Morphology and phylogenetic position of the holodipteran dipnoans of the Upper Devonian Gogo Formation of northwestern Australia

P. A. PRIDMORE, K. S. W. CAMPBELL AND R. E. BARWICK

Geology Department, Australian National University, P.O.Box 4, G.P.O. Canberra City, A.C.T. 2601, Australia

CONTENTS

SUMMARY

Holodipterus (*Holodipterus*) *gogoensis* was first described by Miles (*Zool. J. Linn. Soc.* **61**, 1–328 (1977)) from eight specimens from the Frasnian Gogo Formation of the Canning Basin, Western Australia. In 1991 *H. longi* was described by Campbell & Barwick from a single specimen from the same locality. Subsequent collecting has produced two other new species which we assign to two new subgenera, described herein as *H.* (*Holodipteroides*) *elderae* and *H.* (*Asthenorhynchus*) *meemannae*. Diagnoses of the two new subgenera are given. A small isolated palate, which provides new information on the mode of growth of the group, is described as Holodontid gen. et sp. indet. It is shown that all these holodipterans have a distinctive mode of dental growth involving periodic and extensive resorption of denticles, teeth and calluses. Hypermineralized dentine occurs in both the teeth and the calluses. Smith (in Campbell & Smith, *Rec. Aust. Mus.* **39**(3), 131–167 (1987); and in Smith, *Mém. Mus. natn. Hist. nat., Paris* **C53**, 179–194 (1988)) has argued that because teeth are developed only in dental laminae, which are complicated structures unlikely to have been evolved more than once, they are reliable guides to understanding phyletic relationships. Consequently she considered that holodipterans should be regarded as derivatives of a *Speonesydrion*-like dipnoan that retained and developed numbers of shedding denticles. Campbell (in Campbell & Smith 1987), and Campbell & Barwick (in *Early vertebrates and related problems of evolutionary biology* (ed. M.-m. Chang *et al.*), Beijing Science Press (1991)) argued that teeth have evolved several times in dipnoans and that their presence in holodipterans is not indicative of relationship. The latter authors have given reasons for considering *Holodipterus* to be a member of the so-called 'rasping' or 'denticle shedding' lineage which can be traced back to the Early Devonian *Uranolophus*. The newly described subgenera add information vital for clarifying the position of the holodipterans. *H.* (*Holodipteroides*) had no true teeth, but it produced radial ridges on the palate and prearticulars simply by adding new raised tissue at the end of the radial ridges, and it had denticulated plates attached to the surface of the basihyal. *H.* (*Asthenorhynchus*) had a pectoral girdle of the same kind as *Griphognathus* and a number of dermopalatines and other denticulated plates at the anterior end of the palate, as does *H.*

Phil. Trans. R. Soc. Lond. B (1994) **344**, 105–164
Printed in Great Britain

(*Holodipterus*) *gogoensis* and *Griphognathus whitei*, which is the best documented member of the 'denticle-shedding' lineage. It is also shown that holodipterans and *Griphognathus* shared a distinctive pustulose/perforate structure of the head bones. We therefore conclude that holodipterans, *Griphognathus* (and perhaps other rhynchodipterids) developed from some unspecified Middle Devonian stock that underwent rapid radiation either at the end of the Middle Devonian or in the early Late Devonian (Frasnian).

1. INTRODUCTION

Six species of lungfish belonging to four genera have been described from the Frasnian (Upper Devonian) Gogo Formation of northwestern Western Australia (Miles 1977; Campbell & Barwick 1990, 1991, 1994). Two of these, *Griphognathus whitei* and *Chirodipterus australis*, are represented in Australian and overseas collections by a substantial number of specimens, some of which are quite exquisitely preserved. Studies of the skull material have resulted in a considerable body of information on the cranial and dental anatomy of these two species becoming available (Miles 1977; Campbell & Barwick 1983, 1987; Campbell & Smith 1987; Smith & Campbell 1987; Cheng 1989). Material assignable to the other four recognized species is much rarer, and the skulls that have been described are less complete.

Amongst these lesser known Gogo dipnoans is a species assigned by Miles to the genus *Holodipterus* White & Moy-Thomas. Moy-Thomas & Miles (1971) had erected a new Order, the Holodipterida for this genus and *Devonosteus*, a genus based on a skull from Wildungen. The species, *Holodipterus gogoensis* Miles, was erected on the basis of material from eight very incomplete specimens (Miles 1977, p. 14). Since then a more gracile species named *Holodipterus longi* (Campbell & Barwick 1991, p. 435) has been described from the palate and mandible of a single specimen.

This paper describes the results of further investigations of Gogo holodipterans. Recently prepared material includes a single well-preserved specimen showing the structure of the skull, the pectoral girdle, most of the mandible, and the scalation of a new species assigned to a new subgenus *H.* (*Asthenorhynchus*). New material, in conjunction with earlier prepared incomplete material, also establishes the presence of a second new subgenus *H.* (*Holodipteroides*). The available material of the latter form is limited, and although it comes from several specimens it does not allow for a complete account of the skull or the remainder of the skeleton. Nevertheless it provides data on aspects of the hyoid arch not available from *H.* (*Holodipterus*) *gogoensis*. Furthermore, it should be noted that one specimen, the palate of which was sectioned and described by Campbell & Smith (1987) in their study of the dentition of *H.* (*Holodipterus*) *gogoensis* and referred by them to that species, is attributable to this new subgenus. These subgenera display a number of features which link them (and hence all holodipterans) to *Griphognathus*.

The present work has also seemed an appropriate place to present a full description of *H.* (*Holodipterus*) *longi*. Campbell & Barwick (1991) provided a diagnosis of this taxon and presented several photographs of the holotype, but a full description has not been published. Initially it had seemed to us that some of the new Gogo material might be attributable to *H.* (*Holodipterus*) *longi*, but as preparation proceeded it became evident that this is not the case. We argue that holodipterans are members of the group of primitive dipnoans that shed their buccal denticles, teeth and marginal ridges episodically, at which times they remodelled their dental apparatus.

2. HOLODONTIDAE (Gorizdro-Kulczycka, 1950)

Remarks. This family was erected for *Holodipterus*, but in the opinion of Miles (1977) it may also contain *Devonosteus*. Campbell & Barwick (1990) suggested that the genus *Conchopoma* also belongs with it, but the supporting evidence is, and remains, weak. Despite the lack of other genera that could be considered to be sufficiently closely related to *Holodipterus* to be included in the family, we consider that the genus is sufficiently distinctive to warrant its isolation in a distinct family. We predict that other older genera of the family will be discovered in the Middle Devonian marine rocks of Europe or Australia.

Note that in this text we use the word 'holodipteran' as an informal adjective to refer to the members of the genus *Holodipterus* and its subgenera.

3. HOLODIPTERUS (White & Moy-Thomas, 1940)

Type species. H. kiprijanovae Pander from the Upper Devonian of the Orel District, Russia.

Diagnosis. Large dipnoans with a concave dorsal lateral skull profile and a broad, depressed and ventrally recurved snout in the adult; paired C and E bones, and a small D; bone I with a long buried posterior projection; lateral line present in J; K not present as an independent bone; the lateral line from J joins the main line in bone X; in lateral profile the ventral edge of the cheek strongly arched to accommodate a large soft preorbital cheek; lateral line retained in bone 3; snout, if ossified, covered with continuous dentine that contains only the lateral line pores and those from the rostral tubuli; a little cosmine present behind this dentine; surface of the remainder of skull roofing bones with variably developed porous cosmine-like material or bone, with pustules made of dentine separated by bone perforated with large regularly spaced pores.

Endocranium suspended from the skull roof by a median crista that terminates well forward of the posterior end of the skull, and much longer dorsolateral cristae that extend back well beyond the occiput; no adlateral cristae, nor fenestrae in the lateral cristae, nor f.mm.l of Miles (1977) present; endolymphatic ducts open at the transverse level of the posterior end of the median crista; jugular vein opens into the temporal chamber beside the orbital artery foramen, as well as into the orbital chamber via the foramen sphenoticum minus.

Outline of dentary rectangular, with parallel sides and a transverse anterior edge; crest of dentary carrying a row of teeth with hypermineralized cores; three infradentaries, surangular, angular and a single splenial/postsplenial; anterior furrow covered by a large transverse adsymphysial plate and ends of the prearticulars; a small median pit between the dentary and the adsymphysial plate opens down into the covered anterior furrow; labial furrow long and deep. Lateral lines deeply buried in or beneath the bone on both skull and mandible, consisting of a circular tube and a slit-like extension towards the external surface; canals open to the surface by large pores.

Pterygoids and prearticulars with radiating rows of teeth or radial ridges without teeth; callus usually present on posteromedian part of palate and on heel of prearticular in adults; variable amounts of the buccal surfaces of both bones covered with denticles and a continuous sheet of white superficial dentine (see Campbell & Smith 1987, p. 166); all tissues of the buccal surface episodically resorbed, the white superficial dentine and the denticles being removed over wide areas and regrown after modification of the underlying bone had taken place to accommodate shape change; the more medial teeth also progressively removed; failure to remove patches of dentine permitted pleromic ingrowth of dark-coloured hypermineralized dentine, which in some places formed elevated calluses; lateral margins of pterygoids and prearticulars armoured with large denticles that are overgrown by bone during growth phases and then replaced by similar denticles during intervening phases. X-radiographs show the centre of ossification is close to the midline, indicating that growth was restricted to the anterior, lateral and posterior margins of the bone. Several unattached dermopalatines and small tooth plates present.

Parasphenoid hollow, with a moderately long stalk, and a wide corpus with a distinct layer of bone rising to form a ploughshare-shaped front to the bone, meeting the thickened ridges forming the quadrate rami of the pterygoids.

Large basihyal carried four denticulated tooth plates similar to, although much shorter than, those of *Griphognathus*; ceratohyal large and stout, although poorly ossified.

Anocleithrum large, deep-bodied and non-planar; cleithrum and clavicle, whose external surfaces were partly buried, have very deep branchial laminae set at a low angle to the external surfaces.

Remarks. H. kiprijanovae Pander and *H. santacrucensis* Gorizdro-Kulczycka are both European Late Devonian species that are known from partial lower jaws only. We have not seen the material of the type species of the genus, and consequently we are unable to comment on the validity of the assignment of either *santacrucensis* or *gogoensis* to *Holodipterus*. However, the illustrations of *H. santacrucensis* (Gorizdro-Kulczyzcka 1950) show that it is sufficiently well preserved for us to judge that it is close to *H. gogoensis* in gross morphology and in details of the dentition. We are satisfied that those two species are congeneric. Meanwhile we accept the judgment of Miles (1977) that all three are congeneric, in preference to the erection of a new genus based on the new data from *H. gogoensis*.

So that the name *Holodipterus* will have some morphological content, the generic characters listed above are derived from the more abundant and better preserved species from Gogo, on the assumption that they are congeneric with the European species.

We are still then faced with the taxonomic problem of how to handle the morphological diversity of the Gogo holodipterans, given that the amount of material is small. In the first place, five species can be easily discriminated: *gogoensis*, *longi*, *elderae*, *meemannae* and the palate referred to as holodontid sp. indet. All save the last are represented by enough material to make an extensive description. Although *meemannae* is known only from a single individual, this is exquisitely preserved. Reviewers have suggested that all four named species should simply be referred to *Holodipterus*, because the type species of that genus is so poorly known, our material is so scanty, and we know little about species variation in the group as a whole. All these are points with some force, but following their suggestions would result in the following anomalies.

1. The range of diversity of the genus would be so broad that another colleague has suggested that one species, *longi*, should be placed with *Griphognathus*. We considered that option and rejected it firmly for reasons given in the text.

2. One of the species, *elderae*, has no real teeth but grows its palate by the unique method of adding enamel-clad dentine to the ends of the ridges. Among other Palaeozoic Dipnoi, a difference of this magnitude would be regarded as sufficient justification for its separation into a supra-specific taxon.

With regard to the abundance of specimens, we point out that this is frequently a problem with palaeontological material. Decisions have to be taken on the degree of morphological difference rather than on an analysis of the distribution of morphologies across a large range of specimens.

We have to take into account the geological as well as the morphological information available. The Gogo specimens come from an area of some ecological diversity: a basin off the front of a reef in which there were embayments, one of which was partly closed off by an atoll (Campbell & Barwick 1988). Modern analogies suggest that rapid speciation among small populations would have taken place in such an environment, and that groups of related species would have quickly developed. We can expect further discoveries in the Gogo region to clarify the extent of such taxonomic diversity in this area. The discovery by Long (1992) of additional features that distinguish *Chirodipterus paddyensis* from *C. australis* indicates that this process of discrimination is already happening, although we do not necessarily agree with his decision to separate that species as a full genus.

This raises the suggestion put to us by a reviewer that we should not use subgenera but rather raise our subgenera to the status of full genera. We do not accept that advice. In the first place, it seems unwise to create more full genera while details of the roof and palate of the type species of *Holodipterus* remain unknown. We cannot know at present if *meemannae* differs from *kiprijanovae* in the same skull features as it does from *gogoensis*, although we are confident that it differs from both in the same mandibular characters. Consequently it is impossible to define a new genus for *meemannae* using as full a range of criteria as are normally considered appropriate for generic diagnosis.

The subgeneric solution does justice to the range of morphologies at present known and to the exigencies imposed by the present lack of knowledge of the type species. Another possible solution to the problem might be to invoke the Rules of Zoological Nomenclature. As it seems unlikely that more material of the type species will be found from the vaguely localized 'Orel District' of Russia, it may be possible to apply to the Commission of Zoological Nomenclature for suppression of *H. kiprijanovae* as the type species and the substitution of *H. gogoensis*. We are at present seeking support for such a move.

4. HOLODIPTERUS (HOLODIPTERUS)

(White & Moy Thomas, 1940)

Remarks. We define this subgenus to include forms that have true teeth on the palate and prearticulars, and well-ossified snouts and dentaries.

5. HOLODIPTERUS (HOLODIPTERUS) GOGOENSIS (Miles, 1977)

Previous accounts of H. (Holodipterus) gogoensis. Miles (1977, p. 14) listed eight specimens which he studied in preparing his original description of *H. (Holodipterus) gogoensis*. The holotype (P52569) is a relatively complete skull prepared in palatal aspect (Miles 1977, figure 4*b*). Prior to acid etching the nodule containing this specimen was embedded in plastic on its dorsal surface; in consequence the dorsal roof of its skull is unknown. However, two other specimens examined by Miles (P52568 and P56044) include articulated bones of the dermal skull roof. One of these (P52568) also includes the palate so that it can be confidently assigned to the same species as the holotype. The second specimen (P56044) cannot be so unequivocally assigned to *H. (Holodipterus) gogoensis*. However, in the absence of features indicating that this material is more properly assigned to any of the other Gogo holodipterans considered in this paper, and in so far as its available morphology is congruent with P52568, it seems reasonable to regard it as a specimen of *H. (Holodipterus) gogoensis*.

Miles (1977) has given an extensive account of the palate and prearticulars of *H. (Holodipterus) gogoensis*, and these features have been more completely described by Campbell & Smith (1987).

New material referable to H. (Holodipterus) gogoensis. Ongoing preparation of Gogo nodules collected by Dr Gavin Young (Australian Geological Survey Organisation), and made available to us for preparation and study, together with nodules collected by members of the 1990 A.N.U. collecting trip to Gogo, have revealed four significant new individuals of *H. (Holodipterus) gogoensis*.

Both the braincase and dermal bones of the snout are largely complete in specimen ANU49102, which is probably the largest individual collected to date. CPC25740, which is a young individual about half the size of ANU49102, also includes a number of semi-articulated dermal roofing bones. ANU25738, the dentition of which was figured and partly described by Campbell & Smith (1987), has also provided information on the detailed structure of both the pterygoids and the mandible. The fourth specimen, ANU49104, is an almost complete lower jaw which lacks the articulations and is pathological on the left side. It provides information on the shape of the external dermal bones and the growth of the prearticulars.

The following description deals with features not available to Miles when he wrote his account in 1977, together with an elaboration of other features for which more data have become available. In addition, it has been necessary to reinterpret some of the material on which Campbell & Smith based their account of the dentition of the species, because it is now evident that they dealt with more than one taxon.

Description. The snout is well preserved on ANU49102, and on CPC25740 which is only half the size. The larger specimen is comparable in dimensions with the holotype P52569, and it has a comparably broad snout (figures 1, 2 and 6*a*; tables 1 and 2). The smaller specimen has a very narrow snout, indicating positive allometric growth in this feature (figures 5*a*,*b* and 7*a*,*b*). Campbell & Smith (1987, figure 9) had suspected this from an examination of the growth pattern of the palates, which in general become disproportionately broader with age. The smaller specimen also shows a distinctly recurved ventral surface similar to that of *G. whitei*; although the snout of the larger one is more upright anteriorly, it is never as steep as that of *C. australis*.

In terms of relationships, we consider the presence of denticles on the bone forming the inner edge of the external nares (figure 3*b*), together with the shape of the excavation that housed the anterior edge of the cheek, to be important. The former feature is known from *Griphognathus*, but not from any dental-plated genus of which we are aware. The denticles are of the same type as those on the palate. The termination of the subnasal ridge (Miles 1977, figure 40), is distinguished by the continuation of its inner edge back as far as, or a little farther than, the outer edge, so that it makes a broad and deep surface for the attachment of the anterior edge of the soft lip (figures 2 and 3*b*). This arrangement is seen also in *Griphognathus*. In *Chirodipterus*, on the other hand, the outer edge of this cavity extends farther back than the inner edge (Miles 1977, figure 67). The situation in *Dipnorhynchus*,

Figure 1. *H.* (*Holodipterus*) *gogoensis*. Dorsal view of ANU49102, showing the perichondral ossification of the inner and outer walls of the neurocranium, the dorsolateral and median cristae, the nerve canals in the snout and the remaining external dermal bone of the snout. Scale bar = 10 mm.

Speonesydrion, *Dipterus* and *Scaumenacia* is not completely clear, but in all of them the outer edge seems to extend a little further posteriorly than the inner. This suggests that the anterior edge of the soft lip of *Holodipterus* and other denticulated dipnoans was not confined laterally and so was able to flex outwards extensively, whereas in dental-plated genera it was more confined.

The end of the right subnasal ridge on CPC25740 has a number of well-developed hypermineralized teeth on a patch of the same material. In larger specimens similar teeth are also present, although they show evidence of greater wear. Specimens of *G. whitei* show teeth in the equivalent position, and in two patches mesially, but we can find no evidence of such structures in any dental-plated form.

The external surface of the front of the snout of ANU49102 is covered by an essentially continuous sheet of dentine, broken only by the pores of the lateral line canals and other sensory organs (figure 6*a*). The posterior edge of this dentine sheet is highly irregular. In places it passes back without a break into highly perforate dentine, the perforations being *ca.* 0.12–0.38 mm in diameter. Elsewhere isolated patches of the same material occur, and these extend farthest back along the bone immediately above the lateral lip. Through this material pass the openings of the lateral line canal. Bone is exposed between the patches, and on the bone there are small pustules composed of dentine. Large pores like those found elsewhere on the dermal bone also appear.

