promontorium). In therians, duct and fenestra separated by bony processus recessus to give separate external opening of →cochlear aqueduct.

Multis.: (figures 1, 6, 8 and 20c) duct and fenestra share common opening.

#### Fenestra vestibuli (*fenestra vestibuli*)

Gen., Multis.: (figures 1, 6, 8 and 20c) opening from cochlear capsule facing laterally into →facial sulcus, site of footplate of stapes.

\*Foramen of ?maxillary artery (*foramen arteriae maxillaris*): →canal of maxillary artery

Foramen ovale (*foramen ovale*)

Gen.: in mammals aperture of exit of mandibular branch of trigeminal nerve.

Multis.: probably always multiple with at least →foramen masticatorium and →foramen ovale inferium, and possibly also →dorsal foramen of anterior lamina.

Foramen masticatorium (*foramen masticatorium s. crotaphiticobuccinatorium*)

Gen.: subdivision, uncommon in therians, of →foramen ovale carrying anterior division of →mandibular nerve.

Multis.: (figures 6, 8, 20c and 26–28) always present.

Foramen ovale inferium (*foramen ovale inferium*)

Gen.: subdivision, uncommon in therians, of →foramen ovale carrying posterior division of →mandibular nerve.

Multis.: (figures 6, 8, 20c and 28) always present.

Foramen pseudoovale (*foramen pseudoovale*)

Gen.: in mammals; foramen ovale so designated in monotremes (Simpson 1938) to distinguish from foramen ovale recognized only in alisphenoid. Proposed as standard term (MacIntyre 1967) for foramina transmitting mandibular nerve but not piercing alisphenoid. This usage rejected here in accord with Griffiths (1978). Thus we retain same name for homologous foramina (a standard usage as in e.g. carotid foramen, ethmoid foramen) irrespective of bony surrounding. Homology of foramen ovale here taken to relate to mandibular nerve. Also 'pseudoovale' rejected as prejudicial to possible homology of anterior lamina of petrosal with part of mammalian alisphenoid (Presley 1981; Kemp 1983).

Foramen rotundum (*foramen rotundum*)

Gen.: in mammals, for →maxillary branch of trigeminal nerve.

Multis.: figured (without description) for *Ectypodus* as perforating the 'alisphenoid' anterior to an undivided foramen ovale (Sloan 1979). Not previously described, not found in present study.

Foramen stylomastoideum (*foramen stylomastoideum*)

Gen.: in therians, exit foramen for facial (VII) nerve behind styloid process and antero-medial to →mastoid process. This is foramen stylomastoideum secundarium, between →mastoid and →squamosal. In monotremes and therian embryos, nerve emerges immediately caudal to attachment of styloid process to →crista parotica, this is foramen stylomastoideum primitivum. See also →facial canal.

Multis.: probable exit of facial nerve, and →primary head vein from postero-lateral part of →facial sulcus here termed stylomastoid notch in view of likely homology of this site with foramen stylomastoideum primitivum of other mammals.

\*Glenoprootic canal (*canalis glenoprooticalis*)

Multis.: (figure 26) canal through substance of →petrosal connecting →supraglenoid foramen with ventral part of prootic canal.

\*Glenoprootic vein (*vena glenoprooticalis*)

Multis.: vein passing through →glenoprootic canal connecting supraglenoid vein with ventral part of prootic vein.

Hiatus Fallopii (*hiatus canalis nervi petrosi majoris*)

Gen.: defined in human: anterior orifice of canal carrying superficial petrosal nerve forwards from geniculate ganglion, is on endocranial aspect of tegmen tympani of petrosal. Tendency in palaeontology to describe 'hiatus Fallopii' on ventral aspect of cranium: probably a misnomer, though conceptually representing course of same nerve. Therefore this here entered in quotation: 'hiatus Fallopii', to relate notch or foramen to past literature.

Multis.: (figures 1, 6, 8 and 20c) groove or notch at antero-medial extremity of facial sulcus, related to →'Vidian groove', here interpreted as for →meningeal vessels as well as for →superficial petrosal nerve.

\*Hyoid muscular pit (*fossa muscularis hyoidei*)

Multis.: (figure 1C) distinct hollow postero-lateral to fenestra cochleae and medial to →paroccipital process (figure 1c, C). Here interpreted as for levator hyoidei or posterior belly of digastric muscle.

Hypoglossal foramen (*foramen hypoglossale*)

Gen.: also referred to as (anterior) condylar foramen. In mammals (and other vertebrates) canal, often multiple, for passage of hypoglossal (XII cranial) nerve through the occipital bone. The nerve runs forward into immediate contact with nerves IX, X and XI in →jugular fossa. Recess of this fossa for this part of the nerve called condylar recess. In monotremes hypoglossal foramen is absent, nerve passing directly through →jugular foramen.

Multis.: double in *Paulchoffatia* (Hahn 1969), single in *Ptilodus* (Simpson 1937) and *Ectypodus* (Sloan 1979) opening into condylar fossa anterior to occipital condyle. Absent, possibly confluent with jugular foramen or indiscernible in jugular fossa in Taen. (Kielan-Jaworowska 1971, 1974).

Inferior petrosal sinus (*sinus petrosus inferior*)

Gen.: dural sinus joining →cavernous sinus to →jugular foramen along junction between petrosal and sphenoccipital. In therians leaves skull independently to join internal jugular vein outside cranial margin of jugular foramen, typically separating nerve IX from nerve X. May be extracranial in large part in mammals. Can be only large vein leaving the jugular foramen, when '→sigmoid' joins →vertebral veins.

Multis.: no clear evidence for its course or size.

Inferior ramus of stapedia artery (*ramus inferior arteriae stapediae*)

Gen.: in modern mammals, branch of →stapedial artery which can supply maxillary, infraorbital, meningeal and sometimes lower jaw territories. Runs forward immediately above stapes as most medial content of facial sulcus. Runs infero-lateral to trigeminal ganglion, sometimes in alisphenoid canal. May be functionally replaced by →stylomastoid branch of external carotid artery, e.g. *Ornithorhynchus*, young opossum.

Multis.: evidence very strong for →maxillary, →meningeal, and possibly '→Vidian' branches.

Inferior sagittal sinus (*sinus sagittalis inferior*)

Gen.: in many modern mammals, dural sinus in free edge of falx cerebri, receiving blood from deep in sagittal sulcus and →dorsal aspect of diencephalon. Connected to →transverse sinuses by →straight sinus.

Multis.: no clear evidence for separate existence from →superior sagittal sinus.

Inner ear (*auris interna*): →petrosal\*Interglenoid canal (*canalis venae interglenoidalis*)

Multis.: (figure 1) a canal within the substance of the petrosal bone, usually in the anterior lamina, connecting →supraglenoid and →postglenoid foramina. This region very variable, and term, chosen for brevity rather than anatomical precision, indicates functional similarity rather than necessarily implying homology.

\*Interglenoid vein (*vena interglenoidalis*)

Multis.: (figures 8 and 33) vein connecting →supraglenoid with →postglenoid vein. Because of great variability, the name regarded as descriptive, not an index of homology.

Internal auditory meatus (*meatus acusticus internus*)

Gen.: for →facial nerve VII and auditory–vestibular nerve VIII.

Multis.: (figures 1D and 8B) above nerves not combined in common pit in Jurassic *Paulchoffatia* (Hahn 1969). In later forms (Simpson 1937; this paper), shallow, small compared with subarcuate fossa. Divided by transverse crest into: posterolateral small foramen for →cochlear nerve and anteromedial to crest, smaller foramen for →vestibular nerve, and larger anterior foramen for facial nerve.

Internal carotid artery (*arteria carotis interna*)

Gen.: principal artery of forebrain, running, from common carotid, under basicranium beneath region of tympanic cavity, sometimes piercing basisphenoid, but in therians usually entering →carotid canal (foramen lacerum medium). In tympanic region may have laterally running →stapedial branch.

Multis.: (figure 32) posterior part of its course not known. Opening of →carotid canal here identified as laterally placed (as in therians) in Late Cretaceous forms.

Internal jugular vein (*vena jugularis interna*)

Gen.: vein of neck derived from anterior cardinal vein of early embryo. Can regress completely in mammals, often very small, with →inferior petrosal sinus its principal tributary. Joined by →sigmoid sinus when inferior segment of this present, and in jugular fossa extracranially by →inferior petrosal sinus and →lateral head vein, either directly from tympanic cavity or via →stylomastoid vein.

Multis.: no clear evidence for ventral part of sigmoid or →petrosal sinuses of significant size. Since lateral head vein joining internal jugular found in embryos of all modern mammals and retained in adult monotremes, and since absence of internal jugular vein is unusual, here considered simplest to reconstruct monotreme-like pattern.



\*Internal parietal groove (*sulcus internus parietalis*)

Multis.: (figures 10 and 24–28) groove on cranial surface of parietal in *Nemegtbaatar* and *Chulsanbaatar*, and presenting distinct rounded ridge on endocranial casts. Runs from foramen of →ascending canal, antero-dorsally, to postorbital foramen. From here, intracranially as shallow indistinct groove on parietal, then frontal, extracranially forward from postorbital foramen as postorbital groove. Here interpreted as primarily arterial, part of course of →orbito-temporal vessels, and equated with →sinus canal of cynodonts, morganucodonts and tritylodonts.

Jugular foramen: (*foramen jugulare*)

Gen.: In mammals, derived from embryonic metotic fissure, and sometimes called posterior lacerate foramen. Aperture through which nerves X (vagus) and XI (accessory) consistently, and IX (glossopharyngeal) usually (though in *Tachyglossus* sequestered into separate passage) leave the cranial cavity. Name derived from human, where large sigmoid sinus passes through lateral part of fissure to become internal jugular vein. Human is not of general mammalian pattern (Padget 1957; H. Butler 1967).

Multis.: →jugular fossa.

Jugular fossa (*fossa jugularis*)

Gen.: in mammals, concavity, often large, ventral to →jugular foramen, behind →promontorium, containing ganglia of IX and X and bulb of internal jugular vein when present. Posterior recess is →condylar fossa.

Multis.: (figures 6 and 20*c*) very large and deep in Taen. (Kielan-Jaworowska 1971, 1974) lying obliquely between low occipital condyle and base of promontorium: distinct jugular foramen in middle of roof. →Hypoglossal foramen not identified, therefore jugular foramen presumed to transmit IX, X and XI nerves with internal jugular vein in Taen. Size of fossa suggests presence of large ganglia. Jugular fossa smaller in Plag. and Ptil. (Hahn 1969; Simpson 1937; Sloan 1979), which have more prominent occipital condyles and hypoglossal foramen.

Lateral flange (*lamina lateralis*)

Gen.: term introduced by Kermack (1963) in description of triconodont petrosals for ventrally projecting crest lateral to '→lateral trough'.

Multis.: (figures 1, 6, 8, 20*c* and 26) very similar ridge on ventral aspect of petrosal, anterior part parallel to →promontorium, posterior part turning laterally, forming immediate medial boundary of →epitympanic recess and lateral margin of →facial sulcus, which it overhangs ventrally. If reconstruction correct, lateral flange corresponds to →crista parotica of mammalian embryos.

Lateral head vein (*vena capitis lateralis*)

Gen.: a term frequently used for lateral segment of →primary head vein of vertebrates, typically lateral to cranial nerve ganglia in posterior part of cranio-quadrate passage (see Goodrich 1930). In monotremes and early embryos of other mammals, lies in →facial sulcus lateral to facial nerve and leaves through →foramen stylomastoideum primitivum to join →internal and →external jugular veins. (In squamates large non-homologous vein given same

name can extend forward from it to orbit outside the cavum epiptericum. This has caused considerable misunderstanding in mammal–reptile comparisons.)

Multis.: entered by →prootic vein and by →post-trigeminal vein from semilunar fossa. Communications (pattern variable) with →supraglenoid, →postglenoid veins. Blood may leave through postglenoid or stylomastoid veins, to join external jugular vein or run medially to join internal jugular vein.

#### Lateral sinus (*sinus lateralis*)

Gen.: in human anatomy used to mean composite of →transverse and →sigmoid sinuses. Not recommended for use, and removed from recent *Nomina* as it embraces too much territory to be useful analytical unit. Because of this prior use, ‘lateral sinus’ (Parker 1885) and ‘lateral cerebral sinus’ (P. Butler 1948), often mentioned in accounts of ‘sinus canal’ (Watson 1911), are probably invalid.

Multis.: term not used here, and no evidence for completion of ventral part.

#### Lateral trough (*sulcus lateralis*)

Gen.: term used by Kermack (1963) for elongate depression on ventral aspect of triconodont petrosal, medial to →lateral flange and lateral to →promontorium.

Multis.: equivalent but more complex sulcus here identified as →facial sulcus.

#### Masticatory foramen (*foramen masticatorium*): →foramen masticatorium.

#### Mandibular nerve (*nervus mandibularis*)

Gen.: third principal branch of trigeminal nerve. In mammals, leaves →cavum epiptericum either through →foramen ovale in →alisphenoid or wholly behind alisphenoid, in →carotid canal (foramen lacerum medium). In some forms, anterior division through →foramen masticatorium, posterior division through →foramen ovale inferium. Anterior division motor to muscles of mastication and sensory to oral vestibule (buccal nerve), posterior division motor to floor of mouth (mylohyoid nerve) and sensory to tongue (lingual nerve), lower jaw (inferior alveolar nerve) and side of face (auriculotemporal nerve). In *Ornithorhynchus*, deep temporal branch of anterior division sometimes enclosed in separate foramen in anterior lamina.

Multis.: (figure 32) as here interpreted, →foramen masticatorium and →foramen ovale inferium present, and in some Taen. deep temporal foramen possibly represented by →dorsal foramen of anterior lamina.

#### Mastoid (*pars mastoidea ossis petrosi*)

Gen.: in mammals, posterior part of petrosal bone, derived from →crista parotica behind level of styloid process and postero-lateral to jugular fossa. Possibly partly equivalent to reptilian opisthotic.

Multis.: contributes to occiput. Bone previously reported as ‘→tabular’ shown here to be mastoid.

#### Mastoid emissary vein (*vena emissaria mastoidea*)

Gen.: in modern mammals, emissary vein running from prootic vein through occipito-capular fissure of chondrocranium to join occipital veins. Paracranial part, between squamosal and petrosal, probably homologous with the →post-temporal vein of Multis.

Mastoid foramen (*foramen mastoideum*)

Gen.: foramen of →mastoid emissary vein, probable homologue of →post-temporal fossa.

Maxillary artery (*arteria maxillaris*)

Gen.: extracranial or paracranial artery, usually branch of carotid system, supplying face and jaws. In mammals may be supplied via →stapedial or →external carotid arteries. Can run through alisphenoid canal, and a terminal branch runs through infraorbital canal.

Multis.: here considered to be present, running in some genera through →canal from facial sulcus to foramen near →foramina masticatorium and ovale inferium.

Maxillary nerve (*nervus maxillaris*)

Gen.: second principal branch of →trigeminal nerve. In many vertebrates leaves →cavum epiptericum with →mandibular nerve, behind ascending process of epipterygoid, but in mammals leaving either through →foramen rotundum, anteriorly placed in →alisphenoid, or wholly in front of alisphenoid, through →sphenorbital fissure (foramen lacerum anterior).

Multis.: here interpreted as passing through →sphenorbital fissure.

Medial head vein (*vena capitis medialis*)

Gen.: in vertebrates, longitudinal vein collecting blood from brain, orbit and rostrum, lying medial to cranial nerve ganglia. One of earliest recognizable veins in embryos, major tributary of anterior cardinal vein. In mammals, becomes plexiform and persists as the →cavernous sinus, but otherwise in large part superseded by other channels, principal early one being through →post-trigeminal vein to →lateral head vein.

Multis.: here presumed represented in cavum epiptericum by veins including →cavernous sinus.

Medulla oblongata (*medulla oblongata*)

Gen.: portion of hindbrain caudal to →pons, and merging with spinal cord caudally. Includes →pyramids and olives as surface markings in mammals, and gives origin to roots of cranial nerves IX, X, XI and XII.

Meningeal vessels (*vasa meningeae*)

Gen.: in mammals, arteries and veins usually running together between bone of neurocranium and dura mater, supplying latter, bone and red marrow of skull. In man, largest artery is middle meningeal, entering middle cranial fossa in posterolateral part of cavum epiptericum near to petrosal nerves.

Multis.: large size of ‘→hiatus Fallopii’ and association with ‘→Vidian groove’, and dorso-lateral fissure in *Nemegtbaatar* suggest analogous vessels.

Neocortex (*neocortex*)

Gen.: in mammals, lateral and dorsal part of cerebral cortex with characteristic laminar histology. May be smooth (lissencephalic) or sulcate.

Multis.: poorly demarcated on endocast. Smooth when seen.

Occipital bone (*os occipitale*)

Gen.: complex of basioccipital, exoccipital and supraoccipital. Basioccipital forms caudal element of basicranium, and complex surrounds foramen magnum.

Multis.: (figures 6, 20c and 21) elements completely fused in Asian Taen. form extensive bone, ventral aspect triangular, posterior aspect roughly rectangular. Suture with →basisphenoid transverse at level of foramen ovale inferium. Sutures with petrosal (occipital parts of this previously incorrectly identified as →tabular) well preserved in juvenile skull of *Kamptobaatar* (Kielan-Jaworowska 1971). Also →occipital condyle and →jugular fossa.

Occipital condyle (*condylus occipitalis*)

Gen.: in mammals, usually bilateral, partly on →basioccipital and partly on →exoccipital.

Multis.: (figures 6, 11, 12 and 20c) in numerous Taen. very low in ventral aspect, more prominent in endocranial aspect (Kielan-Jaworowska 1971, 1974; Kielan-Jaworowska & Dashzeveg 1978), hollow inside. Deformation artefact referred to as 'basioccipital box' (Kielan-Jaworowska & Dashzeveg 1978). Presumably a resonatory air space together with cavity of paroccipital process. In other Taen., Plag. (Hahn 1969) and Ptil. (Simpson 1937; Sloan 1979) occipital condyles prominent externally, state of interior not known.

Occipital sinus (*sinus occipitalis*)

Gen.: in mammals, median dural sinus running to superior sagittal sinus over occipital, with tributaries from dorsal surface of cerebellum.

Occipital vein (*vena occipitalis*)

Gen.: in mammals, plexus of veins in neck muscles, draining extracranially to →internal and →external jugular veins. Receive blood from →vertebral, →mastoid emissary, →spurious jugular and →condylar emissary veins.

Olfactory bulb (*bulbus olfactorius*)

Gen.: anterior lobe of cerebrum lying upon →cribriform plate in mammals. Primary connection of olfactory nerve, connected to rest of cerebrum by olfactory tracts.

Multis.: (figures 7, 16, 18, 20a and 32) proportionately larger than in other mammals.

Ophthalmic vein (*vena ophthalmica*)

Gen.: in mammals, superior and inferior groups, former drains to cavernous sinus, latter to →cavernous sinus and →pterygoid plexus. Blood here gets impulsion from eye movements. These also drain superficially to →external jugular tributaries in skin of face and receive blood from the →ethmoidal veins.

Optic foramen (*foramen opticum*)

Gen.: in →orbitosphenoid, for optic nerve, usually at or just anterior to level of optic chiasma.

Multis.: (figure 29) piercing anterior part of sphenoid bone in *Pseudobolodon* (Hahn 1981). In *Nemegtobaatar*, possibly piercing orbitosphenoid just lateral to →taenia clino-orbitalis to enter anterior part of →cavum epiptericum.

Orbital fissure (*fissura orbitalis*) →sphenorbital fissure

\*Orbital groove (*sulcus orbitalis*)

Multis.: (figure 20*b*) faint extracranial groove, possibly vascular. In various Taen. running from postorbital process over parietal and orbitosphenoid, turning down at rear of postorbital ridge to reach ethmoid foramen.

\*Orbital ridge (*crista orbitalis*)

Multis.: (figure 20*b*) vertical ridge in medial wall of orbit on posterior part of frontal. Bounds orbitonasal fossa posteriorly and supports cranial roof overhanging orbit.

Orbitonasal foramen (*foramen orbitonasale*) →orbitonasal fossa.

\*Orbitonasal fossa (*fossa orbitonasalis*)

Multis.: (figure 20*b*) deep, rounded fossa in cranial roof of orbit, in frontal; in Asian Taen., described for *Kamptobaatar* and *Sloanbaatar* (Kielan-Jaworowska 1971), two fossae in latter, anterior largest. Minute →orbitonasal foramen in fossa on left in *Kamptobaatar*. Possibly for gland.

Orbitosphenoid (*ala orbitalis (s. minor) ossis sphenoidalis*)

Gen.: usually endochondral wing of →sphenoid anterior to pituitary fossa forming medial wall or roof of orbit.

Multis.: (figures 20*b* and 29) in *Kamptobaatar* (Kielan-Jaworowska 1971) very large fan-shaped bone constituting most of interorbital wall, shape here confirmed in other Asian Taen. Continuous posteriorly below anterior lamina of petrosal with medial wall of cavum epiptericum as →taenia clino-orbitalis.

\*Orbito-temporal vessels (*vasa orbitotemporales*)

Multis.: term employed here for the vessels in →post-temporal canal, →ascending canal and →internal parietal groove system. These vessels may be major arteries with venae comitantes, and show signs of being affiliated to the →sinus canal of therapsids, triconodonts and tritylodonts. Morphologically distinct from →dural sinuses, as are the →meningeal vessels of modern mammals.

Palaeocortex (*palaeocortex*)

Gen.: in mammals, cerebral cortex of very primitive structure, ventrally placed in →pyriform lobe with olfactory connections, distinct from archaeocortex of hippocampal formation and →neocortex.

Palatonasal foramen (*foramen palatonasale*): →palatonasal notch

Palatonasal notch (*sulcus palatonasale*)

Multis.: (figures 6 and 20*c*) slit-like notch lateral to postpalatine torus, previously interpreted as palatonasal foramen in *Kamptobaatar* (Kielan-Jaworowska 1971) but now shown by sections of *Nemegtbaatar* not to penetrate bone fully.

Paraflocculus (*paraflocculus*)

Gen.: in mammals, part of cerebellar palaeocortex immediately cranio-lateral to flocculus. Absent in some mammals but in many a very prominent lobe entering →subarcuate fossa. Function disputed, but very large in aquatic mammals with sophisticated use of axial muscles.

Multis.: as appears from cast of subarcuate fossa, relatively very large.

Parietal bone (*os parietale*)

Gen.: paired dermal bone in skull roof, in mammals suturing anteriorly with frontals, laterally with →alisphenoid and →squamosal and posteriorly with →occipital. Parietals meet in mid-line sagittal suture. Separate postparietals may lie behind parietals.

Multis.: forms whole cranial roof posteriorly, no postparietals.

Paroccipital process (*processus paroccipitalis*)

Gen.: in therapsids, lateral projection of posterior part of petrosal, supporting →squamosal and ventral to →post-temporal canal. Exposed on occipital aspect of skull ventral to →tabular. In mammals, part of →mastoid, ventrally directed behind and lateral to →jugular fossa, often associated with origin of digastric muscle. To be distinguished from paracondylar or jugular process of →occipital, often erroneously called paroccipital, which forms posterior margin of jugular fossa.

Multis.: (figures 1 and 20c) in Taen. prominent, roughly triangular, in ventral aspect lateral to base of →promontorium, posterior to →postglenoid foramen. Constituted by petrosal, in juvenile *Kamptobaatar* showing suture along edge probably between incompletely fused prootic and opisthotic (mastoid) elements. Hollow internally to form small cavity lateral to →condylar cavity. In *Lambdopsalis* (Chow & Qi 1978) paroccipital process and mastoid strongly expanded to form 'tympanic bulla'. '→Hyoid muscle pit' lies medial to it.

Periotic (*os perioticum*): →petrosalPetrosal (or periotic) (*os petrosum s. perioticum*)

Gen.: endochondral ossification in otic capsule surrounding inner ear and vestibular apparatus, lateral to basicranium and forming ventral part of lateral wall of posterior part of cranial cavity. In mammals, fused complex with no distinct reptilian prootic and opisthotic indicated in adults.

Multis.: (figures 1, 4, 8, 9 and 21–29) fusion between elements not complete in juvenile *Kamptobaatar* (→paroccipital process). In mature forms fusion apparently complete, hence mammalian terminology adopted. Inner ear having straight cochlea (lagena). Cochlear aqueduct confluent with fenestra cochleae, vestibule and semicircular canals therian in pattern. Anterior lamina very large, constituting almost the whole posterior part of lateral wall of braincase.

New data from present study: great thickness of vertical part of anterior lamina, housing →prootic canal, and protruding markedly into cranial cavity: structure and connections of →prootic canal, detail of →paroccipital process, →semilunar fossa, →subarcuate fossa. The large area of bone on occipital aspect previously referred to as →tabular now found to house

semicircular canals and corresponding to reptilian opisthotic or mammalian mastoid. Pierced by →post-temporal fossa in some forms but this small in many forms and more similar to →emissary mastoid foramen of modern mammals.

See also: →ascending canal, →canal of subarcuate fossa, →dorsal foramen of anterior lamina, →facial sulcus, →foramen masticatorium, →foramen ovale inferium, '→hiatus Fallopii', internal auditory meatus, →lateral flange, →postglenoid foramen, post-temporal canal, →post-temporal recess, →promontorium, →semilunar fossa, →supraglenoid foramen, →tympanic foramen.

#### Pharyngeal plexus (*venae pharyngeae*)

Gen.: in mammals, plexus of veins around pharynx pumped by swallowing movements. Joined to →pterygoid plexus, and also via →carotid canal and →foramen ovale to →cavernous sinus.

#### Pila antotica (*pila antotica*)

Gen.: endochondral connection between →orbitosphenoid anteriorly and prootic or dorsum sellae of →pituitary fossa posteriorly, forming medial wall of →cavum epiptericum. Cartilaginous in embryos of some mammals, bony in adult *Tachyglossus* where better referred to as →taenia clino-orbitalis since posterior part attached to clinoid processes only, with no attachment to petrosal.

Multis.: extensive →taenia clino-orbitalis present.

#### Pituitary fossa (*fossa hypophysialis*)

Gen.: site in basicranium of pituitary gland (hypophysis) and surrounding vessels and tissues. In man, saddle-shaped (hence 'sella turcica'), with prominent posterior dorsum sellae of basisphenoid forming posterior margin. Clinoid processes form projections at corners of fossa. →Pila antotica or →taenia clino-orbitalis can form lateral wall.

Multis.: (figures 3, 28 and 29) present, dorsum sellae not prominent, →taenia clino-orbitalis present.

#### Pons (*pons*)

Gen.: in mammals, rostral portion of hindbrain named from bridge of fibres running transversely into cerebellar hemispheres on ventral surface. If these middle cerebellar peduncles small, →corpus trapezoideum may be seen caudally. In therians cranial nerves V, VI, VII and VIII emerge from pons.

Multis.: possibly, as in monotremes, the pons lies posterior to the emergence of V.

#### Postglenoid foramen (*foramen postglenoidale*)

Gen.: in mammals, venous foramen posterior to and usually somewhat laterally placed with respect to glenoid fossa of dentary-squamosal jaw-joint. Often situated between prominent retroglenoid tubercle and wall of external auditory meatus. Conveys →postglenoid vein.

Multis.: (figures 1, 20c, 26 and 33) one of the external openings of prootic canal. See Simpson (1937) for *Ptilodus* and Kielan-Jaworowska (1971) for *Kamptobaatar* and *Sloanbaatar*. In present study, used for ventrally placed foramine external to →facial sulcus where connection may be visualized with →external jugular system ventral to confines of temporal fossa. This usage not intended to imply homology between genera.

Postglenoid vein (*vena postglenoidale*)

Gen.: in mammals often largest venous pathway from cranial cavity, fed by →prootic sinus, then normally drains to external jugular system via retromandibular vein. During development, connected with →lateral head vein. This connection the major one in adult monotremes.

Multis.: (figure 32) usually connected with →prootic sinus by →glenoprootic vein and with →supraglenoid vein by →interglenoid vein.

\*Postorbital foramen (*foramen postorbitale*)

Multis.: (figures 20*b* and 28) foramen in parietal at caudal end of →orbital groove, just below or within postorbital process. Here interpreted as transmitting vessels from →internal parietal groove to orbit.

\*Postorbital process (*processus postorbitalis*)

Multis.: (figure 20) projection of parietal bone behind orbit, placed far posteriorly on parietal in Taen. Long, peg-like in *Catopsalis* and *Chulsanbaatar*. Occurrence not known in Plag. and Ptil.

Post-temporal canal (*canalis posttemporalis*)

Gen.: in therapsids, a passage leading from post-temporal fossa forward over paroccipital process to temporal fossa, bridged externally by tabular and squamosal bones.

Multis.: (figure 1) not leading to temporal fossa, but to →ascending canal either in suture between →petrosal and →squamosal, or, in forms with large →post-temporal fossa, through →post-temporal recess in →subarcuate fossa.

Post-temporal fossa (*fossa posttemporalis*)

Gen.: hollow on occipital aspect of skull associated with opening of →post-temporal canal. In therapsids, enclosed in →tabular bone with squamosal laterally and paroccipital process ventrally.

Multis.: (figures 1, 5, 19, 20*c* and 21) described by Kielan-Jaworowska (1971, 1974) in many Taen. as a very large opening on the occipital plate in the →tabular bone, now regarded as →mastoid. Sections of *Nemegtbaatar* show fossa leads to large post-temporal recess in subarcuate fossa. In this case post-temporal canal corresponds only to thickness of petrosal bone pierced by this communication. In *Catopsalis* (figure 1) and the eucosmodontid skull from Djadokhta Formation (figure 5), post-temporal fossa reduced to small opening comparable with →emissary mastoid foramen of modern mammals. This fossa in *Catopsalis* leads to relatively short post-temporal canal joining ascending canal, both canals exterior to wall of subarcuate fossa.

\*Post-temporal vessels (*vasa posttemporales*)

Gen.: vessels passing through →post-temporal canal, in therapsids connecting temporal fossa with occipital region, equated with →arteria diploetica magna of *Tachyglossus* and its accompanying veins. In other modern mammals, →mastoid emissary vein to →occipital veins may be a vestige.

Multis.: extended via →ascending canal to rest of →orbitotemporal system. In *Catopsalis*



communicates with →postglenoid foramen and in unidentified Hell Creek petrosals with →stylomastoid foramen.

\*Post-trigeminal canal (*canalis posttrigeminalis*)

Multis.: (figures 1, 8 and 27) canal leading from posterior end of →semilunar fossa back to anterior end of →facial sulcus. Here interpreted as associated with →post-trigeminal vein and →superficial petrosal branch of facial nerve.

Post-trigeminal vein (*vena posttrigeminalis*)

Gen.: in mammals, used by Padgett (1957) and H. Butler (1967) for that portion of →primary head vein connecting →medial head vein (→cavernous sinus) with →lateral head vein in →facial sulcus. In modern mammals present only in embryos.

Multis.: here interpreted as present in adults, because of size of →post-trigeminal canal.

Primary head vein (*vena capitis prima*)

Gen.: usage after Padgett (1957), principal longitudinal cephalic vein in the embryos of all vertebrates, superseding →medial head vein prior to the condensation of the chondrocranium. Subdivided into segments: medial segment (→medial head vein), post-trigeminal segment (→post-trigeminal vein) and lateral segment (→lateral head vein). In monotremes, medial and lateral segments retained. In other modern mammals, only medial segment retained as →cavernous sinus, otherwise superseded by communications with →external jugular system and sometimes by later development of →petrosal sinuses connecting with internal jugular system medial to petrosal bone.

Multis.: here interpreted as being fully present.

Promontorium (*promontorium cochleae*)

Gen.: strictly applies to eminence in tympanic cavity over first turn of cochlea, hence term properly used only in therian mammals. Has been loosely applied in palaeontology to ventral prominence of petrosal where cochlea or lagena is enclosed.

Multis.: (figures 1, 6, 8 and 20c) usually narrow, parallel-sided, relatively long, housing nearly straight cochlea (lagena). →Fenestra cochleae facing postero-medially into jugular fossa, with groove for →cochlear aqueduct leading from fenestra medially into fossa. →Fenestra vestibuli separated from fen. cochleae only by narrow bridge of bone, faces antero-ventro-laterally.

Prootic canal (*canalis prooticus*)

Multis.: (figures 1, 8 and 27) relatively broad vascular canal in anterior lamina of petrosal. Runs between intracranial foramen at anterior end of groove for →prootic vein and →tympanic foramen where it enters →facial sulcus. Joined by →glenoprootic canal from laterally at its ventral end.

Prootic vein (*vena prootica*)

Gen.: in mammals, large venous channel leading from →transverse sinus forwards and downwards in front of otic capsule to join the →primary head vein (embryos, adult monotremes) or →external jugular venous system. In many modern therians forms part of

major drainage pathway of intracranial veins (Padget 1957; Butler 1967). In development, first joins →primary head vein near junction of →post-trigeminal segment with →lateral segment, later principally drains into external jugular system via →postglenoid vein. This portion of its course often directed laterally and then parasagittally within cancellous bone of squamosal to reach →postglenoid foramen, and may receive supraglenoid veins from dorsally. Primary head vein connection persists in monotremes, leaves mainly via stylomastoid veins to external and internal jugular.

Multis.: (figures 32 and 33) prootic vein dorsally lies in groove on →anterior lamina (strictly prootic sinus) and then enters vertical canal (strictly only then becoming 'vein') to connect ventrally with →lateral head vein and →glenoprootic vein.

Pterygoid plexus (*plexus venosus pterygoideus*)

Gen.: in modern mammals, venous plexus associated with bellies of deep jaw-muscles. An important site of muscle-pumping in recent mammals. Connected to →external jugular veins for superficial drainage, and to →postglenoid system, through →supraglenoid foramen and bony canal in squamosal.

Pyramid (*pyramis medullae oblongatae*)

Gen.: in modern mammals, when present, longitudinally directed elevations close to mid-line containing cortico-spinal fibre tracts prior to their decussation.

Pyriform lobe (*corpus pyriforma cerebri*)

Gen.: in modern mammals, infero-laterally placed part of cerebral cortex with characteristic and simple histology (archaeopallium), just behind olfactory tracts, associated with olfaction.

Rhinal fissure (*sulcus rhinalis*)

Gen.: in modern mammals, sulcus bordering lateral margin of →pyriform lobe, demarcating cortex with primitive structure (archaecortex) from the more laterally and dorsally placed more complex cortex (neocortex).

Multis.: (figure 7) indistinct.

Rhombencephalon (*rhombencephalon*)

Gen.: collective term for hindbrain, containing →cerebellum →pons and →medulla oblongata.

Sagittal sinus (*sinus sagittalis*)

Gen.: equivalent of →superior sagittal sinus, present in forms with very shallow sagittal fissure and correspondingly low falx cerebri so that →inferior sagittal sinus absent and its functions assimilated into sagittal sinus.

Multis.: uncertain whether single or double.

Semicircular canals (*ducti semicirculares*)

Gen.: lateral (horizontal), anterior (superior) and posterior canals enclosed within →petrosal in mammals. Anterior and posterior canals meet in crus commune connecting with vestibule.

Multis.: (figures 10, 15 and 20*b*) here found to show typical mammalian pattern, but in small forms with thin skull bones, raising ridges on outer surface.