From the limited dissociated dermal skull bones of ANU49102, we can confirm many of the features described by Miles. However, in two points we note a difference. Bone J has a lateral line canal that extends to the bone labelled X by Miles (1977, figure 122), and bone I has a strong attachment for the dorsolateral crista on its ventral surface anteromesial to the ossification centre.

The palate of ANU49102 is well-preserved, and as large as any available (figures 2 and 14). Each pterygoid has three or four distinct radial tooth rows with discrete teeth, the longest row having four teeth. There are no signs of resorption surfaces at the mesial ends of the rows which fade away without trace, indicating that they were effectively resorbed at an earlier phase of growth. The highest tooth in each row

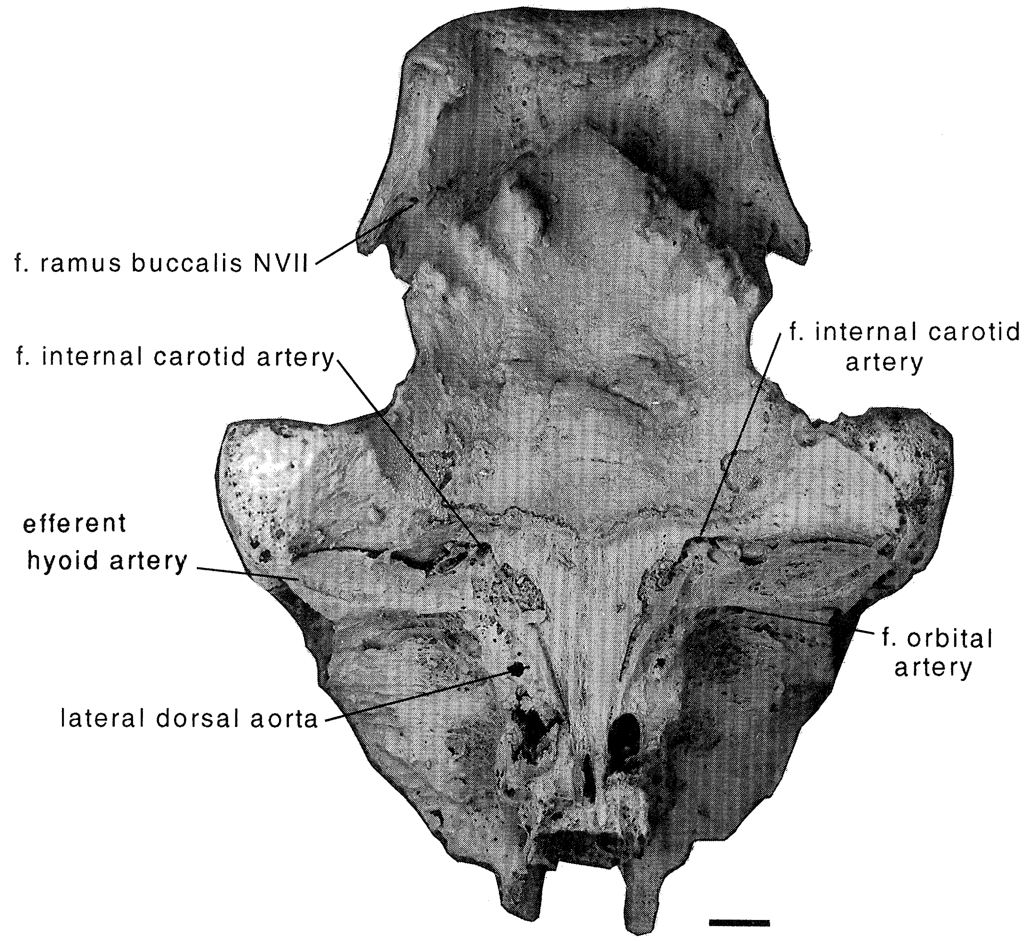
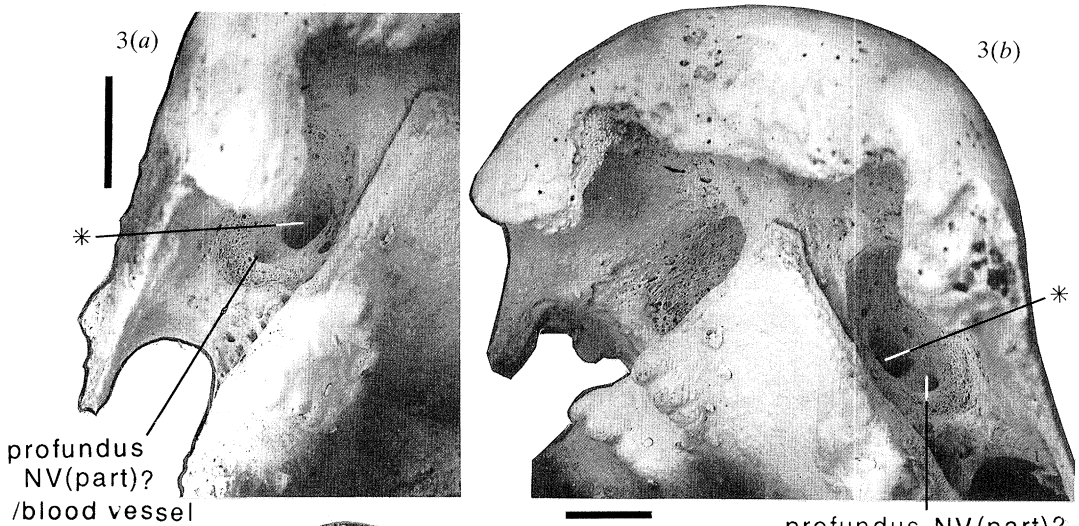


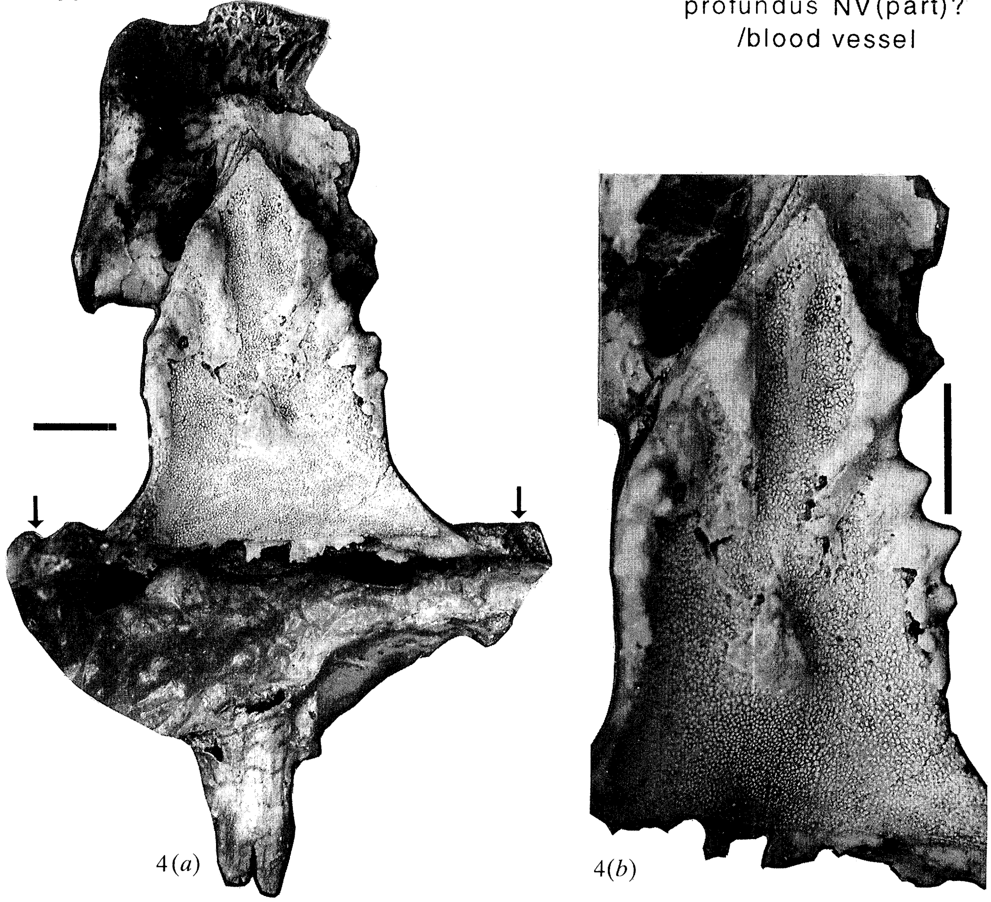
Figure 2. *H.* (*Holodipterus*) *gogoensis*. Ventral view of ANU49102 showing palate, roof of nasal capsules, parasphenoid and occipital area. Scale bar = 10 mm.

Table 1. *Palatal dimensions for the four Gogo species of* Holodipterus

(Total palatal length is the sum of the length values for the buccal palate and the palatal stem. Several of the values given in columns 5, 6 and 7 were calculated by doubling values obtained when the distance between the midline and the appropriate anatomical point on the side of the specimen was measured.)

species/specimen	total length of palate/cm	length of buccal palate/cm	length of palatal stem/cm	width of palate at quadrate rami/cm	minimum width of anterior palate/cm	width of corpus of parasphenoid/cm
H. (*Holodipterus*) *gogoensis*						
P52569 (holotype)	*ca.* 10.7	7.1	*ca.* 3.6	*ca.* 10.5	5.2	*ca.* 3.5
ANU49102	*ca.* 13.1	8.4	*ca.* 4.7	10.5	5.7	*ca.* 3.9
CPC25738	—	*ca.* 6.7	—	6.4	3.8	—
CPC25740	9.7			5.7	2.9	—
H. (*Holodipterus*) *longi*						
WAM86.9.684 (holotype)	—	*ca.* 6.3	—	*ca.* 5.4	3.2	—
H. (*Holodipteroides*) *elderae*						
ANU49101 (holotype)	*ca.* 15.0	*ca.* 9.5	*ca.* 5.5	*ca.* 12.0	6.6	*ca.* 5.6
CPC30838	*ca.* 15.8	*ca.* 10.3	5.5	—	7.0	>4.5
CPC25739	—	—	*ca.* 4.1	—	*ca.* 7.0	*ca.* 4.6
WAM86.9.649	—	*ca.* 11.2	—	*ca.* 13.0	*ca.* 9.0	—
H. (*Ashenorhynchus*) *meemannae*						
ANU49103 (holotype)	*ca.* 9.6	6.0	*ca.* 3.6	6.4	3.9	*ca.* 3.8





Figures 3 and 4. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figure 3. (*a*) Ventral view of roof of the right nasal capsule, and (*b*) slightly oblique anteroventral view of both nasal capsules of ANU49102. Olfactory foramina labelled (asterisk).

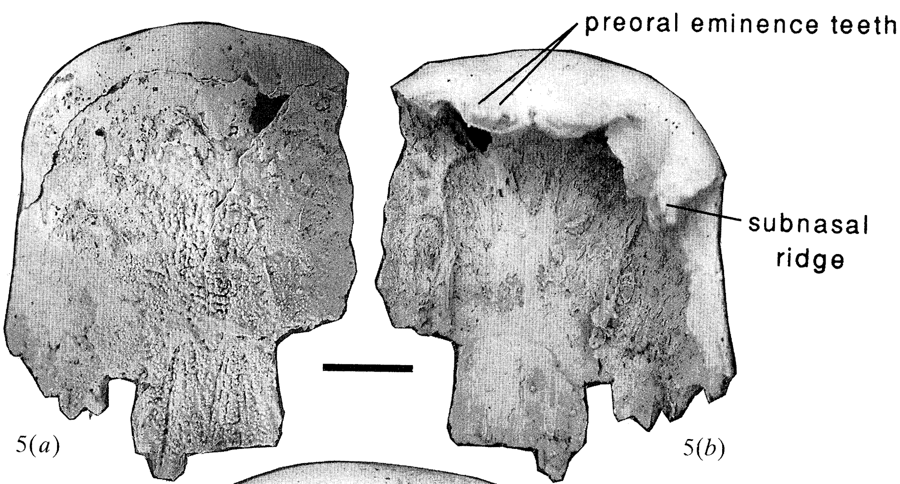
Figure 4. (*a*) Ventral, and (*b*) ventrolateral views of CPC25740. The stem of the parasphenoid is in natural position except for slight lateral displacement, but is separated by plastic from the rest of the specimen. An articulatory facet for the mandible on the quadrate is arrowed on each side of the specimen in (*a*); (*b*) is tilted to show the extent of the resorption at the lingual ends of the tooth rows.

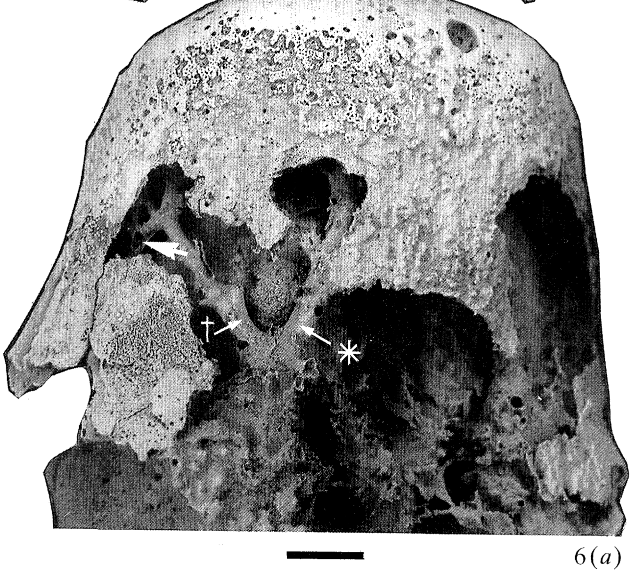
is always labial. Along the palatal edge the large rounded denticles characteristic of holodipterans are present.

The posteromedian callus is large and flanked anterolaterally on each side by two smaller calluses. Each of these is separated by a shallow depression that marks a previous resorption episode. This pattern is similar to that shown by P50999, figured by Campbell & Smith (1987, figure 5A), although in the ANU specimen the calluses do not diverge so strongly and do not align with a tooth row as in that specimen (figure 2). This supports the view of those authors that

Table 2. *Snout dimensions for* (H. Holodipterus) gogoensis *and* (H. Holodipteroides) elderae

species/specimen	width across nasal capsules/cm	breadth of snout at tip of plate/cm	minimum breadth of nasal buttress/cm
H. (*Holodipterus*) *gogoensis*			
P52569 (holotype)	*ca.* 3.7	6.3	0.8
ANU49102	4.5	6.7	0.8
CPC25740	—	4.1	0.6
H. (*Holodipteroides*) *elderae*			
ANU49101 (holotype)	4.4	—	1.3
CPC25739	4.5	*ca.* 7.7	1.3



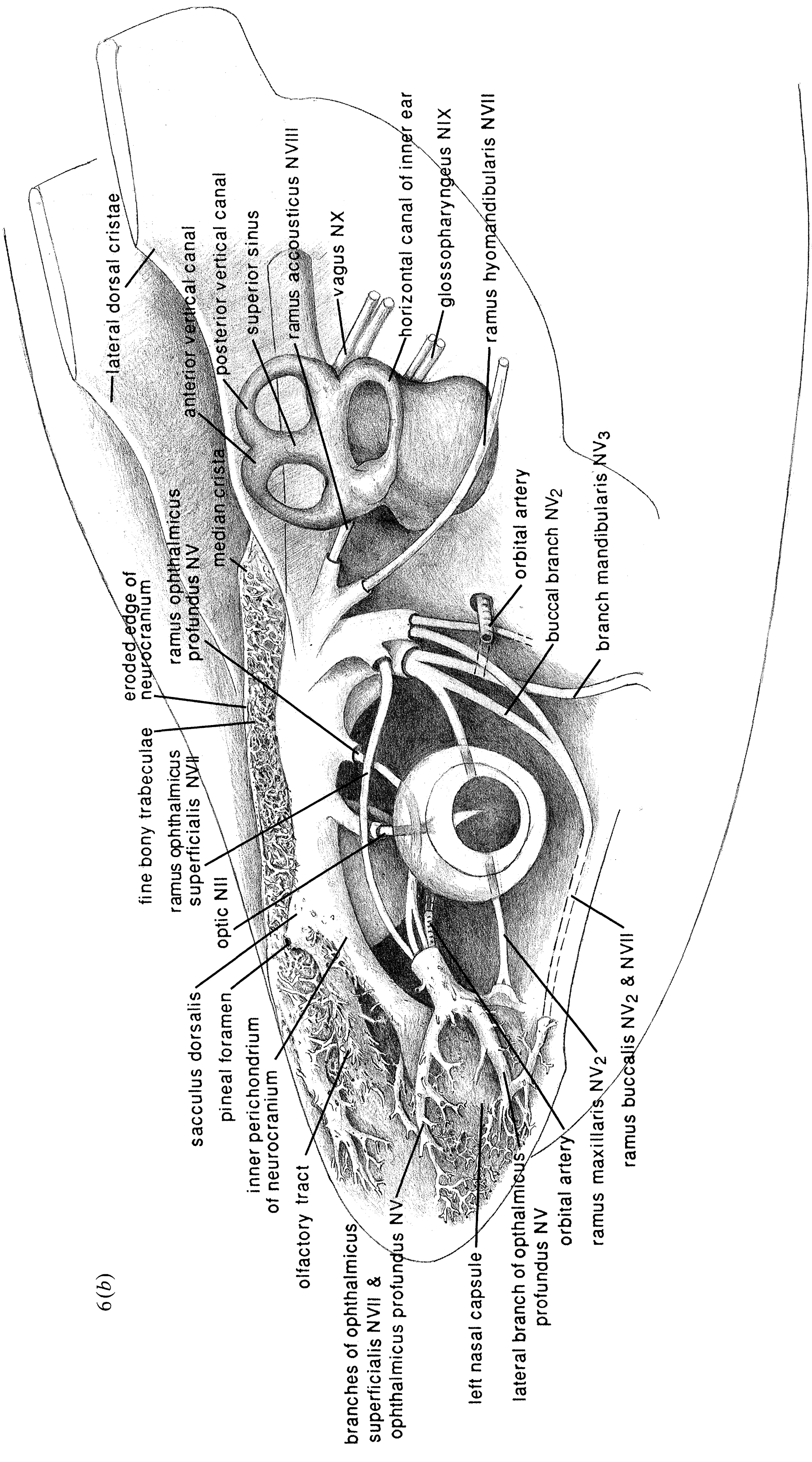


6(*a*)

Figures 5 and 6. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figure 5. (*a*) Dorsal view of snout of CPC25740 showing ossification centres. (*b*) Ventral view of same showing remnants of the lateral line canals, and teeth on the subnasal ridge and the preoral eminence.