Semilunar fossa (*impressio trigeminale*)

Gen.: name from human, where →trigeminal ganglion also called semilunar ganglion. Is shallow fossa on petrosal in which ganglion lies. Represents most of →cavum epiptericum in man.

Multis.: (figures 1, 4, 7 and 8) large posterior compartment of →cavum epiptericum, impressed into antero-medial aspect of →anterior lamina of petrosal. →Foramen ovale inferium, →foramen masticatorium, and in some cases →dorsal foramen lead from its lateral aspect, while →post-trigeminal canal leads posteriorly to →facial sulcus. In some forms separated from more anterior part of cavum by ridge of bone on →anterior lamina.

Semilunar ganglion (*ganglion semilunare*) →trigeminal ganglion

Sigmoid sinus (*sinus sigmoideus*)

Gen.: in man, where name introduced, dural sinus inscribed on posterior aspect of petrosal and adjacent bones running from →transverse sinus to →jugular foramen. By definition becomes →internal jugular vein at internal margin of jugular foramen. Not usually joined within skull by →inferior petrosal sinus. May receive posterior →cerebellar veins. In many mammals communicates with →vertebral venous plexus extensively or exclusively, running back within foramen magnum, or through posterior condylar canal. In such cases, inferior segment connecting with jugular foramen is absent.

Multis.: (figures 7, 10, 20*c*, 32 and 33) seen running caudally from →transverse sinus, but no evidence for course to →jugular foramen.

Sinus canal (*canalis sini*)

Gen.: term frequently used in therapsid literature, following Watson (1911) for groove in epipterygoid–parietal suture, usually considered (but questioned here) to be venous, following Parker (1885) in therians.

Multis.: here equated with part of →internal parietal groove, and held to be primarily arterial (also →orbito-temporal vessels).

Sphenoid bone (*os sphenoidale*)

Gen.: in mammals, complex of basisphenoid and presphenoid in basicranium, joined ventral to →pituitary fossa by cartilage or bone. These have appended wings: →orbitosphenoid joining presphenoid and →alisphenoid joining basisphenoid at about level of →pituitary fossa. In modern mammals →pterygoids fused to →alisphenoid.

Sphenorbital fissure (*fissura sphenorbitalis*)

Gen.: in mammals, aperture (also called orbital fissure or anterior lacerate foramen), usually approximately triangular with apex dorsally, between orbitosphenoid and alisphenoid (therians) or anterior lamina (monotremes). Allows passage of contents of →cavum epiptericum forward to orbit.

Multis.: (figure 20*b*) in *Pseudobolodon* (Hahn 1981) large opening connected by long channel with cavum epiptericum. Shown here in Late Cretaceous forms to be scarcely visible in side view, being the forward opening of the →cavum epiptericum into the orbit, with →anterior lamina and minute →alisphenoid laterally, with →taenia clino-orbitalis and orbitosphenoid medially, and floored by floor of the cavum epiptericum.

Sphenopalatine foramen (*foramen sphenopalatinum*)

Gen.: passage for entry of nerves and vessels from outside lateral wall of nasal cavity to interior to supply mucous membrane of nose and palate. See also →superficial petrosal nerve.

Multis.: (figure 20*b*) at junction of maxilla, frontal, orbitosphenoid and palatine in Taen. and seen in sectioned skull of *Nemegtbaatar*. From it, wide sphenopalatine groove runs posteriorly along ventral part of orbitosphenoid to cavum epiptericum.

Sphenopalatine groove (*sulcus sphenopalatinus*): →sphenopalatine foramen

Spurious jugular foramen (*foramen jugulare spurium*)

Gen.: in mammals, venous foramen for an analogue of the →mastoid emissary vein, connecting →prootic vein with →occipital veins through capsulo-parietal foramen in chondrocranium and thus in adult skull between mastoid part of petrosal and occipital. In some mammals functionally replaces →internal jugular vein.

Spurious jugular vein (*vena jugulare spurium*) →spurious jugular foramen

Squamosal (*os squamosum*)

Gen.: in mammals, dermal bone bearing glenoid fossa for dentary–squamosal jaw-joint and making variable contribution to wall of braincase.

Multis.: (figures 6, 20 and 22–26) insignificant contributor to braincase, placed far posteriorly and building the strong, prominent lambdoid crests characteristic of multituberculates. Forms strong zygomatic arch with large glenoid fossa, and anteriorly contacts maxilla directly, also jugal, see note 2 on page 602.

Stapedial artery (*arteria stapedis*)

Gen.: lateral branch of internal carotid artery, widespread in early development of mammals, representing branch of second aortic arch distributed to face and jaws. Can have →inferior ramus to upper and lower jaws and infraorbital region, superior ramus to meninges, cranial bones, orbit and supraorbital region, and posterior ramus to occiput and →stylomastoid region. In view of prevalence in modern mammals, and in other vertebrates, should be considered as possibly primitive structure, but its distribution can be frequently annexed by branches of the →external carotid artery.

Multis.: here shown probably to be present, with evidence for maxillary and meningeal connections.

Straight sinus (*sinus rectus*)

Gen.: in mammals, a dural sinus running through tentorium cerebelli in midline, thus along posterior aspect of falx cerebri, only in contact with bone at its junction (confluence or torcula)

with →superior sagittal sinus and →transverse and →occipital sinuses. Can receive blood from →inferior sagittal sinus, and from dorsal aspect of brain stem, thalamus, basal ganglia, etc. (great cerebral vein in man).

#### Stylomastoid vessels (*vasa stylomastoidea*)

Gen.: in mammals, →lateral head vein may leave facial sulcus caudal to exit of facial nerve by turning laterally as stylomastoid vein, which may then communicate with →external or →internal jugular systems away from contact with the skull. In some mammals a stylomastoid artery, arising from →external carotid artery or →stapedial artery can be major supply to occiput, meninges and more anterior regions.

Multis.: here →lateral head vein is reconstructed in all forms continuing caudally as stylomastoid vein. In the isolated Hell Creek petrosals stylomastoid foramen, and in *Catopsalis* the postglenoid foramen, connected with the →ascending canal, raising the possibility that an arterial connection may have been present between stylomastoid-like vessels and →orbito-temporal system.

#### Stylomastoid foramen (*foramen stylomastoideum*) →foramen stylomastoideum

#### Subarcuate fossa (*fossa subarcuata*)

Gen.: in mammals, recess in medial aspect of →petrosal beneath anterior →semicircular canal and behind →internal auditory meatus. In many but not all mammals houses →paraflocculus of cerebellum and hence often called 'parafloccular recess'.

Multis.: (figures 1, 4, 8 and 21–24) proportionately larger than in other known mammals. In some Taen. also connected with body of cranial cavity by →ascending canal and with →post-temporal fossa by →post-temporal canal. In *Catopsalis* communication from fossa to post-temporal canal is minute.

#### Superficial petrosal nerve (*nervus petrosus major*)

Gen.: in modern mammals, pathways for secretomotor fibres from facial (VII) nerve to join →maxillary (to lacrimal, nasal and palatal glands). Superficial petrosal branch of facial known as →Vidian nerve or nerve of pterygoid canal after joining deep petrosal (sympathetic) nerve from internal carotid artery. Nasal and palatal branches distributed after sphenopalatine ganglion, with maxillary nerve and vessels, through →sphenopalatine foramen. Lesser superficial petrosal nerve connects tympanic branch of glossopharyngeal nerve (IX), via otic ganglion, to parotid gland through auriculotemporal branch of mandibular nerve.

#### Superior petrosal sinus (*sinus petrosus superior*)

Gen.: in mammals, dural sinus joining cavernous and sigmoid sinuses along crista petrosi. Late development in embryos of modern mammals.

Multis.: no clear evidence for its presence.

#### Supraglenoid foramen (*foramen supraglenoidale*)

Gen.: in mammals, site of connection of posterior deep temporal veins through squamosal bone with →prootic vein and →postglenoid vein.

Multis.: (figures 1, 8, 20c and 26) vascular foramen entering lateral aspect of anterior lamina

facing into temporal fossa. Connected by interglenoid canal to postglenoid foramen, and the canal also connected to →prootic canal by →glenoprootic canal. In view of variable pattern described here, and marked irregularity of walls of interglenoid and glenoprootic canals in sectioned skulls, the term is to be regarded as descriptive rather than an indication of homology.

Supraoccipital (*os supraoccipitale*) →occipital bone

Sympathetic nerves (*nervi sympathetici*)

Gen.: in mammals, after relay in cervical sympathetic ganglia, fibres distributed along →internal (deep petrosal nerve), →external carotid and →vertebral arteries.

Tabular (*os tabulare*)

Gen.: in therapsids, dermal bone on occipital plate, associated with →post-temporal fossa.

Multis.: described as large bone, pierced by large post-temporal fossa, between squamosal and exoccipital–supraoccipital on basis of comparison with cynodonts, in *Kamptobaatar* and *Sloanbaatar* (Kielan-Jaworowska 1971). Study of new material, especially *Chulsanbaatar*, *Nemegtbaatar* and *Catopsalis*, shows this bone to house semicircular canals that form ridges on its outer surface (subvertical ridge, medial to post-temporal fossa related to posterior canal; transverse ridge below fossa related to horizontal canal). Sections of *Nemegtbaatar* show no trace of separate tabular. This region should therefore be regarded as mastoid. In some genera the →post-temporal fossa is only a small foramen.

Taenia clino-orbitalis (*taenia clinoorbitalis*)

Gen.: Ossified →pila antotica of flat, ribbon-like form running from posterior clinoid process behind →pituitary fossa to →orbitosphenoid. Gaupp (1908) showed essential homology of this in monotremes with →pila antotica of squamate reptiles, but this term retained here for monotreme bony form to emphasize its flattening, the lack of strong connection with the otic capsule, and its situation wholly medial to abducent (VI) nerve, features not seen in squamates.

Multis.: (figures 28 and 29) here found to be similar to that of monotremes, but much more extensive, possibly secondarily, in relation to the general robustness of the cranial bones.

Temporal fossa (*fossa temporalis*)

Gen.: cranial region behind orbit, in mammals between braincase and zygomatic arch, mainly containing bellies of muscles of mastication and coronoid process of lower jaw.

Multis.: boundary with orbit not clear. Posterior part flares outwards more than in other mammals.

Tentorial sinus (*sinus tentorii*)

Gen.: term employed by Padget (1957), equivalent to posterior rhinencephalic vein in older mammalian terminology. Very mobile in development, and very variable in position in mammals, superseded in man, hence not widely used in *Nomina*. Drains lateral surface cerebral hemisphere, and runs back to join →straight, or →transverse, or →prootic sinuses.

Multis.: (figures 7, 28, 29 and 32) seen in cast in *Chulsanbaatar* joining prootic sinus above semilunar fossa, and as groove anteriorly on anterior lamina in sections of *Nemegtbaatar*.

Transverse sinus (*sinus transversus*)

Gen.: in mammals, dural sinus in attached margin of tentorium cerebelli running from →superior sagittal sinus to →sigmoid or →prootic sinus, boundary recognized by divergence from tentorium.

Multis.: (figures 7, 10, 16, 20*a* and 32) diverges from →sagittal sinus, joins →prootic and →sigmoid sinuses.

Trigeminal ganglion (*ganglion trigeminale*)

Gen.: in mammals, combined ganglion of the three major branches of the trigeminal nerve (unlike other vertebrates where ophthalmic and maxillo-mandibular ganglia separate). Often called semilunar ganglion, hence →semilunar fossa.

Multis.: (figure 32) possibly very large, judged from size of →semilunar fossa.

Tympanic bone (*os tympanicum*)

Gen.: found only in mammals, widely held to be derived from angular bone of lower jaw of therapsids.

Multis.: not described, but figured as preserved as a crescent in *Ectypodus* (Sloan 1979).

Tympanic bulla (*bulla tympanica*)

Gen.: found only in mammals as bone-enclosed expanded tympanic cavity.

Multis.: described as rounded hollow structure postero-lateral to promontorium in *Lambda-psalis* (Chow & Qi 1978). Homology of this as bulla challenged (Kielan-Jaworowska & Sloan 1979). Regarded here as an expansion of →mastoid including paroccipital process. Also →occipital condyle.

\*Tympanic foramen (*foramen tympanicum*)

Multis.: used here in text to denote openings of →facial and →prootic canals into →facial sulcus, to distinguish from endocranial openings of canals. Abbreviated in figures, where no ambiguity, to 'facial canal foramen' and 'prootic canal foramen'.

Venae comitantes (*venae comitantes*)

Gen.: descriptive term for interconnected veins clustered around large arteries, taking name of related artery. Venous blood in them gains impulsion from systolic pulse wave.

Vertebral vessels (*vasa vertebrales*)

Gen.: in mammals, major artery and accompanying plexus of veins that enter subarachnoid space between cervical vertebrae and occiput, or between vertebrae more caudally to supply substantial posterior part of brain and meninges. In modern mammals, vertebral veins form alternative pathway draining venous blood through the foramen magnum, instead of to the internal jugular vein.

Vestibular nerve (*nervus vestibularis*)

Multis.: here used in sense of abbreviated term for superior division of auditory-vestibular (VIII cranial) nerve, being the major nerve supply of the vestibular apparatus.

Vidian (*Vidii*)

Gen.: structures described in human anatomy by Vidius. Has come into widespread use in palaeontology in relation to markings related to nerve of pterygoid canal. This should strictly lie between alisphenoid and pterygoid components, and contain →sympathetic fibres from →internal carotid plexus and the immediate pre-ganglionic fibres of →superficial petrosal branch of the facial nerve, running to sphenopalatine ganglion. Nerves or vessels not conforming to these criteria, but functionally related, are in this paper referred to in quotation marks as 'Vidian', to relate to the previous literature, but to draw attention to the possible misnomer.

Vomer (*vomer*)

Gen.: dermal bone, paired in palate in lower vertebrates, single in secondary nasal septum in advanced therapsids and mammals.