Figure 6. (*a*) Dorsal view of snout of ANU49102, showing detail of surface of dermal bones and branching canals both for the ophthalmicus superficialis and a mesial ramus of the ophthalmicus profundus (asterisk), and for a lateral ramus of the ophthalmicus profundus (dagger) nerves. The large white arrow indicates a branch of the buccalis nerve. (*b*) Reconstruction of the orbit and snout in left dorsolateral view to show the positions of the major nerves and the orbital artery. The reconstruction is based mainly on ANU49102 in which the neurocranium has been weathered through dorsal to the perichondral bone investing the the brain. The fine bony tubules and struts joining the inner and outer perichondrial layers of the neurocranium have been omitted on the left side for clarity. Instead we have shown the passage of the nerves and artery between the inner and outer neurocranial walls as encased in a bony collar. Details of the inner ear are not well known in *H.* (*Holodipterus*) *gogoensis*, and for this figure data from *H.* (*Holodipteroides*) *elderae* has been used. The size of the eyeball is arbitrary.


lateral dorsal cristae
anterior vertical canal
posterior vertical canal
superior sinus
ramus accousticus NVIII
vagus NX
horizontal canal of inner ear
glossopharyngeus NIX
ramus hyomandibularis NVII
median crista
ramus ophthalmicus profundus NV
eroded edge of neurocranium
orbital artery
buccal branch NV_2
branch mandibularis NV_3
fine bony trabeculae
ramus ophthalmicus superficialis NVII
optic NII
sacculus dorsalis
pineal foramen
inner perichondrium of neurocranium
olfactory tract
branches of ophthalmicus superficialis NVII & ophthalmicus profundus NV
left nasal capsule
lateral branch of opthalmicus profundus NV
orbital artery
ramus maxillaris NV_2
ramus buccalis NV_2 & NVII

6(*b*)

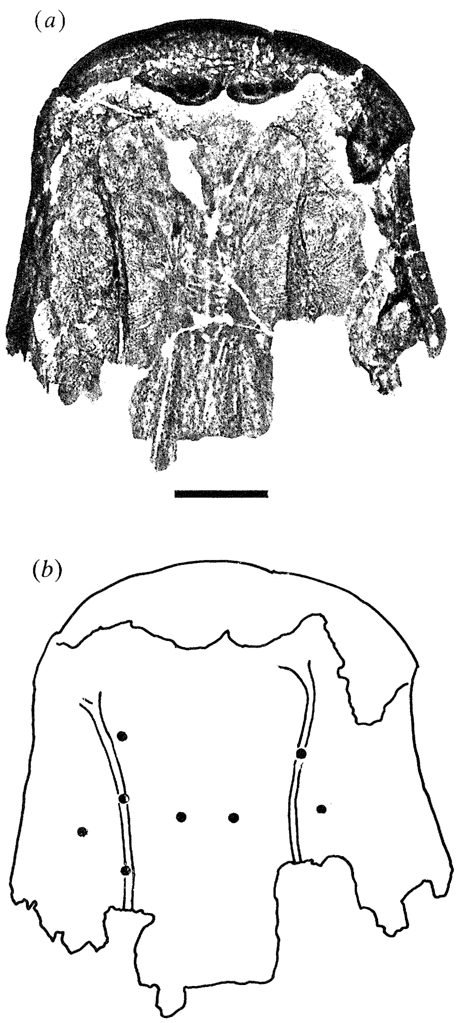


Figure 7. *H.* (*Holodipterus*) *gogoensis*. (*a*) X-radiograph of CPC25740 showing ossification centres and lateral line canals. (*b*) Diagram of same with ossification centres indicated by dots and the lateral lines shown. Note that bones were rejoined to the right side of the specimen between the time that the photographs for figures 5*a*,*b*, and the radiographs for this figure were made (cf. figures 5*a*,*b*). Scale bars = 10 mm.

the isolated lumps are not the relicts of old teeth. They are patches of dentine that were not resorbed during successive growth phases, and whose capacity to resist wear has been increased by progressive hypermineralization.

The front edge of the main callus in ANU49102 shows strong resorption. A patch of white superficial dentine, within which are scattered columns of hypermineralized dentine, occupies an area along the midline from the callus to the anterior margin. Immediately in front of the callus a few new denticles lie in a resorption area, a feature not seen on any other specimen. All these structures together indicate that the variation of the conformation of the central part of the palate results from the apparently capricious nature of the resorption process; but the amount of resorption that took place at any point apparently depended on the thickness of superficial dentine at that point, and this in turn depended on its proximity to previous hypermineralized dentine that stood slightly proud of its surrounds.

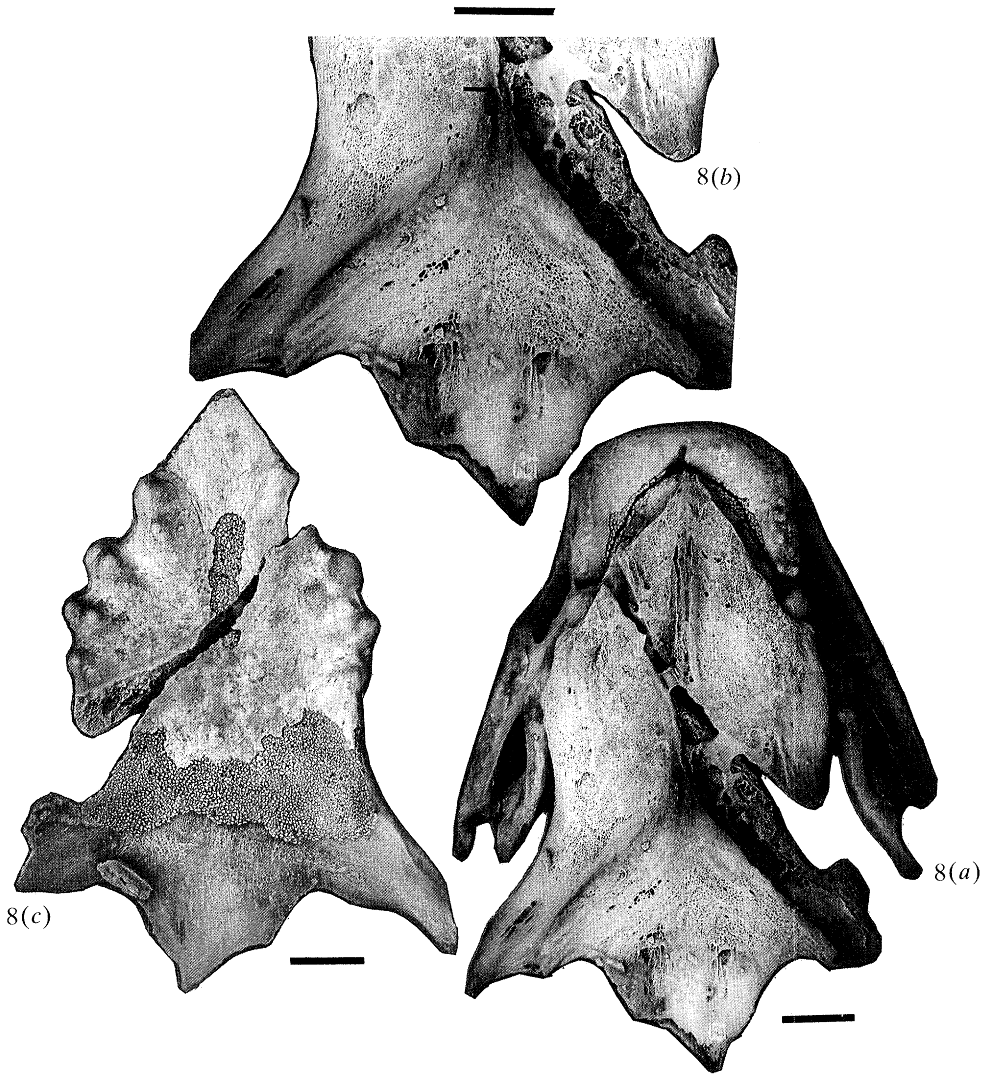
Like P50999 this specimen also shows denticles and sheets of superficial white dentine posterolateral to the callus. In places these sheets and calluses show resorbed and undercut edges. Similar patches of superficial dentine are present in the anterior midline and between the rows of teeth. CPC25738 also shows the palatal detail well (figure 8*c*), with superficial dentine widespread in the early phases of a resorption episode.

The parasphenoid was well described by Miles (1977, p. 154). We add a couple of points on structure not preserved, or poorly preserved, in his material. The anterior edge is never visible on the buccal surface because of the extensive denticulation or callus covering. On CPC25738 the dorsal surface is well exposed (figures 8*a*,*b*), and the anterior margin, which forms part of the dorsal layer described below, is shown to be more elongate and acute than Miles (1977, figure 77) has illustrated. This is also shown by the specimen figured by Miles, which has been examined by K.S.W.C. X-radiographs of CPC25738 show the centre of ossification near the anterior extremity of the bone, and confirm the observation that it extends as a short process in the midline between the posterior end of the pterygoids. This arrangement is also shown by other Gogo holodipterans (see below). The posterior end of the stalk also is more acute than Miles shows, lying as it does between the slightly protruding margins of the occipital endocranium.

Transversely the stalk of the bone is hollow. It is deepest mesially and thins out dramatically to the lateral edges (figures 2 and 14) where it is almost paper thin and tends to break away during preparation.

Each pterygoid has a posterior ridge on the dorsal surface, the 'ridge on the quadrate ramus of the endopterygoid' of Miles, which in X-radiographs is seen to be formed of a very open meshwork of bone quite unlike the dense texture of the other parts of the pterygoids. The parasphenoid has a ploughshare-shaped front face to abut the back faces of these ridges. Although this is superficially like the parasphenoid of *Chirodipterus*, *H.* (*Holodipterus*) *gogoensis* differs in that a distinct layer of bone covers the dorsal surface of the corpus of the parasphenoid and rises gradually to its anterior edge. This is well shown on CPC25738 (figure 8*a*,*b*) where the texture of the bone readily defines both the anterior and posterior edges of this layer. The interior of the corpus of the bone is largely open, but it contains a few struts as shown on CPC25740. In *C. australis* the parasphenoid is as described by Campbell & Barwick (1982, figure 6). This feature of the anterior end of the parasphenoid in *H. gogoensis* is also unlike that of *Griphognathus*, in which the parasphenoid has a much flatter corpus. We suggest that in *Holodipterus* the pterygoids are ridged to carry the impact and pressure of the stronger marginal bite, and consequently the anterior end of the parasphenoid is thicker to abut their posterior ends.

As Miles (1977, figure 77) indicated, three longi-



Figures 8. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm. (*a*) Dorsal view of palate of CPC25738 with the mandible in position. Note the teeth on the dentary, and the three major ridges on the palate. (*b*) Enlargement of dorsal view of parasphenoid of same showing differences in bone texture between the corpus and the stalk. Note the foramina for the vascular canals at the posterior of the corpus, and the forward extension of the tip of the parasphenoid between the pterygoids (arrowed). (*c*) Ventral view of the same palate showing resorption of white superficial dentine and replacement by denticles.

tudinal nutrient canals run into the parasphenoid. X-radiographs of CPC25738 show such canals running forwards in the bone and joining anteriorly before entering the hypophysis.

From our new material, we have been able to locate only isolated palatal tooth plates such as those figured by Miles (1977, figures 88 and 89) in the holotype. Re-examination of the holotype shows a number of interesting points. First, marginal denticles continue around the anterior end of the pterygoids (Campbell & Smith 1987, figure 2B), indicating that any dermopalatines were not applied closely to the ventral edge of those bones. Second, the bones labelled dermopalatine 1 by Miles (1977, figure 72) have a recessed bony flange along their inner edges (figure 9) and there is no surface on the lateral edge of the pterygoids with which this flange could articulate. We have another isolated plate that matches his dermopalatine 1 (figure 10*a*,*b*) and this has given further information. The evidence is that it was embedded in soft tissue or articulated with another bone that separated it from the pterygoid. Third, the right plate has a large lateral notch, in the wall of which are closely spaced denticles of the shedding type. Its palatal surface is covered with a sheet of superficial dentine and some shedding denticles. Fourth, the same bone shows a truncated front edge which has a steep face. One isolated plate of this type in our collection shows that the front face of this bone carries no scattered denticles, indicating that it abutted another bone. Fifth, we know what dermopalatines 1 are like in this group because they are well displayed (figures 73 and 74) by *H.* (*Asthenorhynchus*) from which we have other notched plates of the same type as those described above.

From all these points we conclude that the deeply notched bone identified as dermopalatine 1 by Miles is a more laterally placed tooth plate that formed the inner margin of the posterior naris. In fact it matches

9

Figure 9. *H.* (*Holodipterus*) *gogoensis*. Ventral view of the anterior part of the holotype showing the loose plates in the subnasal region. Scale bar = 10 mm.

the plate labelled dermopalatine 3 in *Griphognathus whitei* by Miles (cf. our figure 10*c*,*d*). That bone has a lateral embayment for the anterior naris, and its front edge lies against the inner margin of the preoral eminence. The bone in question in *H.* (*Holodipterus*) *gogoensis* would fit well into such a position.

The holotype (figure 9) has an apparently symmetrical bone that Miles considered to be a vomer. We have not found a similar bone in our material. In the holotype this bone was not attached to the internasal septum as there is neither a flattened surface of attachment nor a scar on the septum like that in *Chirodipterus australis*. ANU49102 also has a very well preserved sharp keel on its median septum, indicating that no median plate was attached in that specimen either. We also note that the median bone in the holotype has a transverse posterior edge that does not allow it to be fitted against the front of the pterygoids. Presumably it was a loose bone lying in front of the so-called dermopalatines. It may have articulated laterally with the dermopalatine 3 bone, making possible the reconstruction as in figure 10*c*. As

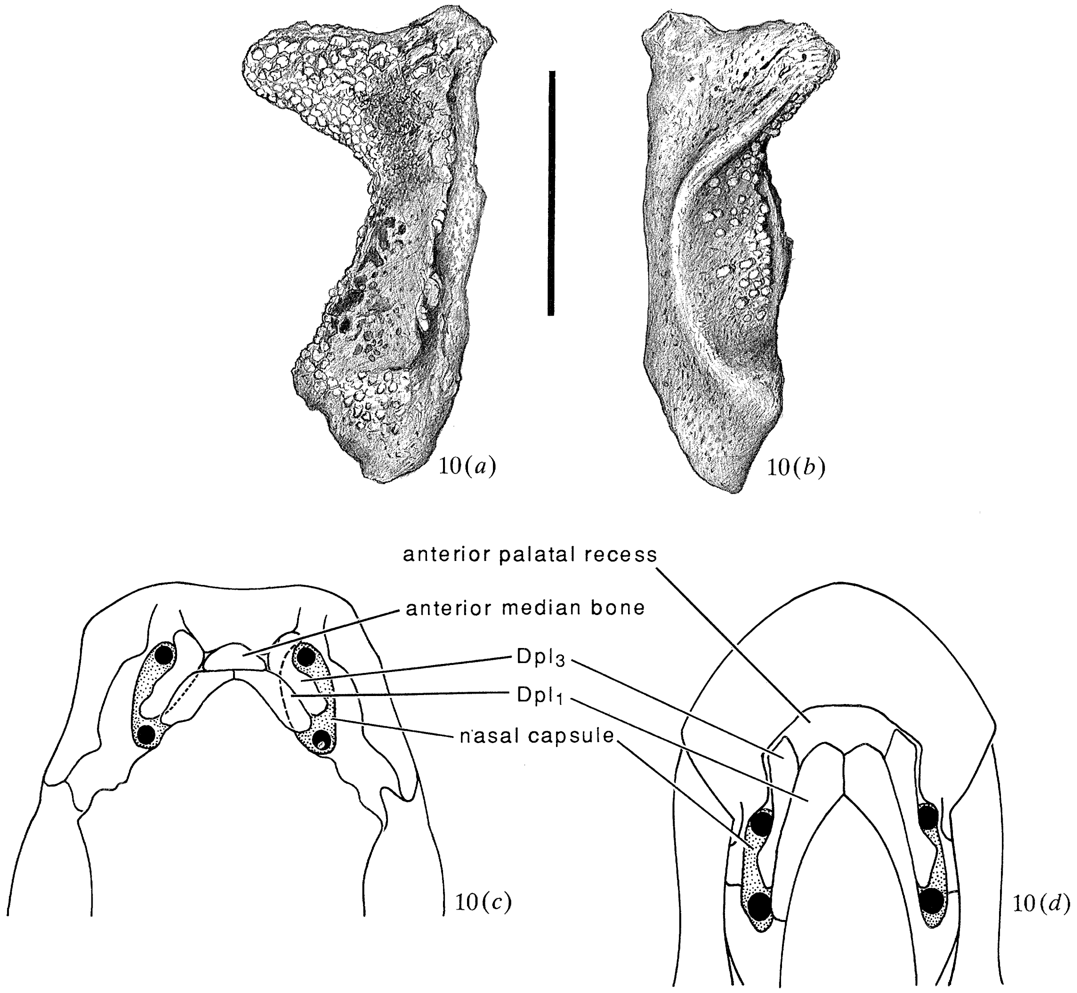


Figure 10. *H.* (*Holodipterus*) *gogoensis*. (*a*,*b*) Drawings of an isolated dermopalatine 3, ANU49179, from an unidentified specimen in ventral and ventrolateral views. (*c*) Reconstruction of the anterior half of the palate of the holotype showing the inferred relative positions of the dermopalatines. (*d*) Comparative diagram of *Griphognathus whitei* based on Campbell & Barwick (1984, figure 7E). Scale bar = 10 mm

we have shown elsewhere (Campbell & Barwick 1984) median bones in front of the pterygoids are inappropriately referred to as vomers.

As Miles showed, there are four other small loose tooth plates on the right side of the holotype. Occasional loose bones of a similar kind have been found in our preparations, but they cannot be reassembled to form any pattern. We note, however, that *H.* (*Asthenorhynchus*) has similar bones and we conclude that they are a feature of the genus as a whole.

Specimen ANU49102 is weathered through the neurocranium to show the shape of the braincase particularly well (figures 1 and 6*b*). The first observation is the smallness of the volume (somewhat less than 50%) lying internal to the inner perichondrium (i.e. the bone enclosing the brain tissue and cerebrospinal fluids) compared with the whole volume enclosed by the outer perichondrium. The second observation is the general absence of swellings in the walls of the inner perichondrium. There are no lateral expansions apart from a very slight one in the region of nerve II and another in the region of nerves V and VII. Behind the latter the nerve tube gradually decreases in diameter. As shown on figure 6*b*, swellings occur around the pineal structure (sacculus dorsalis) and the region of nerves V and VII. Significantly there are no swellings of any sort in the region of the telencephalon. It is well known that the walls of the inner braincase do not necessarily reflect details of the structure of the underlying brain (Rudebeck 1945). However, the diagrams of *Neoceratodus* and *Protopterus* brains provided by Northcutt (1987) show features that one would expect to be reflected in the walls because they are of such magnitude as to require special spaces. In particular the telencephalon in both genera is greatly expanded, its margins lying farther laterally than any other part of the brain. As the braincases of all four Devonian genera we have been able to examine have a pattern like that of *Holodipterus*, it is reasonable to infer that the expansion of the telencephalon is a post-Devonian feature of the group. This may be correlated with an increased role for olfaction in post-Devonian dipnoans which is correlated with a reduction in the importance of other sensory systems including those represented by the tubule systems in the snout. A second point is that both extant genera show swelling in the position of nerves V and VII, but they also show a continuation of the swelling back behind the otic region: that is, the region of the whole of the fourth ventricle is expanded. No such pattern is known in any Devonian dipnoan. The significance of this cannot be understood in detail, but we note that in the extant genera much of the space is occupied by the choroid plexus, and by neural tissue containing fibres of passage and aggregates of motor nuclei. We therefore infer that these had not yet developed to the same extent in the Devonian genera. A third observation is that the otic complex has a narrow connection with the inner perichrondrial ossification. This is similar to the arrangement in extant dipnoans, but entirely different from that found in such rhipidistians as *Eusthenopteron* (Jarvik 1980) and *Megalichthys* (Romer 1937). In the latter the perichondrial ossification swells laterally around the otic chambers.

The occiput is moderately well preserved on ANU49102 (figures 2, 11, 12 and 14). The ossification around the notochordal chamber is light and its posterior edge is very thin. Surrounding the chamber there are numerous hollow struts that do not connect to any openings in the outer wall, but whose inner ends form a well-defined ring. This indicates that the wall around the notochord was thick cartilage, strengthened by hollow bony trabeculae. This ring of tubules is not complete dorsally where there is continuity between the chambers for the notochord and the brain stem. The latter is surrounded by a thin sheath of bone except on its ventral side. The diameter of this sheath at the position of nerve X is *ca.* 4.5 mm.

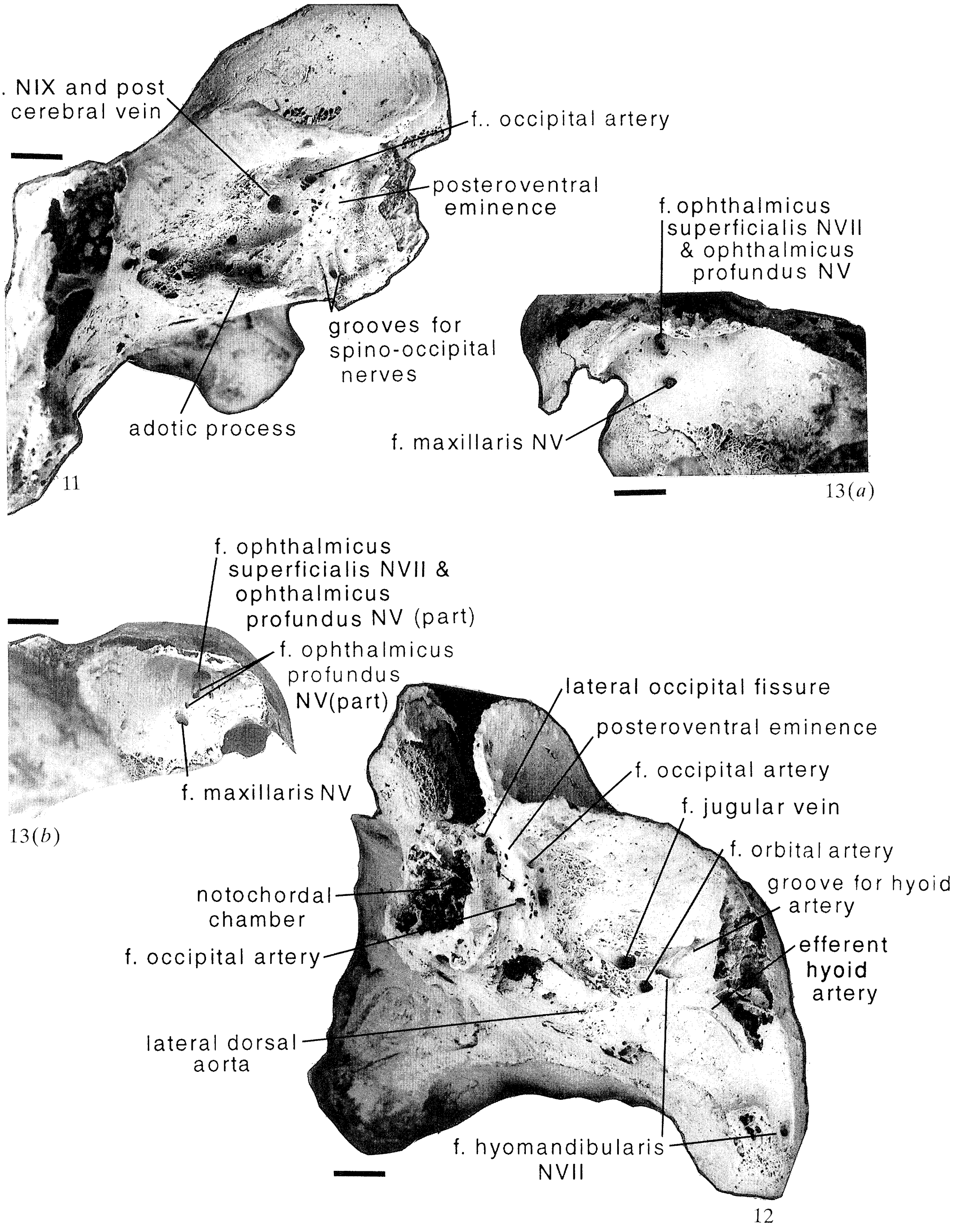
Miles (1977, figure 23) showed a well-developed ventral otic fissure, and a lateral occipital fissure in both lateral and dorsal positions. We have confirmed this on the holotype. On ANU49102 we have been unable to find a ventral otic fissure, and the lateral occipital fissure is present only dorsally. It lies mesially to a strong vertical ridge (the posteroventral eminence of the otic region of Miles (1977, figure 23)) that is situated immediately below the dorsolateral crista. The fissure runs up to a position immediately beneath the posterior end of the fossa for the temporal muscle, but does not complete the ring dorsally. The difference between these specimens shows that the cranial fissure is variable in this species.

Several foramina open through the lateral occipital fissure. In ANU49102 there are three of moderate size on each side, and some of them cannot be traced through the bone into the braincase. However, the middle one opens into a long bony tube that runs anteriorly into the wall of the braincase at a very acute angle. Because of the position and orientation of the foramen and tube, we consider them to mark the course of nerve X. This interpretation is consistent with that of Miles (1977, figure 40).

Another slightly narrower, more posterior tube runs parallel with the tube for nerve X, and opens through a small foramen in the furrow behind the lateral occipital fissure, a little dorsad of the foramen for nerve X. A second small foramen in this furrow dorsad of the one previously mentioned, enters a more poorly preserved tube lying posterior to the other tubes and at a high angle to the brain stem. These two tubes are interpreted as transmitting spino-occipital nerves.

Immediately ventral to the fissure is a foramen for the occipital artery that enters a vertical canal rising through the end of the posteroventral eminence and issuing at a foramen high on its lateral face. The occipital artery impinges on the ventrolateral wall of the neurocranium in a deep groove well to the side of the parasphenoid. Behind this groove are two or three smaller vertical grooves that seemingly open down into the groove for the lateral dorsal aorta. These are shown as vague lines by Miles (1977, figure 23). Presumably they carried supplementary arteries serving the posteriorly extended temporalis muscles.

Anterior to the posteroventral eminence and dorsal



Figures 11–13. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figure 11. Posterolateral view of the left side of the occiput of ANU49102 (fNIX lies 10 mm anteroventrally to the indicated post-cerebral vein foramen).

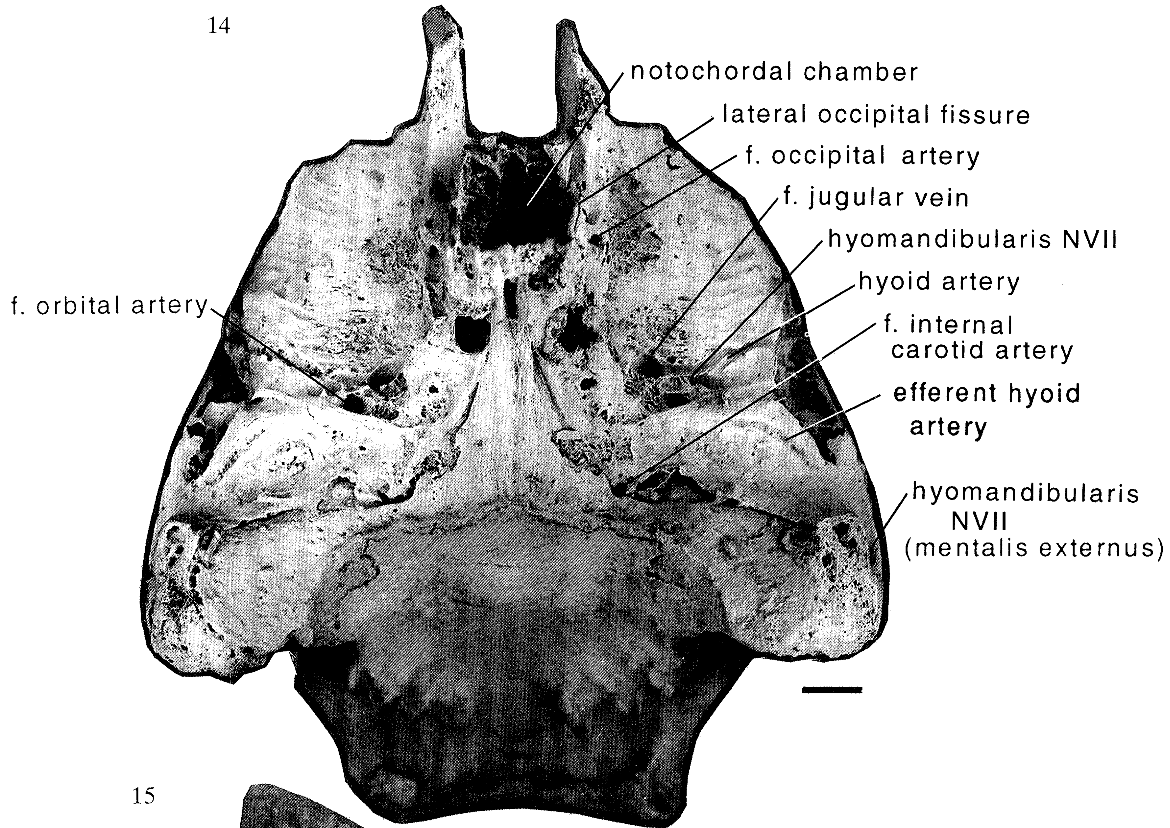
Figure 12. Posterolateral and slightly ventral of the rear of the skull of ANU49102.

Figure 13. Posterior views of the antorbital walls of (*a*) the left and (*b*) the right sides of ANU49102.

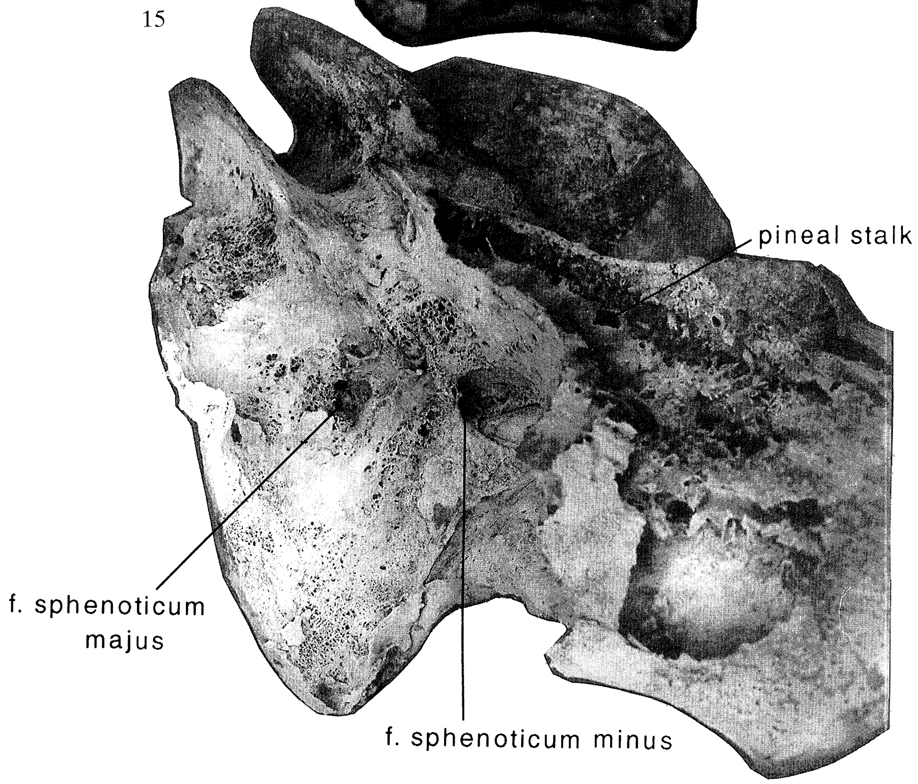
to the adotic process are two large foramina. The posterior compound one we interpret as carrying the posterior cerebral vein, and the anterior one nerve IX. This is in agreement with Miles (1977, figure 23), except that in our specimen the foramina for the posterior cerebral vein exit from a common cavity rather than from three isolated foramina.

A groove for the lateral dorsal aorta is clearly visible in the neurocranium lateral to the stalk of the parasphenoid, in front of which it makes a broad curve laterally to run to the foramen for the orbital artery (figures 2 and 12). This foramen is the most ventral of a group of three and is connected to the temporal chamber by a canal passing straight through the bone. Immediately lateral to the foramen and connected to it by a short passage, is a second foramen

14



15



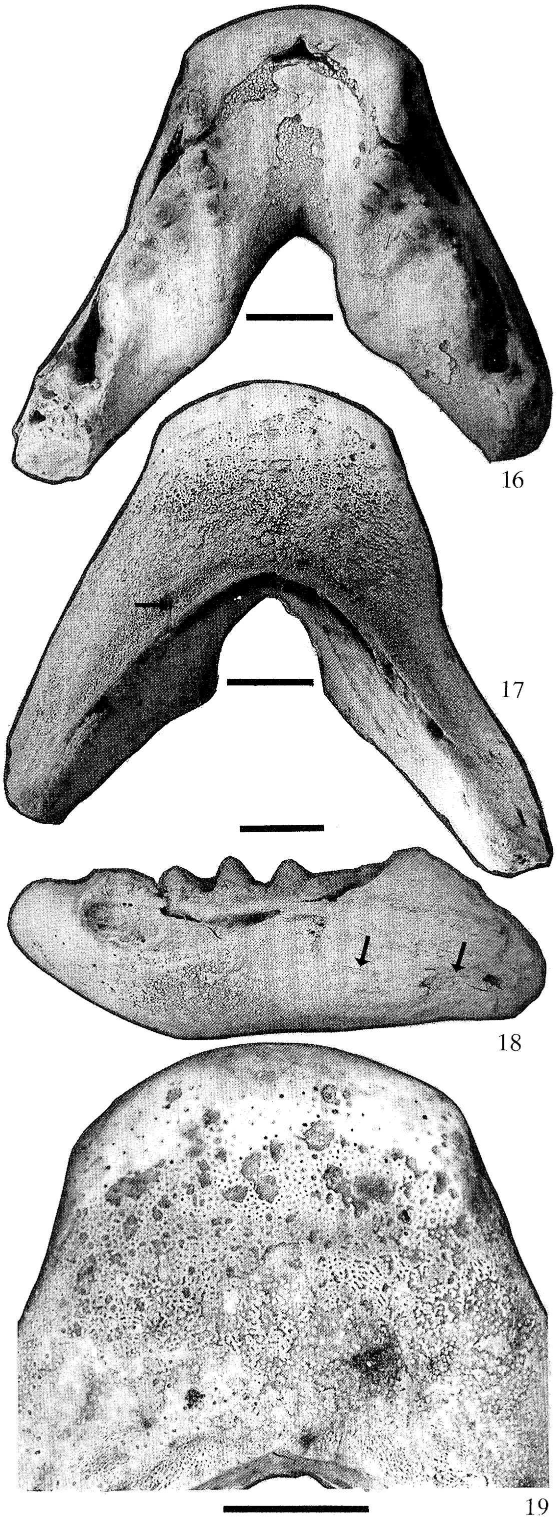
Figures 14 and 15. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figure 14. Posteroventral view of skull of ANU49102.

Figure 15. Antero-dorso-lateral view of same.

opening laterally into a distinct broad groove that fades laterally to the hyomandibular attachment. On the right side, before it reaches the hyomandibular facet, this groove divides, its upper branch joining a groove running laterally from the jugular foramen (see below). The bifid groove from the orbital artery foramen carried branches of the hyoid artery (cf. Fox 1965, p. 497) and the hyomandibularis VII. This latter nerve passed from the braincase through a short tube to the chamber also containing the orbital artery.

Dorsomesial to the foramen for the orbital artery is the large jugular foramen. This also opens into a canal



Figures 16–19. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figures 16–18. Dorsal, ventral and lateral views of the mandible ANU49104. Note the suture (arrowed) between angular and the splenial/postsplenial in figure 17, and between the surangular and the angular in figure 18.

Figure 19. Ventral view of the anterior of the mandible of ANU49104 showing variation in the dentine coating and in the shape and size of pores on different parts of the surface.

through the bone into the temporal chamber. In the temporal chamber on both sides there is a large cavity through which both the orbital artery and the jugular vein pass. This cavity lies in the floor of the anterior extension of the masseteric fossa immediately lateral to the foramen sphenoticum majus (figure 15). Within the thickness of the bone of the lateral wing, a short canal extends anteromesially from the jugular canal down to the foramen sphenoticum minus. This must have been for a branch of the jugular vein. Thus there seems to be little doubt that the temporal and orbital chambers were drained by two confluent branches of the jugular vein.

On the posterior face of the lateral wing of the neurocranium, a deep groove runs laterally from the jugular foramen parallel with the groove from the orbital foramen, but narrower and deeper. This deep groove reaches the hyomandibular facet, the edge of which it indents. This groove branches, the dorsal branch running up and off the bone above the hyomandibular facet, and probably ran into the adductor chamber. Miles (1977, figure 44) illustrated a groove in this position which he interpreted as a branch of the hyomandibularis VII. This seems to us to be unlikely as we see no evidence that the groove is continuous with the main groove and canal for the main hyomandibularis nerve. On the contrary, it seems to be a direct branch from the jugular, and hence we consider it to be a venous branch draining the muscles attached to the lateral commissure and perhaps extending around into the adductor chamber.