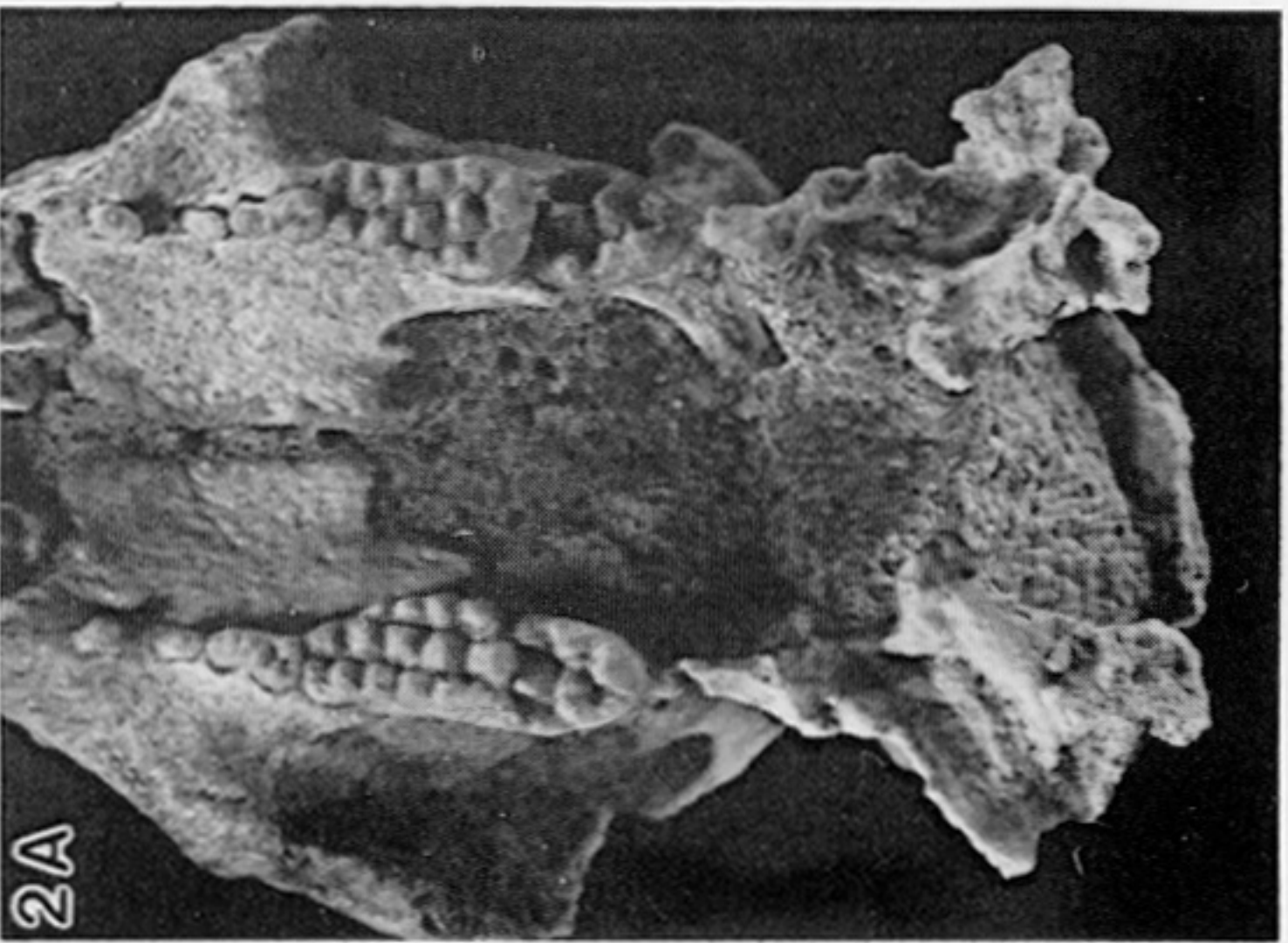
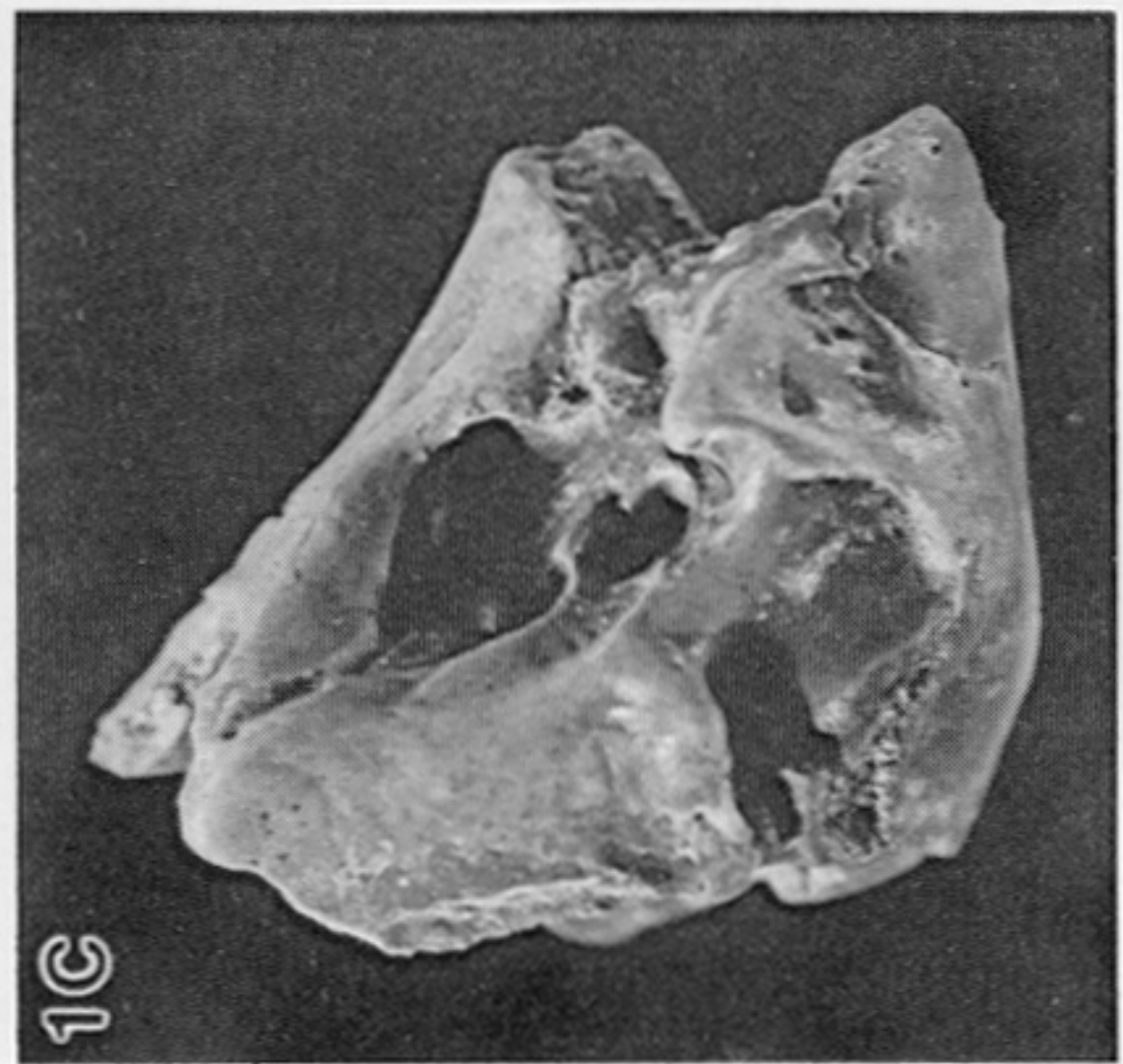
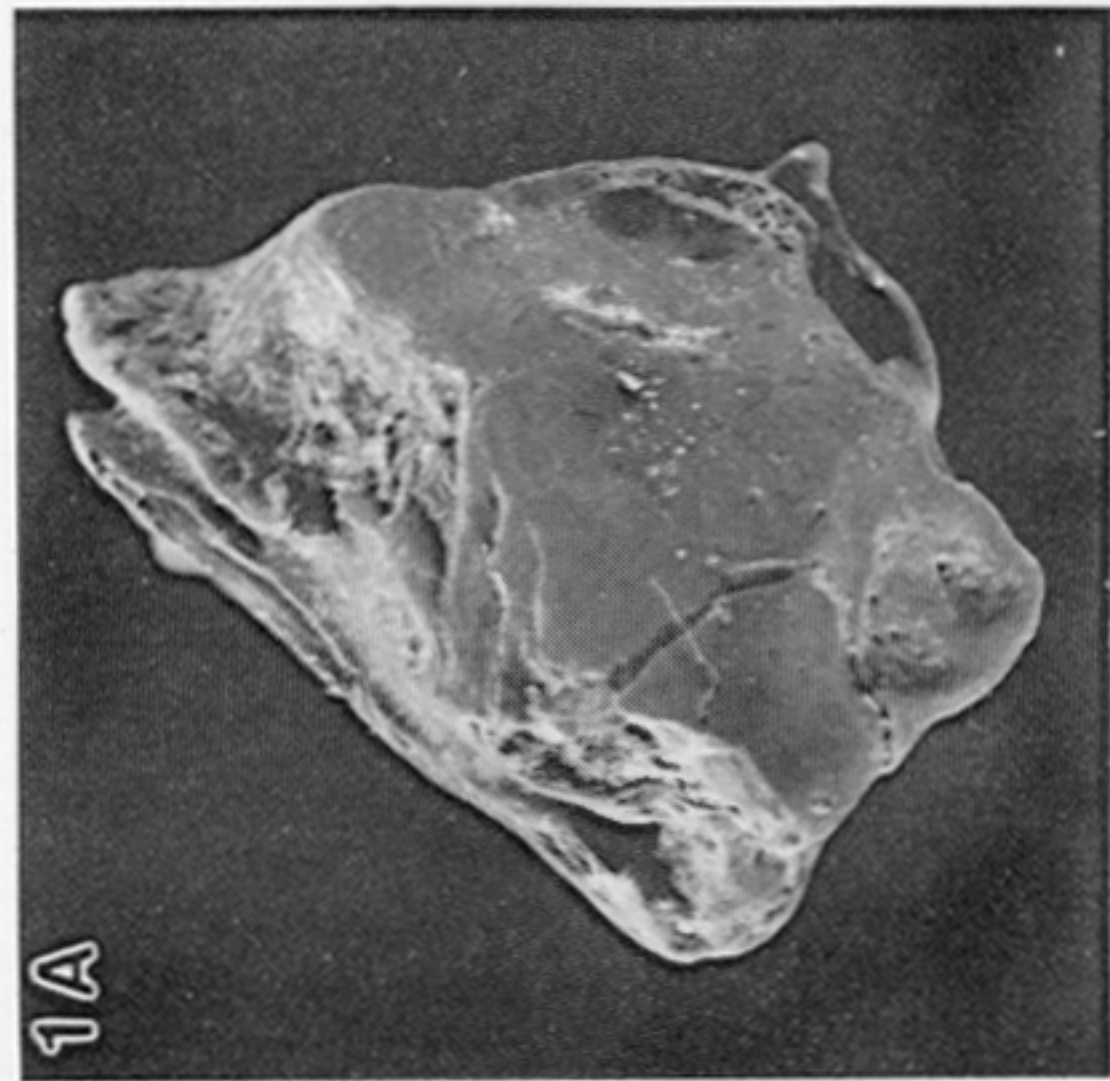
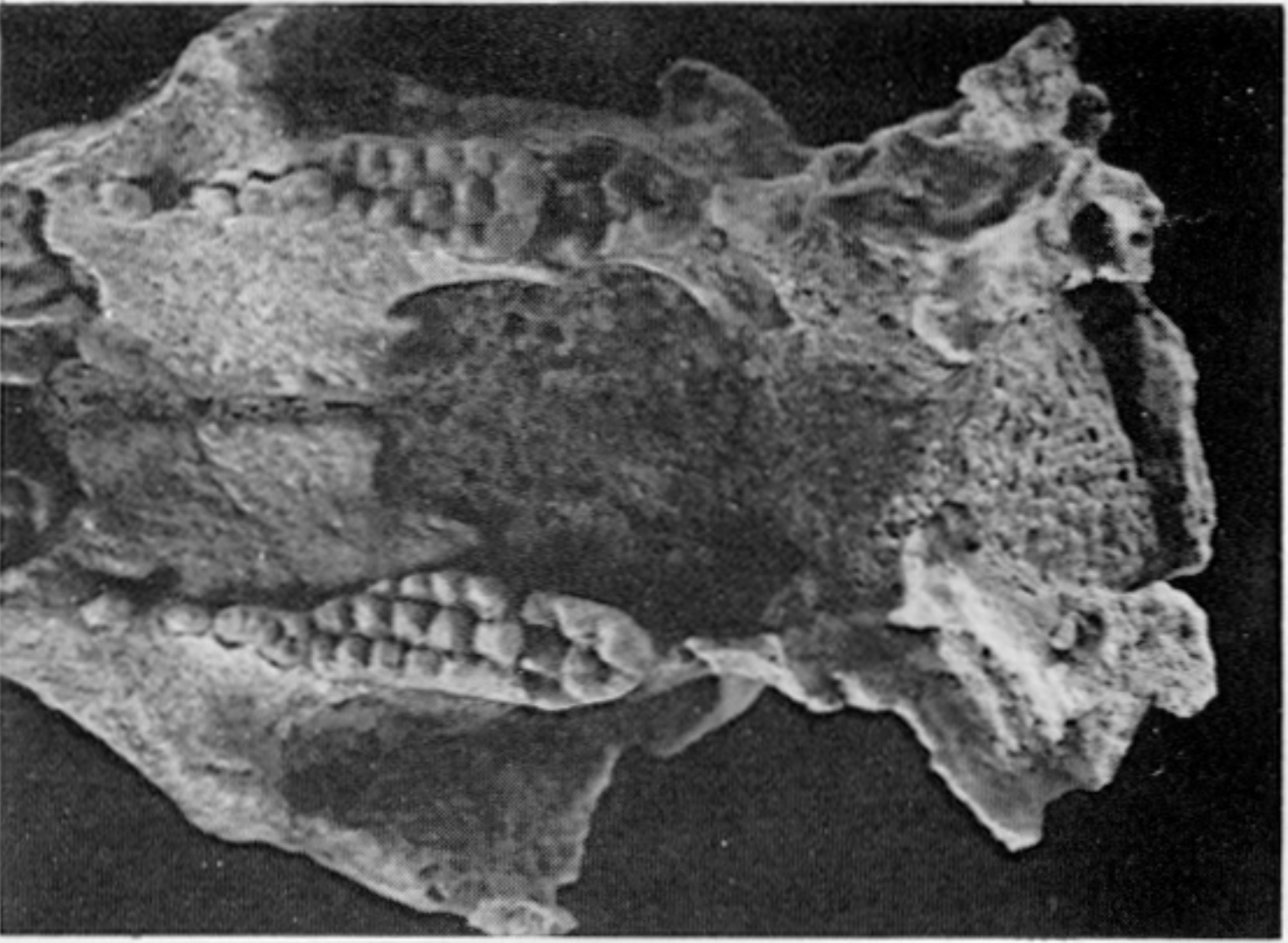
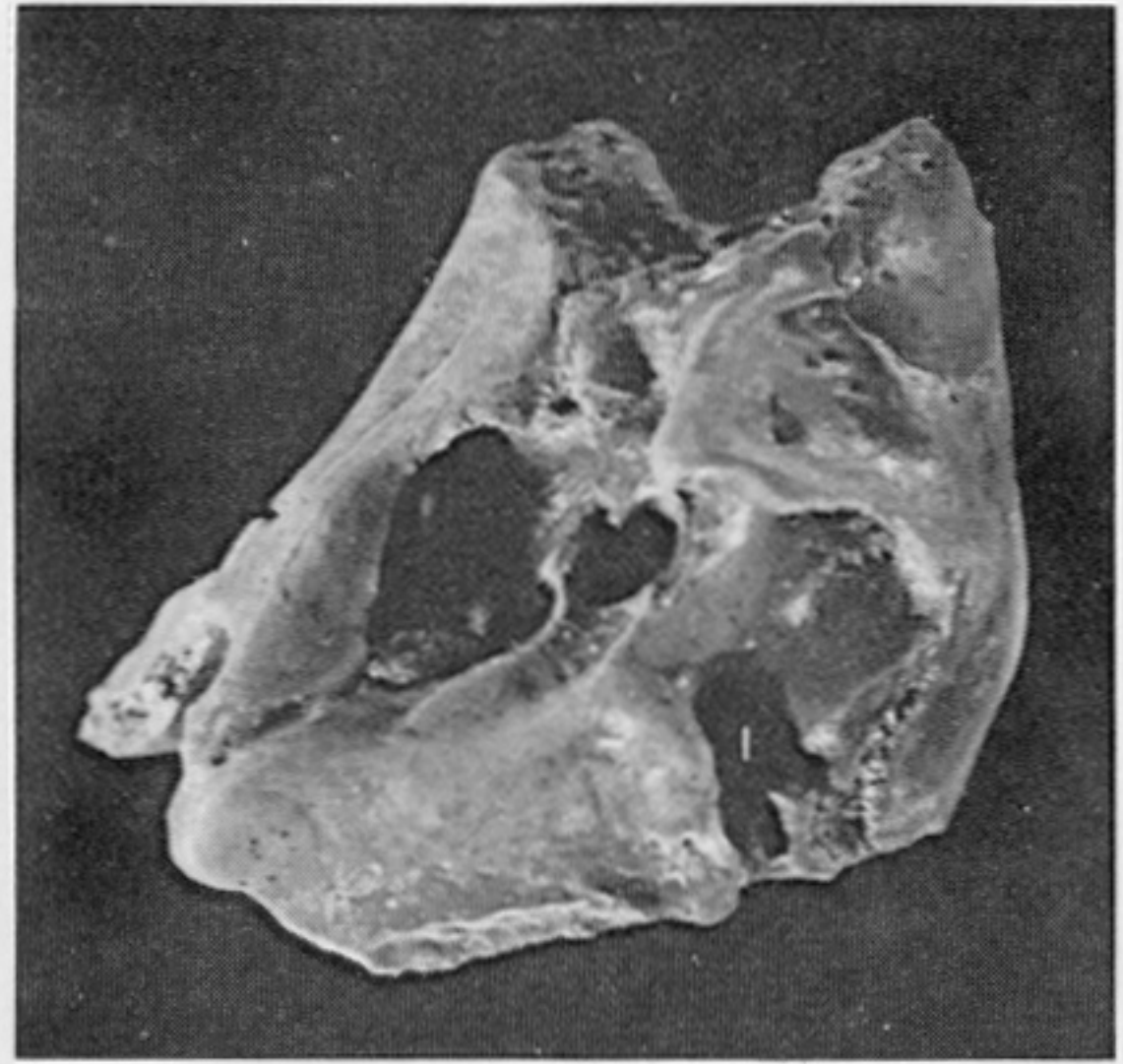
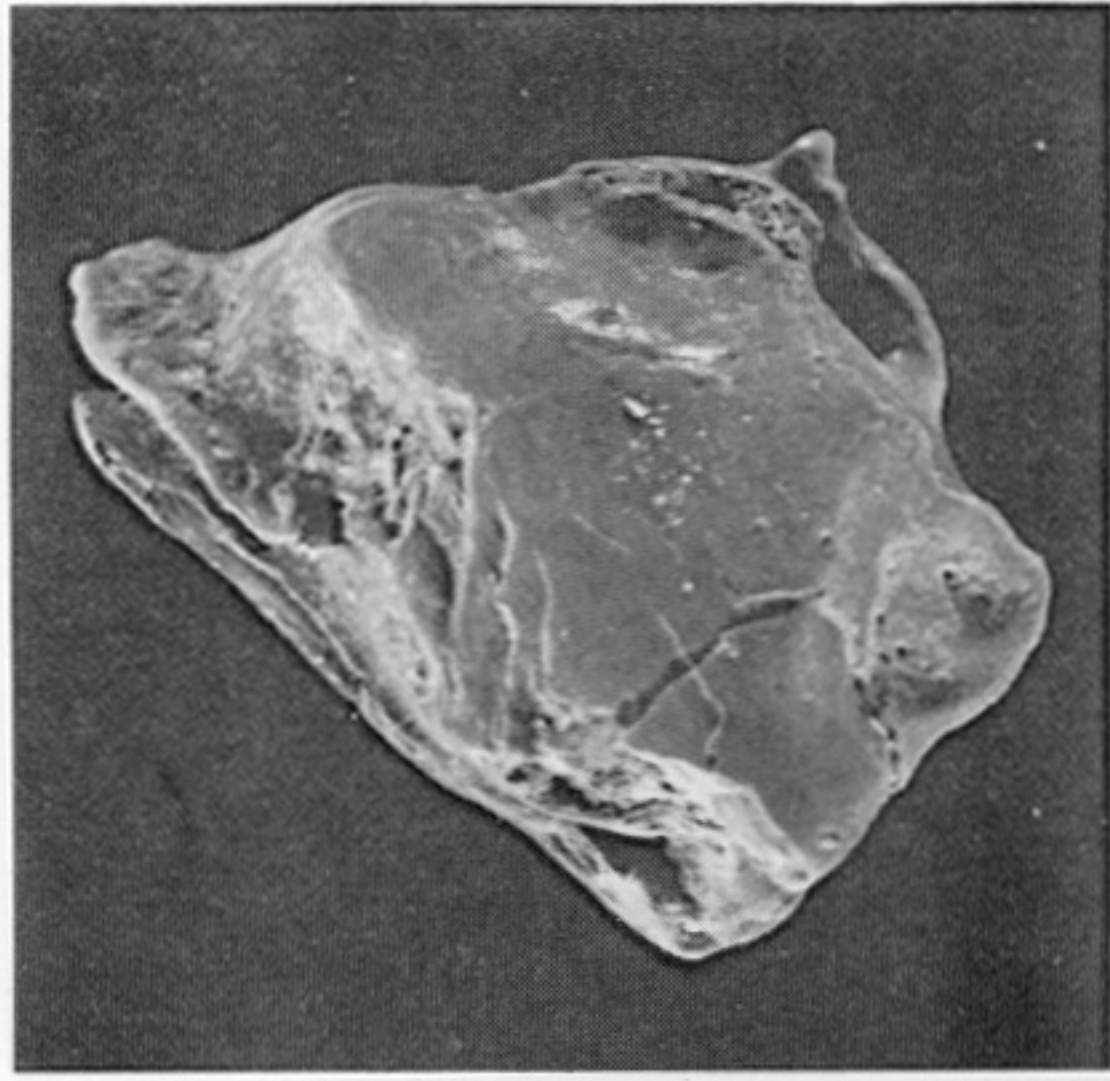
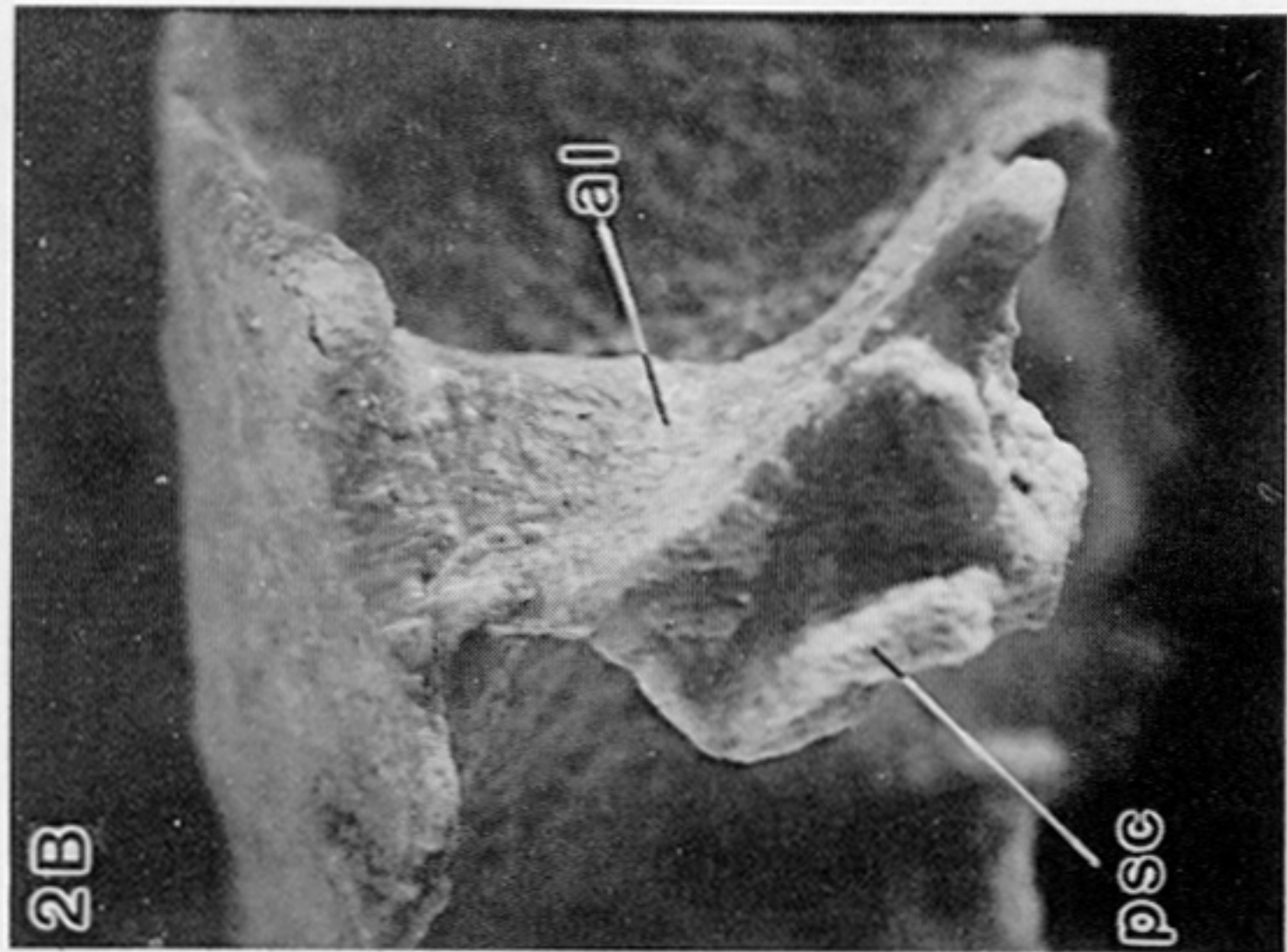
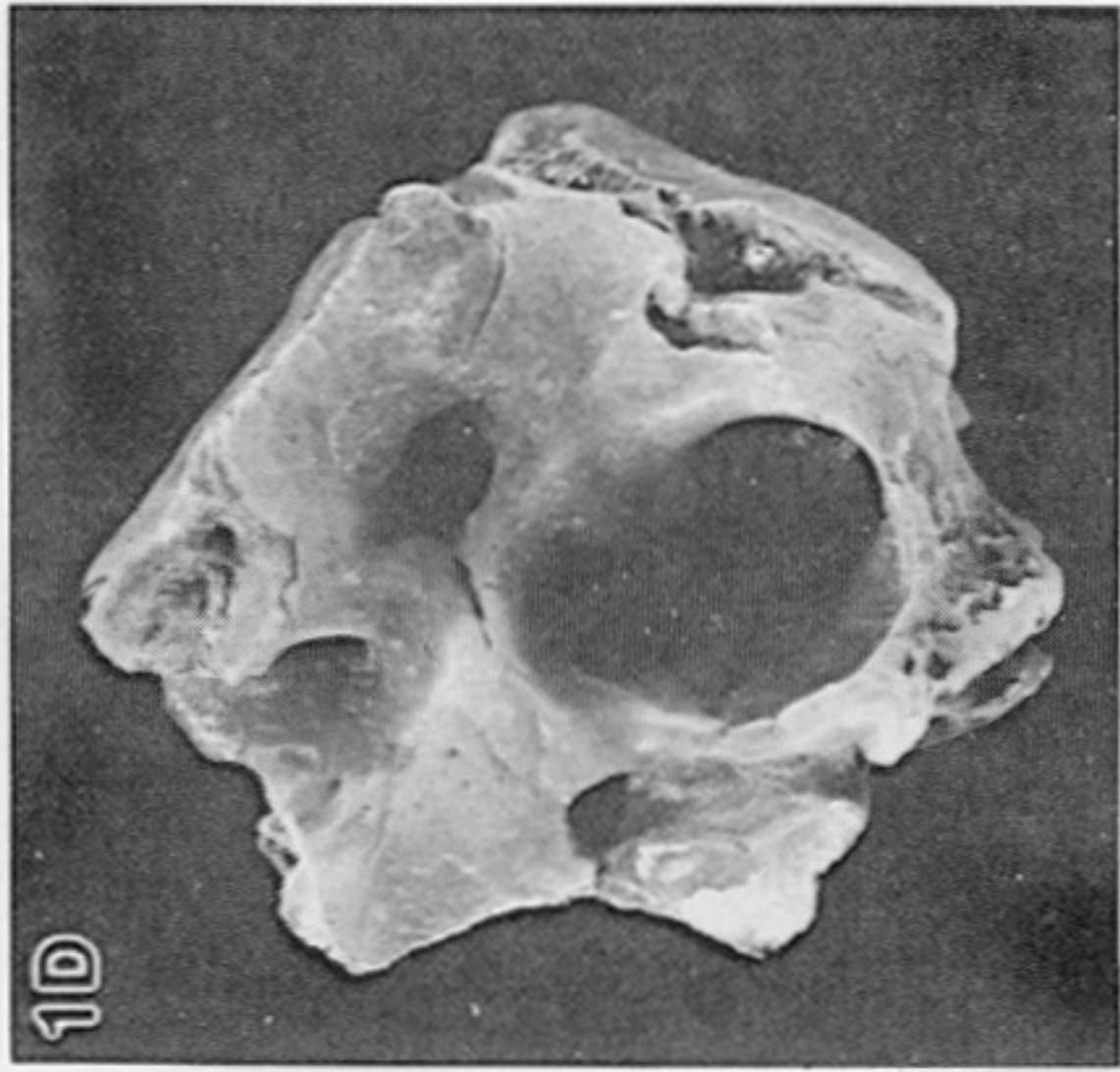
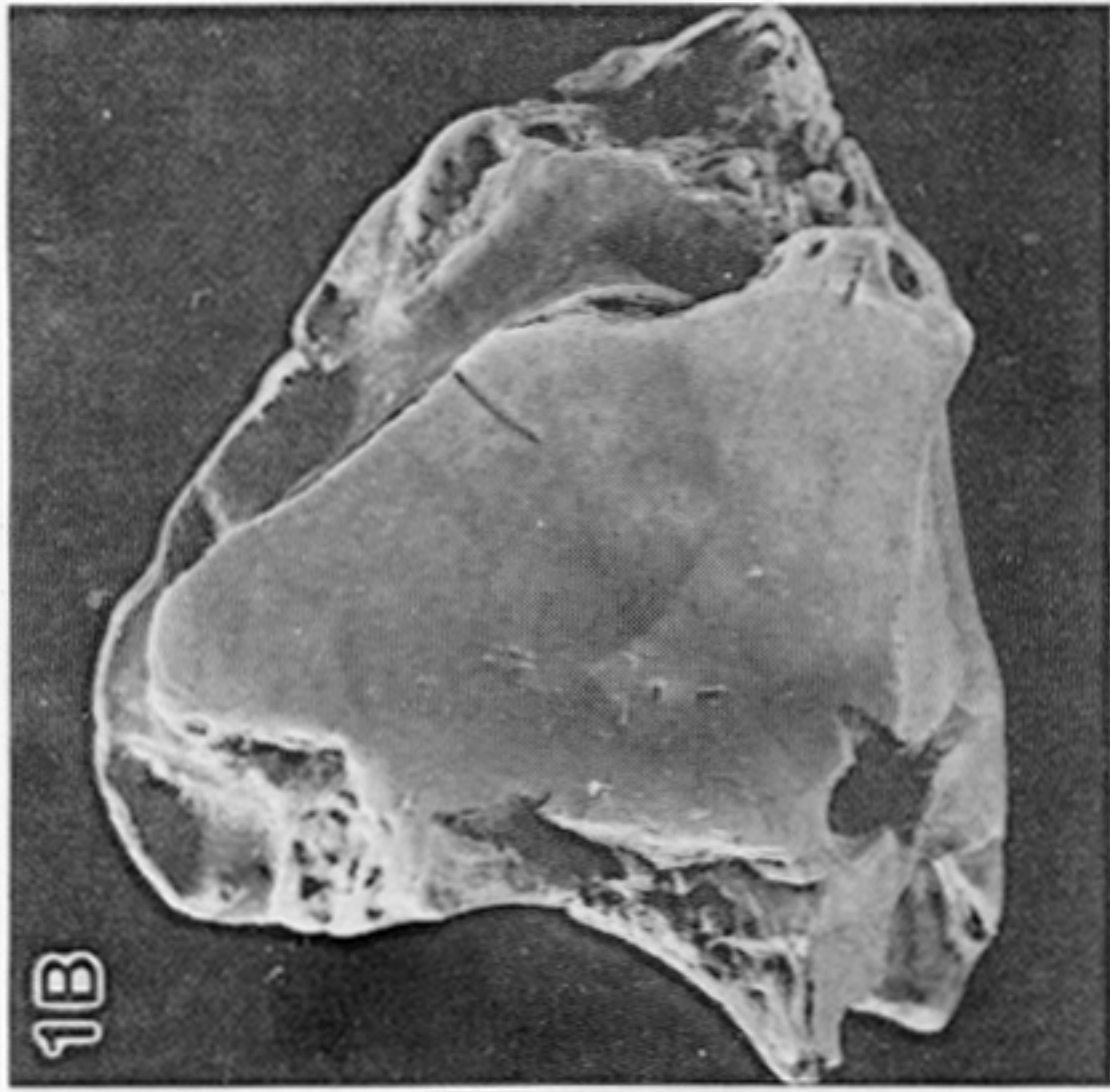
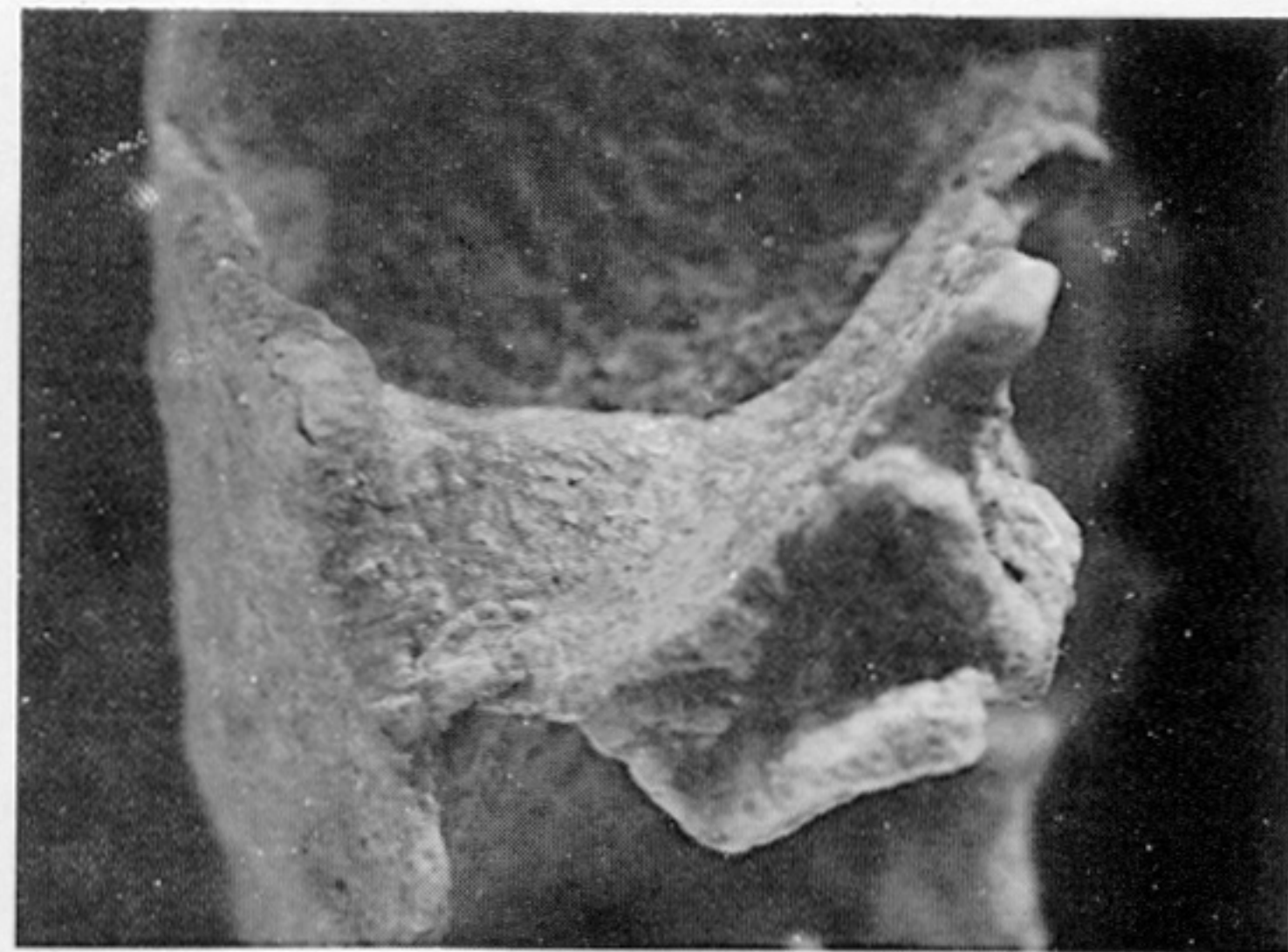
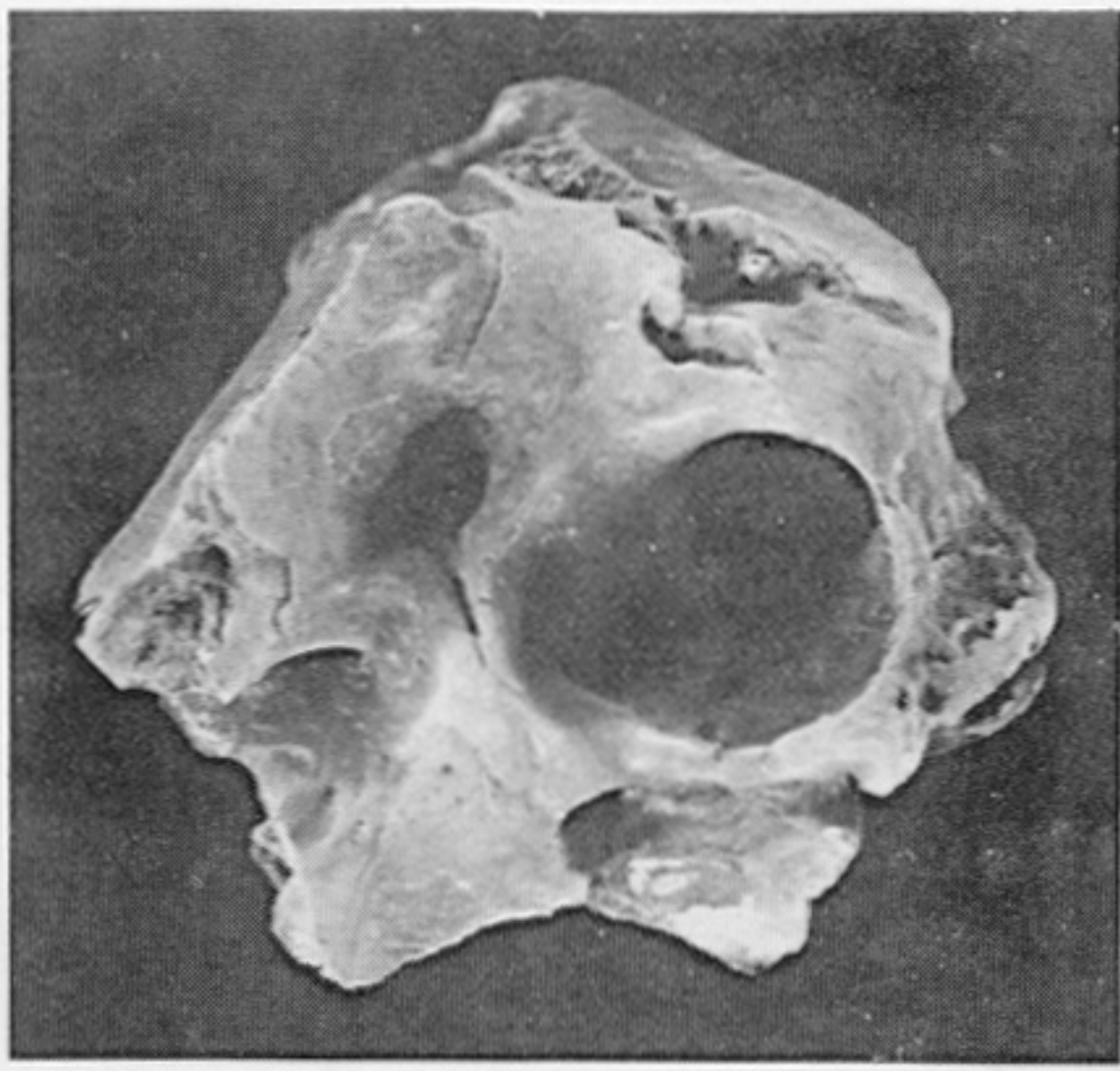
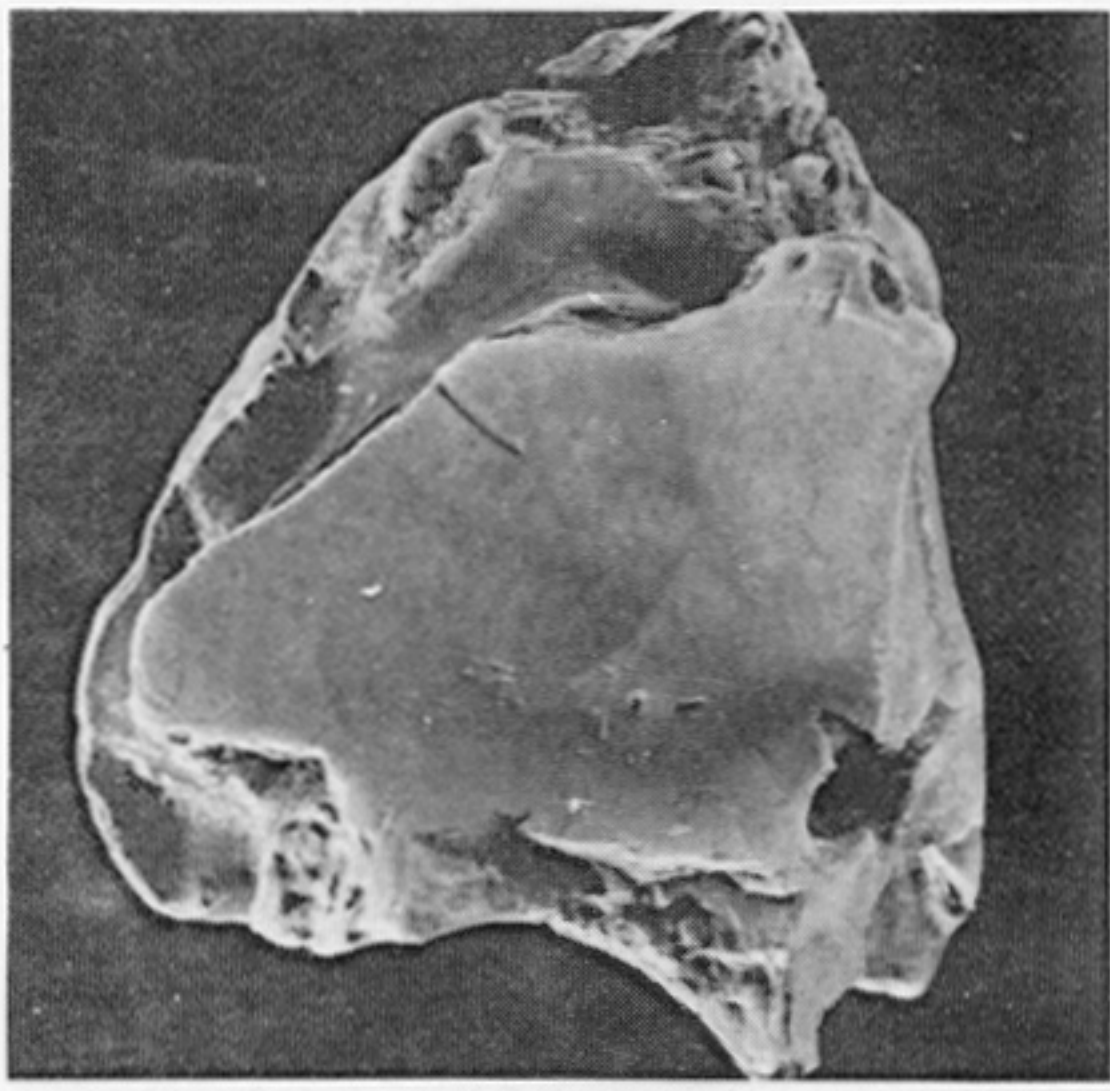
Multis.: (figures 6 and 20 *c*) well preserved in *Kamptobaatar*, proportionately longer in *Pseudobolodon*.