Below the otoquadrate bar is another strong groove that turns ventrally and approaches the mesial margin of the furrow for the mentalis externus branch of the hyomandibularis nerve (Fox 1965, figure 31) before the latter enters the foramen that takes it through the quadrate and into the mandible (figures 12 and 14). This groove impinges on the bar about half way along its length, a fact that we interpret as indicating that it carried an artery looping off the lateral dorsal aorta. On both sides of the specimen a branch of this groove runs down mesial to the furrow for the ramus mentalis externus branch of the hyomandibularis for about 7–8 mm and then runs off the bone. It also lies lateral to and about 1.5 cm. forward of the facet for the articulation of the epibranchial of the first branchial arch. This seems to preclude its having carried the efferent epibranchial artery of this arch, although it would be appropriately placed to carry the efferent hyoid artery. That artery has been lost in *Neoceratodus*, but is well developed in *Protopterus* and is present in *Lepidosiren* and indeed in most gnathostomatous fishes (Goodrich 1930; Bertin 1958). In some specimens of *Chirodipterus australis* and *Pillararhynchus longi* a groove on the ventrolateral surface of the ceratohyal could have been connected with the equivalent groove in these forms and would have been appropriately placed to carry the efferent hyoid artery. The ceratohyal is poorly known in holodipterans, but Miles (1977, figure 150) illustrated an inverted right (misinterpreted by him as a left) ceratohyal of *Holodipterus gogoensis* with a groove in the same place as in *Pillararhynchus*. (We note that in *Sorbitorhynchus deleaski-*

tus, Wang *et al.* (1993) interpreted this structure as the efferent epibranchial artery, making an analogy with *Neoceratodus forsteri*).

Above the level of the jugular and orbital artery foramina the lateral wing of the neurocranium flexes backwards rather sharply so that it lies at about 40° to the palatal plane. As shown by Miles (1977, figure 22) this backwardly deflected part of the lateral wing is crossed by numerous transverse narrow ridges, separated by broader rounded grooves. The lateral edge of this surface, which formed the lateral commissure, consists of perichondral sheets separated by an open space which passes down to the edge of the hyomandibular facet. Between the lateral commissure and the dorsolateral crista is a wide space floored by bone that has a finished posterior edge. In the terminology of Miles this would have been the base of the mesial division of the foramen for the masseter muscle. This foramen is much larger than its homologue in *Griphognathus* or *Chirodipterus*. Its size correlates with the fact that, unlike these other forms, holodipterans do not have an adlateral crista.

Our material does not allow us to add significantly to the description of the labyrinth and supraotic cavities given by Miles. However, we note that there is a thick anterior extension of the dorsolateral crista to house the anterior vertical semicircular canal.

In the posterior wall of the temporalis chamber, the orbital artery and the jugular vein have the courses previously outlined. The foramen sphenoticum majus lies at the base of a broad furrow running down the wall as an extension of the temporalis fossa. Opening into it are small foramina for the branches of V_2, V_3 and VII. We see no reason to disagree with the interpretation of Miles (1977, p. 117).

The antorbital/postnasal bar and the adjacent nasal capsule have a more complicated arrangement of foramina and canals than indicated by Miles. On its dorsal face the antorbital wall is drawn forwards into a deep invagination that houses two large dorsal foramina (figure 13*a*,*b*). These open into thick tubes that run anteromesially and anterolaterally in the ethmoidal space (figures 1 and 6*a*). They branch repeatedly forming an array of tubules decreasing in

Figures 20–23. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figures 20–22. Dorsal, ventral and dorsolateral views of the mandible of CPC25738. Note the resorption and replacement patterns of the dentine in figures 20 and 22.

Figure 23. Enlargement of anterior ventral surface of same. Note the absence of cosmine anteriorly and anterolaterally, and the variation in pore size and structure.

diameter towards the anterior and lateral margins, where they connect with the lateral line canals. In addition they have numerous fine tubules on their dorsal surfaces which ramify into the overlying dermal bone. ANU49102 does not show the tube illustrated by Miles (1977, figure 69, VII_S), the ophthalmicus superficialis VII. Such a tube could not have been present in the specimen originally and destroyed during preparation, because there is no base from which it could have originated, and no space under the dermal bone through which it could have run.

The two large foramina in the deep dorsal invagination are oriented in such a way that the structures entering them must have had a course high across the orbital chamber. Furthermore they pass into tubes that lie in the ethmoid space, completely dorsal to the nasal capsules, and they have numerous tubules running up to enter the dermal bone. These observations are consistent with the course of the ophthalmicus superficialis VII, and with the ophthalmicus profundus V which, in *Neoceratodus*, according to Kesteven (1945, p. 28) and Fox (1965, pp. 505–508), sends two branches dorsomesially and dorsolaterally to the nasal capsule. We therefore consider that the tube labelled mesial profundus by Miles (1977, figure 69) carried both the ophthalmicus superficialis VII, and the mesial dorsal branch of the ophthalmicus profundus V (the *ramus nasalis internus profundus* of Fox). The anterolaterally directed thick tube in the ethmoidal space (the lateral branch of the ophthalmicus profundus V) is joined laterally by a tube that connects with a laterally placed foramen in the tectum nasi lateral to the antorbital wall. This foramen, which lies lateral to the posterior margin of olfactory capsule (figure 2) we interpret as having carried the ramus buccalis nerve VII.

Discussions of the snouts of Gogo dipnoans have almost never taken into account the vascular system. Obviously such a remarkable sensory region would have required a rich blood supply which could only be partly met from the palatine arteries. Bertmar (1966) is the only author to discuss the arterial system in the snouts of extant dipnoans in any detail. He considered that 'the dipnoan orbital artery reaches the snout via a dorsal branch, the a. supraorbitalis . . ., the only artery in the ethmoidal region in the Dipnoi'. It would seem possible therefore that one of the bony tubes extending forwards from the deep invagination in the antorbital wall referred to above as transmitting the ophthalmicus superficialis VII and the ophthalmicus profundus V, also transmitted the supraorbital branch of the orbital artery (figure 6*b*). Because the lateral bony tube within the ethmoid space so clearly joins with the ramus buccalis VII and is only indirectly connected with the main mass of tubules in the snout, it seems most likely that it was the medial bony tube that also carried the artery.

In the antorbital wall, at the bottom of the invagination for the above nerves and artery, lie two or three smaller foramina. On the left the more dorsal one is single and on the right it is paired. These pass through the buttress and open on the back of the nasal capsule just lateral to the olfactory nerve. There is no groove in the nasal capsule that might indicate the subsequent course of this feature, and so we assume that it passed forwards in soft tissues. This seems to be the structure considered by Miles (1977, figure 69) to be the maxillaris V_2, as that also enters the lateral wall of the nasal capsule. According to Fox (1965, figure 30), however, maxillaris V_2 runs well below the nasal capsule, but a branch of the profundus runs into the lateral wall of the capsule. Therefore, we prefer to interpret the canal in question as a branch of the profundus, or alternatively as a blood vessel. In the antorbital wall immediately below this foramen (or foramina on the right) is a smaller foramen that connects via a tube with another small foramen in the ventromesial wall of the nasal capsule. From there the nerve it transmitted ran in a shallow groove along the inner wall of the capsule and then on to the flank of the internasal septum where it disappears. This was also probably a branch of the profundus V.

Mesially in the base of the antorbital wall is another large foramen that opens into a canal that is directed downwards and forwards to open at the base of the nasal capsule where the neurocranium meets the pterygoid. In this latter region there are several foramina, and they all seem to open into the canal in question. Comparison with *Neoceratodus* (Fox 1965, figure 31) suggests that this canal carried maxillaris V_2.

The mandible of *H. gogoensis* is well known from four or five specimens in the BM(NH) Collection and from two in the ANU Collection, and one in the Commonwealth Palaeontological Collection. Mandibular dimensions for six of these specimens are given in table 3. As Miles (1977) observed, there is considerable variation in the relative width of the mandible in this species. (Note, however, that the ratio given by Miles on p. 209 appears to be jaw length/jaw width rather than the reverse as he stated.) The relative length of the mandibular symphysis of P50999 seems to be extreme and it may be that this specimen should not be referred to *H.* (*Holodipterus*) *gogoensis*. Dr Moya Smith has indicated that it is not possible to see if there are isolated teeth in this specimen so that it may be a member of *H.* (*Holodipteroides*) *elderae*, as is suggested by its long symphysis. We now describe a number of features we consider significant for discriminating *H.* (*Holodipterus*) *gogoensis*.

The dentary is a long bone that extends back on the dorsal surface to the end of the first prearticular tooth ridge. Ventrally its boundary with the infradentaries is not distinguishable, and it passes into these bones without even a slight change in slope (figures 17 and 21). Its dorsal edge is well-rounded anteriorly, but becomes sharper laterally. In vertical view its anterolateral corners are almost rectangular, and in these the surface is slightly depressed (figures 16, 20 and 24). When the mouth was shut, these depressions would have lain immediately beneath the external narial notches in the upper lip. We presume that they allowed a flux of water to pass when the mouth was closed. Our specimens, unlike those described by Miles, have several small teeth, or enlarged denticles which have developed hypermineralized dentine,

Table 3. *Mandibular dimensions for Gogo species of* Holodipterus

(The values given here for P50997 and P50999 were suppled by Dr Moya Smith. Those for P52565 are from Table 4 of Miles (1977). WAM86.9.685 is a small incomplete mandible referred to *H.* (*Holodipteroides*) *elderae.*)

species/specimen	total length/cm	length of symphysis/cm	width at articulations/cm	total length/ artic. width	sym. length/ artic. width
H. (*Holodipterus*) *gogoensis*					
P50997	9.8	4.0	*ca.* 11.5	0.85	0.35
P50999	—	9.5	*ca.* 12.0	—	0.79
P52565	9.4	4.1	9.6	0.98	0.43
CPC25341	8.6	3.5	*ca.* 10.0	0.86	0.35
CPC25738	*ca.* 7.0	2.9	*ca.* 6.9	1.01	0.42
ANU49104	*ca.* 5.7	2.7	*ca.* 6.5	0.88	0.42
H. (*Holodipterus*) *longi*					
WAM86.9.684 (holotype)	6.4	2.0	*ca.* 6.4	1.00	0.31
H. (*Holodipteroides*) *elderae?*					
WAM86.9.685	*ca.* 5.4	*ca.* 3.3	*ca.* 6.2	0.92	0.53
H. (*Asthenorhynchus*) *meemannae*					
ANU49103 (holotype)	*ca.* 7.3	*ca.* 3.5	*ca.* 6.5	1.12	0.54

arrayed along the crest of the dentary both mesially and laterally. The spacing between teeth in specimens of different sizes is such that it could not be produced by the posterior addition of new teeth in conjunction with the wear of the older teeth. These therefore must have been episodically shed so that the bone could grow. This is supported by the observation that partly grown specimens, e.g. ANU25738, have denticles around the inner edges of the dentary and a strip of white superficial dentine between these and the teeth, whereas in more mature specimens the whole buccal surface is covered with hypermineralized dentine, and the suture with the prearticulars is obscured by the same substance, as shown especially well by P52565 (Campbell & Smith 1987, figure 7). Plastered against the outer face of the bone below the teeth on the partly grown individual is a layer of dentine whose margins show that it was episodically resorbed (Campbell & Smith 1987, figure 4D). On the largest specimens, e.g. P52565, the teeth are scarcely visible, indicating that resorption increased with age.

The anterior and anteroventral faces of the dentary are covered with dense dentine perforated by openings for the lateral line canals and the symphysial tubuli (figures 19, 23 and 28*a*,*b*). The same substance extends back along the ventral edge of the labial pouch suggesting that the dentary runs that far back at least. Behind this zone of dense dentine, and joining it along a sharp line, is a highly perforated surface, the perforations of which are larger than normal cosmine pores and more irregular in shape. It is not clear if this line marks the boundary between the dentary and the infradentaries.

Miles considered that *H. gogoensis* has four infradentaries on each side, but we have been unable to confirm this. On the contrary, we have some indications that only three are present in at least some specimens. On ANU49104 (figure 18) the left surangular is clearly defined on the outer surface of the mandible by a sigmoidal suture, although this may be distorted because the specimen is clearly pathological

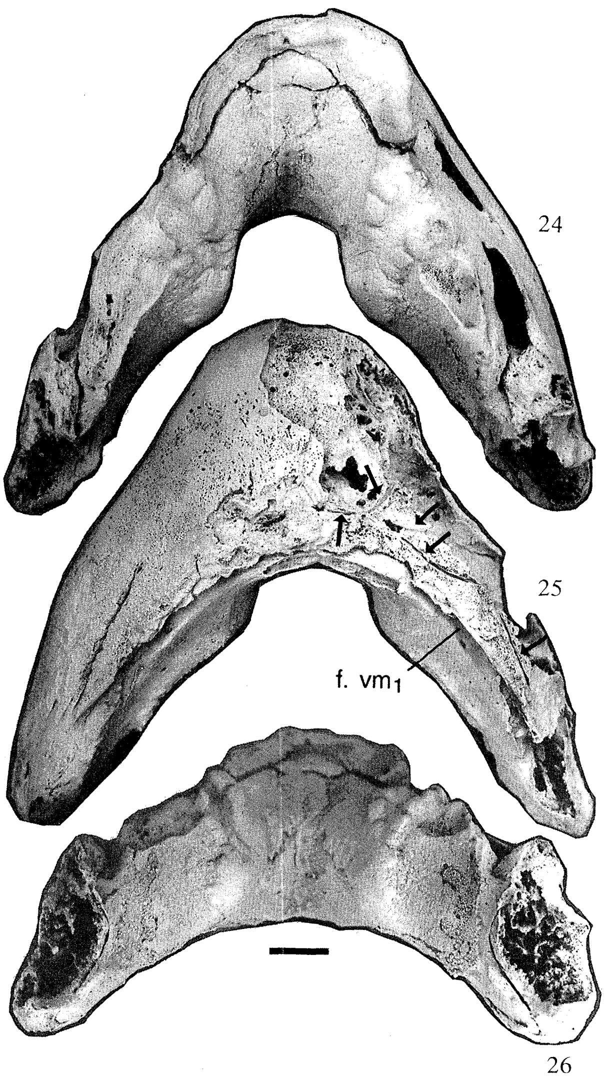
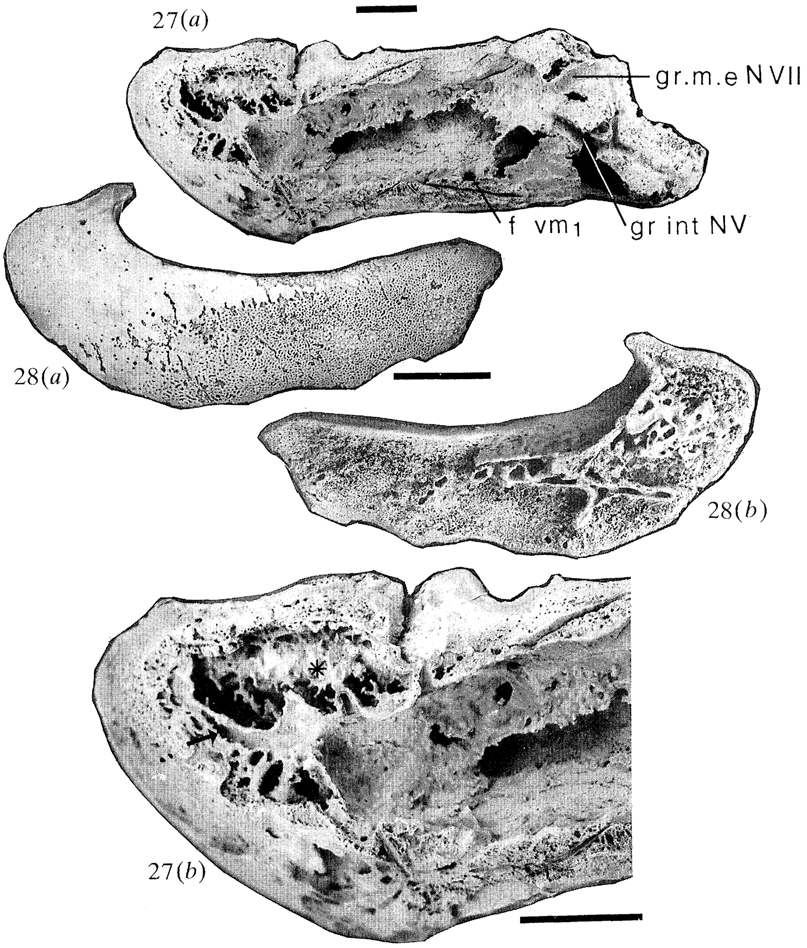


Figure 24–26. *H.* (*Holodipterus*) *gogoensis*. Dorsal, ventral and posterior views of the mandible of CPC25341. Note the arrangement of the lateral line canals (arrowed) on the left side of figure 25.



Figures 27 and 28. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figure 27. (*a*) Left ramus of CPC25341 in lateral view, with the external dermal bones removed, and the mesial wall of the Meckelian cavity partly lost during preparation. (*b*) Enlargement of anterior of same showing the extension of the Meckelian cavity into a branching system of canals. Two major tubes at the anterior of the Meckelian cavity are indicated by an arrow and an asterisk.

Figure 28. (*a*,*b*) External and internal views respectively of the dermal bone flaked from CPC25341. The depth of burial of the lateral line canals and the large tubules extending from them to the surface are shown in (*b*) as well as the tubules connected with the system from the front of the Meckelian cavity.

in this region. The suture is continued forwards across the floor and wall of the labial pouch to a point below the most anterior prearticular tooth. Its anterior course is known to be normal because it is matched on both sides of CPC25738. In these two specimens the course of the suture within the labial pouch has a much less vertical orientation than shown by the illustration given by Miles (1977, figure 109). In our specimens this portion of the suture reaches posterior to the level of the second tooth row before turning posteroventrally over the exposed part of the bone, whereas in Miles's figure it reaches to the first tooth row.

The lateral line canal system, which would be useful in helping unravel the bone pattern, is itself not completely clear. The mandibular canal enters the angular in the normal position for Devonian dipnoans and runs forward to the ossification centre of that bone and then loops down to the ossification centre of the splenial/postsplenial (figure 25), those two bones apparently having fused. Before it reaches this centre it is joined by a canal from a posterodorsal direction. This must be a branch from the oral canal, but such a structure has not been observed on any other species. The oral canal is deeply buried and most of it is not preserved (figures 25 and 28*b*), but on its outer surface it has the slit-like band from which large pores arise.