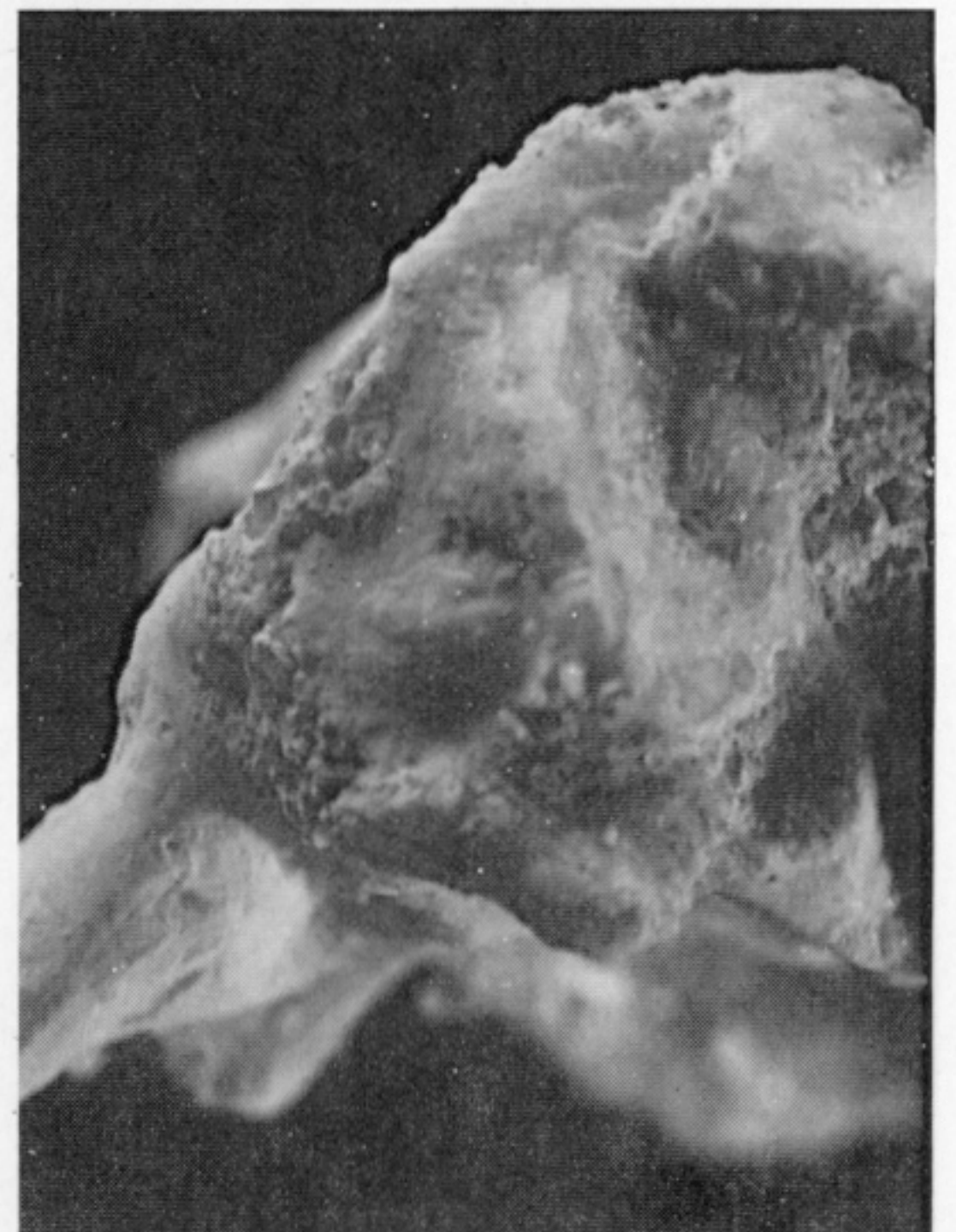
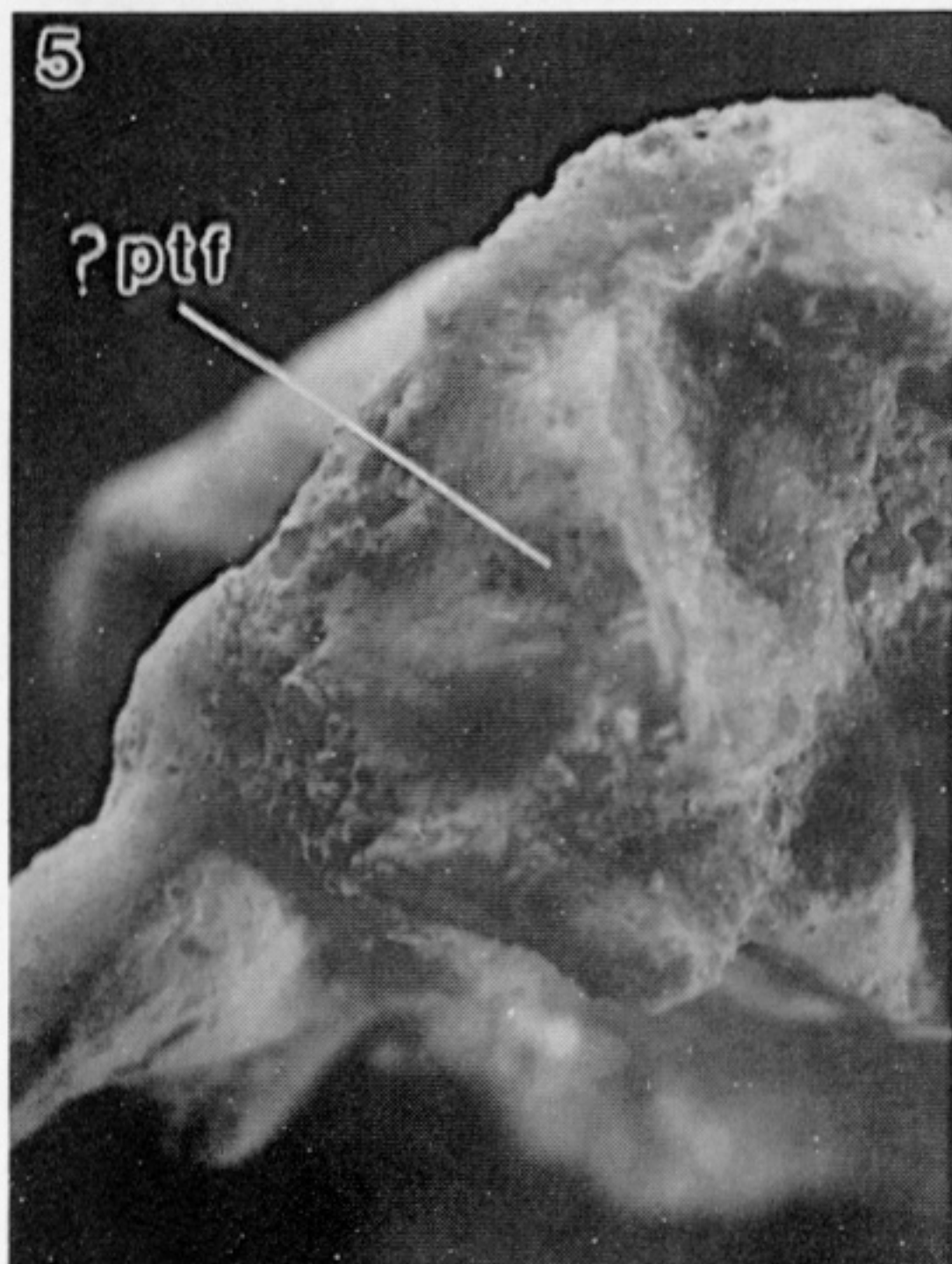
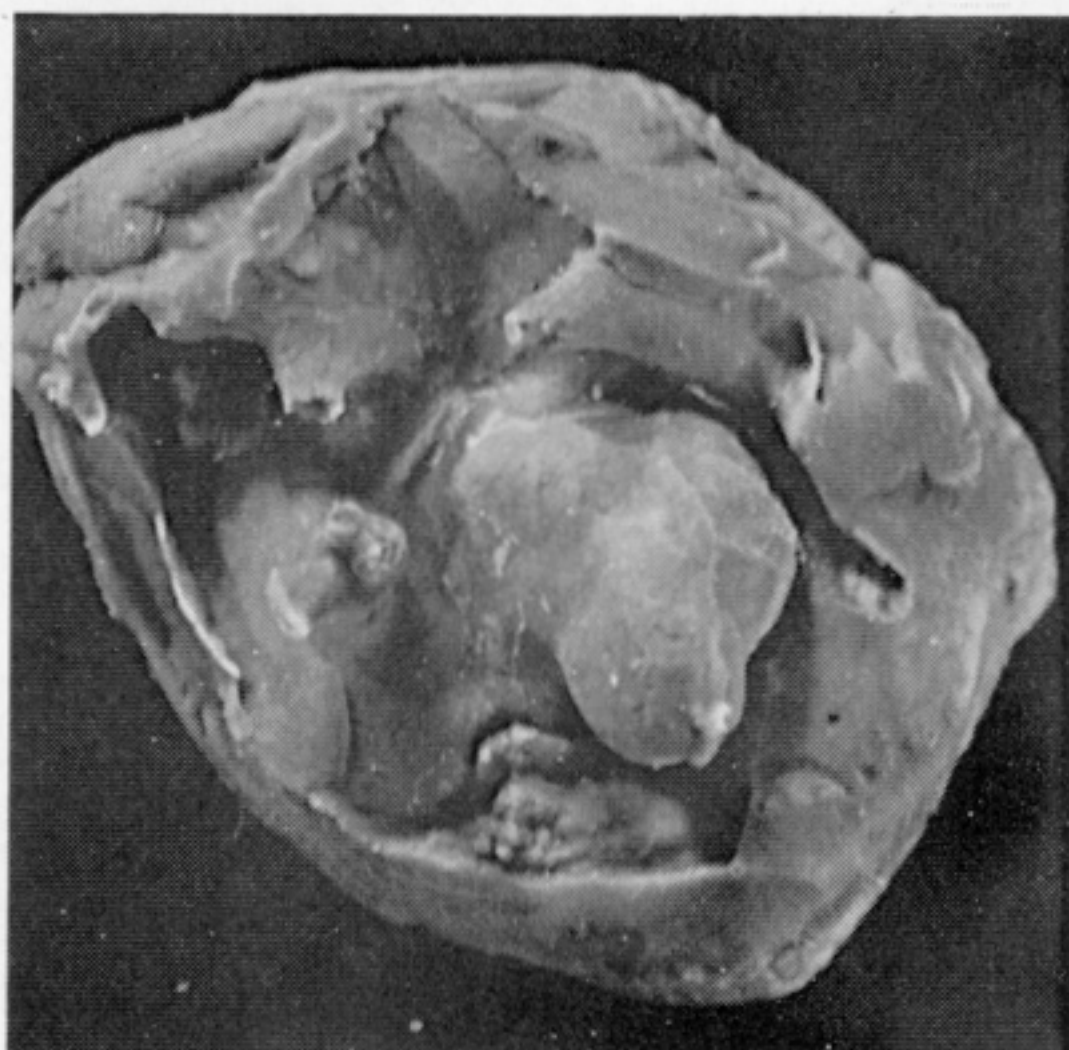
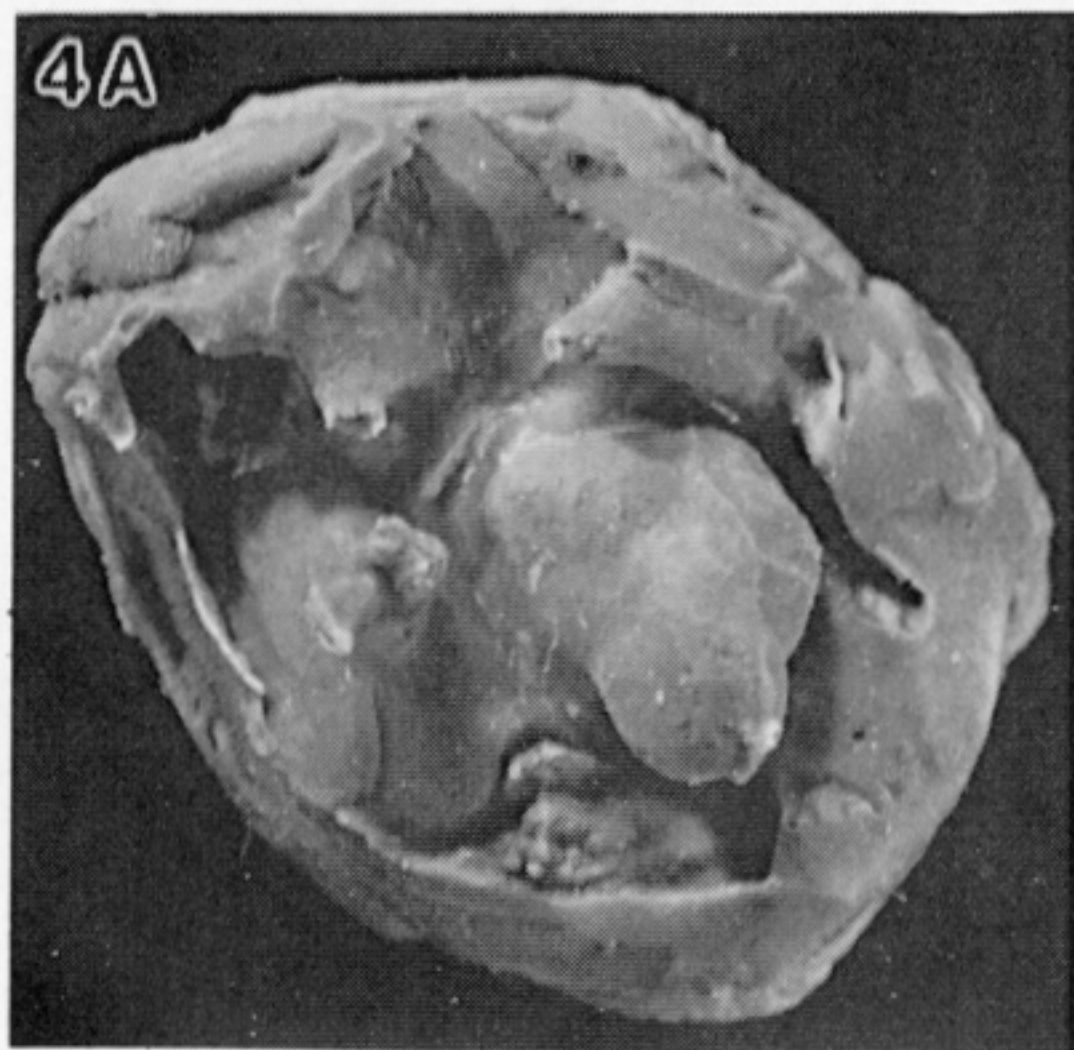
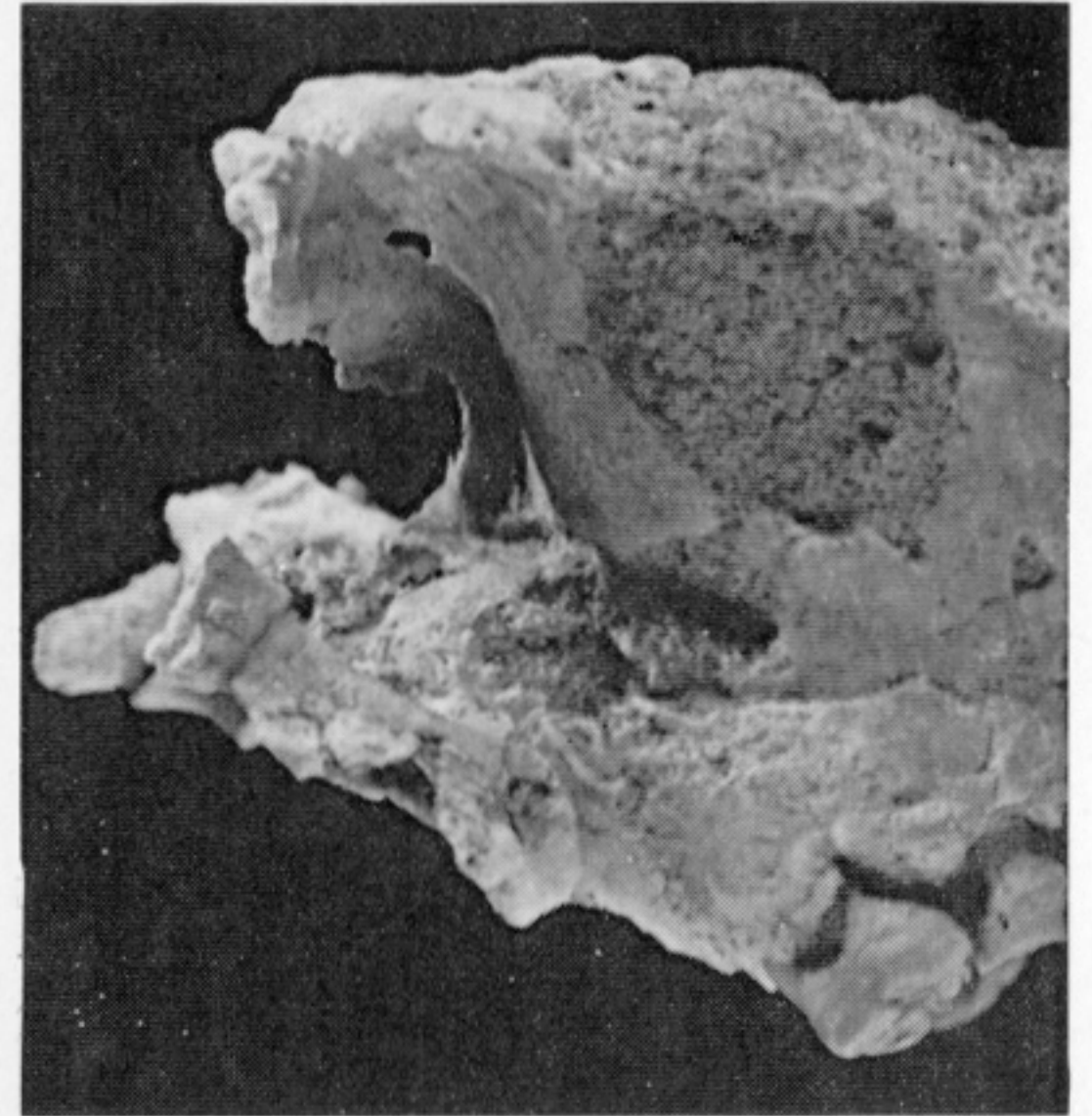
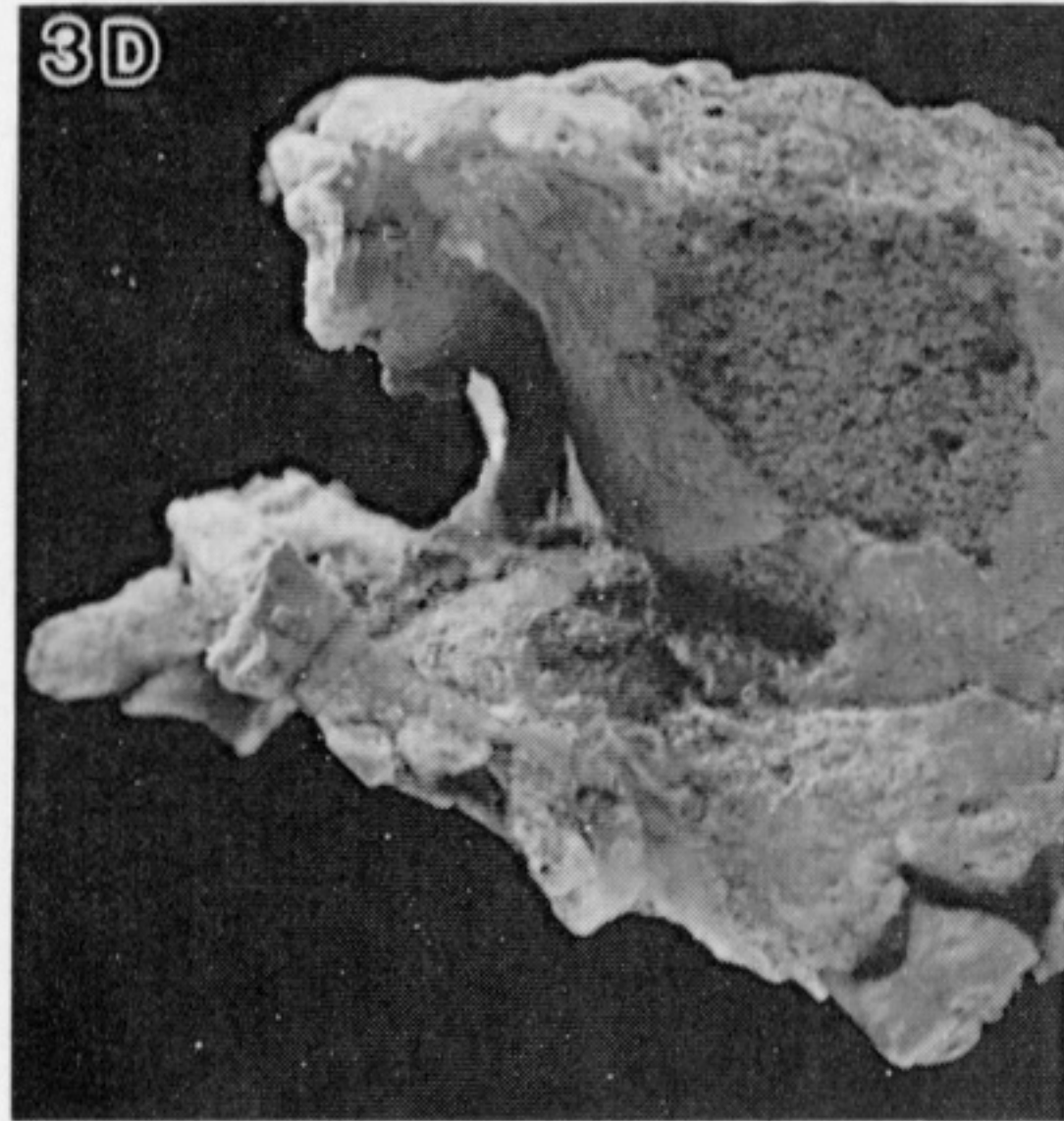
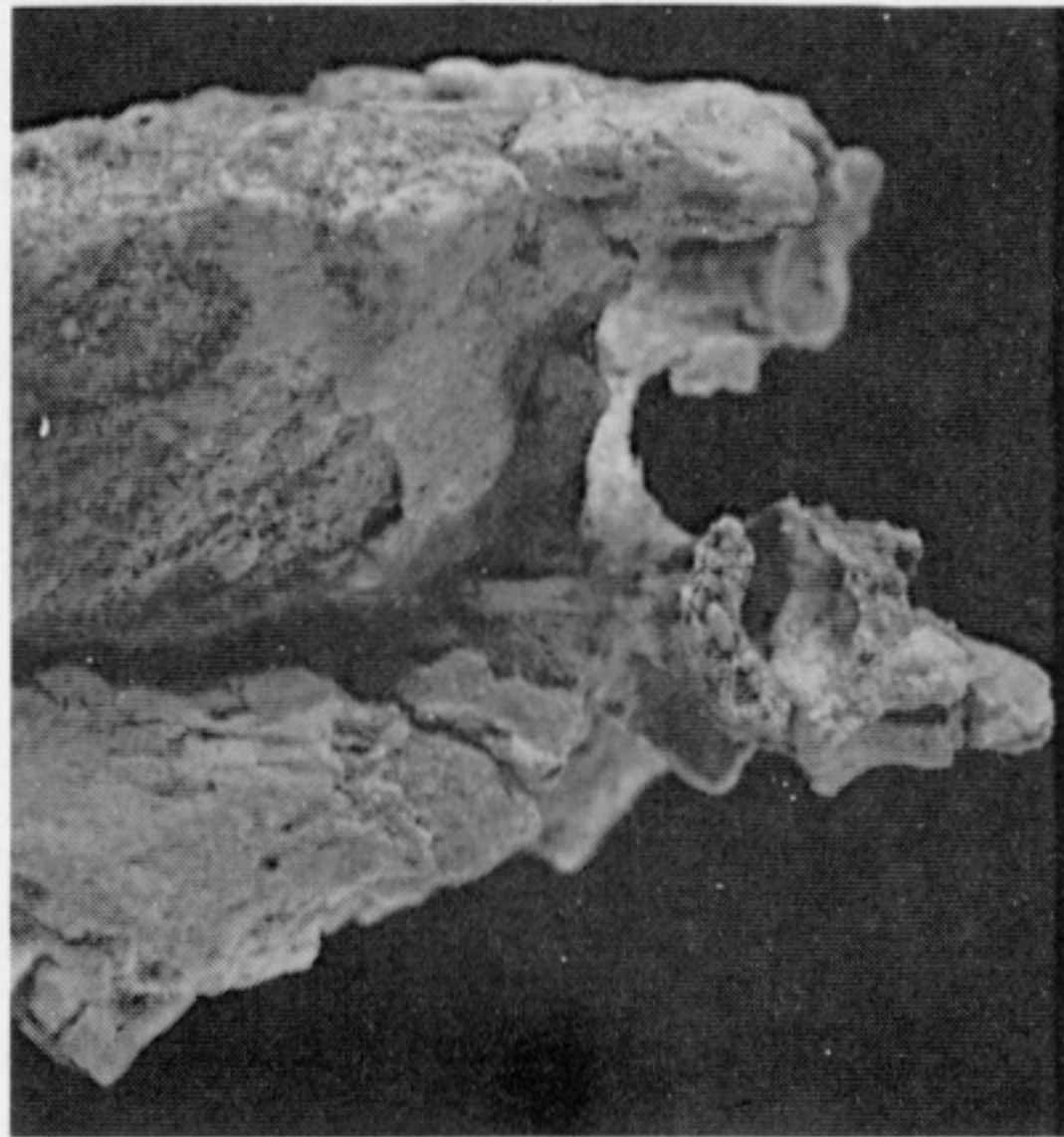
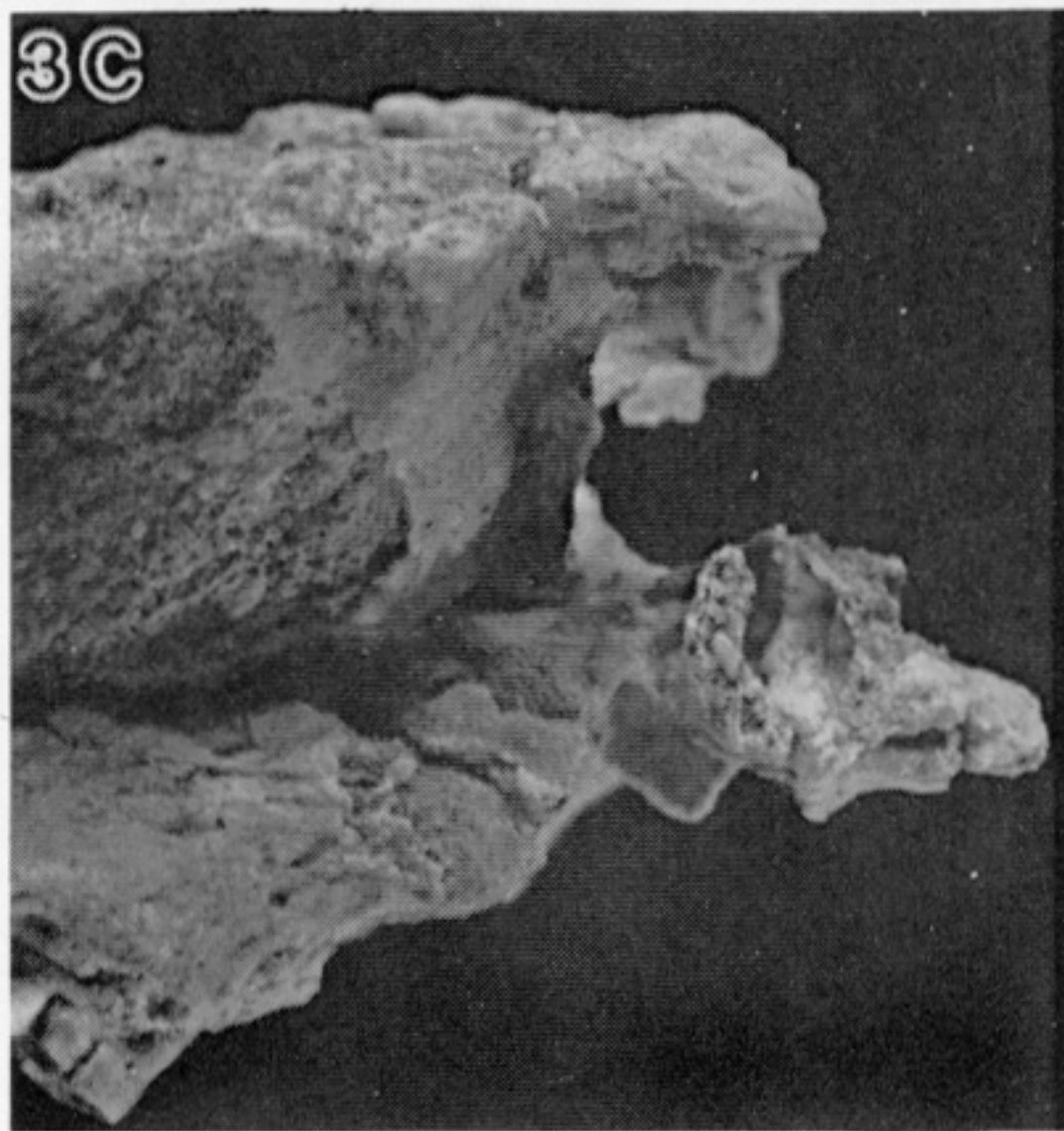
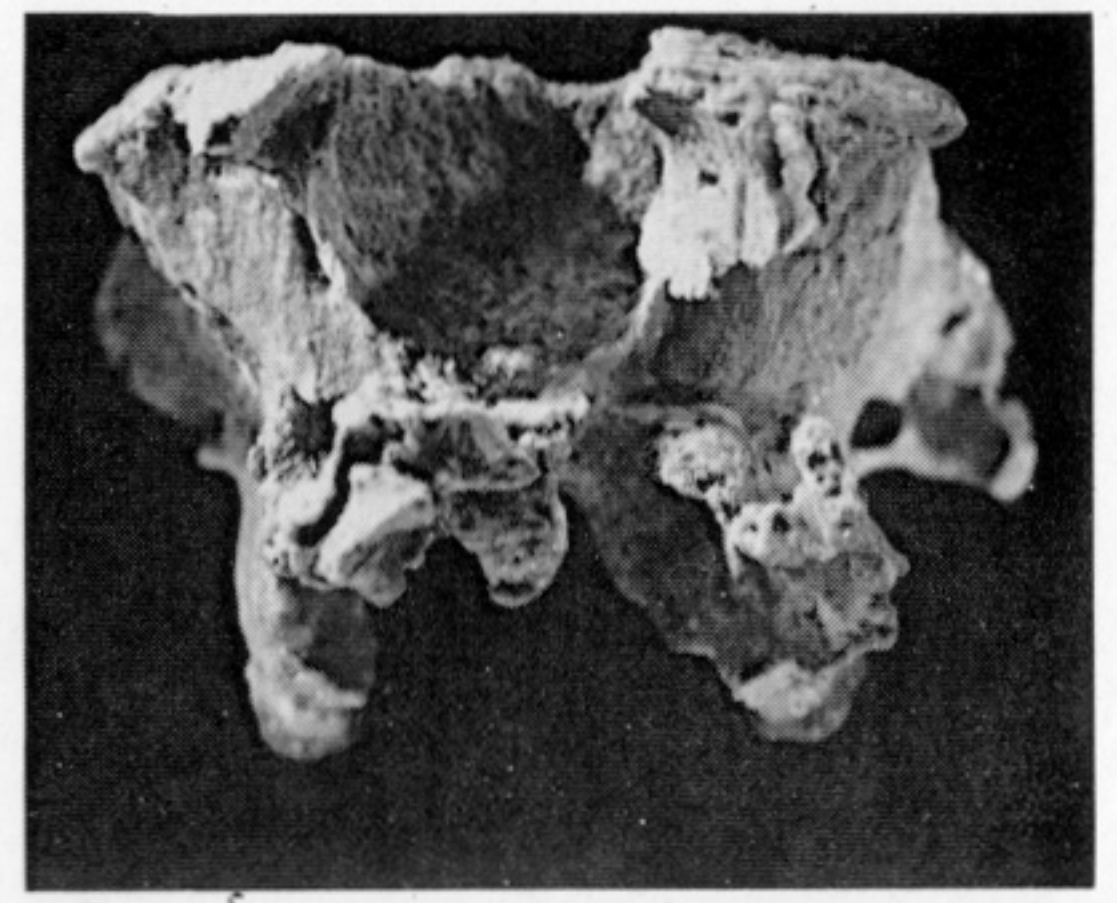
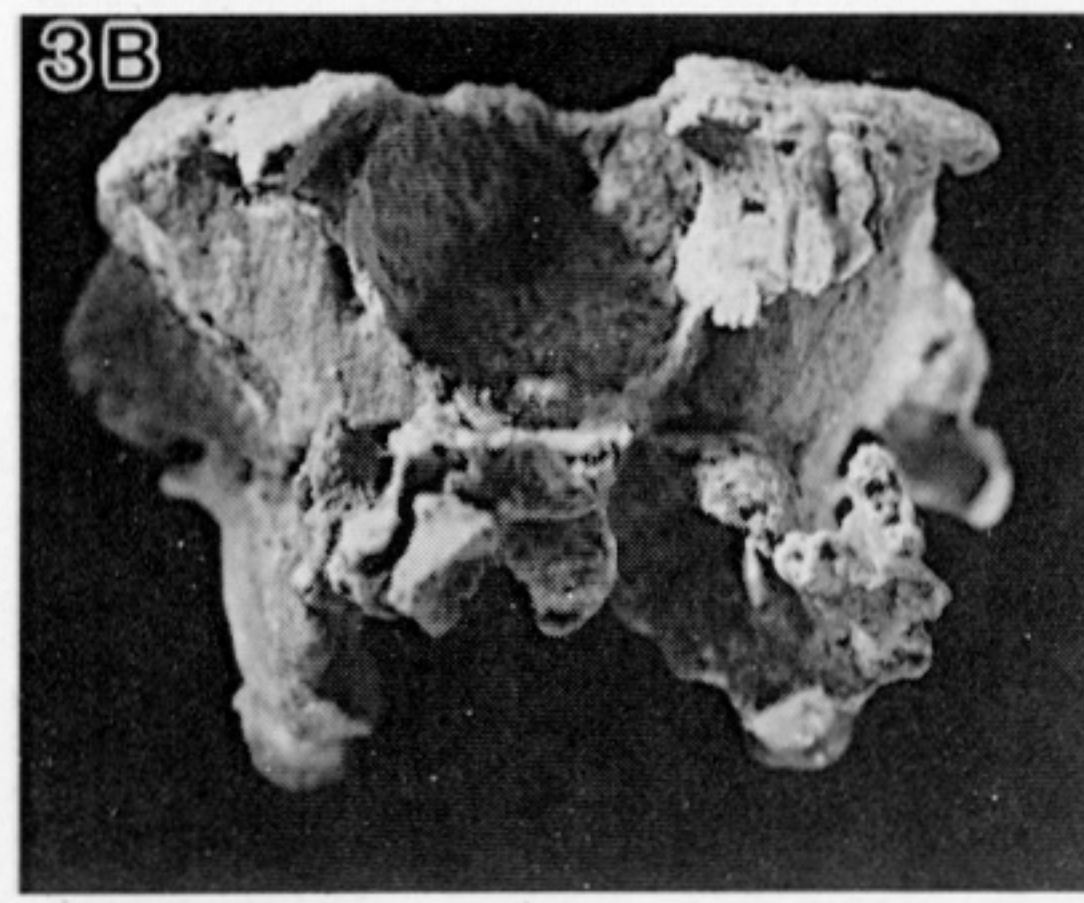
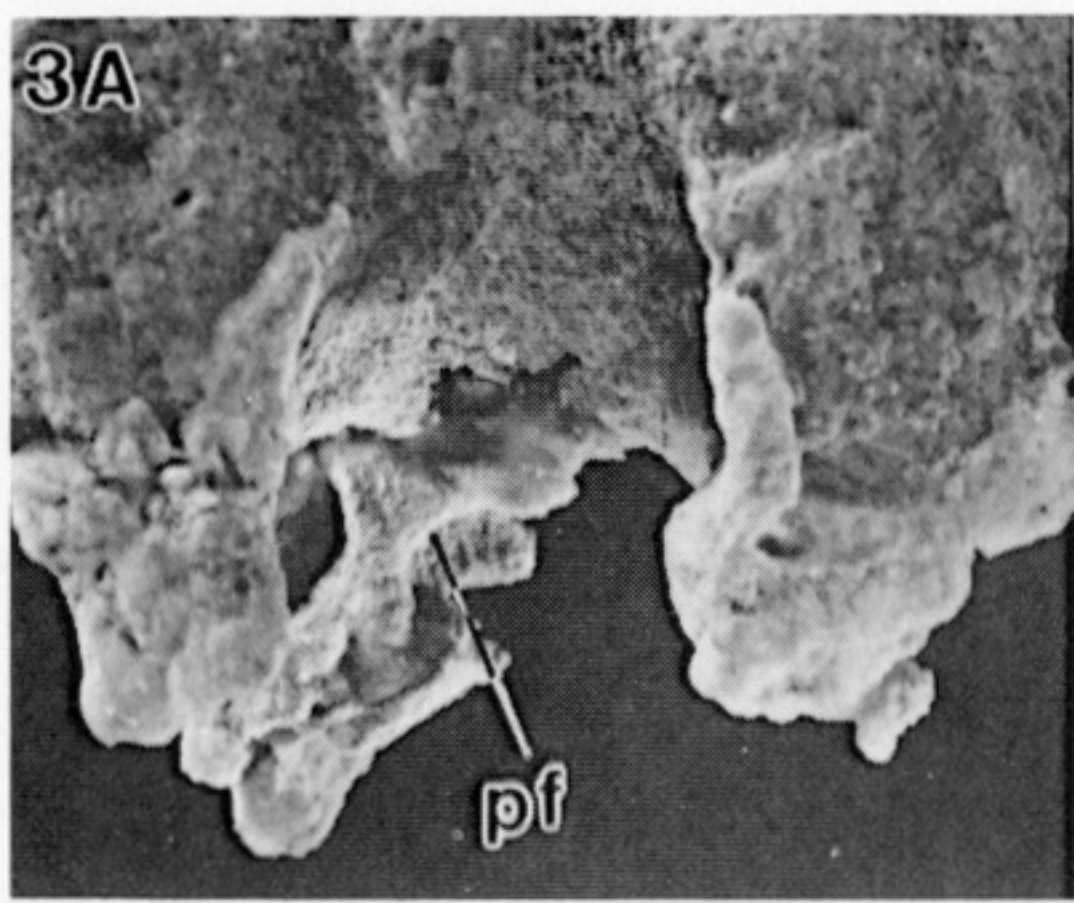
*Notes added in proof (21 July 1986).*

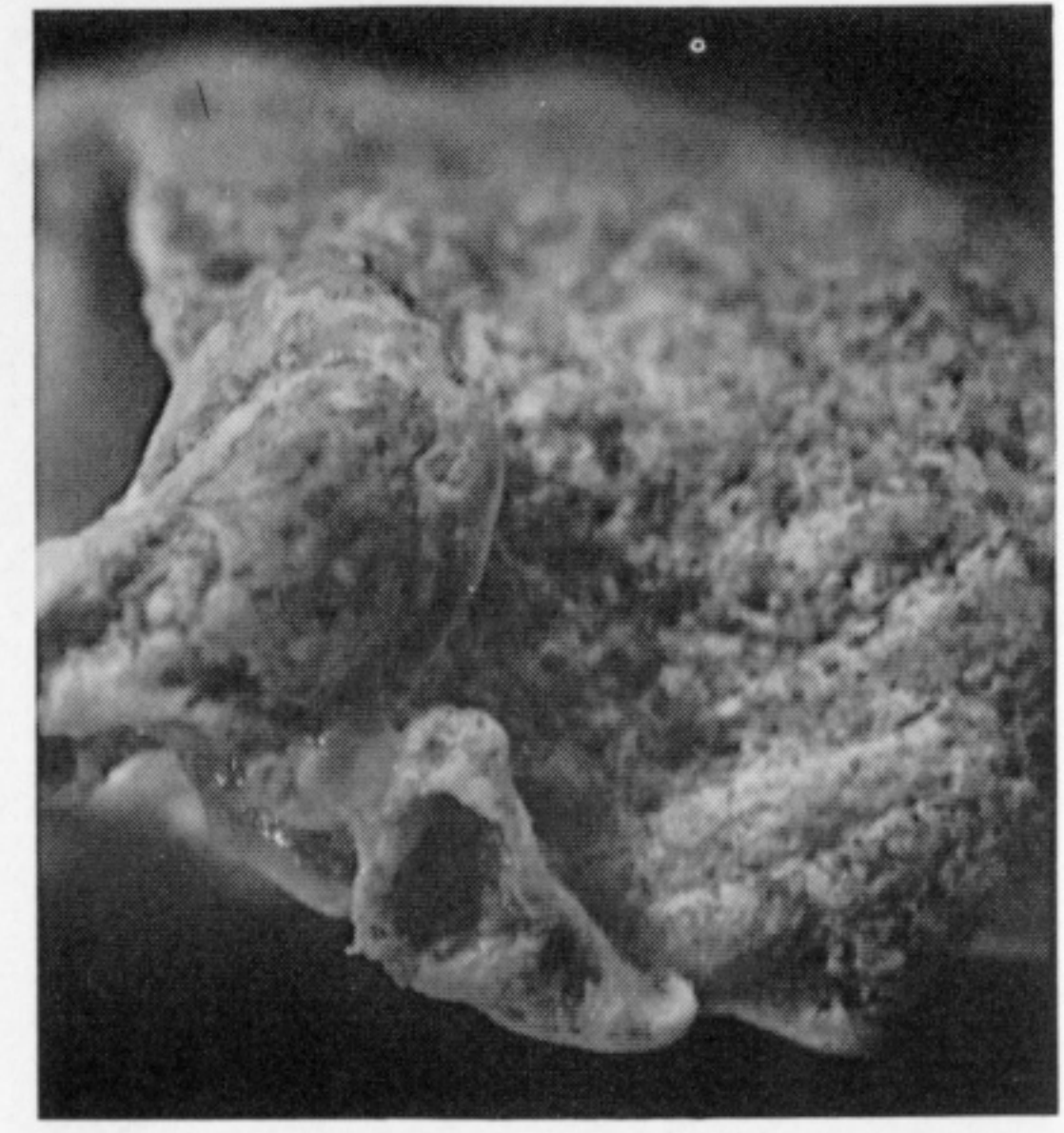
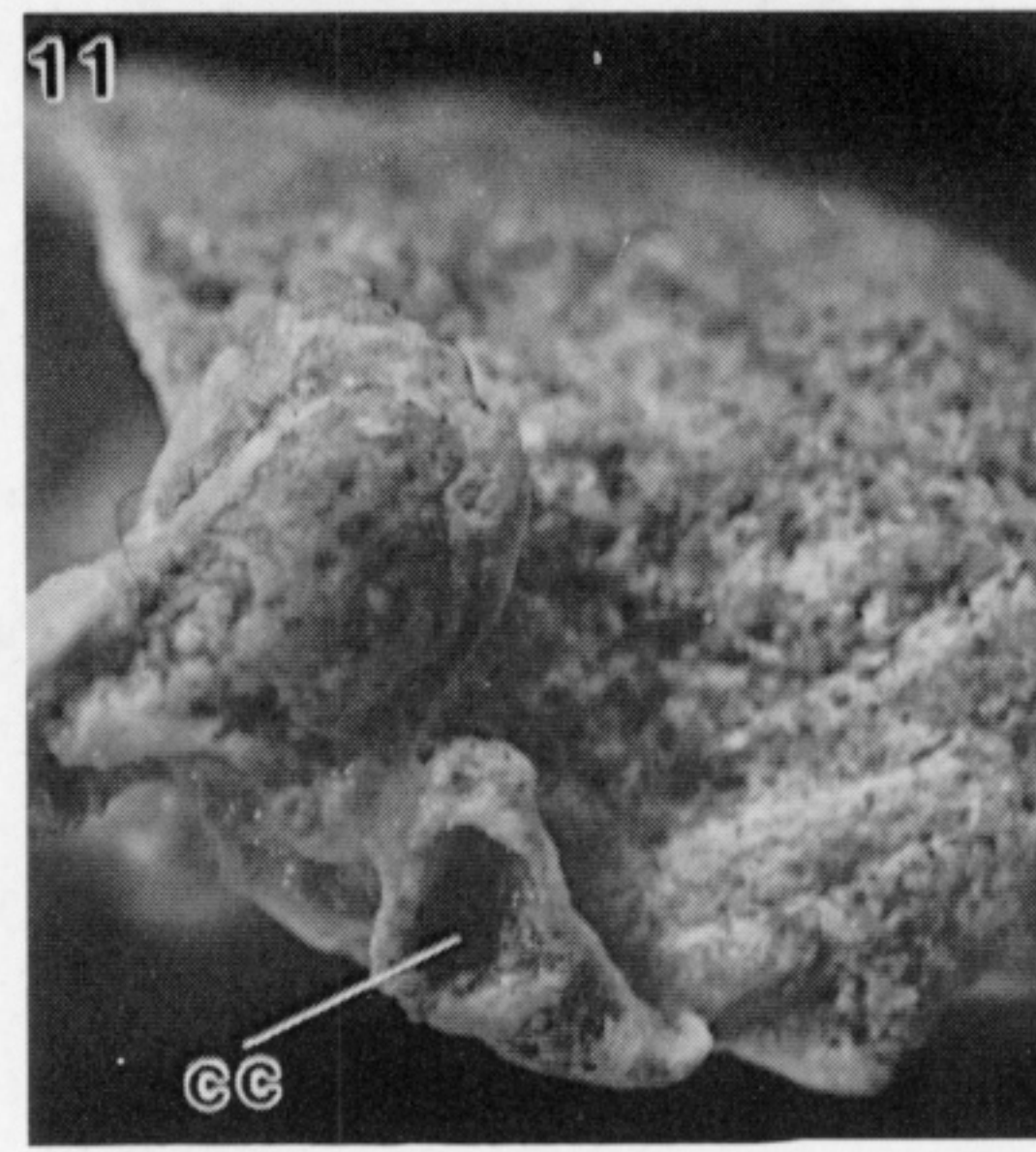
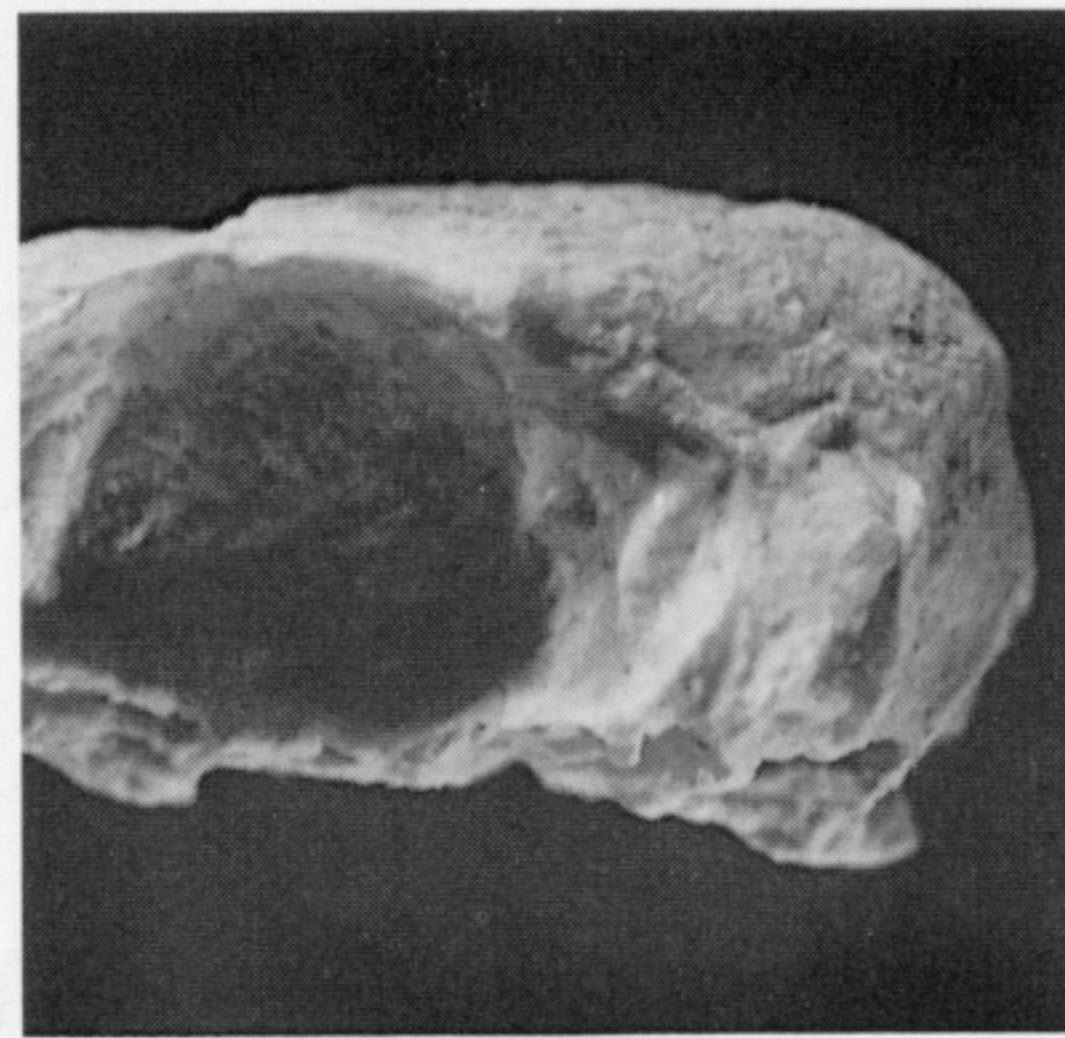
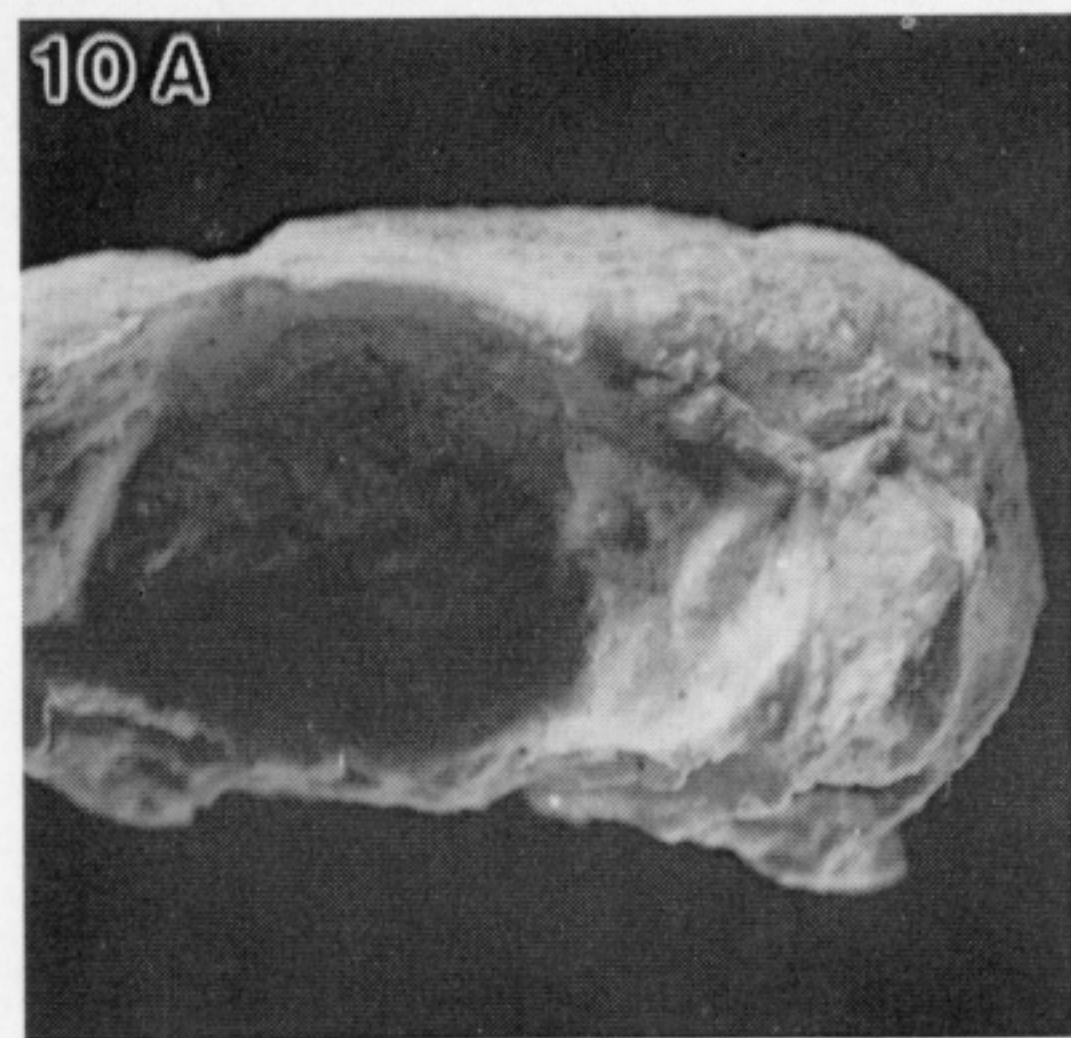
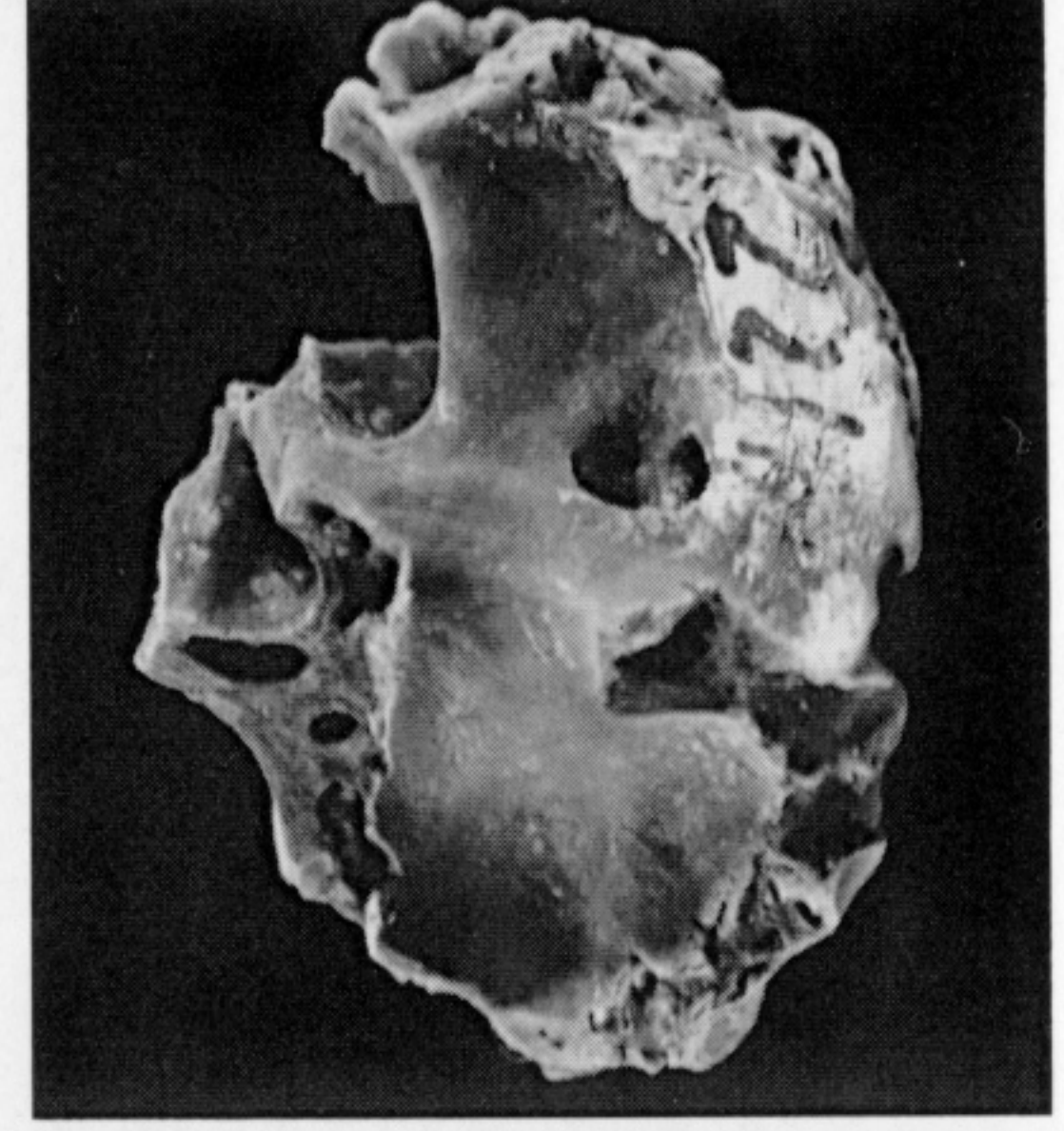
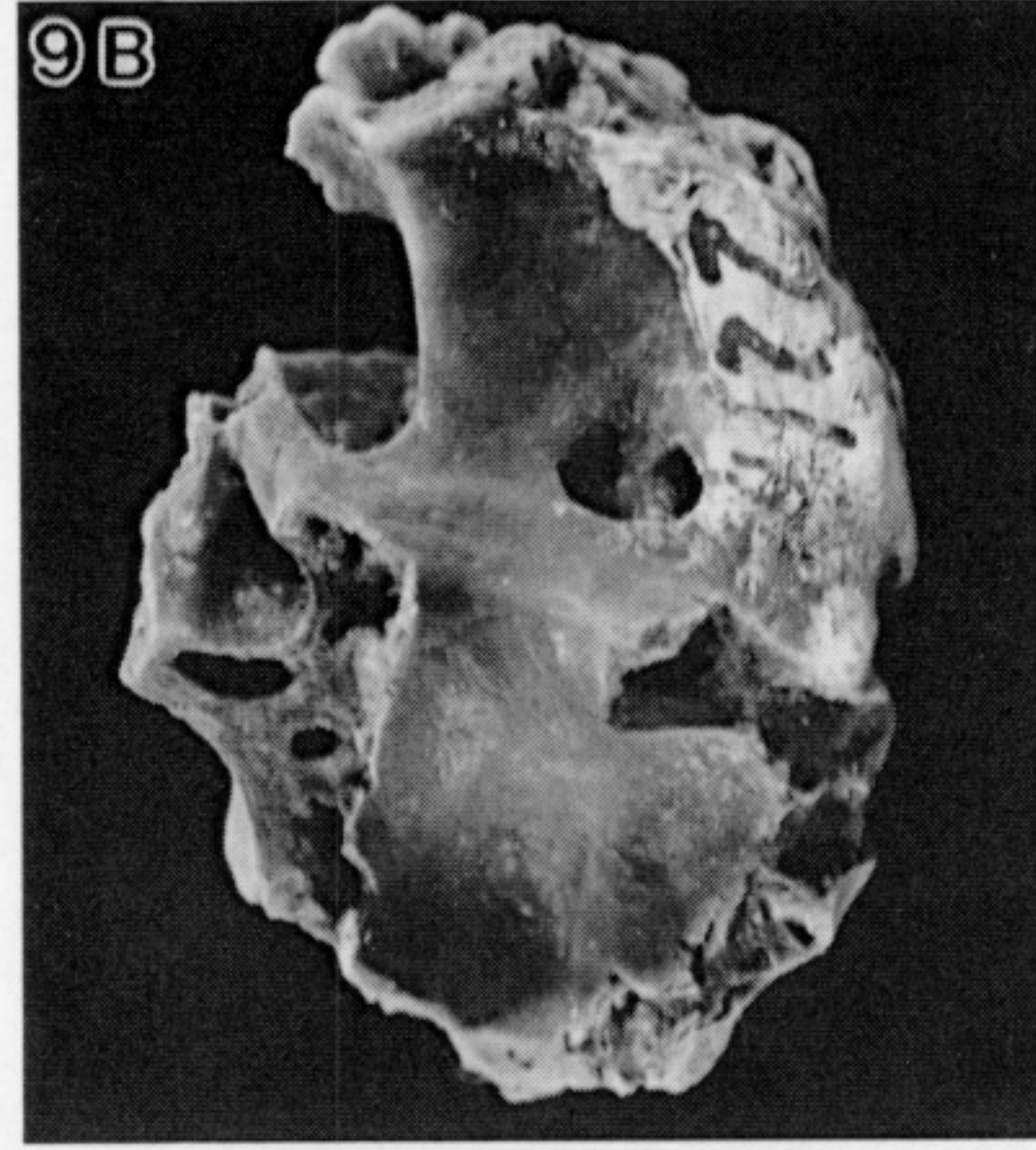
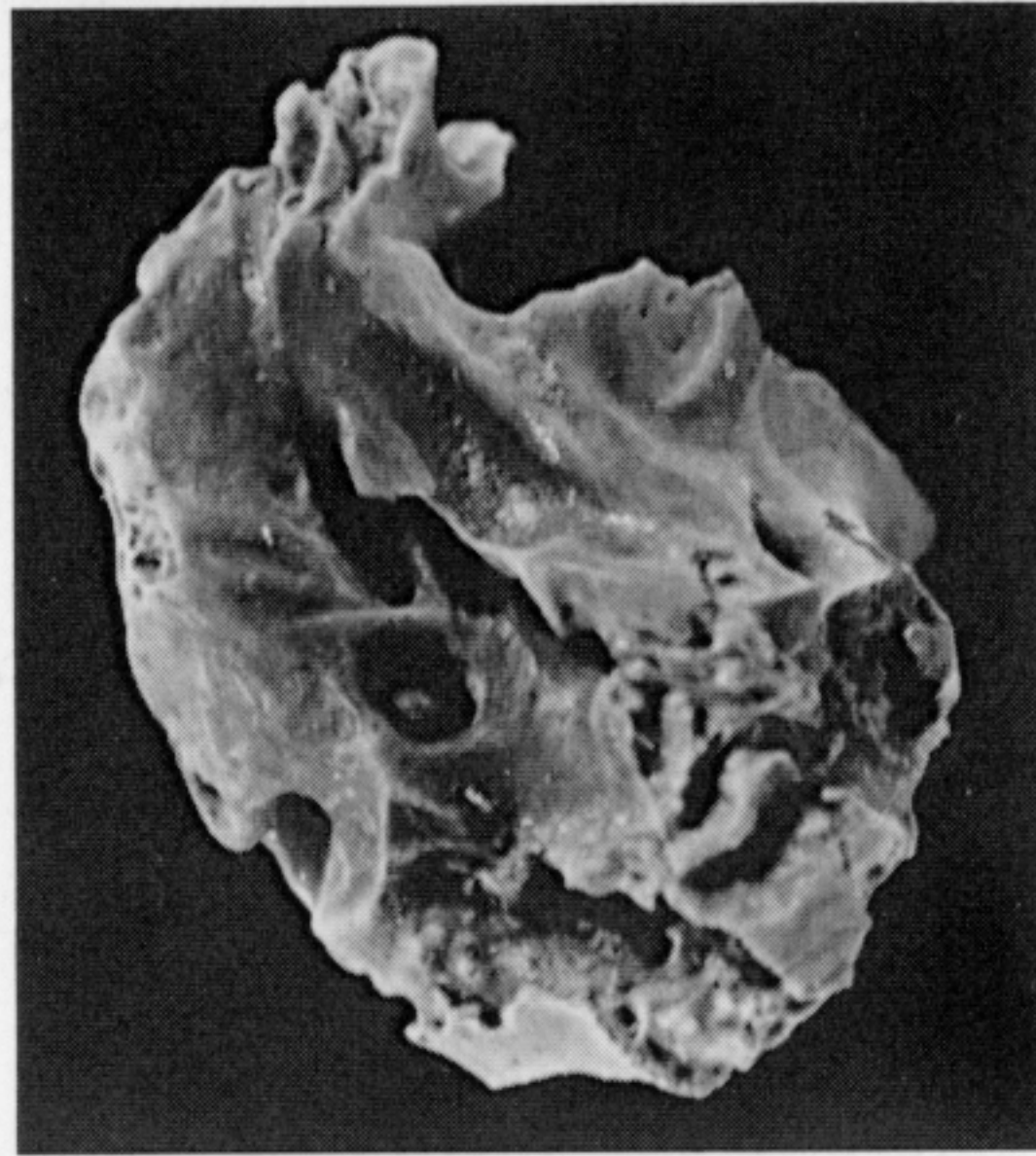
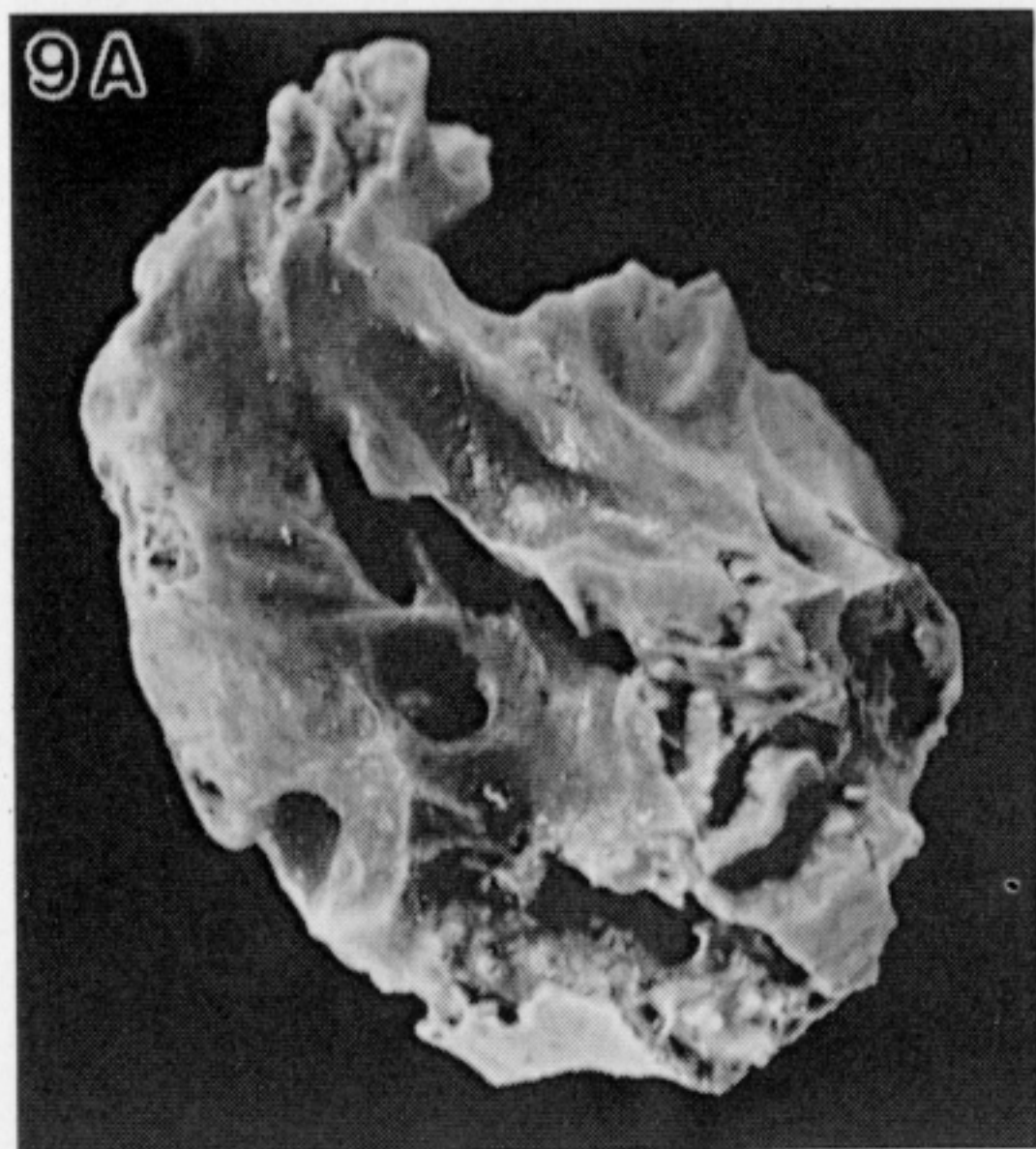
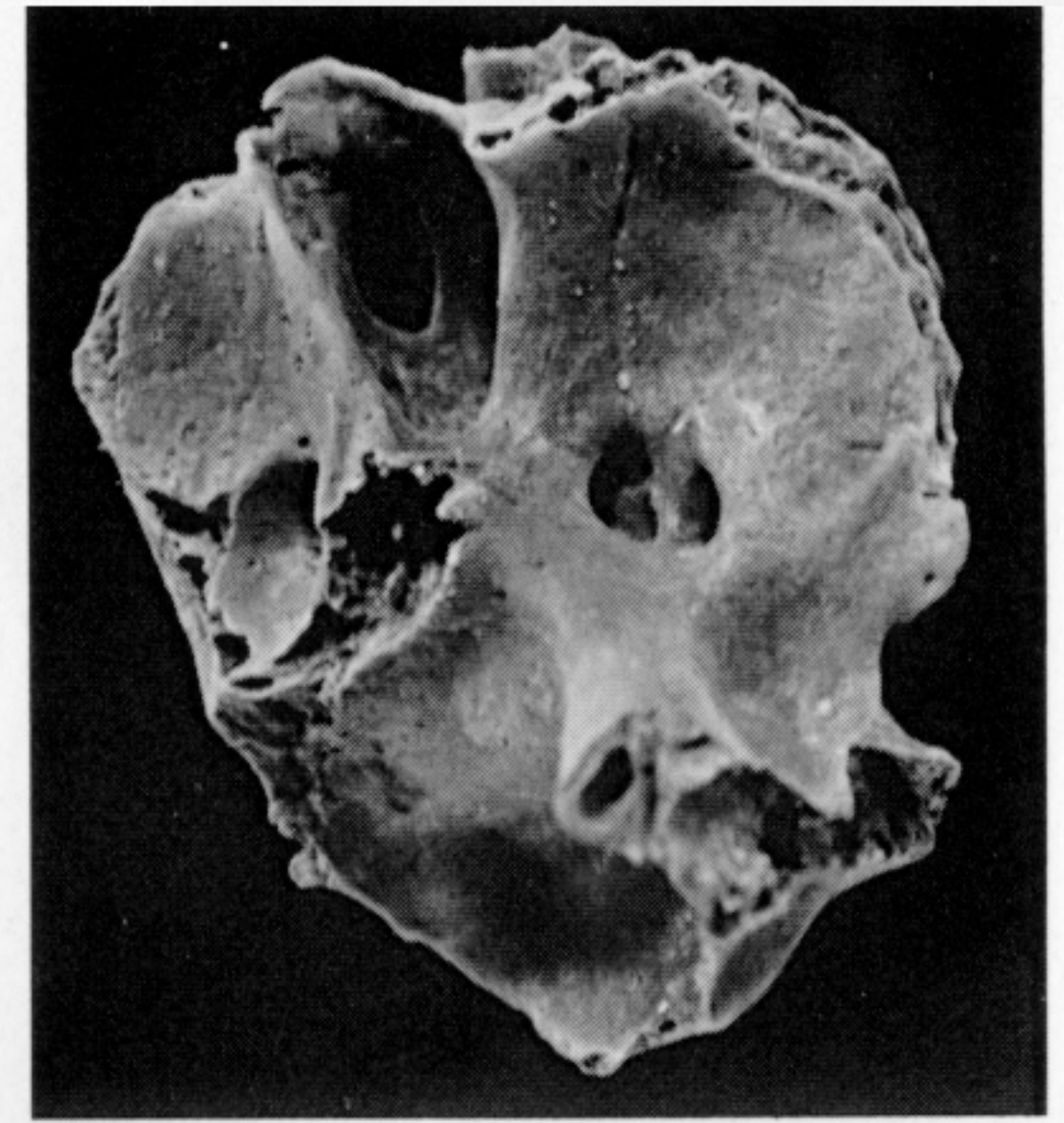
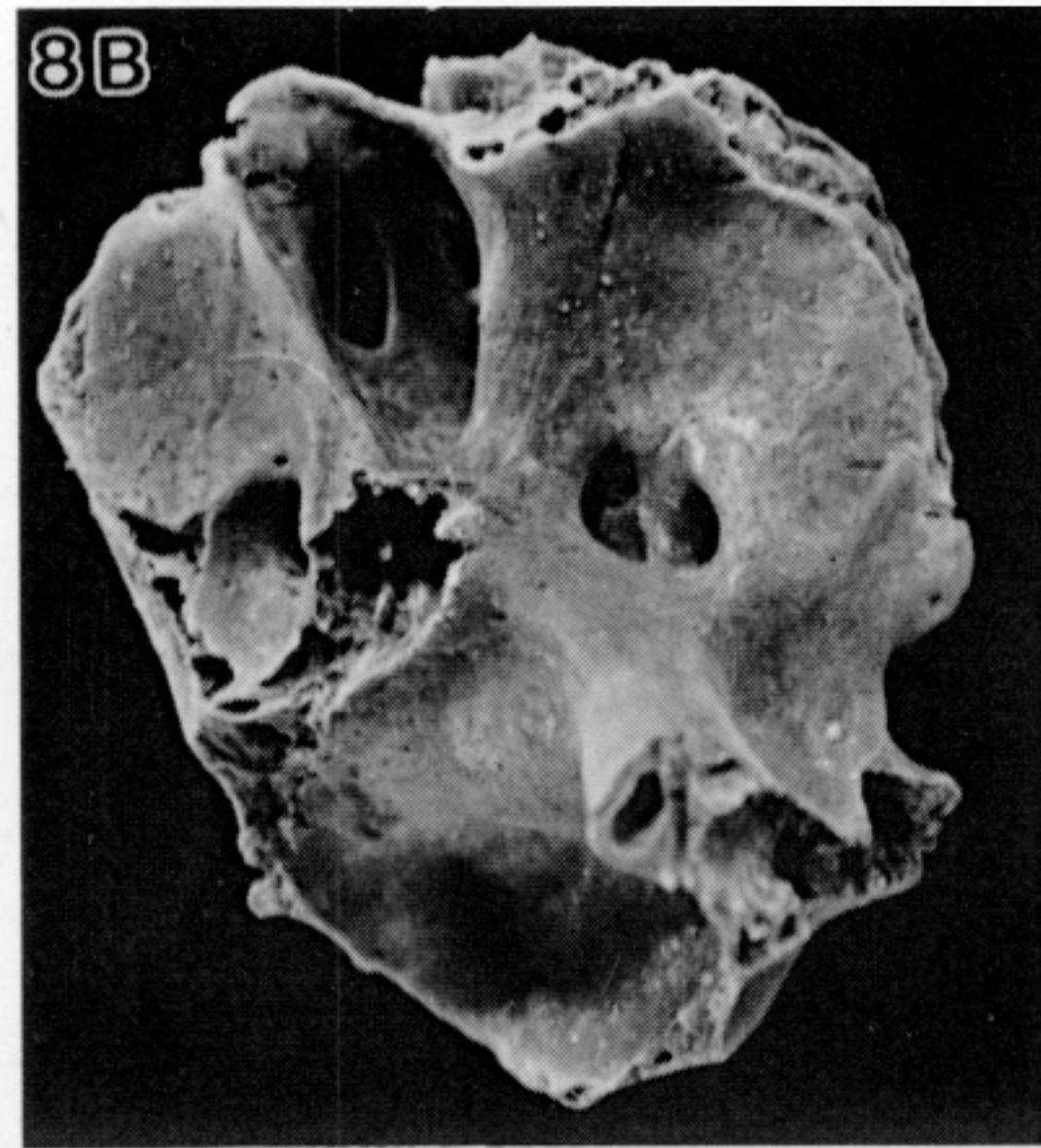
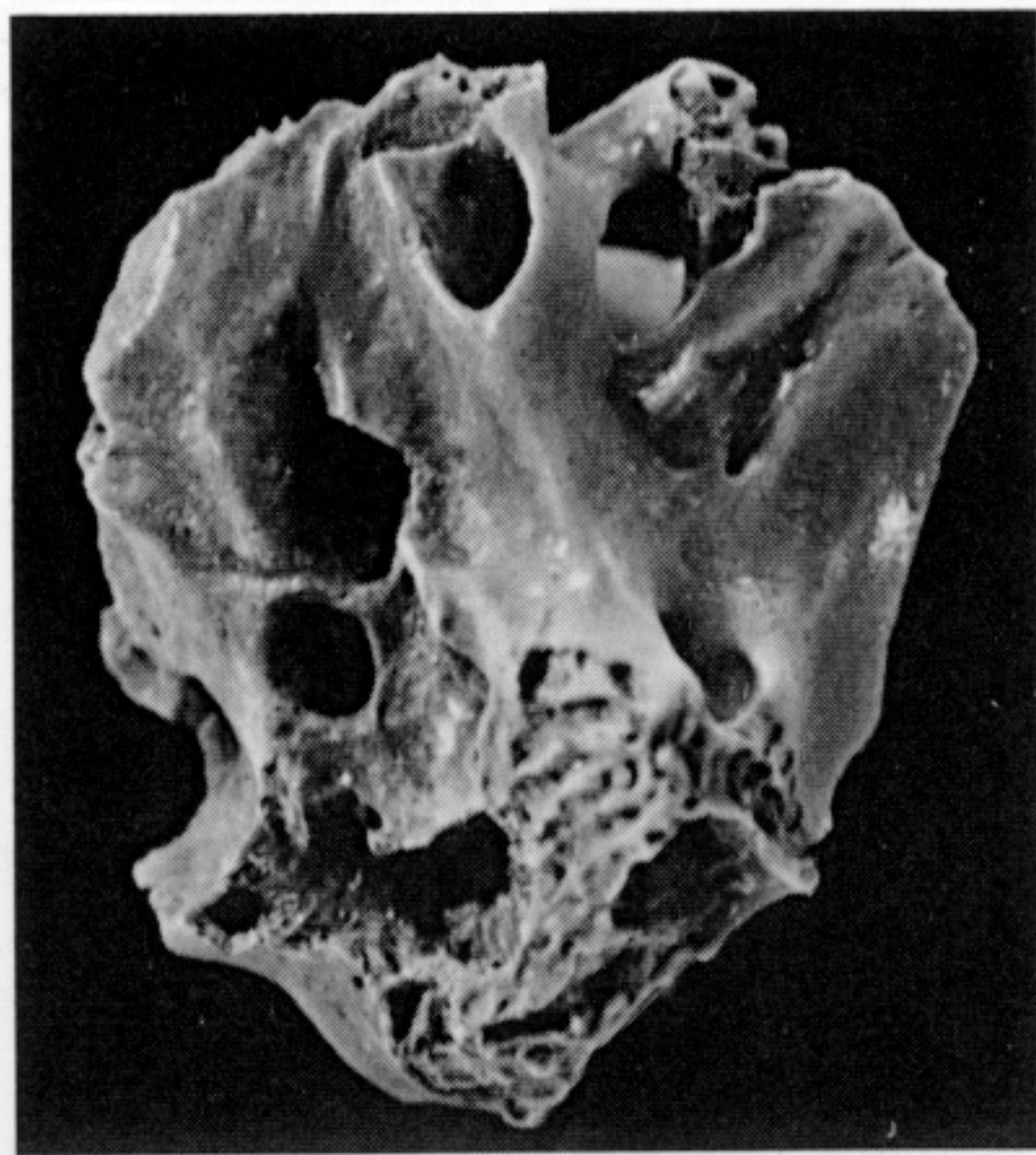
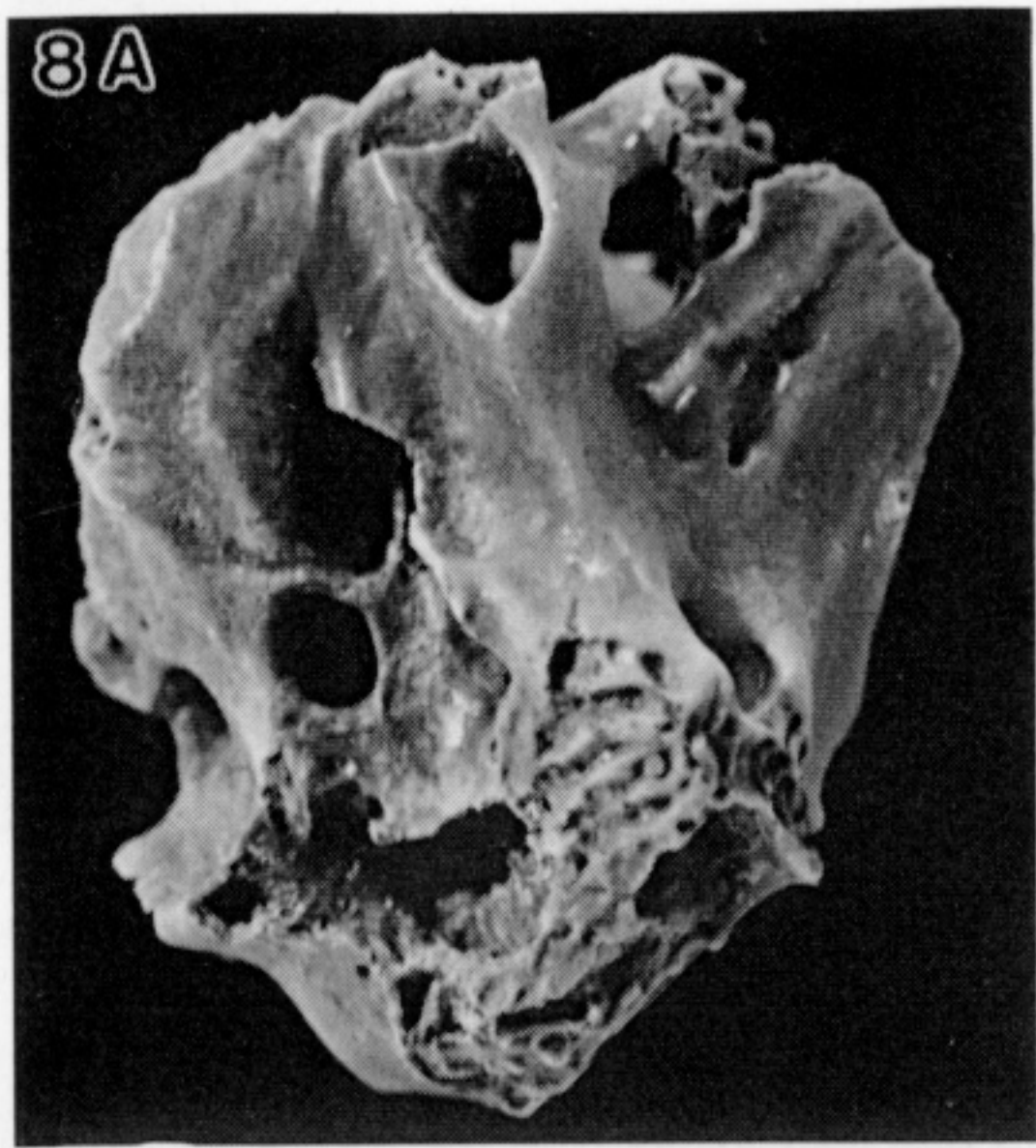
1. Miao Desui of the University of Wyoming is preparing and describing excellent material of the Palaeocene *Lambdopsalis bulla* Chow & Qi 1978, and has kindly shown us specimens. One with the auditory ossicles in place confirms our reconstruction of the incus articulating in the epitympanic recess. The pattern of the vascular canals in the petrosal region corresponds in general with that described here, but there are detailed differences in size and in the position of interconnections. The anterior lamina of the petrosal is proportionately smaller in *Lambdopsalis* and the trigeminal foramina appear to lie within a relatively large alisphenoid.