The interior of the mandible is also well shown by CPC25341 which had the left external dermal bones flaked off on a separate piece of rock when collected. This specimen shows that the Meckelian cartilage was not strongly ossified, but is represented by a thin flaky perichondral layer on the mesial side of the Meckelian cavity (figure 27*a*,*b*). The lateral face of the articular shows to advantage the arrangement of the canals leading down from the foramen hyomandibularis VII and mandibularis V. Two canals run from this foramen. The larger one runs anteroventrally to the back of the Meckelian space where it divides to send one branch for the intermandibularis V (gr.int V of Miles) downwards and backwards to open at the posteroventral edge of the surangular (figure 27*a*), and a second branch that runs anteroventrally down the back wall of the Meckelian cavity to open at the foramen labelled f. vm_1 by Miles (1977, figures 100, 102 and 103). From its position, we conclude that this probably carried a branch of the intermandibularis. The smaller canal runs directly ventrally to open into a canal directed posteroventrally from the gr.int V described above. Neither the larger nor the smaller of these canals has been described from any other species.

A foramen immediately in front of f. vm_1 connects with a shallow furrow that runs anterodorsally along the face of the perichondral Meckelian bone. The alignment of the furrow suggests that it may connect with a foramen (the f_4 sa_1 of Thomson & Campbell 1971, figure 21) exiting the Meckelian bone immediately at the posterolateral extremity of the dentary.

The perichondral bone at the anterior end of the Meckelian cavity carries two tubes (figure 27*a*,*b*). The larger of these (arrow, figure 27*b*) is directed anteriorly and ramifies into a number of tubules some of which join a reticulum below the anterior furrow which they enter, and others which connect ventrally and laterally via more robust tubules to the external dermal bone where presumably they served organs that opened through the external pores. The smaller tube (asterisk, figure 27*b*) referred to above, joins the Meckelian cavity more posteriorly and passes dorsally into the bottom of the anterior furrow.

We have nothing to add to the description of the prearticular tooth plates given by Campbell & Smith (1987).

6. HOLODIPTERUS (HOLODIPTERUS) LONGI

(Campbell & Barwick, 1991)

Holotype. WAM86.9.684, collected by Dr John Long from the Gogo Formation, Paddy's Springs, via Bugle Gap, Canning Basin, Western Australia.

Diagnosis. See Campbell & Barwick (1991, p. 435).

Description. The palate (figures 29 and 30) has an anterior angle of *ca.* 65°, which is comparable with that of juvenile *H. gogoensis*. It is lightly ossified in comparison with specimens of the latter species of comparable size. Most of the surface is covered by normal denticles which are larger towards the front and gradually disappear behind the zone of waisting for the adductores mandibulae. Nine or ten teeth are present along the palatal margins (figures 29 and 31*a*,*b*). These are variable in shape, but most are ovate cones that are concave on their lingual faces. A smaller second tooth sometimes lies in the concavity. Thus several rows with two teeth are present, but none have three. Resorption of the medial tooth in some rows indicates that at a slightly later stage of growth even this would have been removed from all rows, and it also indicates that at a slightly earlier stage three teeth were probably present in some rows.

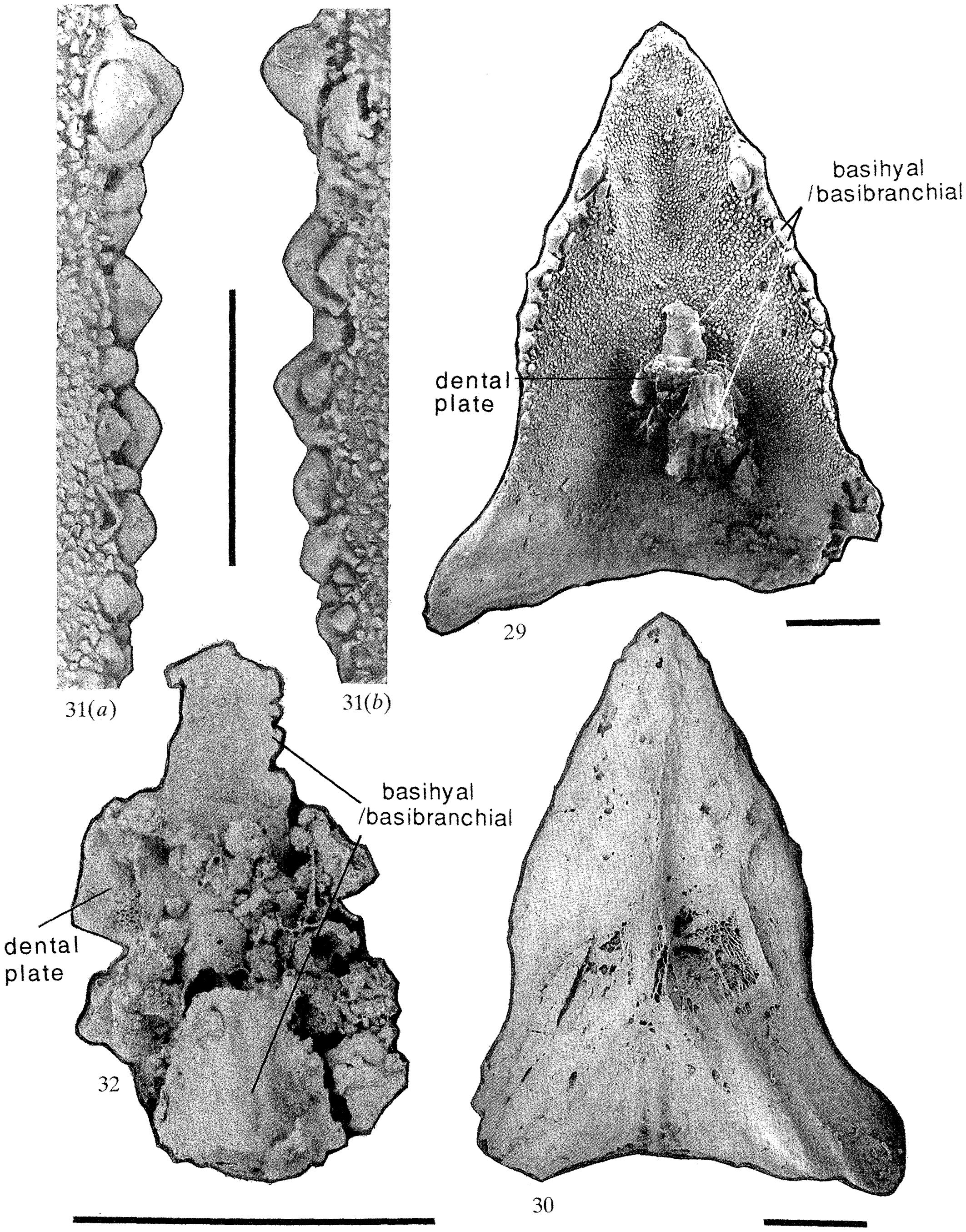
The outline of the parasphenoid is obscured on the buccal surface, but on the visceral surface (figure 30) it is seen to have an acute anterior tip with a layer of tissue plastered on its surface, as in other holodipterans. In this region it is thick and abuts the quadrate ridges of the pterygoids. These latter structures are lightly ossified and supported by internal bony struts.

A small fragment of the partly crushed basihyal/basibranchial, which is very lightly ossified, is preserved on the posterior part of the palate (figures 29 and 32). Of significance are the fragments of two small dental plates that are still attached to its dorsal surface. These plates indicate that the mode of feeding was similar to that of *Griphognathus*, which is what would be expected from the other attributes of the buccal surface.

The mandible is represented by the symphysial region and the complete right ramus (figure 33). The symphysis is short, being only 30% of the total length of the jaw. The lingual groove slopes steeply and is devoid of denticles except anteriorly. The ramus is slender and has only a small heel on the prearticular. The dentary is proportionately longer than in *H.* (*H.*) *gogoensis*, quadrate in outline, and has a slightly concave transverse front and almost straight flanks. At the ends of the front segment the bone rises to a slight peak, behind which is a long and deep depression which lies below what we consider to have been the site of the anterior naris. Along the lateral crest of the dentary is a single row of five teeth which increase in size rearwards (figures 33*b* and 35). At least five similar teeth are recognized across the anterior dorsal edge of the right half of the dentary. Medially the dorsal edge of the anterior face of the dentary is slightly recurved, a feature not observed by us on any other dipnoan. Surrounding the teeth is a layer of white superficial dentine which extends along their flanks. The buccal edge of this layer shows clear evidence of resorption. Mesial to this edge the surface is covered with denticles of the same kind as those on the adjacent prearticulars.

The wide crescentic adsymphysial plate (figure 33*b*) is well defined and is comparable in shape with that of other holodipterans. It is covered with denticles like those of the prearticulars.

The prearticulars join at a clear median suture which is straight except at the posterior end where it is zigzaged. The heel (Smith & Campbell 1987) is much less well developed than on any other holodipteran with which we are familiar. This heel has a weak ridge that extends anterolaterally in alignment with the first tooth row. The surface of the ridge carries a small amount of unresorbed white dentine, but no evidence of callus-forming hypermineralized dentine. Thirteen teeth are arranged along the lateral crest of the bone (figure 36). The most anterior three lie close together and make up a row which is almost in alignment with the posterior teeth of the dentary (figures 33*b* and 35). The fourth and fifth teeth, like the sixth and seventh, are radially aligned. Five of the hindmost teeth fall along the apex of the lateral crest, but the ninth is offset and lies medial to the eighth and tenth teeth. Wrapped around the lateral end of the anterior longitudinal row is an enamel-covered layer of dentine (figure 35, arrows) suggesting that lateral growth took place by the addition of a layer of tissue rather than by the addition of a series of enlarged denticles like those on some other holodipterans. In this layer of



Figures 29–32. *H.* (*Holodipterus*) *longi*. Scale bars = 10 mm.

Figures 29 and 30. Ventral and dorsal views of the palate of WAM86.9.684.

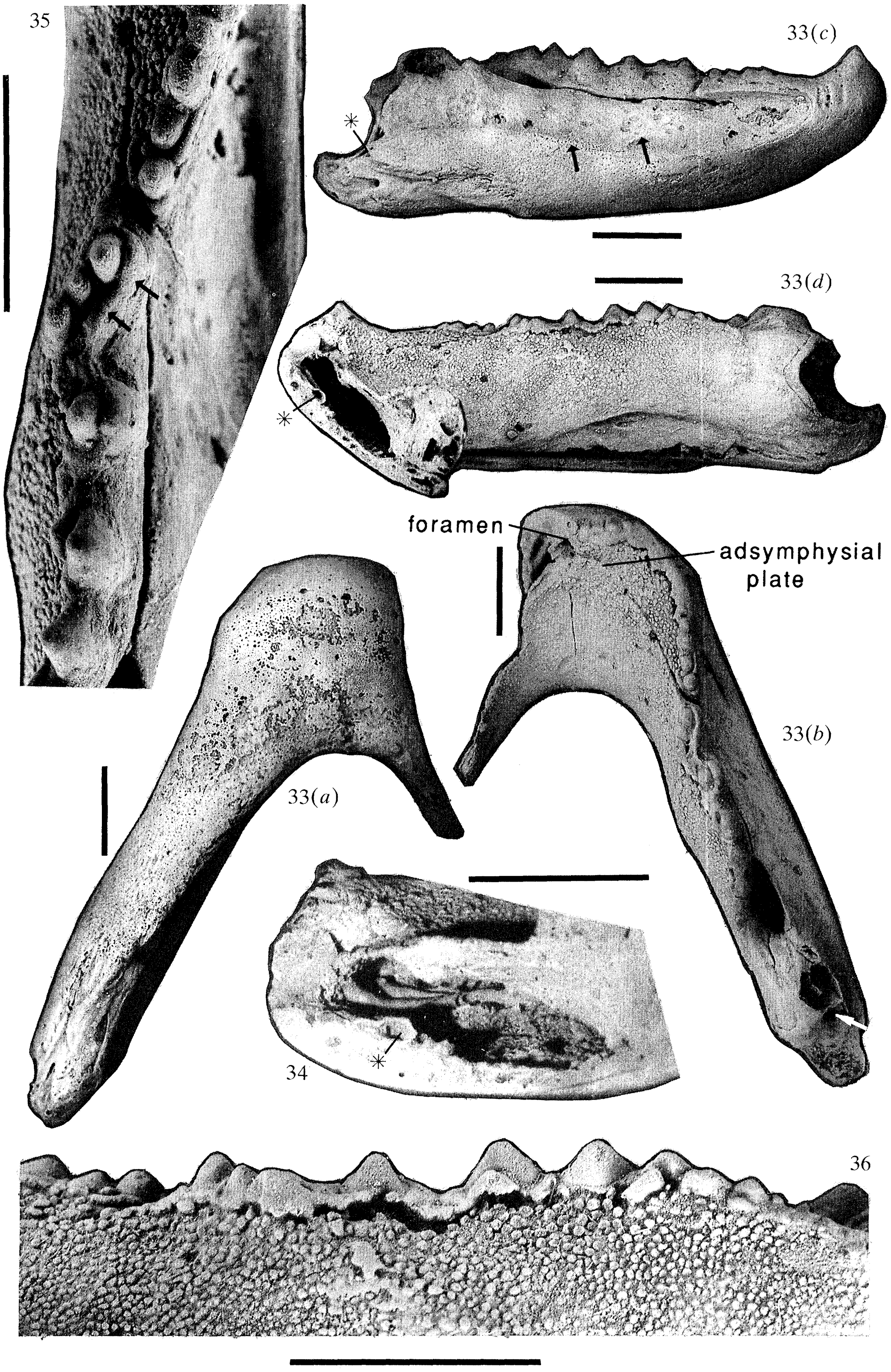
Figure 31. (*a*,*b*) Enlargement of the left and right marginal teeth and adjacent denticles of the same palate showing the effects of resorption.

Figure 32. Enlargement of mesial part of the palate of same showing the remains of the basihyal/basibranchial and one of its denticle bearing plates, tilted to the left with respect to figure 29.

wrap-around tissue two centres of hypermineralization can be distinguished, one opposite the end of the first tooth row, and the other opposite the gap between the first and second rows. The space between adjacent teeth in successive rows is covered with white dentine. The lingual edges of the tooth rows are resorbed, and new denticles have grown in the recently resorbed spaces. On the outer faces of the prearticulars there are no enlarged denticles.

The posteroventral parts of the prearticular are smooth and in life were probably covered in soft tissue. A sharp keel forms the boundary between this surface and the largely denticulated bone forming the remainder of the surface of the prearticular. This smooth bone extends back below the articular. Denticles are also absent from the prearticular immediately in front of the articular.

The articular is narrow (figure 33*b*). As in *Griphognathus*, its glenoid fossa has a narrow lateral rim representing the lateral fossa. It bears a preglenoid



Figures 33–36. *H.* (*Holodipterus*) *longi.* Scale bars = 10 mm.

Figure 33. (*a*) Ventral, (*b*) dorsal, (*c*) lateral and (*d*) mesial views of the mandible of WAM86.9.684. The arrow in (*b*) marks the common foramen for the mentalis VII and the mandibularis V. The arrows in (*c*) mark the suture between the angular and the surangular. In (*d*) an asterisk indicates the tube of the oral lateral line canal.

Figure 34. Internal view of the symphysis of same. Note the ramifying tubules. An asterisk marks the tube of the oral lateral line canal.

Figures 35 and 36. Enlargements of marginal tooth row of WAM86.9.684 in dorsal and medial view. The arrows in figure 35 indicate an enamel-covered rim of white superficial dentine. In figure 36 the anterior is to the left.

process, the top of which has been destroyed, and it forms the back wall of the adductor pit. Ventrally the articular passes around between the inner and outer dermal bones as a strip of Meckelian bone which becomes progressively less well ossified leaving a gap towards the midline (figure 33*a*,*d*).

The external dermal bones are well preserved, and they consist of a relatively narrow exposed part covered by cosmine-like substance at the front, and an extensive, almost vertical, naked blade that runs forward from the glenoid fossa to the anterior of the labial furrow (figure 33*c*). The absence of superficial tissue on the bone suggests that a large muscular lip and cheek were present. The boundary between the dentary and infradentaries is not visible. The suture between the surangular and the angular is the only one distinguishable between the infradentaries. This suture (arrowed, figure 33*c*) runs obliquely upwards from the posterior end of the mandible just below the articular, isolating a small lenticular piece of exposed bone, before passing across the naked bone of the cheek to terminate below the posterior end of the dentary. As is normal in Devonian dipnoans, the surangular has a high peak covering the outer face of the preglenoid process, much of which has been broken away. The surangular and the posterior part of the angular have very little cosmine, but they show well the many pores through the bone that are characteristic of other holodipterans and *Griphognathus*. X-radiographs show only one radiation centre in the splenial/postsplenial position. The anterior parts of the angular and the splenial/postsplenial are cosmine covered, and the sizes of the openings to the flask chambers vary considerably. The lateral lines are marked by their pores, but these are clear only anteriorly. X-radiographs show that the lateral line commissure is posteriorly placed, and that the canal running forwards from its junction with the mandibular canal has a strong anterolateral orientation. Its junction with the mandibular canal is clearly shown on a radiograph.

An unusual feature is the foramen at the rear end of the pustule-covered part of the surangular (figure 33*a*). This foramen lies within the surangular and because of its appearance could be interpreted as the end of the oral lateral line canal. However, in other Devonian dipnoans the oral canal does not extend so far back.

On the external surface between the glenoid and the preglenoid process is a large foramen for the mentalis externus VII and the mandibularis V (arrow, figure 33*b*). As is normal for holodipterans, a second large foramen for the intermandibularis V lies between the articular and the surangular at the rear end of the latter. On the ventral edge at the contact between the Meckelian bone and the prearticular is a foramen that is entered from the rear by a shallow furrow. This corresponds with f.vm_1 (Miles 1977, figure 109). Two other more anteriorly placed foramina lie in the angular against the Meckelian bone. These correspond with the two unnamed foramina on the same figure of Miles.

The interior of the mandible (figure 34) can be seen through the eroded anterior end. Details have been elucidated by radiography. A large tube on the left side near the anterior margin (asterisk, figures 33*d* and 34) is the oral lateral line canal. It is matched by a canal on the right side shown in a radiograph. A large tube runs posteroventrally from the median pit in front of the adsymphysial plate, and lies close to the internal surface of the dermal bone. It is not symmetrically placed, but is displaced to the right. As it runs backwards it receives other tubes from both sides and increases in diameter. It is joined by at least four somewhat smaller tubes, two contacting it mesially, one laterally, and one ventrally. More posteriorly, about half way along the symphysis, it is joined by a large but broken tube from the right. A third large tube lying even further to the right is joined by numerous smaller tubes that ramify around the inner anterior face of the dentary immediately anterior to the labial pit. Fine connections are made between these tubules and the oral lateral line canal where it is preserved on the left side.