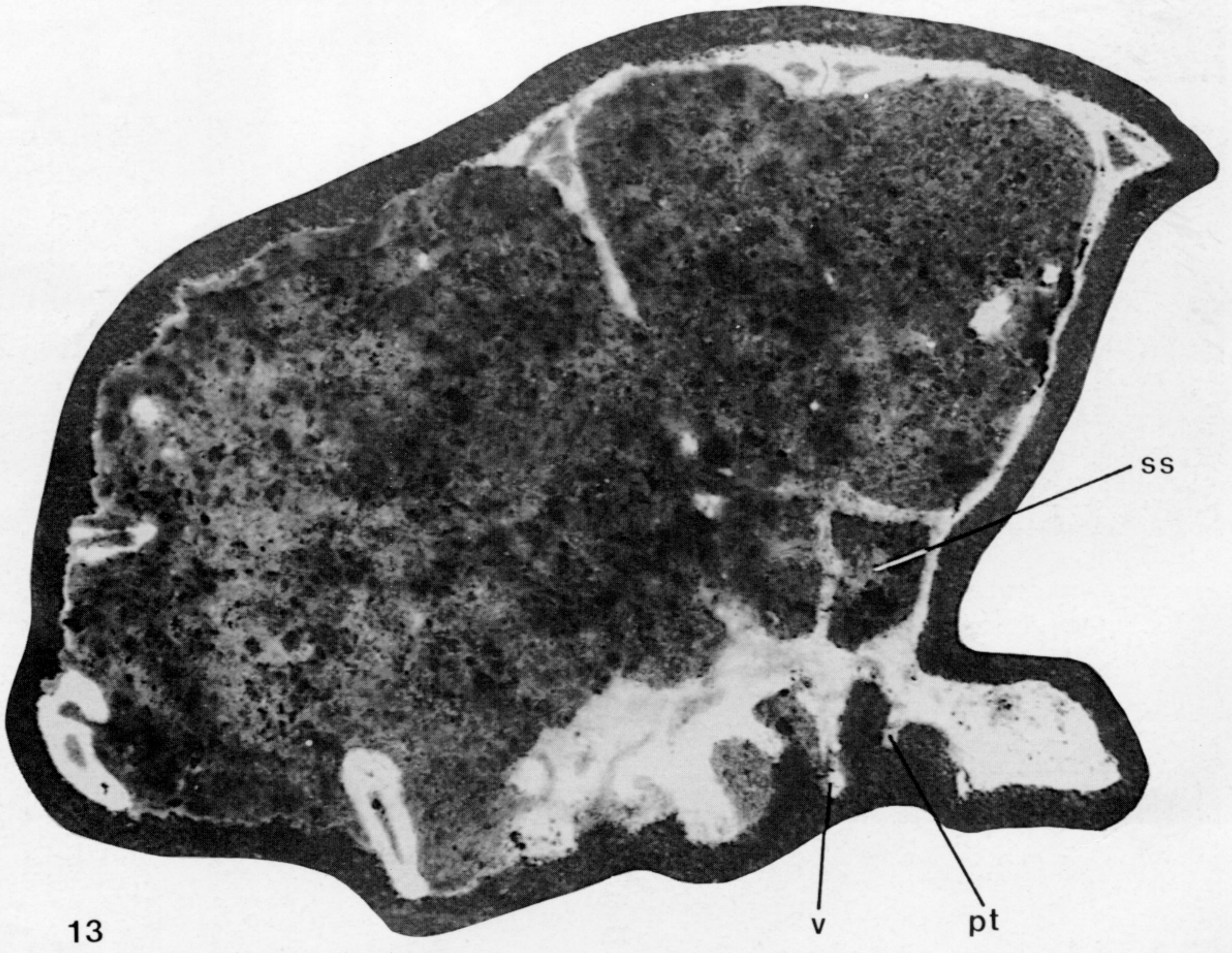
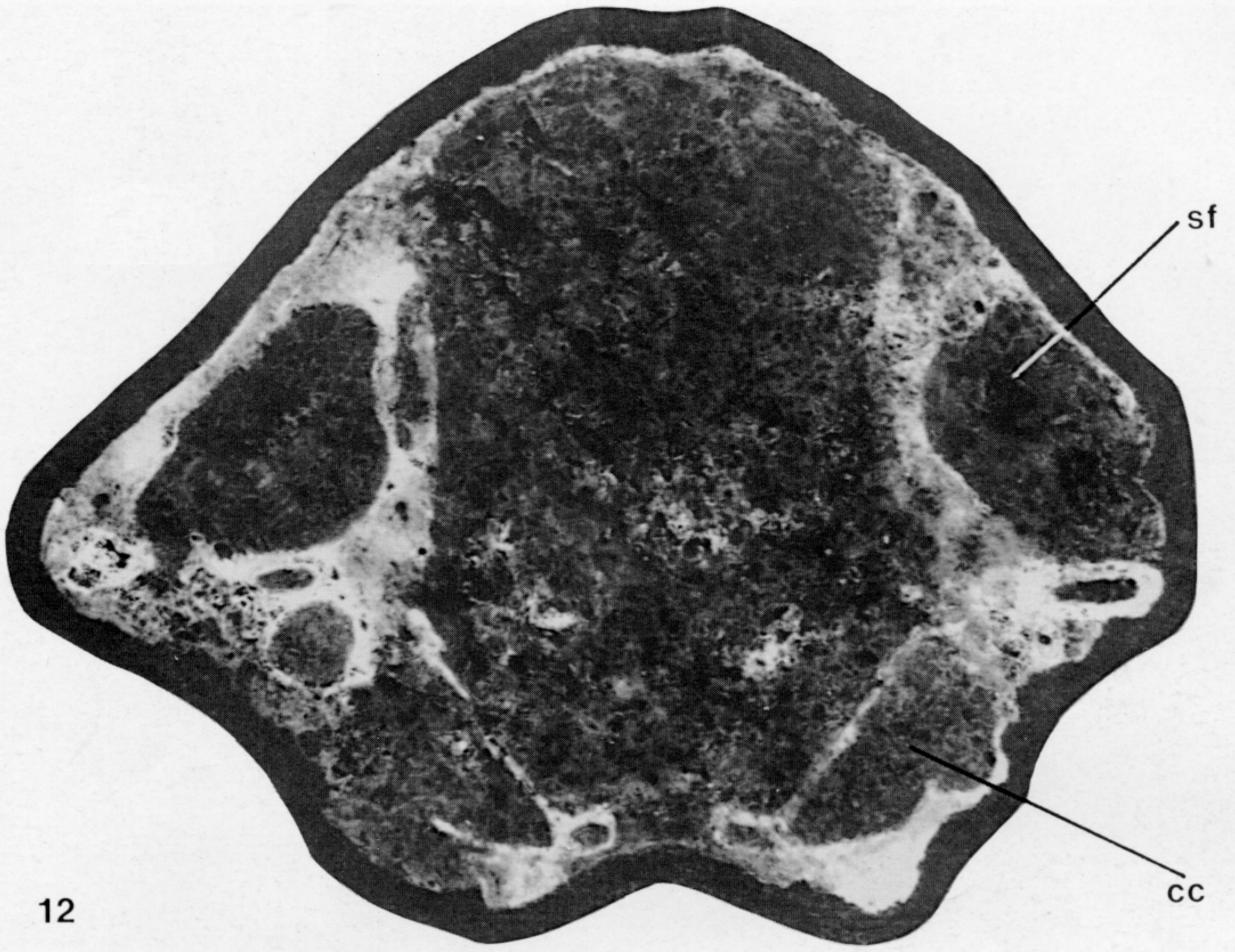
2. J. A. Hopson (personal communication) has informed us of his discovery in *Ptilodus montanus* of a slender jugal, internal to the zygomatic arch. Z.K.J. has since confirmed the presence of a very slender jugal, pointed posteriorly and widening anteriorly, placed medially in the zygomatic arch in several specimens from different genera of Taeniolabidoidea.



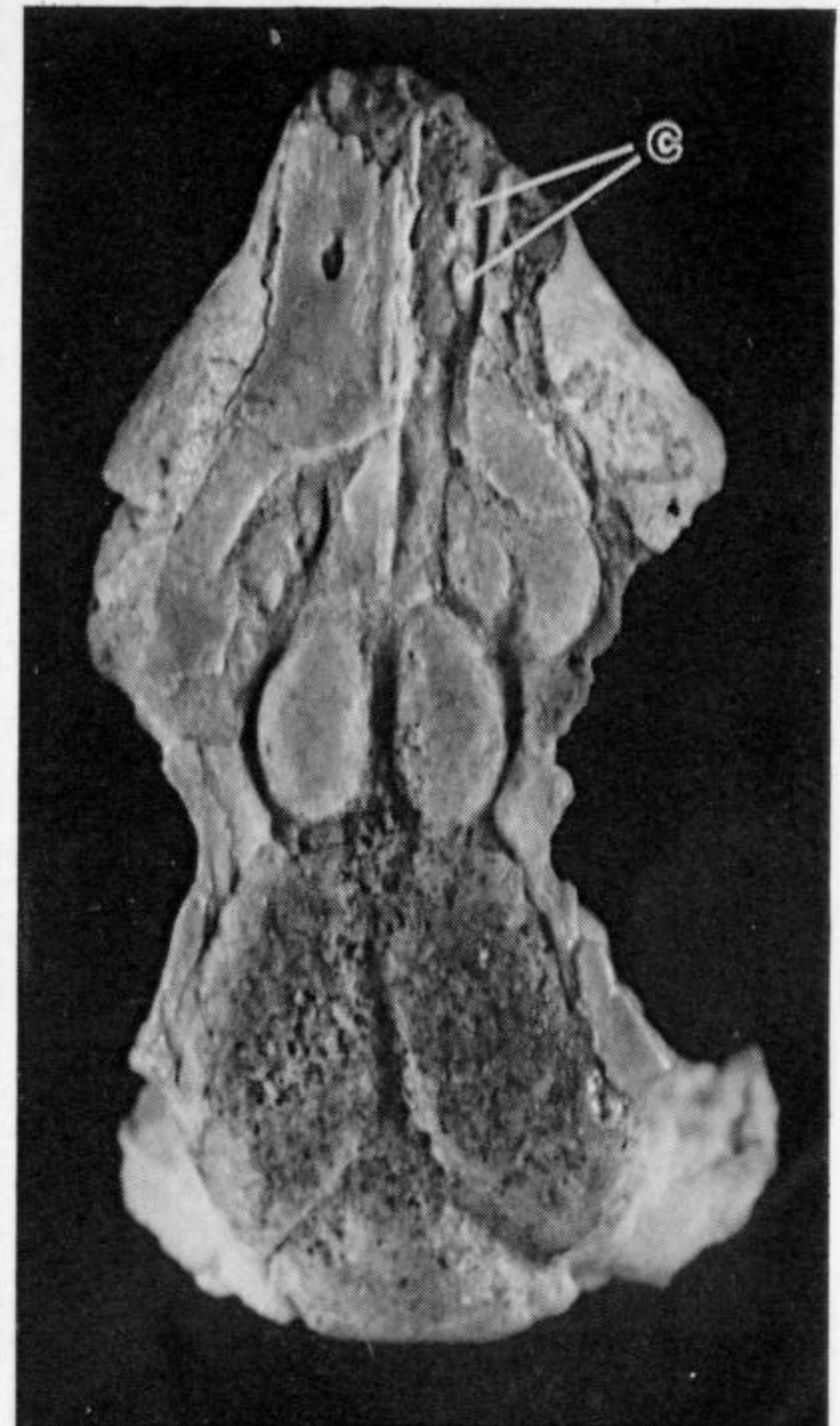
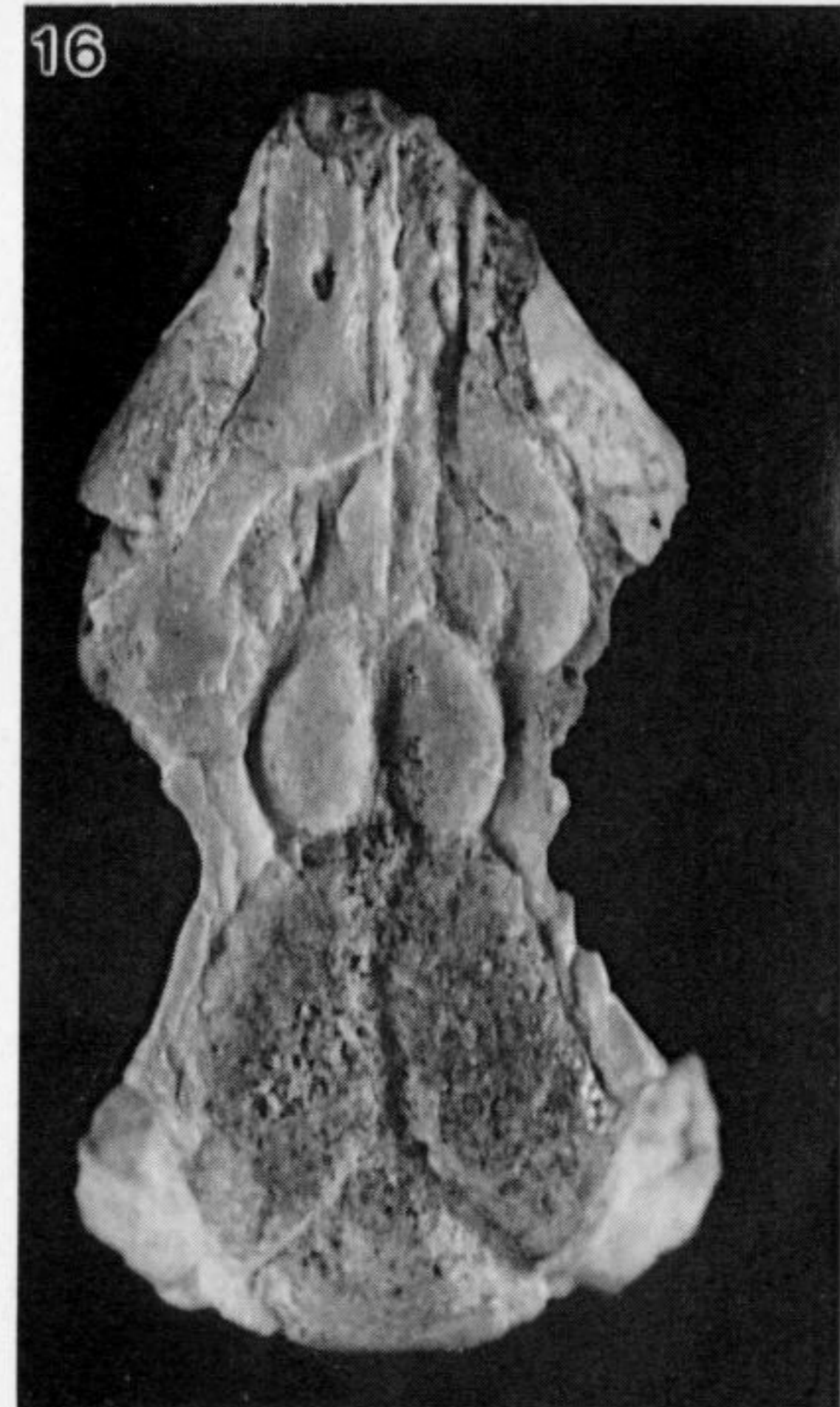
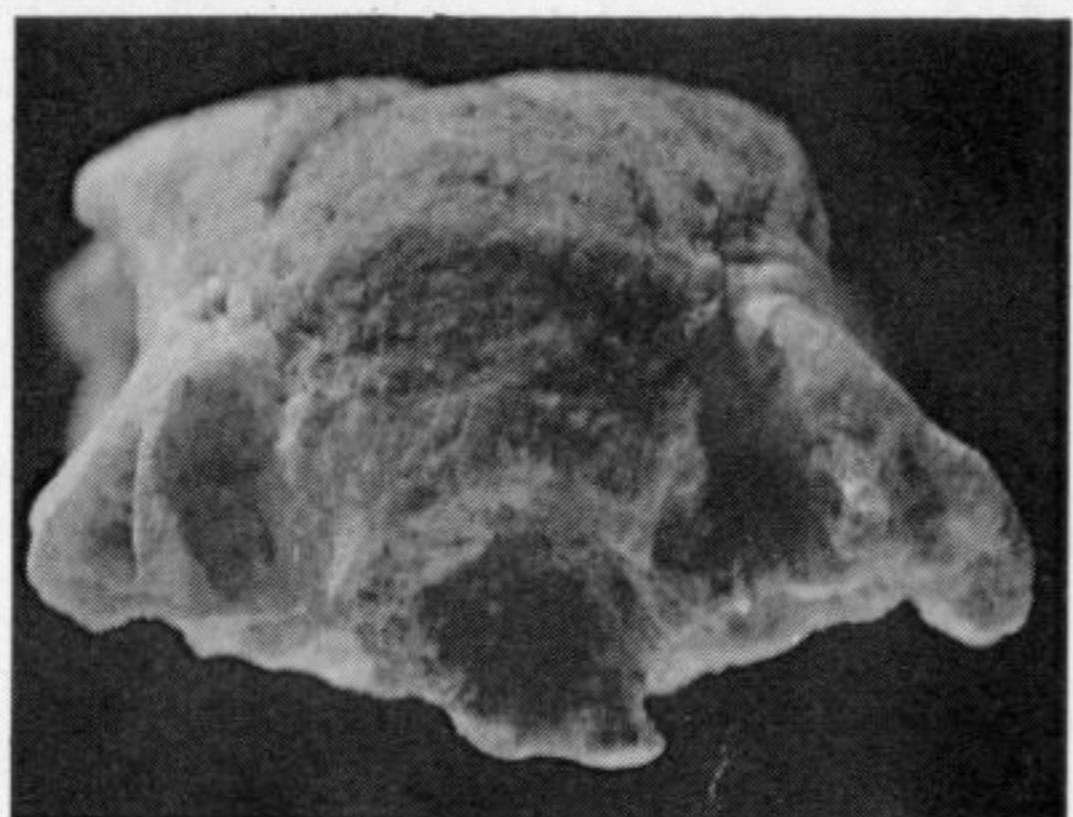
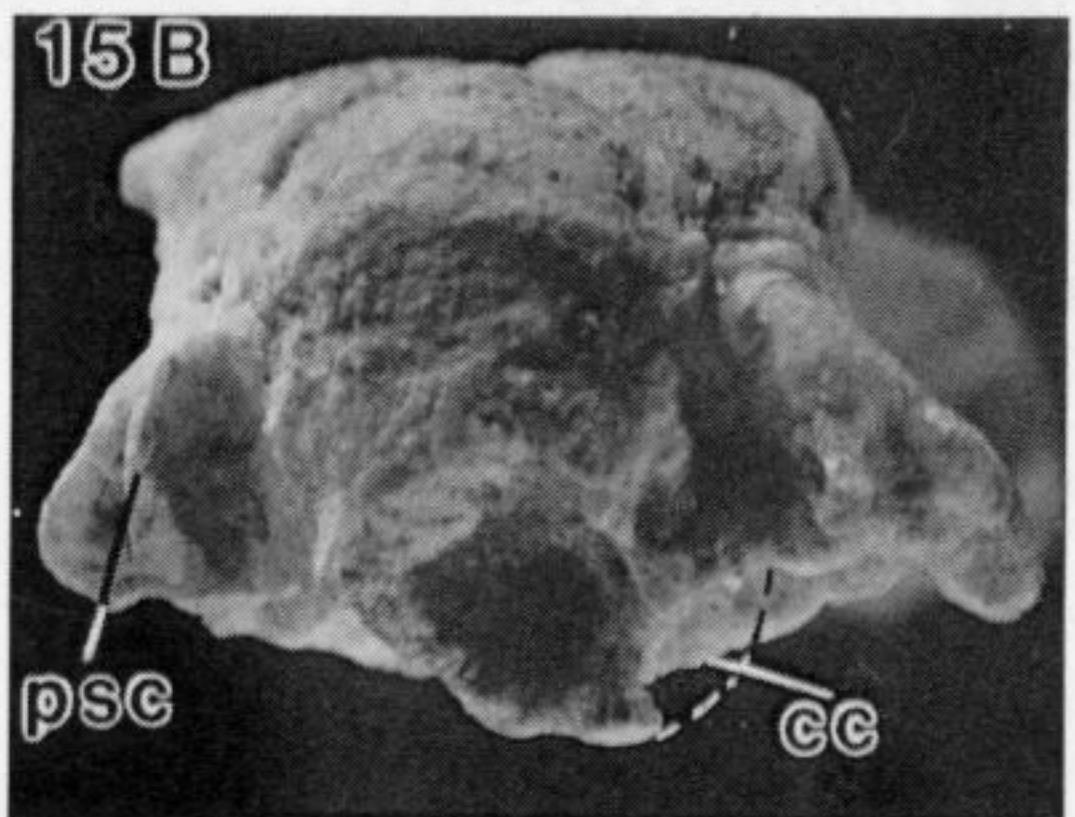
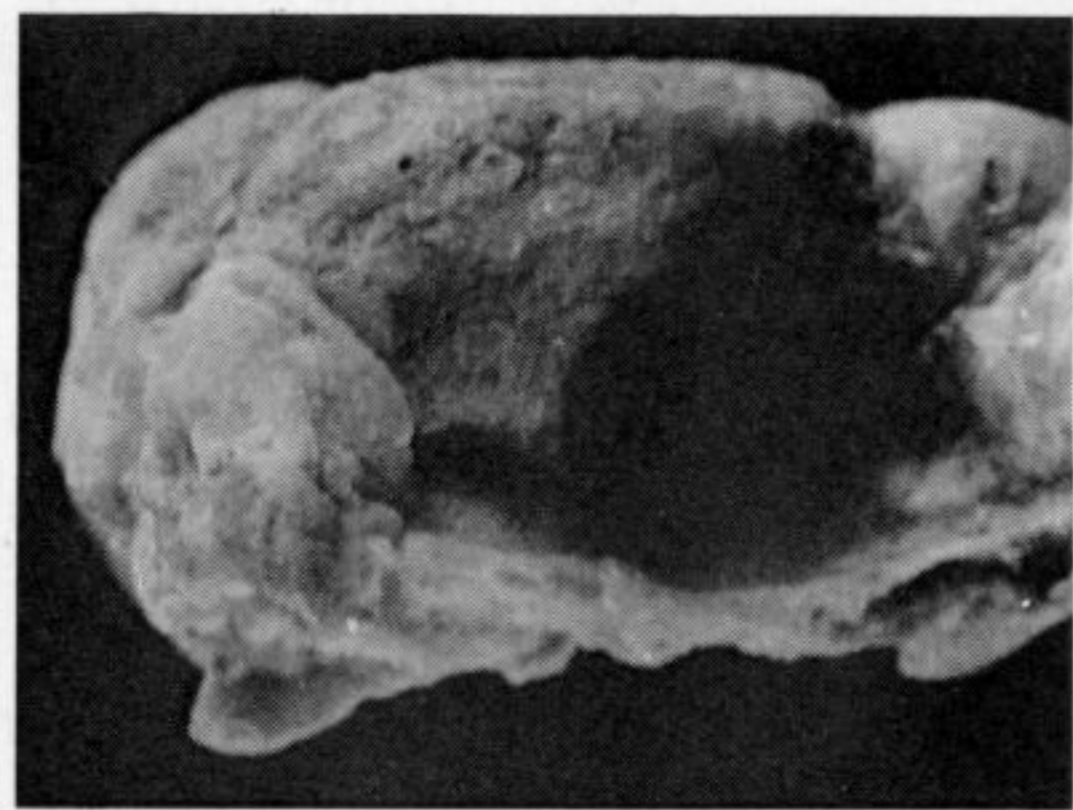
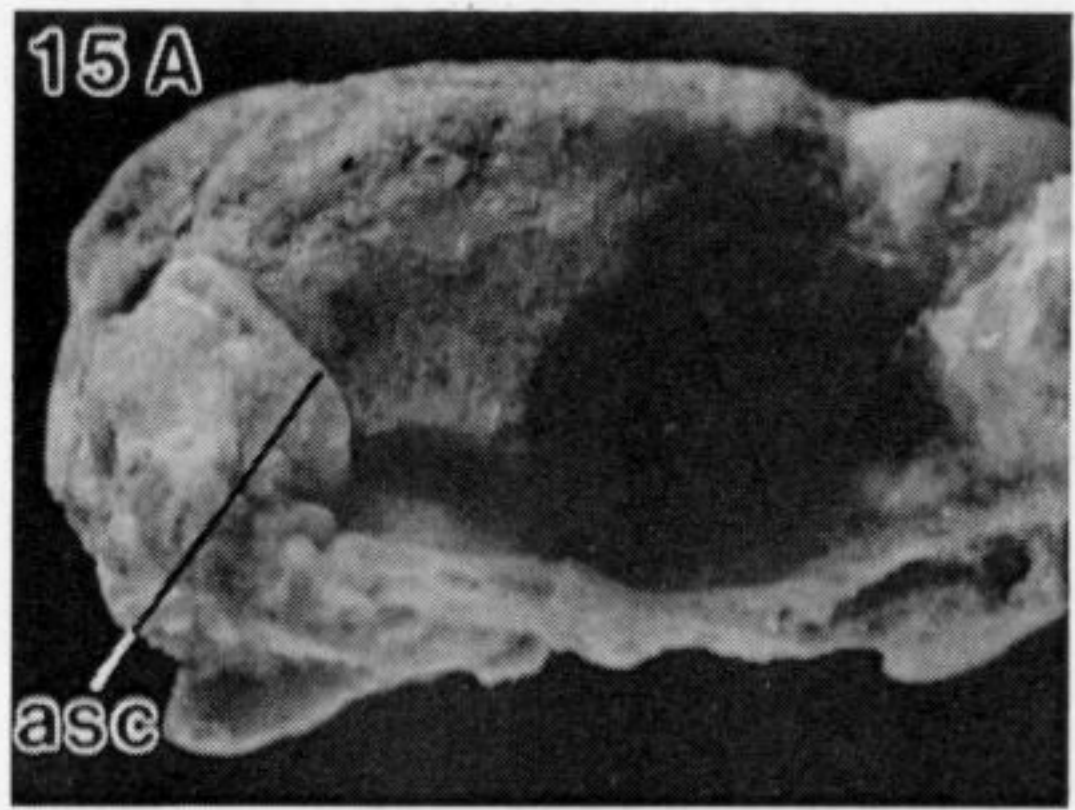
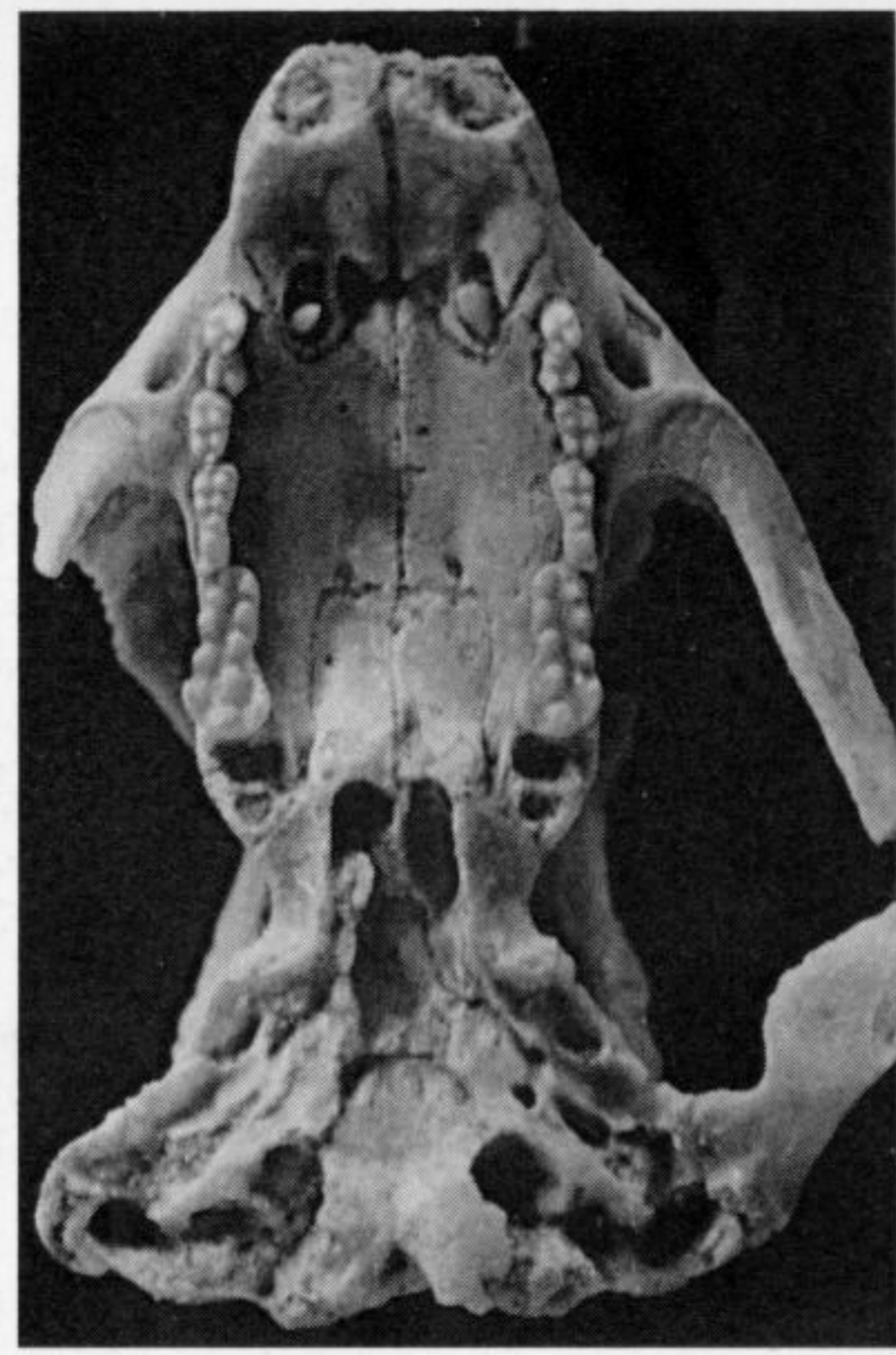
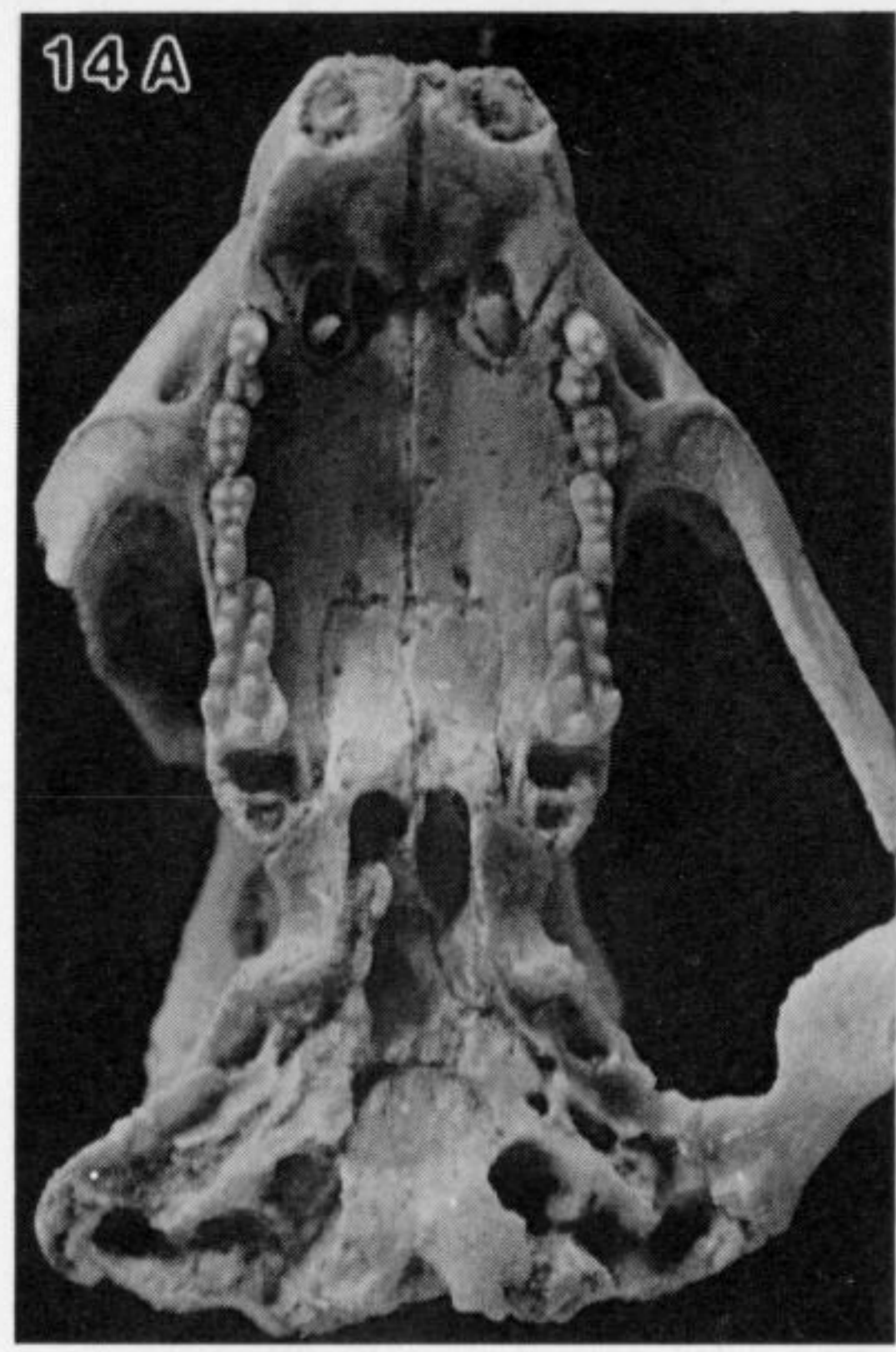