Remarks. This species remains based on a single specimen, represented by a palate and two-thirds of a mandible. The original diagnosis stressed four points: (i) the limited number of teeth in each palatal and prearticular tooth row, which are not sufficiently numerous to form pseudo-tooth plates; (ii) the large number of teeth along the margins of both the pterygoids and the prearticulars; (iii) the lack of strong hypermineralization and hence the failure of calluses to form on the palate and prearticulars; and (iv) the shortness of the median symphysis in the mandible. The specimen has a much lighter construction than *H.* (*Holodipterus*) *gogoensis*, and in many respects it resembles *Griphognathus whitei*. The presence of the foramen in the midline in front of the adsymphysial plate, the presence of a distinct adductor pit in the mandible and the distinctive depression in the dentary below the position of the external naris, give the specimen the clear stamp of the genus *Holodipterus*.

We expect that there will be contention about the definition of the term 'tooth' as used in this description. Certainly, in outline the teeth are not simple cones, but we note that in *H.* (*Holodipterus*) *gogoensis* many teeth of the tooth rows are similarly concave on their mesial faces. This indicates that, like those of *H.* (*Holodipterus*) *longi*, they were added in close proximity to the preceeding tooth in the row to which they belong, thus producing a distorted conical shape. In addition, we note that teeth are more numerous along the palatal margins of *H.* (*Holodipterus*) *longi*, than is usual for tooth-plated Devonian dipnoans. We contend that such a distribution does not bear on the definition of teeth. Finally, it may be argued that we need to establish the presence of petrodentine in the cores of the teeth, as such tissue is characteristic of the cores of the teeth of most Devonian dipnoans (Smith 1988). The single available specimen is too valuable to section, and hence we are unable to refute this potential criticism. On the other hand the presence of dark, hypermineralized dentine in the cores of many of the teeth of *H.* (*Holodipterus*) *longi* is easily established where their tops are worn. This substance is at least superficially similar to the tissue observed in teeth of specimens of *H.* (*Holodipterus*) *gogoensis*, about which there is no contention.

7. H. (HOLODIPTEROIDES) (subgen. nov.)

Etymology. -oides = similar: that is, to *Holodipterus*.

Type species. H. (*Holodipteroides*) *elderae* sp. nov. from the Gogo Formation, Frasnian, Canning Basin, Western Australia.

Diagnosis. A subgenus reaching a greater size than *H.* (*Holodipterus*); snout of adults broad and depressed rather than protuberant; nasal buttress unusually thick; palate thick, with three or four radial ridges and sometimes a weak median ridge, but no conical teeth; buccal surface of adult palates almost completely covered with coarse pustules of hypermineralized dentine separated by less mineralized dentine; small posterior areas of the palate with denticles and superficial white dentine; a large posteromedian callus present.

8. H. (HOLODIPTEROIDES) ELDERAE (sp. nov.)

Etymology. After Valerie Elder, part-time preparator in the Department of Geology at The Australian National University, who prepared some of the specimens described here and who assisted with collecting during the 1990 A.N.U. Gogo collecting trip.

Holotype. ANU49101, from the Gogo Formation (Frasnian) at Lloyd Hill, Canning Basin, Western Australia.

The holotype is a moderately large partial skull. It includes most of the neurocranium, although anteriorly the dorsal portions of this are missing, as also is the extreme posterior of the neurocranium. Almost all of the palate of this specimen is present, although due to its connection to the neurocranium its dorsal surface is not visible. Part of the dermal skull roof, most of a hyoid arch, fragments of the gill arches, an anocleithrum and most of a clavicle, and the articulatory part of one side of the mandible, are also present.

Paratypes. Three specimens, designated as paratypes, are regarded as conspecific with the holotype on the basis of the morphology of their palates and the nature of the dental surfaces.

WAM86.9.649 is a large partial skull collected by J. A. Long in 1986 in the southwestern area of Bugle Gap, approximately 3.2 km east of Lloyd Hill. It includes approximately the posterior two thirds of the neurocranium which bears well developed but incomplete median and dorsolateral cristae, most of the anterior half of the palate, and the dermal bones of the snout and anterior skull roof. The cranial cavity is open posteroventrally and reveals the inner walls of the left sacculus as well as much of the perichondrium surrounding the cavities for the posterior hindbrain and anterior spinal column. The mandible and postcranium are lacking.

CPC30828 which was collected at Long's Well on Gogo Station by G. C. Young in 1972, consists of an almost complete palate with adhering fragments of the palatoquadrate and neurocranium, some other skull fragments and part of the postcranial skeleton.

CPC25739, which was found by G. C. Young at the same locality as CPC30828, consists of diverse and generally fragmentary skull bones as well as part of the dermal bone from the dorsal surface of the anterior of the snout, and a palate which is lacking the anterior margins, but is otherwise relatively complete. The anterior of the body of the palate, which is broken away from the posterior portion a little forward of the junction between the parasphenoid and pterygoids, has been embedded in plastic and sectioned transversely at four levels. These sections were treated by Campbell & Smith (1987) as material of *H.* (*Holodipterus*) *gogoensis*.

Additional material. WAM86.9.685 is an isolated, incomplete, small mandible assigned to this species because of the dentine cover on the buccal surface, and because the length of the symphysis relative to the length of the mandible falls outside the range of *H. gogoensis* (table 3).

Diagnosis. As for the subgenus.

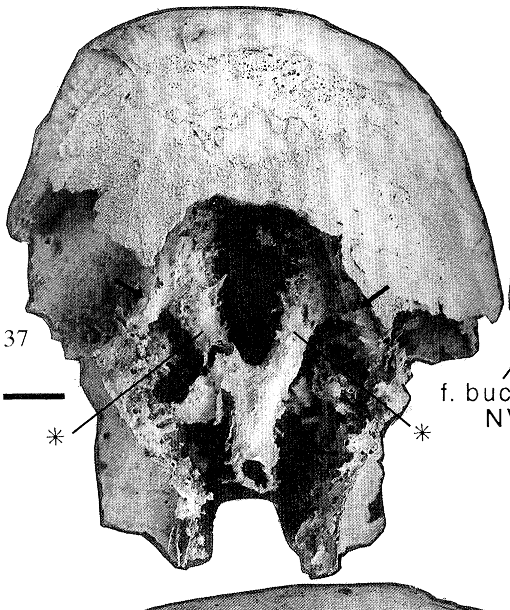
Description. The terminal portion of the snout is missing from all known specimens, but the posterior two-thirds or so of the dermal snout is preserved in CPC25739 (figure 37) and slightly less of it seems to be present in WAM 86.9.649. In comparison with specimens of *H.* (*Holodipterus*) *gogoensis* (ANU49102 and CPC25740) these specimens indicate a flatter dorsal surface to the posterior snout. In addition, the breadth of the snout across the nasal buttresses is almost twice that of *H.* (*Holodipterus*) *gogoensis* (table 2). Otherwise the snouts of these two taxa appear similar.

The preserved (posterior) portion of the dermal snout of specimen CPC25739 shows no evidence of separate ossifications, but bears a broad transverse band of cosmine which covers most of its anterior half (figure 38). This band shows features which we interpret as evidence for multiple phases of resorption. The cosmine is more-or-less complete except for narrow resorption lines and a few cosmine-free patches. Posterior to this band, cosmine is limited to small irregular patches. Some small areas have scattered pustules lacking pore canal openings.

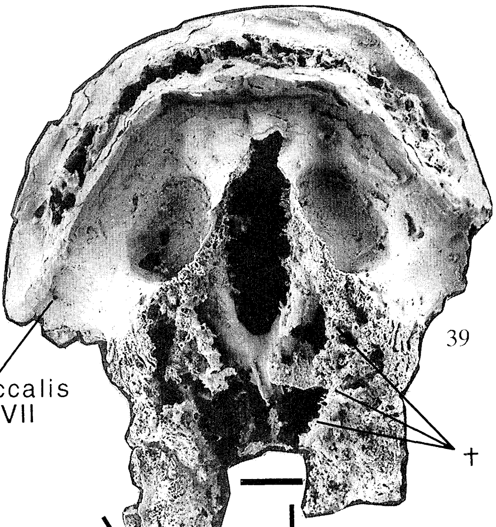
The dermal skull roof and dermal cheek are not well known. The most complete information on these regions comes from CPC25739. The only other specimens in which such bones are known are the holotype and CPC30828, both of which include a few more-or-less complete dermal bones.

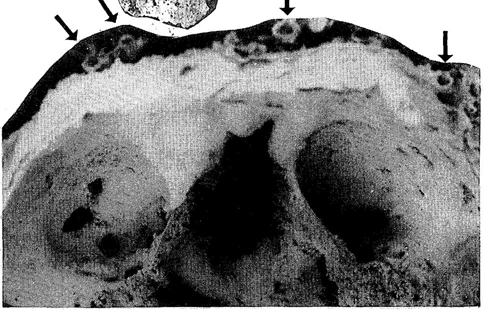
Specimen CPC25739, which has been X-rayed (figure 42), retains bones B, I, J, Y_1, X and L_1, and these appear similar in general configuration to the same bones in *H.* (*Holodipterus*) *gogoensis*. Bone Y_1 appears relatively larger than in that form. Ventrally the anterior third of bone B bears an approximately rectangular area for attachment of the median crista as is the case in *H.* (*Holodipterus*) *gogoensis*. The ventral surface of bone I also bears a faintly corrugated attachment surface for the dorsolateral crista. An equivalent strong attachment surface is known in

37



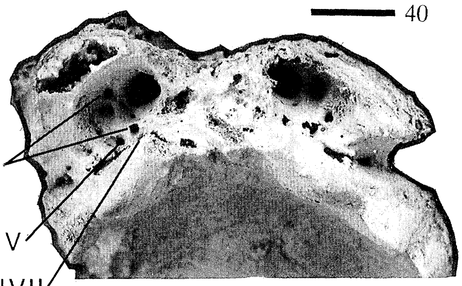
39



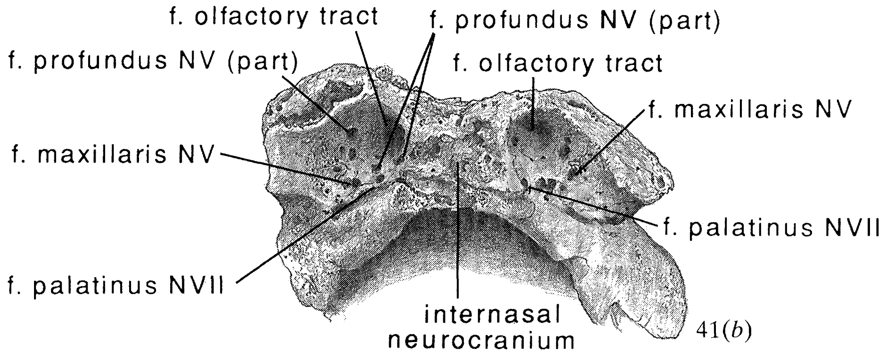


40

38



41(*a*)



41(*b*)

Figures 37–41. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

Figure 37. Dorsal view of the snout of CPC25739 showing the anterior of the braincase, the bony tubes for the olfactory tracts (asterisks) and the tubes for the ophthalmicus profundus (arrows) on each side of the specimen.

Figure 38. Enlargement of part of the dermal bone of the snout of same to emphasize the extent of the cosmine and the porous structure of the bone.

Figure 39. Ventral view into the roofs of the nasal capsules of CPC25739. The longitudinal tube for the palatinus nerve is indicated by daggers. The anterior rim of the specimen is plastic embedding material.

Figure 40. Anteroventral view into the nasal capsules of same to show the foramina in the posterior wall of the nasal capsule. The two anterolateral holes in the roof of the right capsule (tectum nasi) are artifacts. Rostral tubules are preserved (arrows).

Figure 41. (*a*) Anterior view into the nasal capsules of the holotype, ANU49101. (*b*) Drawing of same.

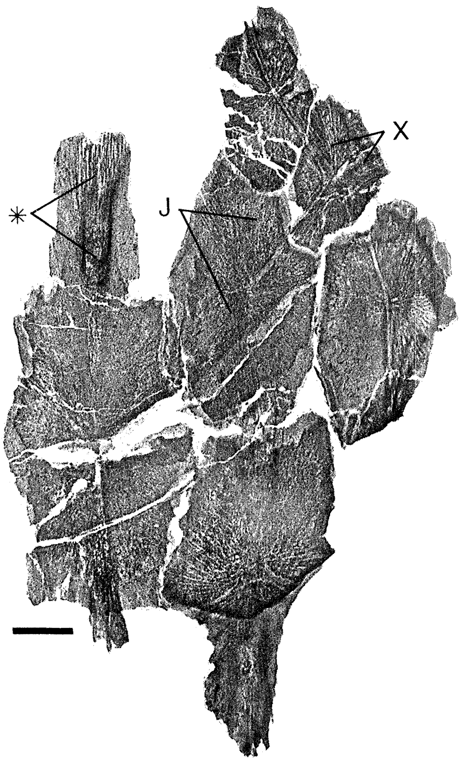


Figure 42. *H.* (*Holodipteroides*) *elderae*. X-radiograph of the right posterior roofing bones of CPC25739, showing radiation centres. Note the canal in bone J and the broad connection of the two canals in bone X. The anterior third of bone B (asterisk) carries the attachment for the median crista. Scale bar = 10 mm.

H. (*Holodipterus*) *gogoensis*. Bone I also has a long and wide posterior subdermal projection for the attachment of the anocleithrum. X-radiographs show a fully developed lateral line canal in bone J, and in bone X the canal from J bends to run forwards into L_1 without actually intersecting the more lateral canal that penetrates $Y_1-X-(4)$. Instead these two canals approach each other and seem to be connected by a broad flat open space (figure 42). A similar situation is found in *H.* (*Asthenorhynchus*) *meemannae* and in *H.* (*Holodipterus*) *gogoensis*, although in the latter the only bone available is not as well preserved as in the other species. The preserved dermal skull bones of the holotype do not appear to articulate with one another and so interpretation is difficult. One of them bears the confluence of the infraorbital and supraorbital lateral line canals and so is identified as bone X.

The pustules on the dermal bones of the skull in *H.* (*Holodipteroides*) *elderae* are finer and more closely spaced than those of *H.* (*Holodipterus*) *gogoensis*. The holotype and CPC30828, which are specimens of similar size, show this difference.

The only bone of the operculo-gular and submandibular series preserved is a right subopercular 1 from CPC30828. It has the normal shape for a holodipteran, but it is 61 mm long and *ca.* 53 mm high, which is very large. The dorsal edge has a deep overlap that extends the full length of the bone and the anterior edge has a much narrower overlap. The external surface is covered with pustules.

The walls of the antorbital chamber agree in their topographic features with those of *H.* (*Holodipterus*) *gogoensis*. Immediately posterior to the excavation in the dorsal part of the antorbital wall the walls of the neurocranium arch upwards, and increasingly outwards, in a smooth curve. There follows a region of the neurocranium, extending from about the level of the optic foramen to the level of the foramen sphenoticum minus, where the outer perichondral layer of the neurocranial walls are essentially planar and vertical in orientation (figure 43). Opposite walls are subparallel in this region. Ventrally this part of the neurocranial wall flares laterally as in *H.* (*Holodipterus*) *gogoensis* to provide a laterally thining layer of bone over the mesial part of the dorsal surface of the pterygoids.

Posterior to this parallel-sided portion of the neurocranium the walls undergo a slight realignment, so that they converge posteriorly and dorsally. These converging walls form the very abbreviated median crista which has a steep and concave posterior edge.

The roofs of the nasal capsules are well preserved only in CPC25739 (figures 39 and 40) but information has been obtained from the the holotype, WAM86.9.649, and CPC30828, all of which have parts of the posterior wall of the capsule preserved.

In CPC25739 the nasal capsules are ovate within the tectum nasi, and have their long axes converging forward towards each other at an angle of 50–60°. The boundary between the roof of the nasal capsule and the tectum nasi of the neurocranium is marked by a distinct change in slope locally, as well as a change in the surface texture of the bone. The dorsal surface of each nasal capsule is gently arched and penetrated by numerous fine foramina which open dorsally and mesially into small bony tubules. Some of these tubules join with the large bony canal for the ophthalmicus superficialis VII and ophthalmicus profundus V discussed below. Others terminate in the open space between the capsules which must have been occupied by cartilage in life.

As in other Gogo dipnoans the olfactory tracts were encased in bony sheaths. These sheaths diverge at 35–40°, and increase gradually in diameter as the nasal capsules are approached (figures 37 and 43). No sharp division between the olfactory tracts and nasal capsules is evident. The large angle of divergence, the smooth transition between the olfactory tracts and nasal capsules, and the relative proportions of the telencephalon and the olfactory tracts, are features that *H.* (*Holodipteroides*) *elderae* shares with *H.* (*Holodipterus*) *gogoensis*. The length of the bony sheath of each olfactory tract is almost equal to the distance between the medial point of conjunction of these tracts and the pineal swelling.