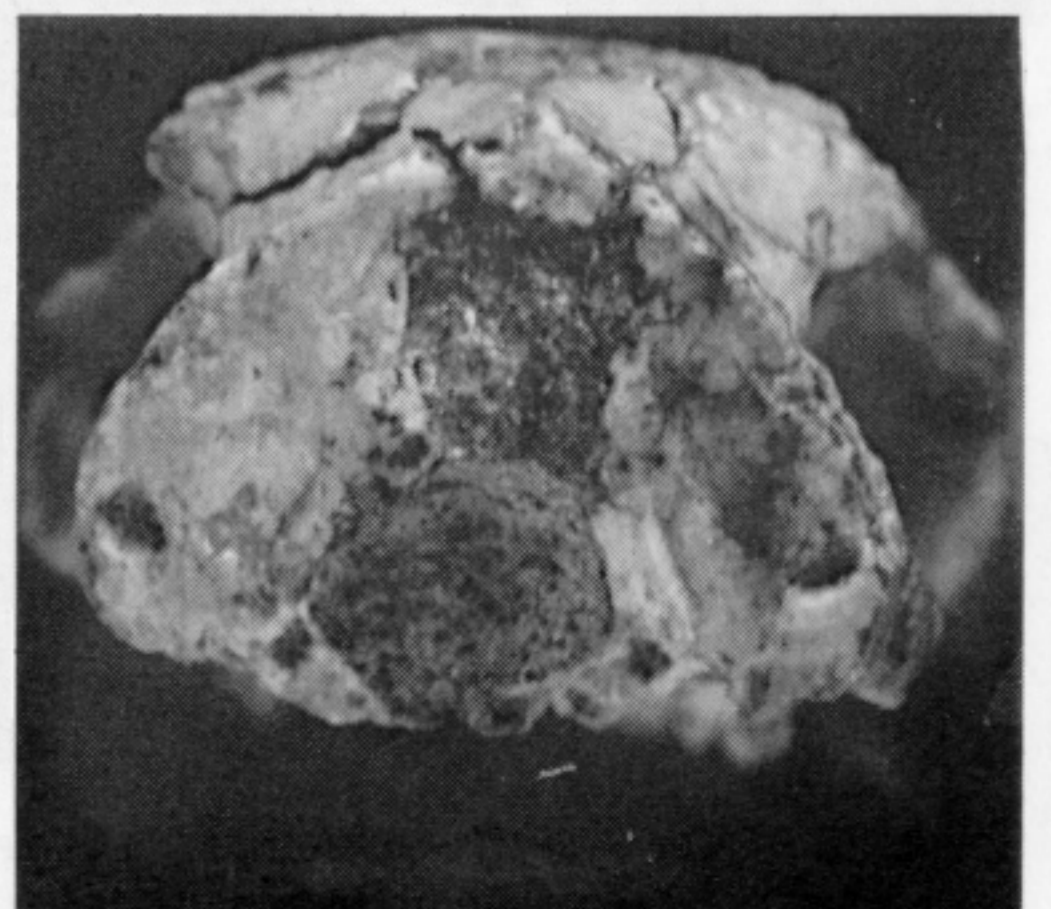
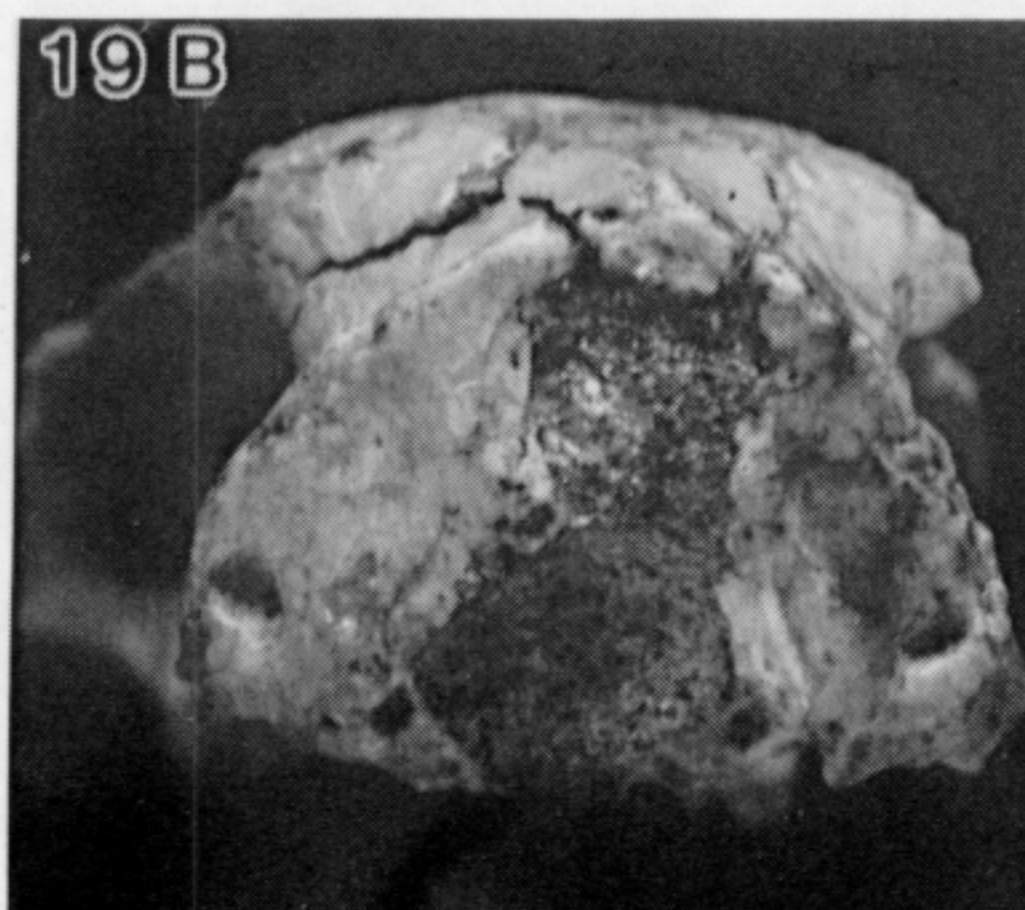
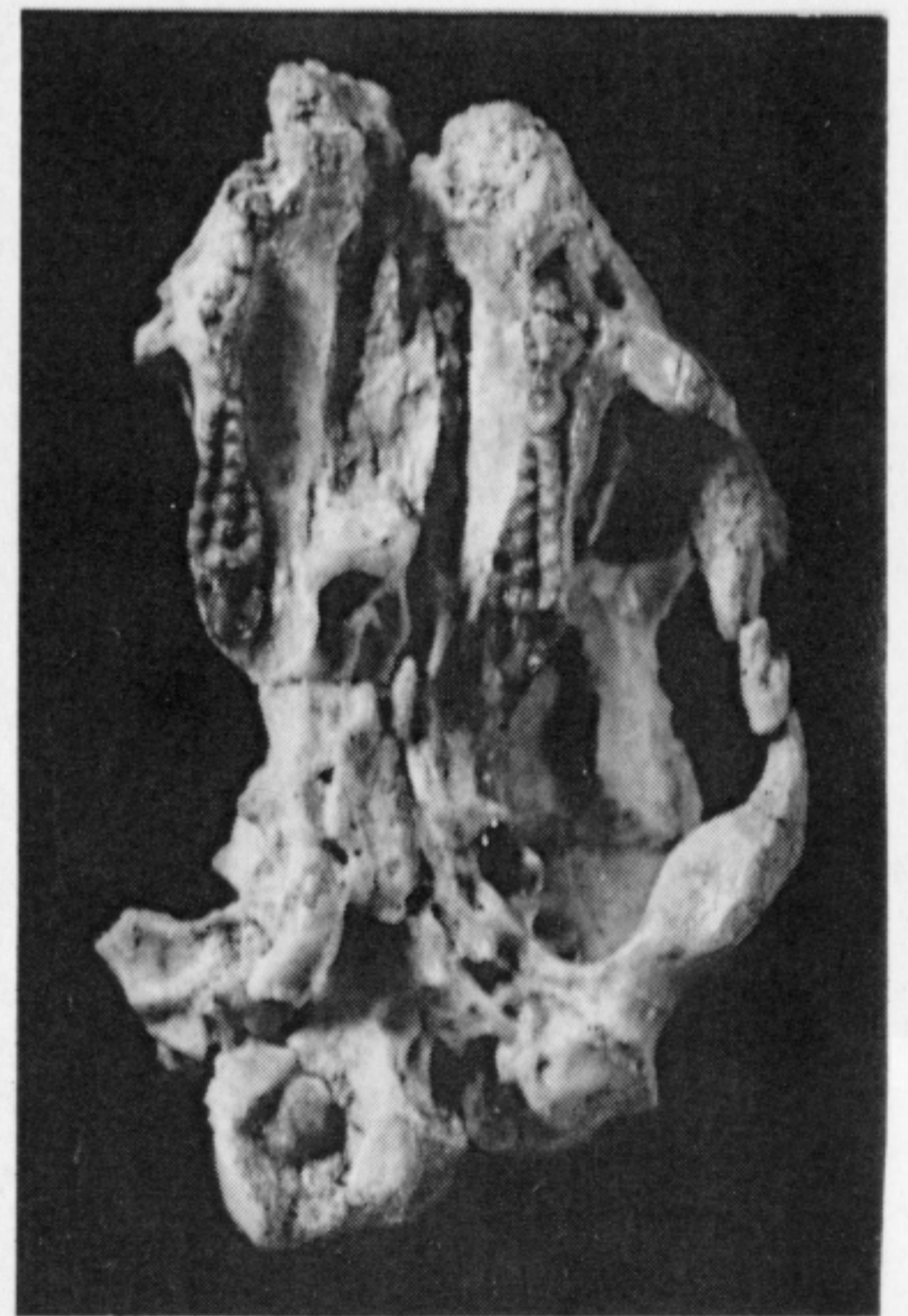
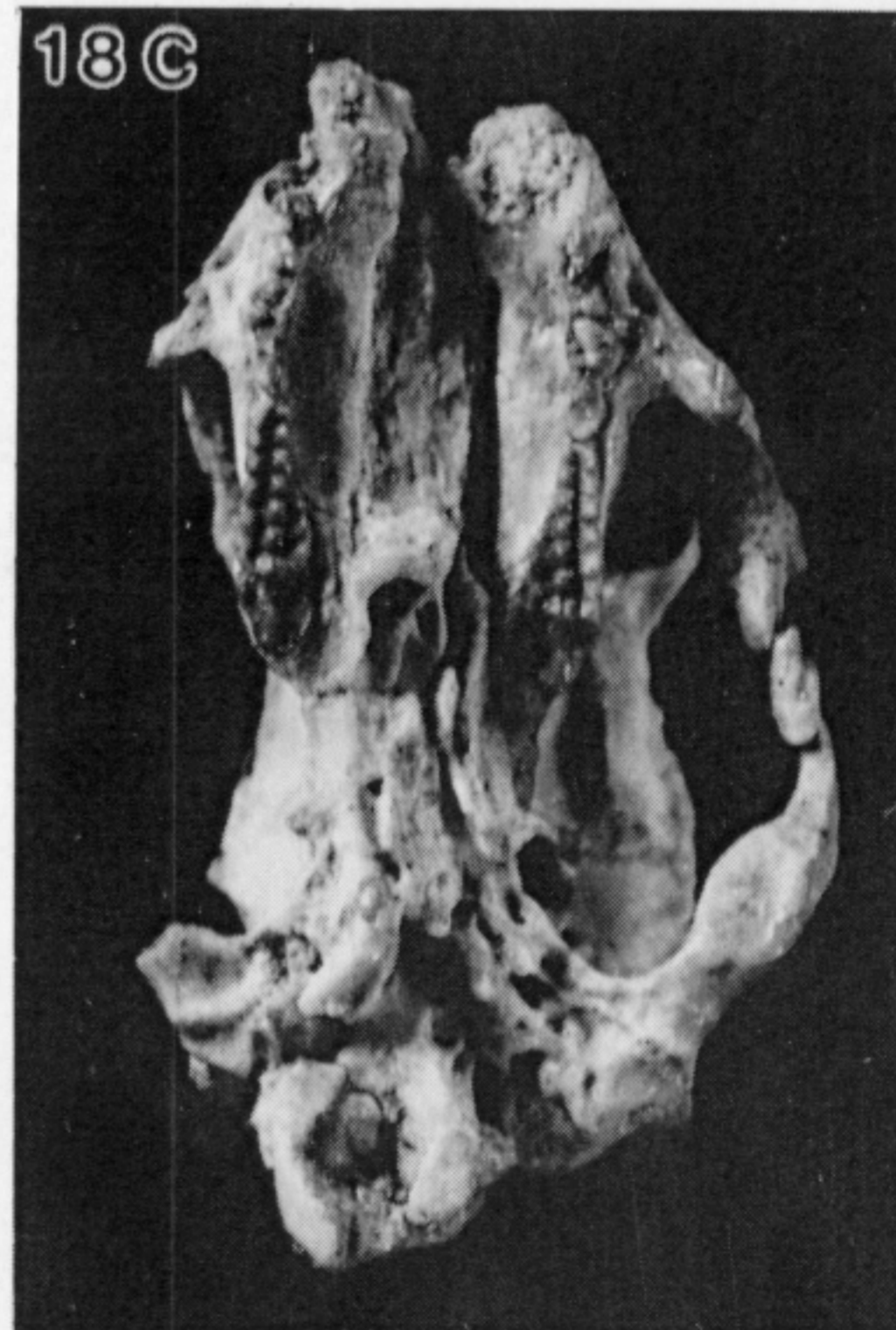
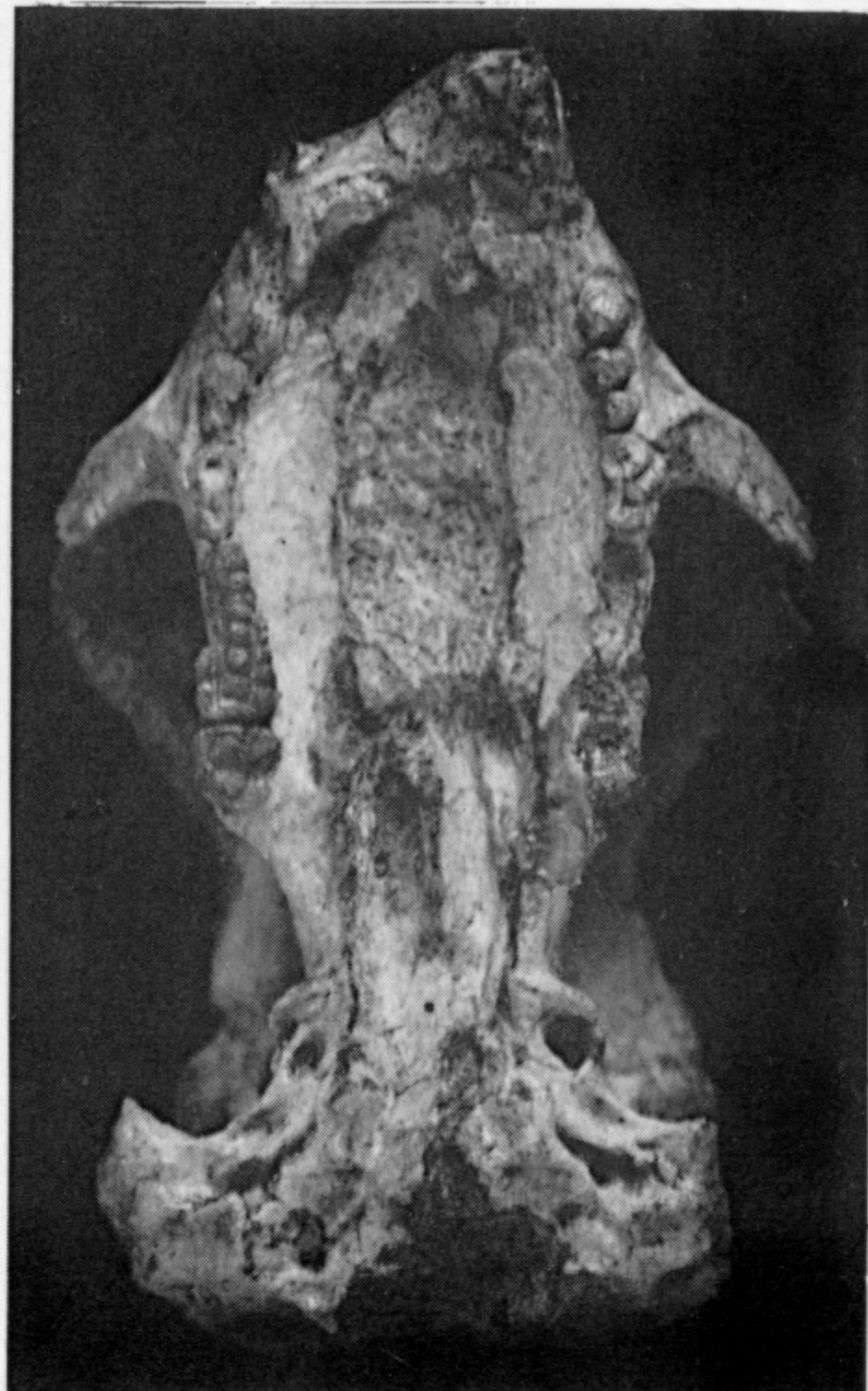
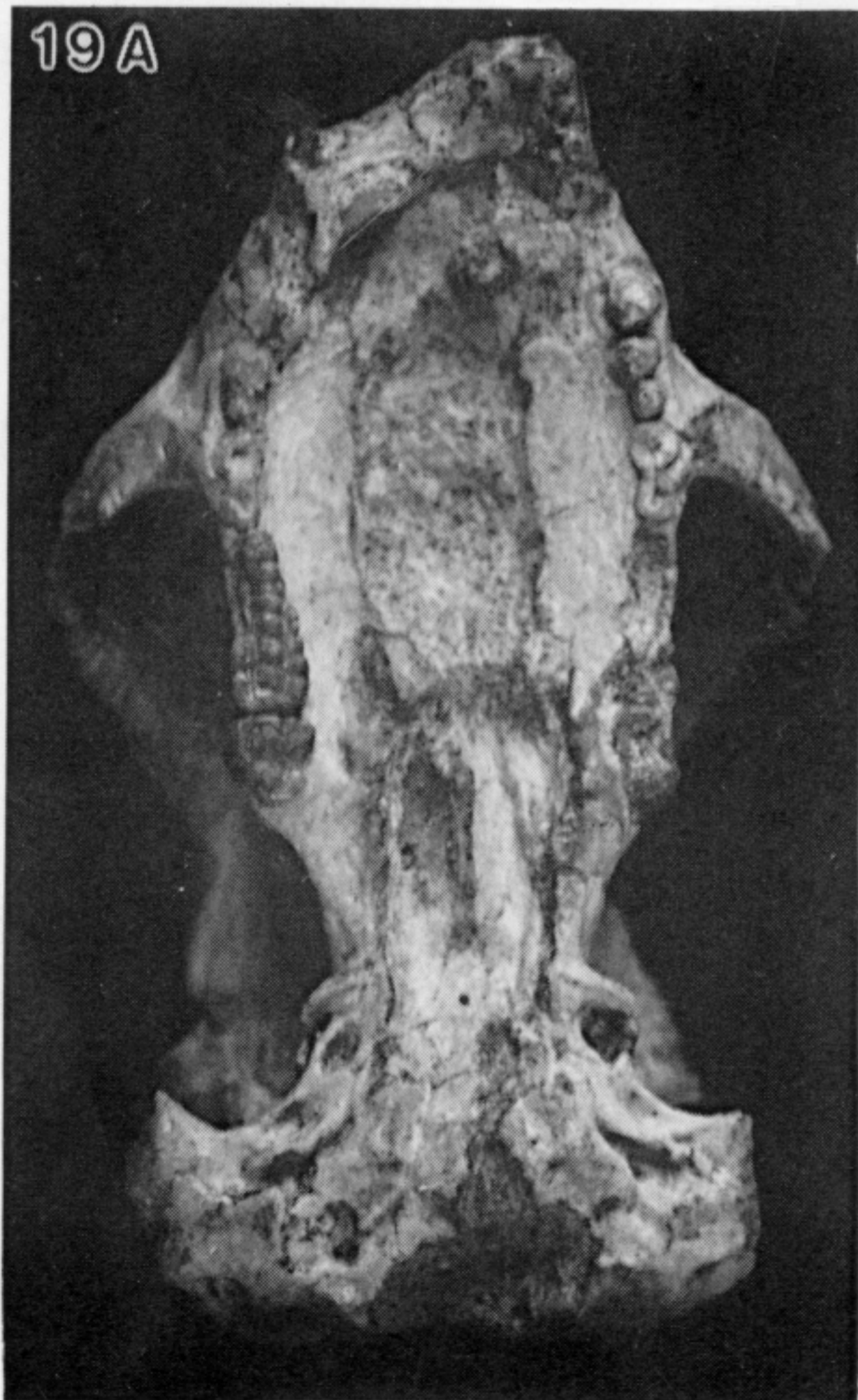
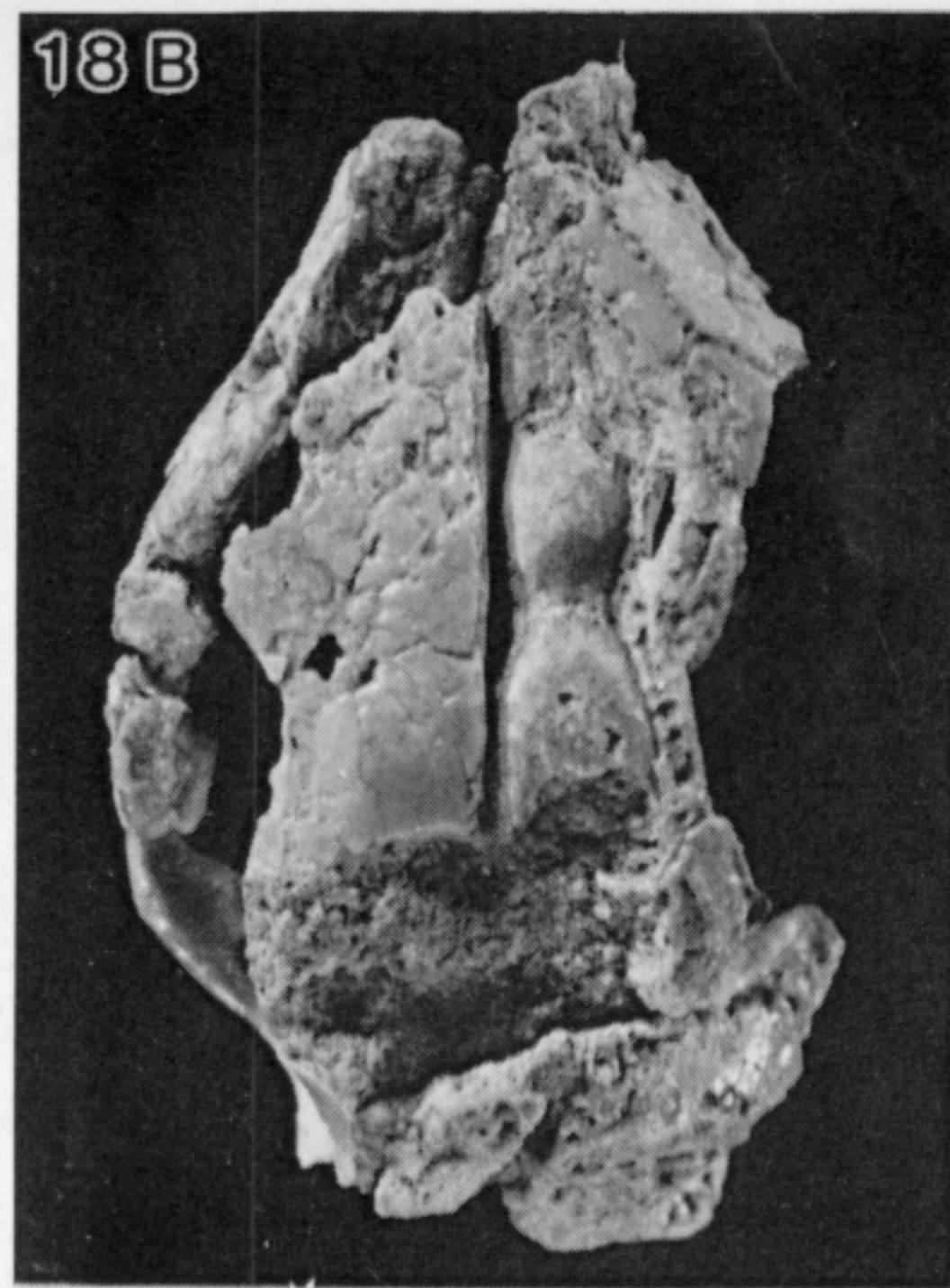
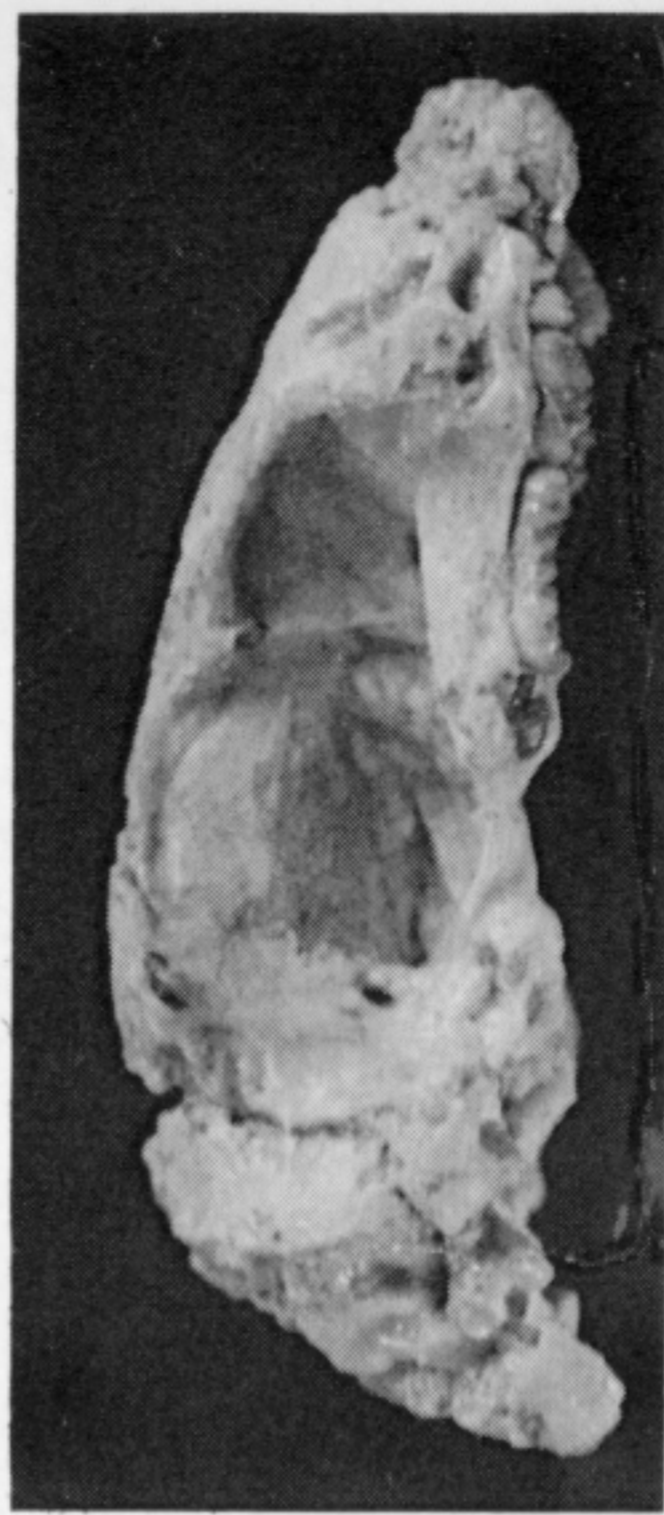
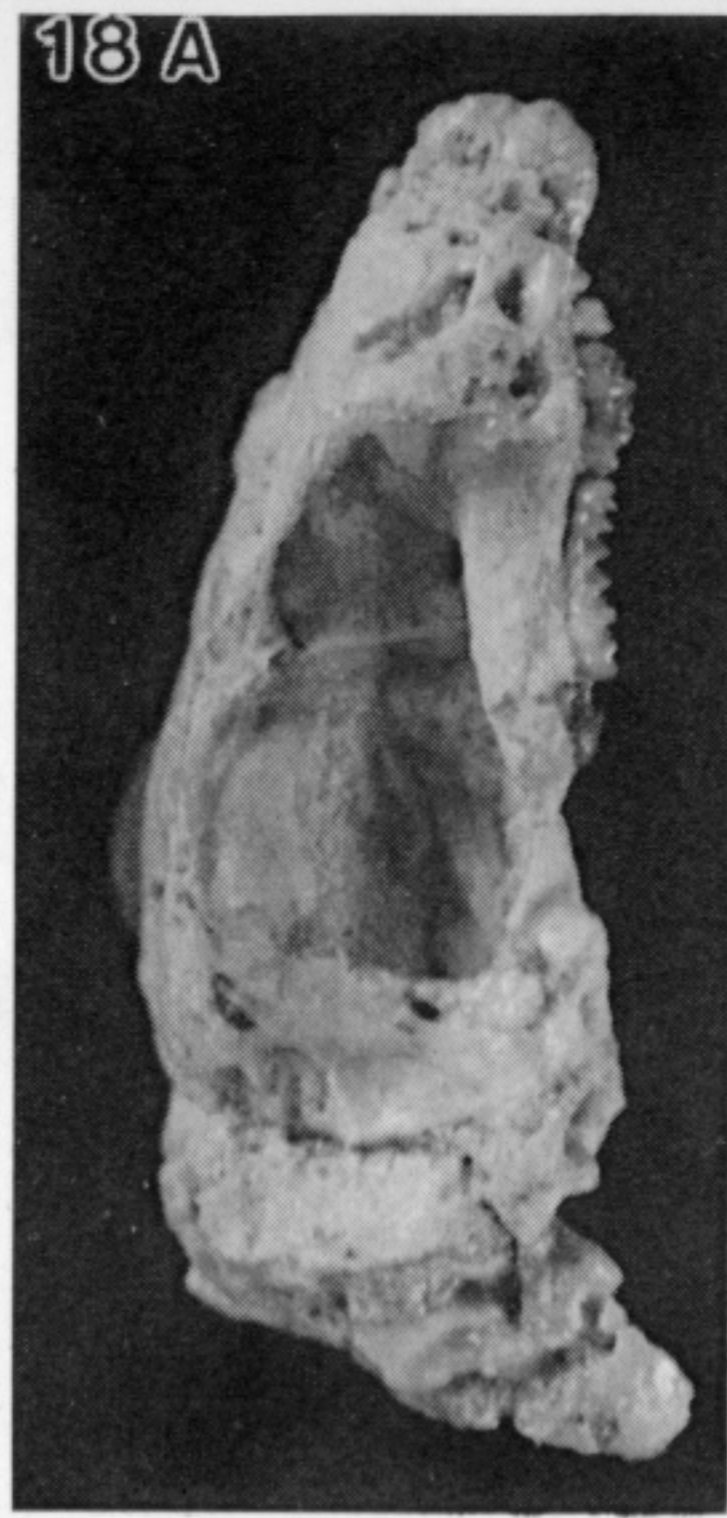
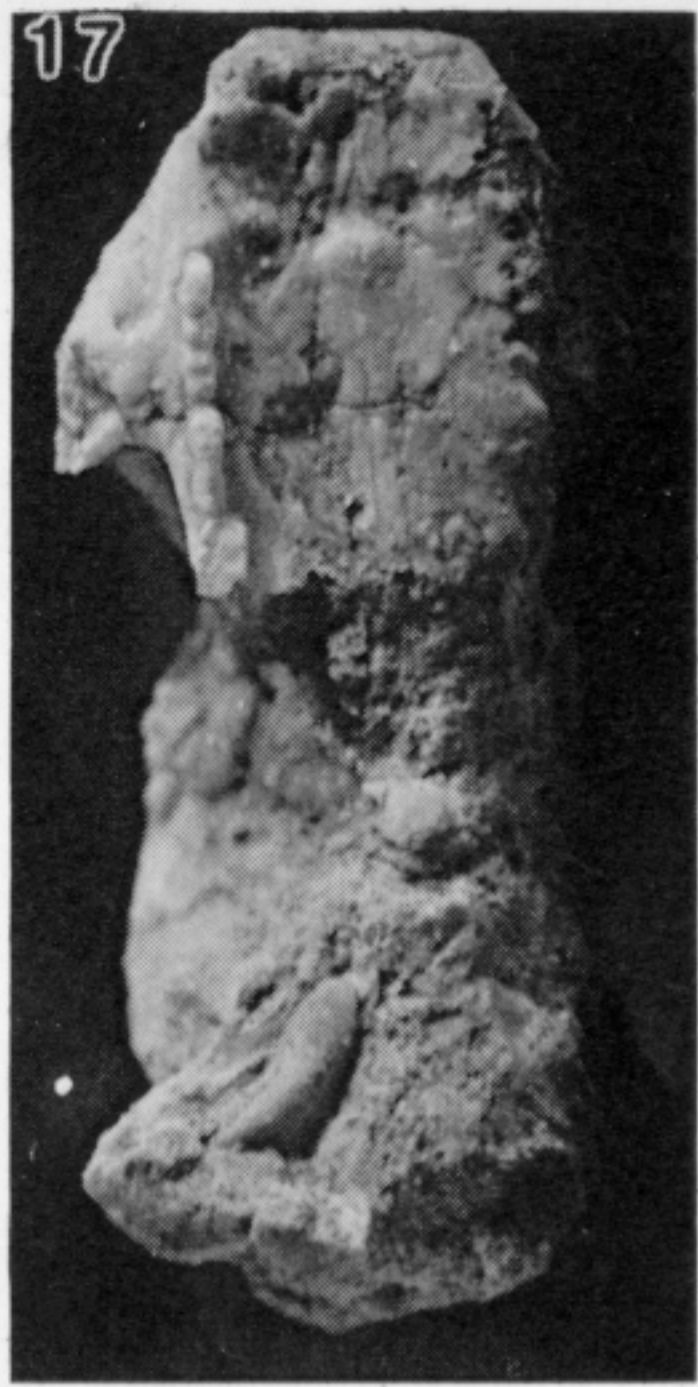




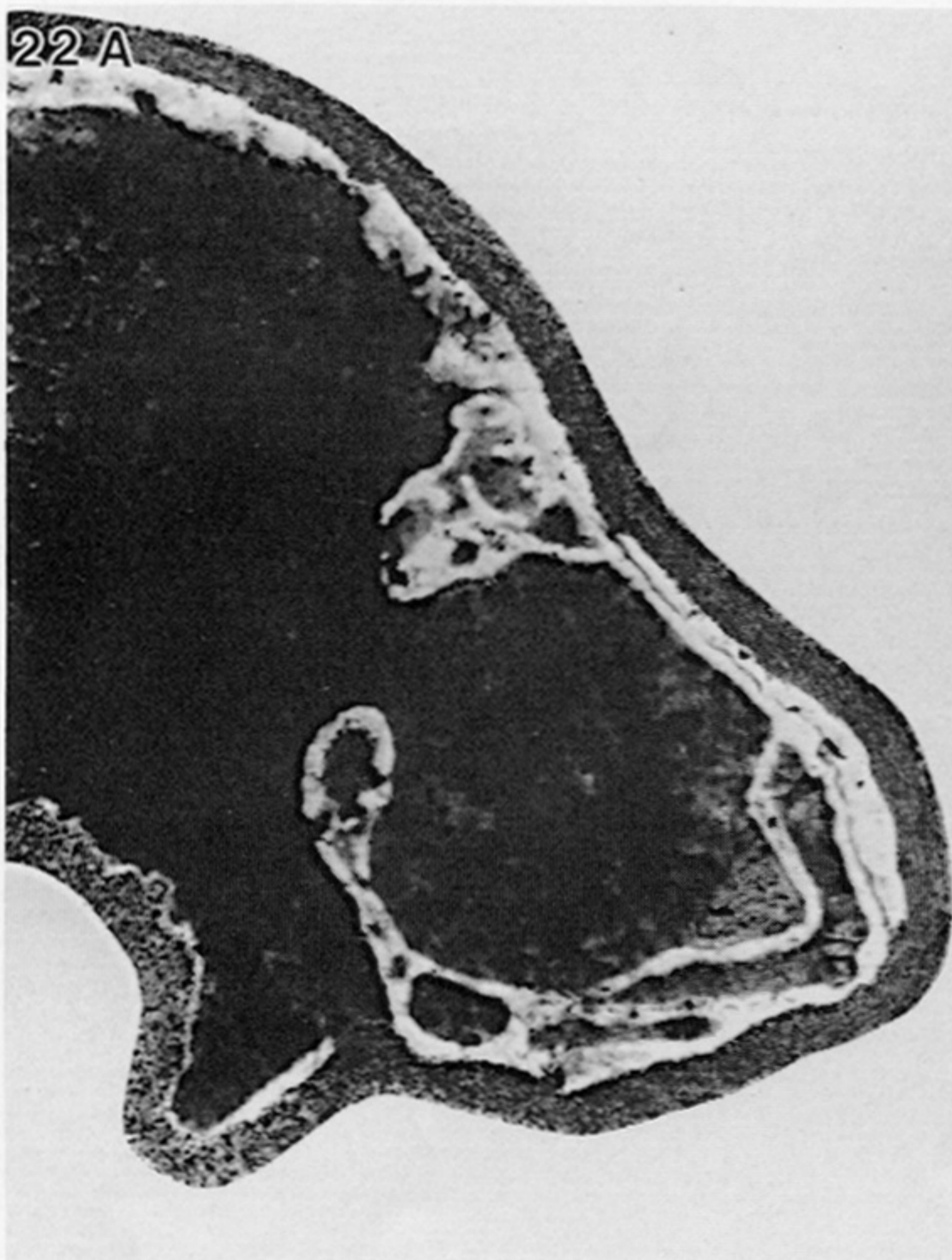
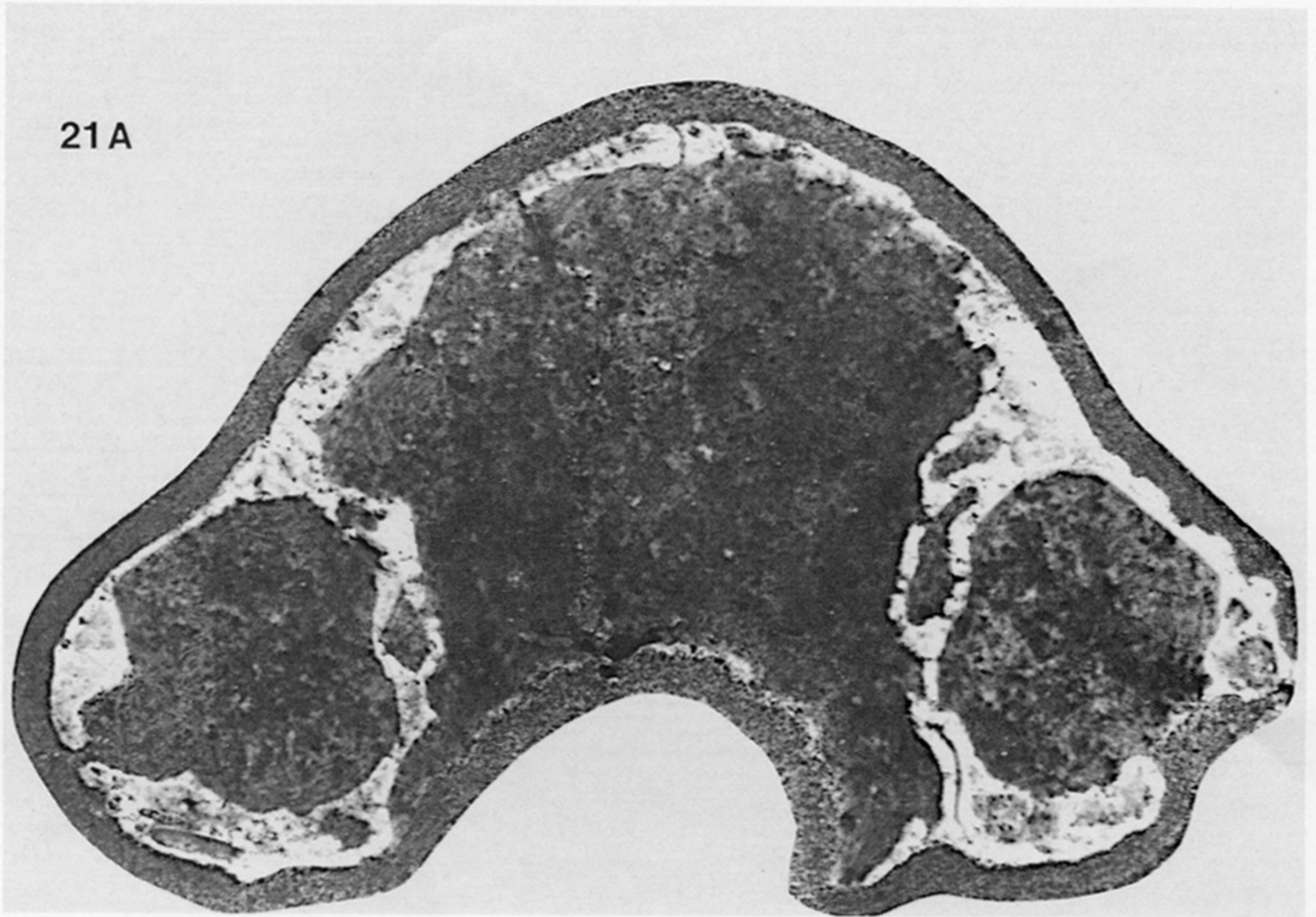
FIGURES 12 AND 13. For description see p. 538



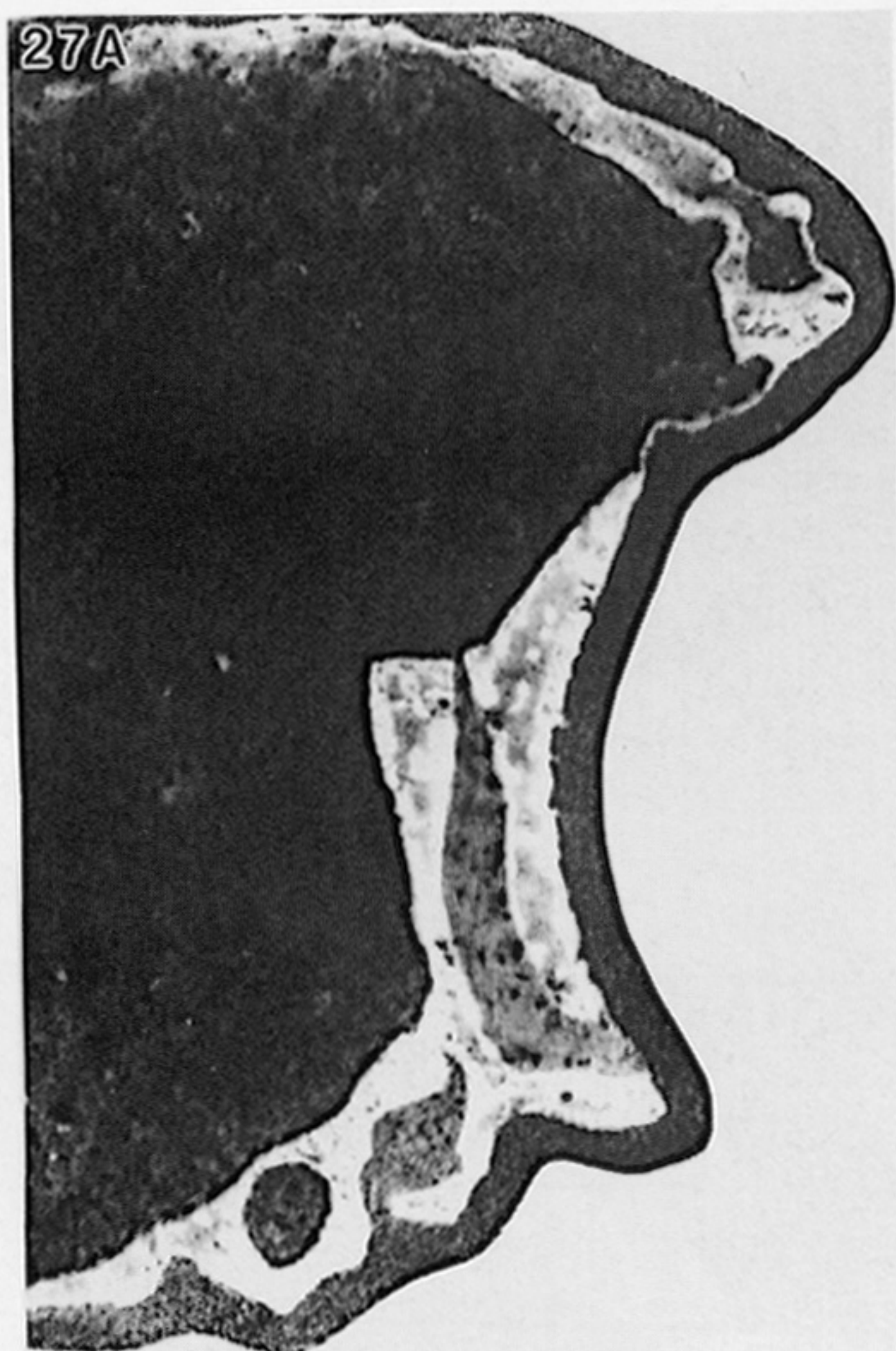
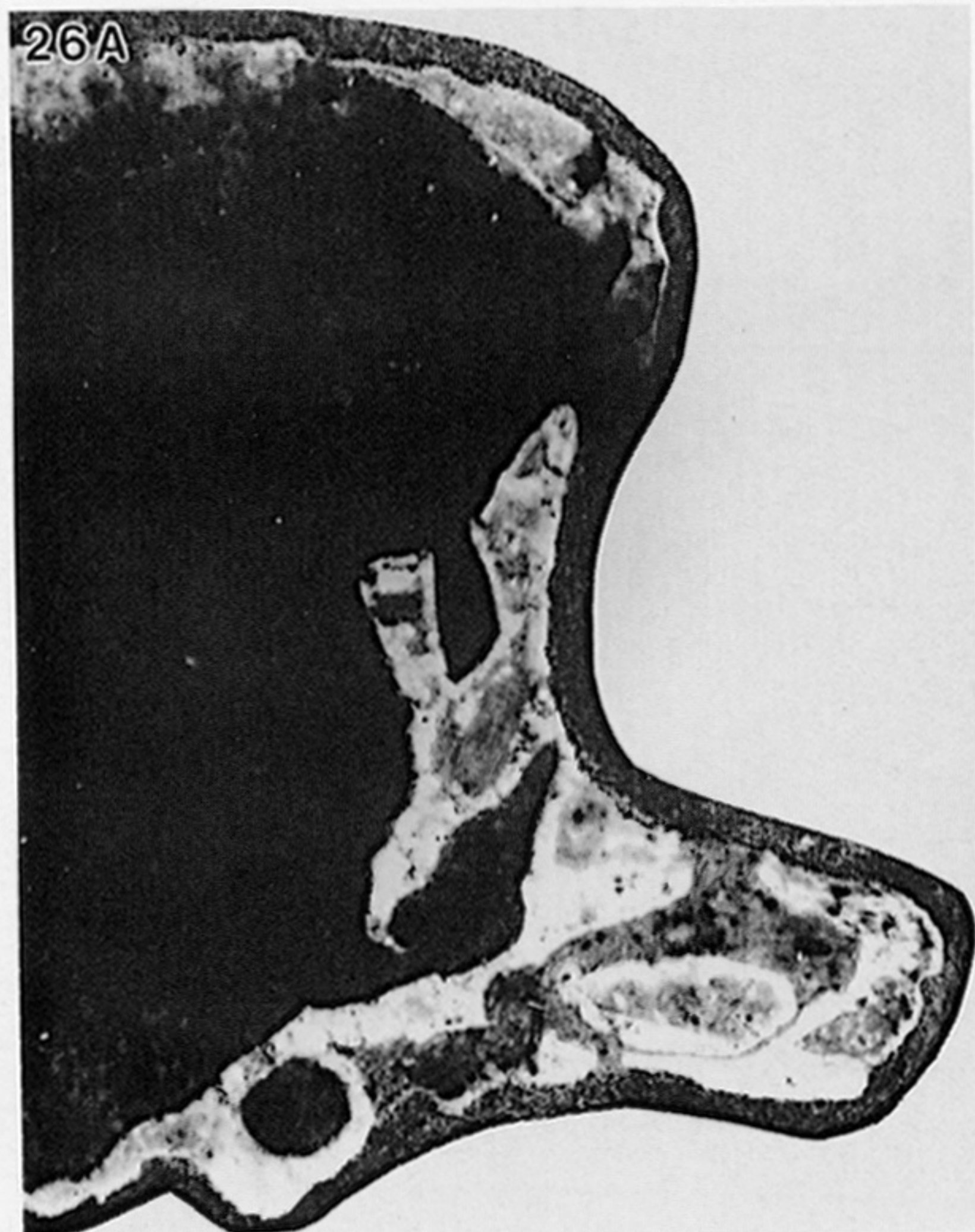
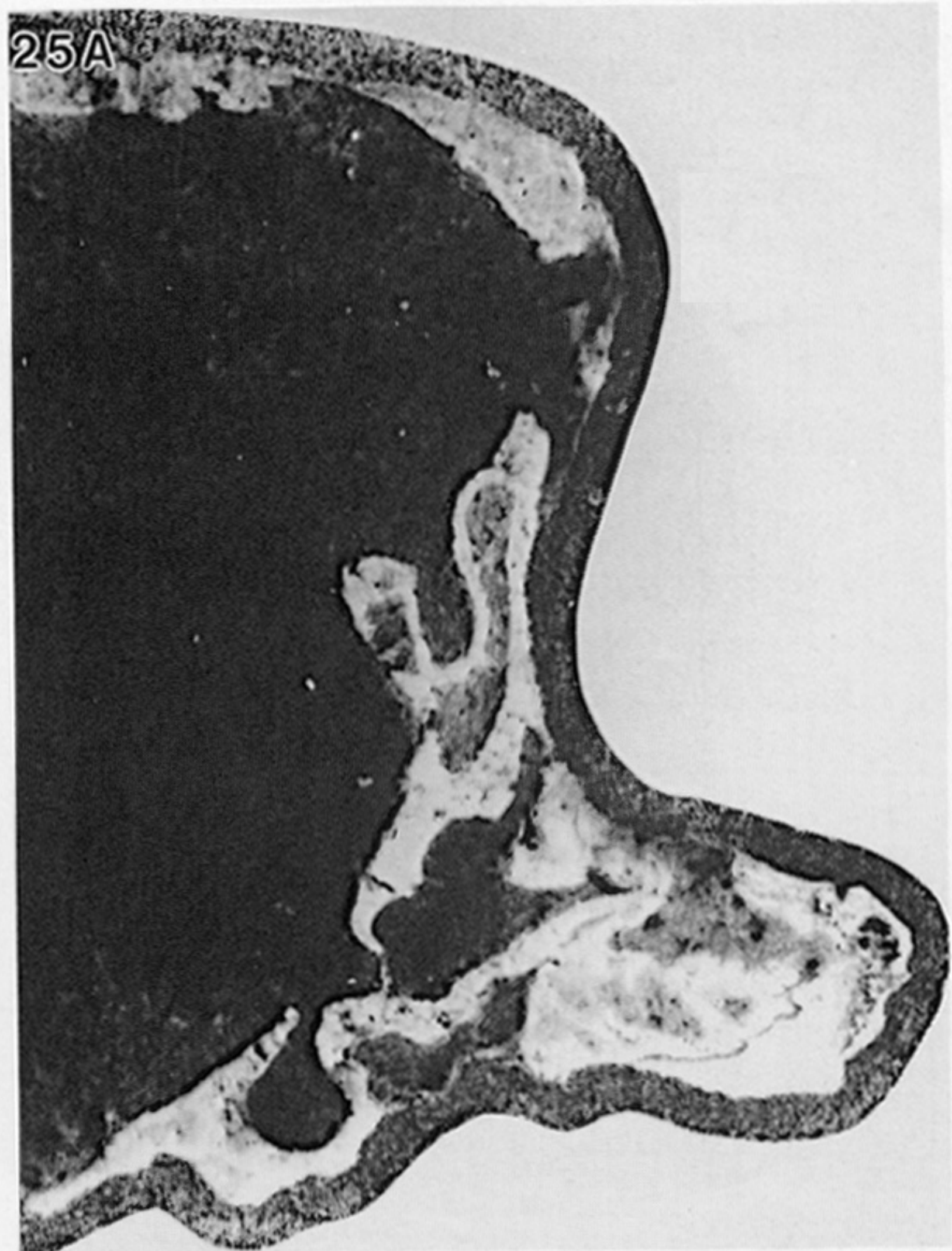
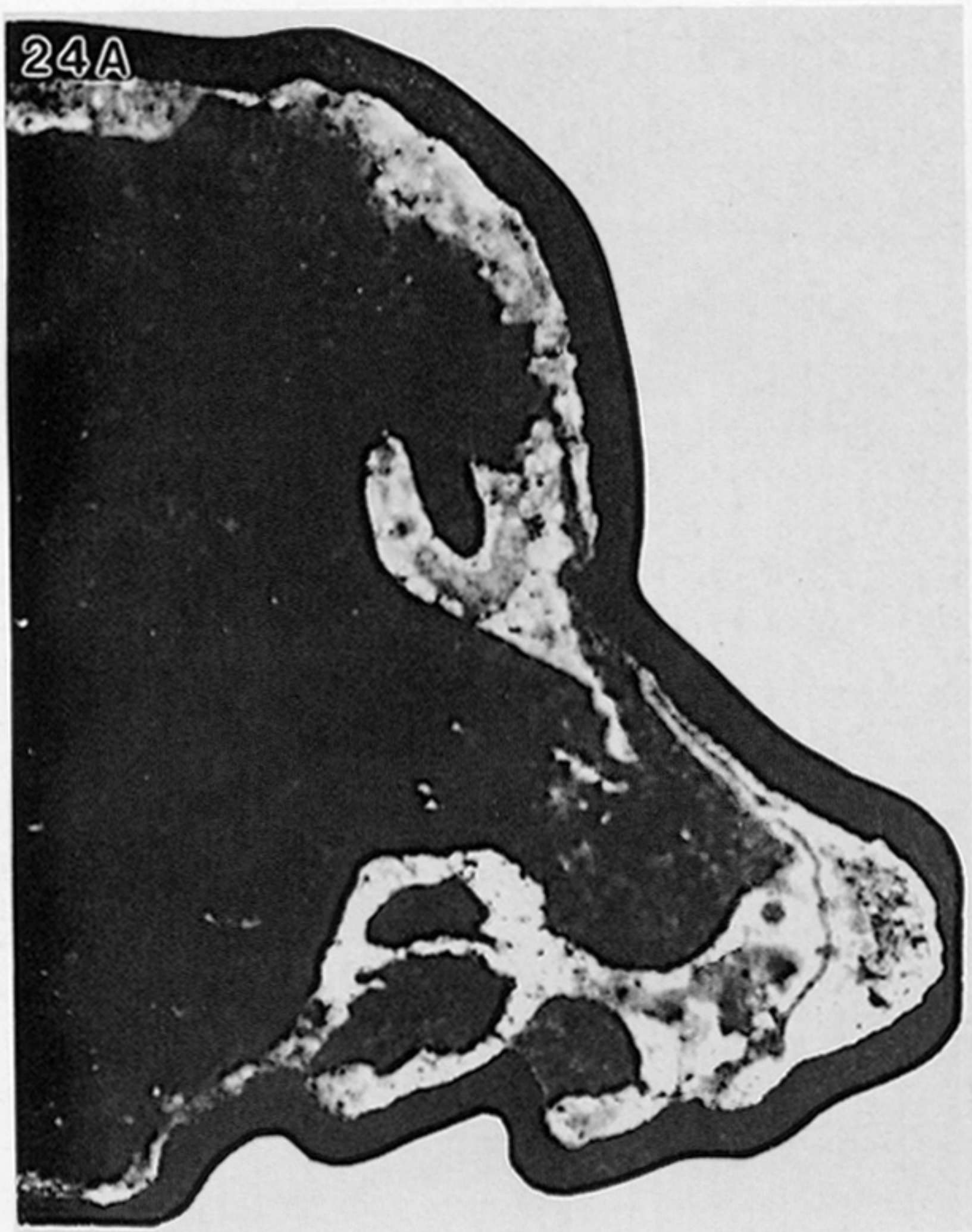
FIGURES 14-16. For description see p. 539.



FIGURES 17-19. For description see opposite.

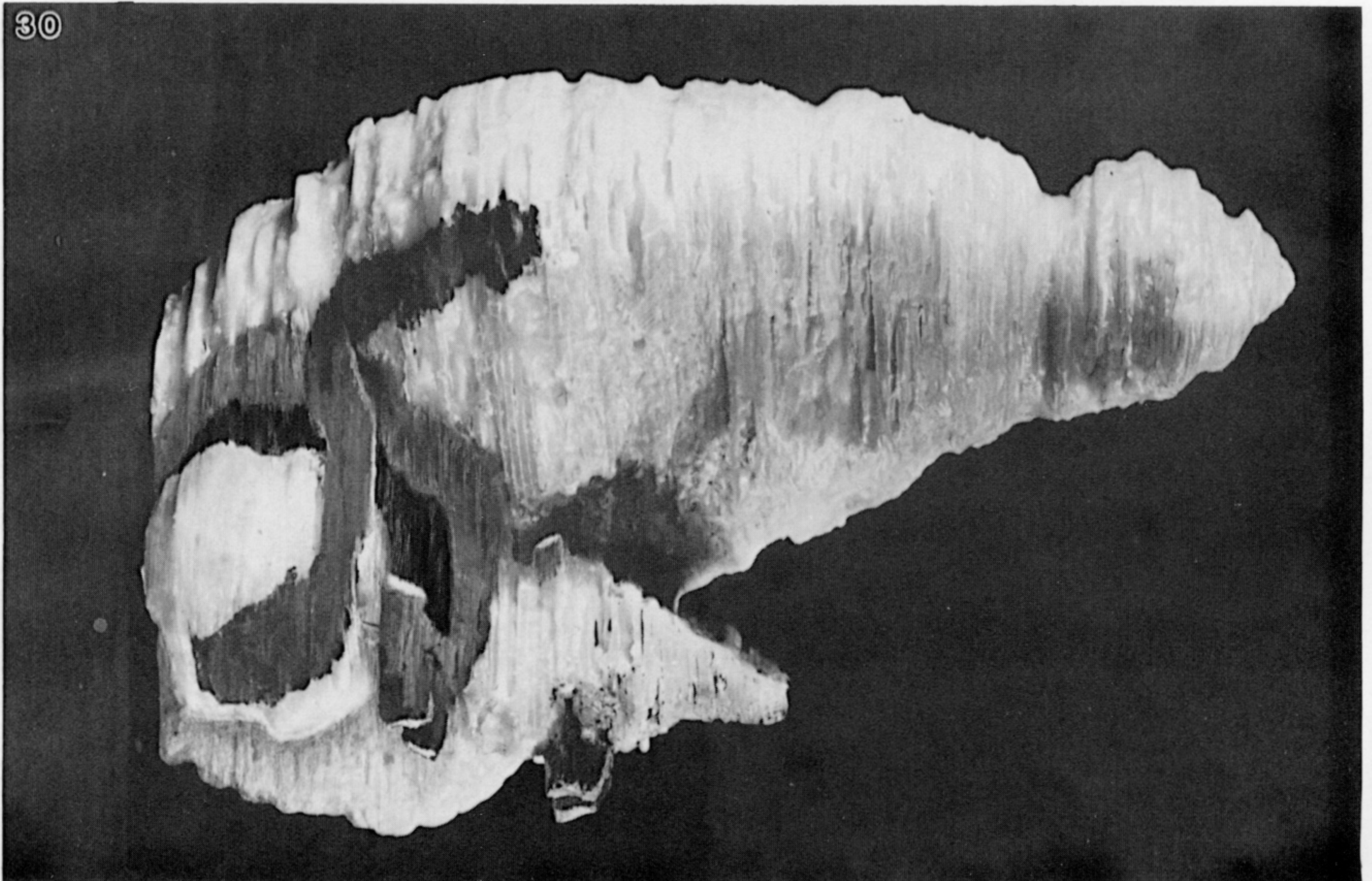
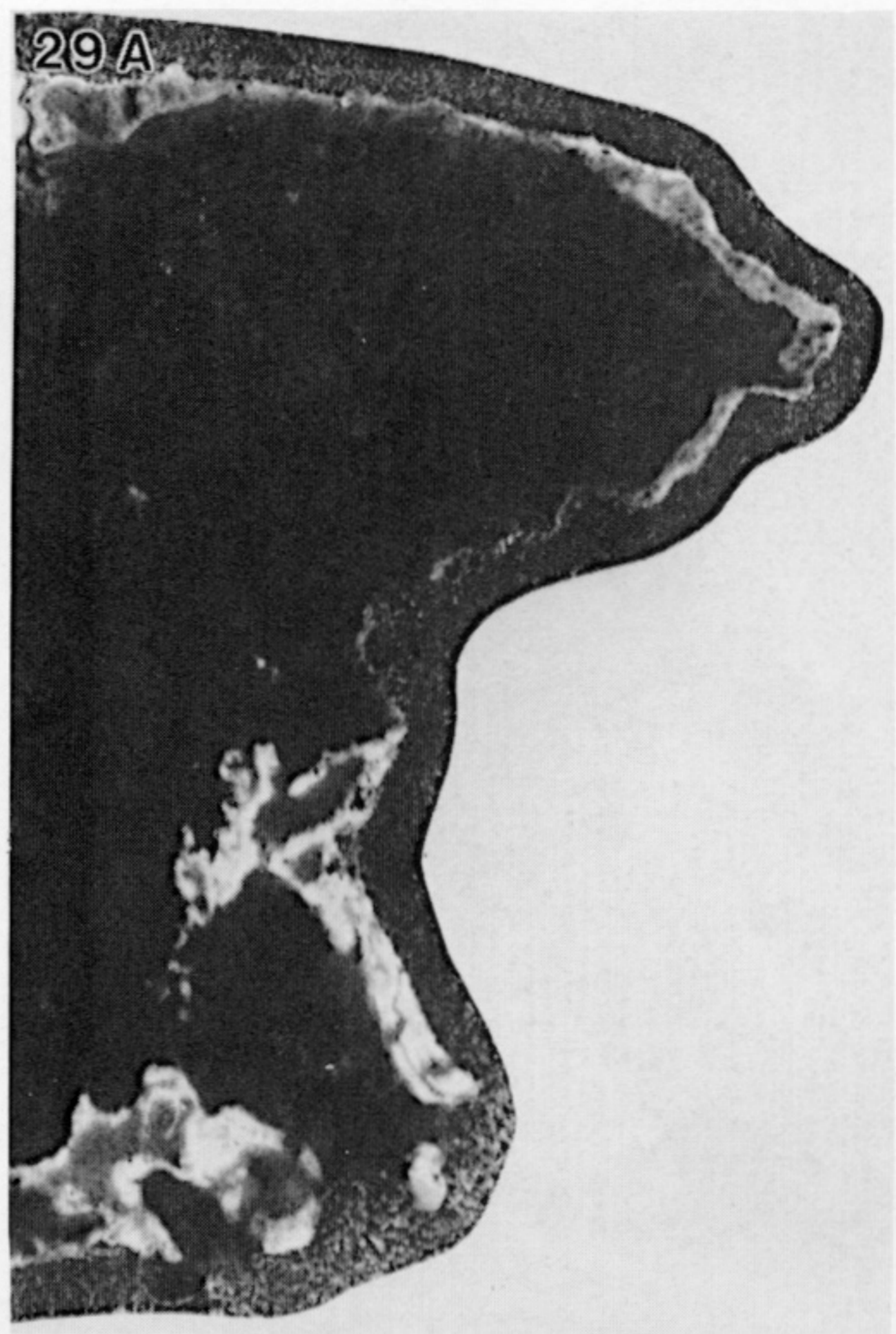
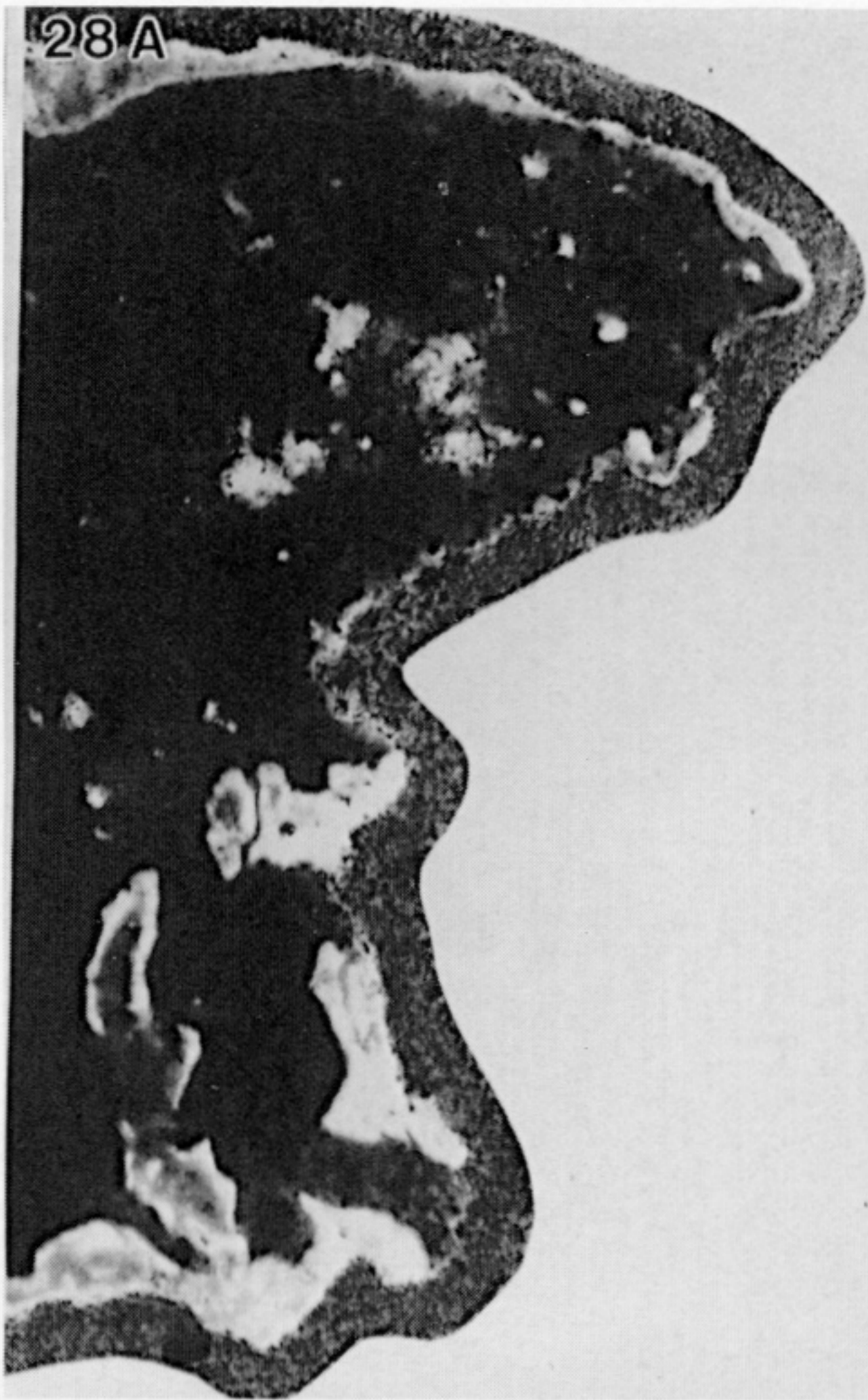


FIGURES 21 A, 22 A AND 23 A. For description see opposite.



FIGURES 24A, 25A, 26A AND 27A. For description see opposite.





FIGURES 28 A, 29 A AND 30. For description see opposite.