In *H.* (*Holodipteroides*) *elderae*, as in other Gogo dipnoans, the posterior wall of each nasal capsule is pierced by a number of foramina in addition to the one that transmitted the olfactory tract (figure 41*a*,*b*). These vary in diameter although they are all considerably smaller than the olfactory foramen. The most easily interpreted specimen is CPC25739 which has had the palate removed (figures 39 and 40). It

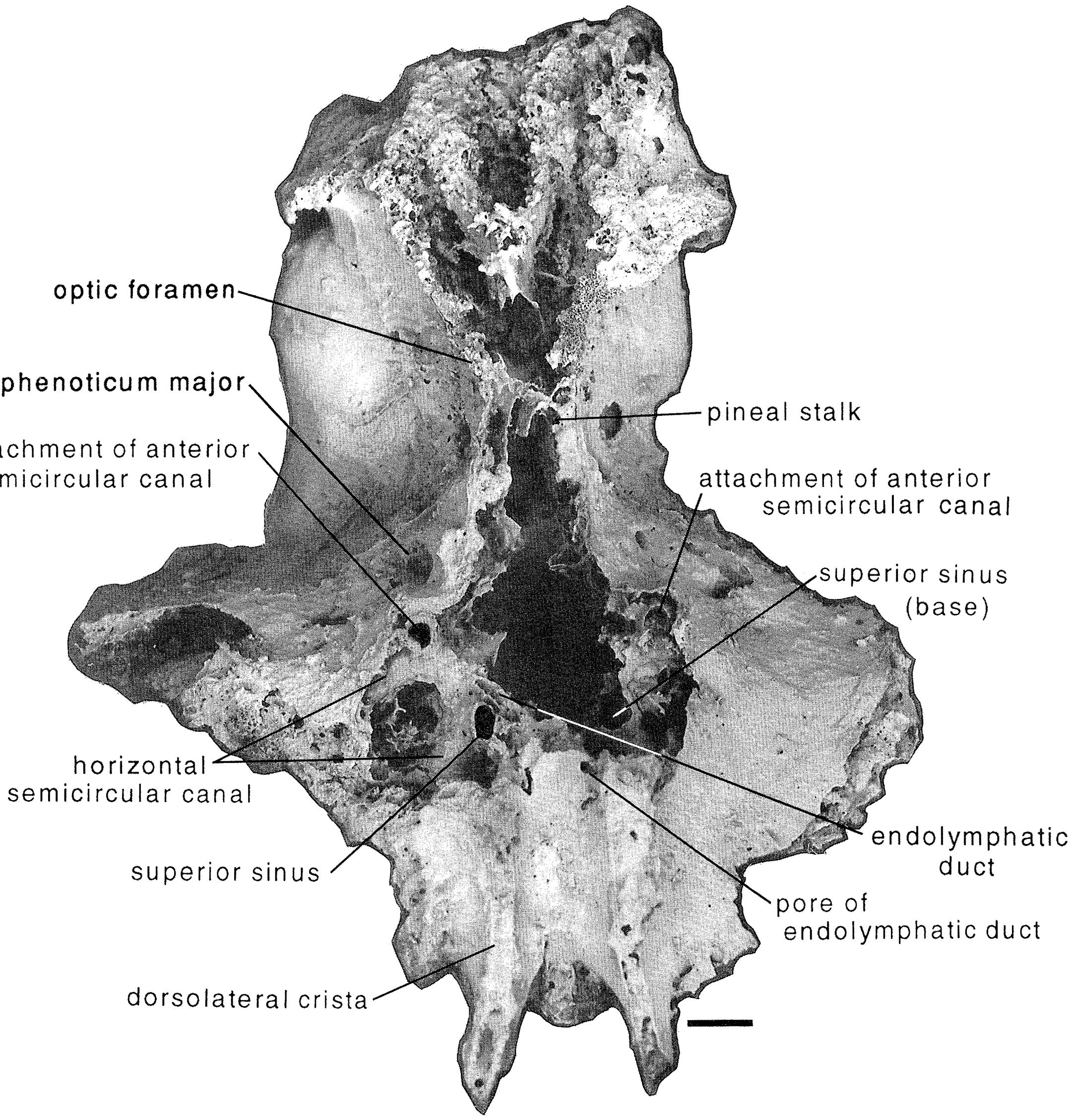


Figure 43. *H.* (*Holodipteroides*) *elderae*. Dorsal view of the holotype, ANU49101, showing the horizontal semicircular canal on the left, and sections through the verticals on the right. Scale bar = 10 mm.

corresponds well with *H.* (*Holodipterus*) *gogoensis*. The dorsal part of the antorbital wall is extended into an invagination from which an anteromesially directed tube proceeds across the top of the nasal capsule (arrows in figure 37). As indicated for *H.* (*Holodipterus*) *gogoensis*, this would have housed the ramus ophthalmicus superficialis VII and a branch of the ophthalmicus profundus V_1, and the supraorbital branch of the orbital artery. An anterolaterally directed similar tube for the lateral branch of the ophthalmicus profundus V_1, is indicated by its broken base on the left and by the more distal part of the tube (concealed) on the right. Laterally the remnant of a tube for the buccalis VII enters the tectum nasi at a foramen (figure 39) on both sides and its junction with the lateral profundus is visible on the right. In the floor of the above-mentioned invagination is a smaller foramen which enters a tube running anteroventrally to emerge in the back of the nasal capsule lateral to the olfactory nerve. This would have been for another branch of the profundus or perhaps a blood vessel. As we have indicated in the description of *H. gogoensis*, we see no evidence of the tube figured by Miles (1977, figure 69) as being for the ramus superficialis VII. Indeed there is no space for such a tube between the roofing bones and the bifurcating tubes in CPC25739. As discussed in our treatment of *H.* (*Holodipterus*) *gogoensis*, Kesteven (1945) indicated that in *Neoceratodus forsteri* branches of both the ophthalmicus profundus V_1 and ophthalmicus superficialis VII nerves pass over the nasal capsules, and so we conclude that the mesial of the above mentioned pair of tubes housed fibres of both these nerves.

Immediately behind the profundus foramen in the antorbital wall on the right side, but about 7 mm further back on the better preserved left side, is a larger foramen that opens anteroventrally into a tube that joins the anterior end of a longitudinal multi-branched tube lying close to the interface between the neurocranium and the palate. Posteriorly the longitudinal tube (dagger, figure 39) runs towards the position of the hypophysis. Anteriorly it opens into the

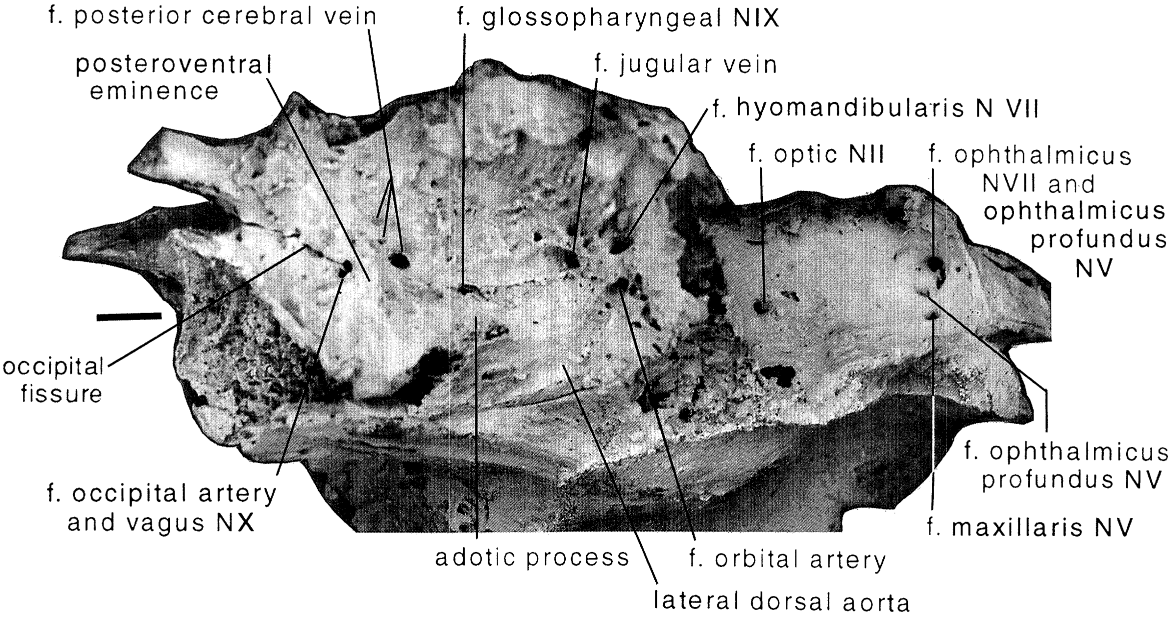


Figure 44. *H.* (*Holodipteroides*) *elderae*. Posterolateral and slightly ventral view of the holotype, ANU49101, showing the foramina in the antorbital wall and the posterior wing of the neurocranium. Scale bars = 10 mm.

posteroventral wall of the nasal capsule. An anterolaterally directed tube from this main tube, joins a parallel but more lateral longitudinal tube that opens through the postnasal wall below the nasal capsule. Similar tubes can be identified in X-radiographs of the neurocranial remnants on the left side of CPC30828. In both specimens these longitudinal tubes are in the appropriate positions to have housed the palatinus nerve and and possibly branches of the palatine artery. The tube from the antorbital wall is therefore reasonably interpreted as carrying the maxillaris V_2 which in *Neoceratodus* joins the palatinus anteriorly (Fox 1965, figure 31). As in *H. gogoensis* there are several small foramina entering the nasal capsule just lateral to the maxillaris foramen. These can be seen to join the palatinus complex, and therefore they are interpreted as carrying branches of either the palatinus artery or the palatine nerve.

In the holotype the number of foramina is larger than in CPC25739, but most of the roof of the snout has been lost and with it the tubes for the ophthalmicus profundus V_1 and ophthalmicus superficialis VII nerves. On the right side the preservation is good enough to permit the establishment of connections through the antorbital wall into the nasal capsule by probing. On the left side the pattern of foramina is slightly different and probing has not been successful. We therefore limit our description to the right side. In the floor of the antorbital invagination is a foramen that enters a tube issuing through a single opening lateral to the olfactory foramen. This is a branch of the profundus as noted above from *H.* (*Holodipterus*) *gogoensis* and for CPC25739. As in *H.* (*Holodipterus*) *gogoensis* a foramen opens into the nasal capsule mesially and runs forwards as a shallow groove along the internasal septum. This foramen, which probably transmitted another branch of the profundus nerve, is obscured by the internasal septum on figure 41*a*. A canal for the maxillaris V_2 enters the antorbital wall ventral to the invagination and passes through it to open in the nasal capsule ventral or ventrolateral to the profundus foramen (figure 41*b*). In the posterior wall of the nasal capsule ventromesial to the profundus and maxillaris foramina is another one which, from its orientation, probably carried a branch of the palatinus VII (figure 41*b*).

In comparison with the adjacent foramina, the optic foramen is a relatively large opening which enters the vertical wall of the braincase with a slightly caudal orientation (figures 44–46*a*,*b*).

The foramen sphenoticum majus is a large compound depression (figures 45*a*,*c* and 46*a*). In the holotype two large foramina pass mesially and anteriorly from the depth of this cavity into bone-walled tubes which join the thin perichondrium lining the braincase. The tube joining the more dorsal of these two foramina attaches to the inner perichondrium dorsal to and slightly posterior of the point of junction with its companion with the perichondrium. The more dorsal of these tubes is joined by a second bone-walled tube a short distance lateral to its junction with the inner perichondrium. This second tube comes from a position more posteriorly and ventrally within the cranium. On the left it is more-or-less intact and it passes below the level of the horizontal canal into the sacculus. We interpret the dorsal tube, and the tube which joins it, as conduits for branches of nerve VII and nerve VIII respectively (Kesteven 1945, figure 2; Northcutt 1987, figure 3). The ventral tube connecting the foramen sphenoticum majus to the perichondrium lining the braincase we interpret (following Miles 1977, figure 47) as the passage that carried branches V_2 and V_3 of the trigeminal nerve (figure 45*c*).

The foramen sphenoticum minus (figures 45*a*,*c* and 46*a*) is a large depression located at the vertex formed

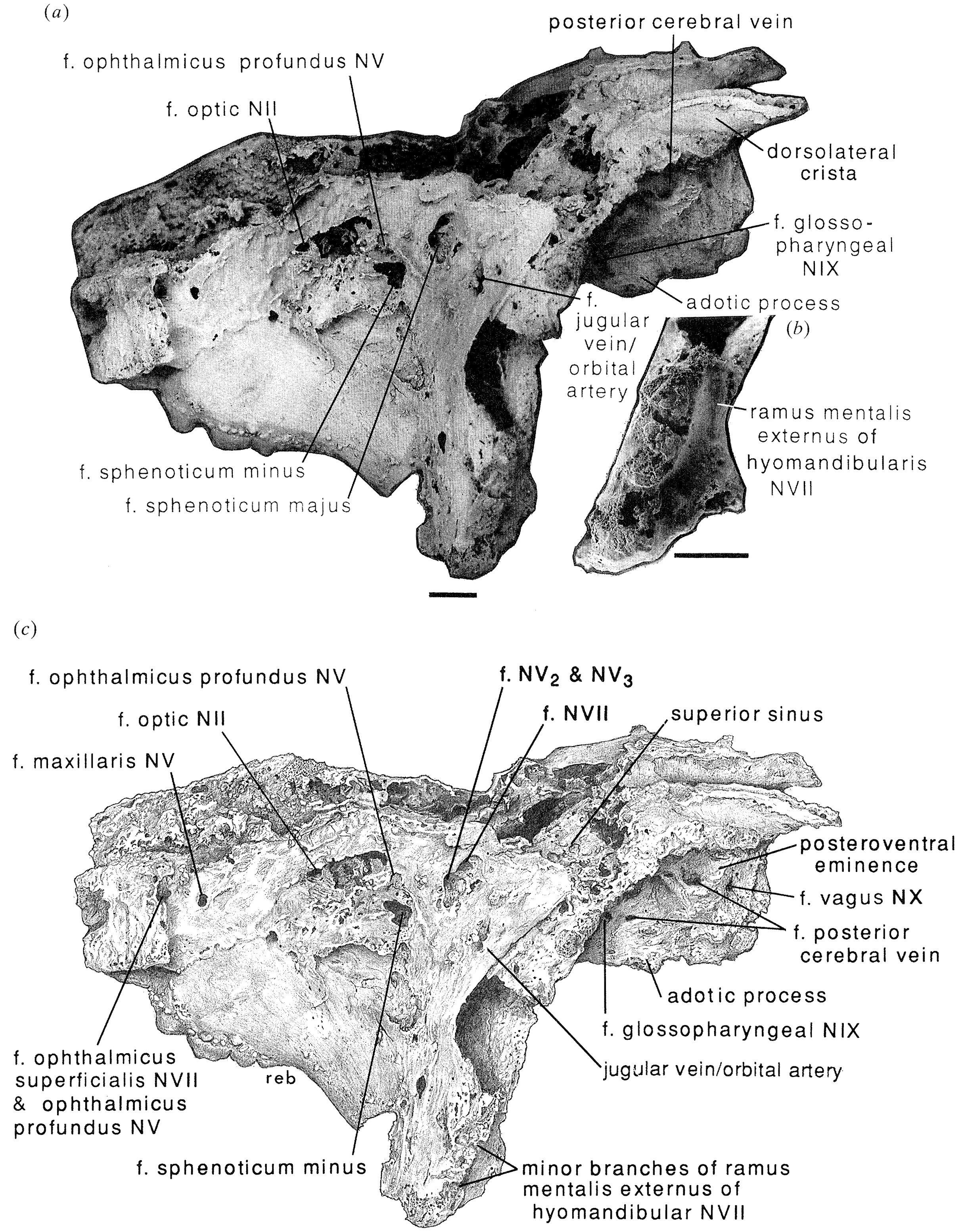


Figure 45. *H.* (*Holodipteroides*) *elderae*. (*a*) Dorsolateral view of the holotype. (*b*) Enlargement of the quadrate region of same. (*c*) Drawing of (*a*) to emphasize detail not shown by the photograph, particularly in the occipital region. Scale bars = 10 mm.

by the conjunction of the vertical wall of the braincase, the lateral wing of the neurocranium, and the almost horizontal portion of the neurocranium that overlies the palate. It penetrates the neurocranial wall as a single very large and high-arched foramen with a posterior and slightly lateral orientation. Due to its position and orientation it is impossible to trace the tube opening through this foramen posteriorly in specimens which include much of the ethmoidal portion of the neurocranium, e.g. the holotype and WAM 86.9.649. However, in CPC30828 which is lacking all of the anterior and much of the rest of the neurocranium, the right foramen sphenoticum minus, although partly obscured, is amenable to investiga-

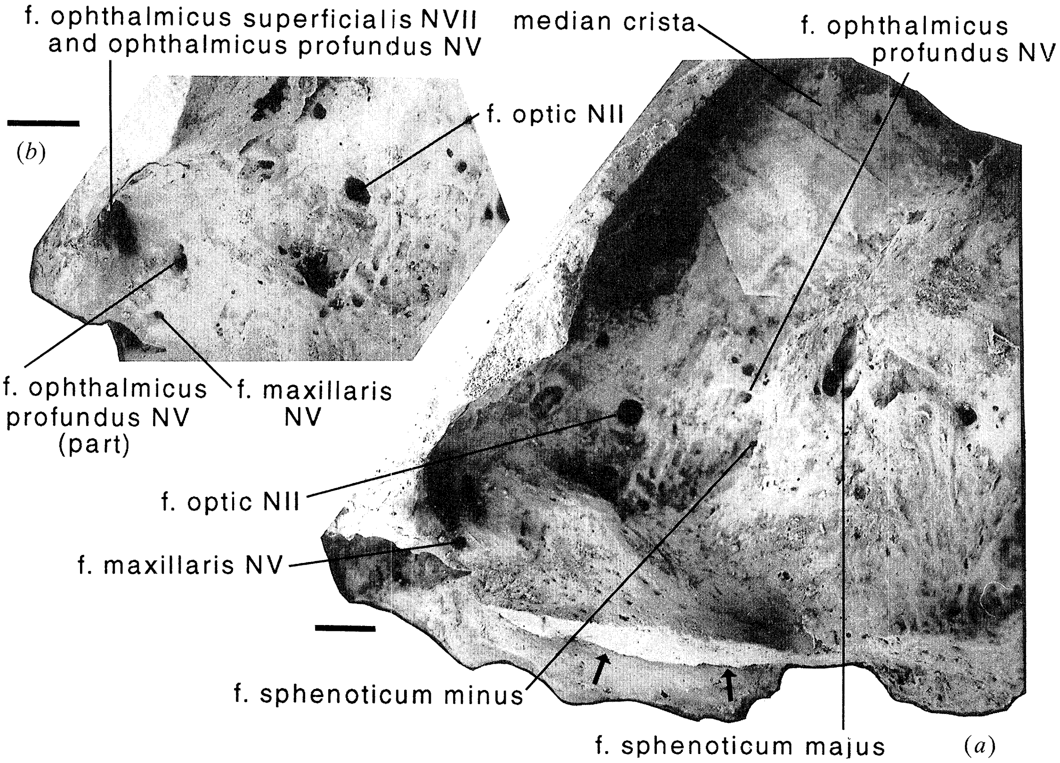


Figure 46. *H.* (*Holodipteroides*) *elderae*. (*a*) Lateral view of WAM86.9.949 showing the fracture (arrowed) within the pterygoid resulting from weathering. The external surface of the snout is covered with plastic used to consolidate the specimen before preparation. (*b*) Posterolateral view into antorbital wall showing foramina. Scale bars = 10 mm.

tion. This specimen reveals that the foramen sphenoticum minus is continuous via the cavum epiptericum with a foramen located on the posterior surface of the lateral wing of the neurocranium. This posterior foramen is the one we identify below as the foramen jugulare. Accordingly we interpret the foramen sphenotium minus as including a passage for a major branch of the jugular vein.

Immediately dorsal to the foramen sphenoticum minus and located on a line joining the optic foramen and the foramen sphenoticum majus, is an intermediate-sized foramen which enters the braincase with a posterodorsal and slightly mesial orientation (figure 45*a*,*c*). In the holotype this foramen opens into a posterodorsally and slightly mesially oriented tube which joins the inner perichondrium of the braincase anterior to the foramina of the foramen sphenoticum minus. We interpret this as the foramen that transmitted the ramus ophthalmicus profundus V_1.

Lateral to (and slightly caudal of) the foramen sphenoticus majus is a large foramen which penetrates the anterior surface of the lateral wing of the neurocranium with a caudal and slightly lateral and ventral alignment (figure 45*a*,*c*). On the left side of the holotype this foramen is obviously double, whereas on the right it appears single. In WAM86.9.649 both of these foramina appear double. As in *H. gogoensis* (see above) this foramen is joined by a bony tube to paired foramina located on the posterior surface of the lateral wing of the neurocranium. We consider that this anterior foramen transmitted both the orbital artery and a branch of the jugular vein.

Proceeding to a discussion of the temporal and occipital areas, we note that as is usual for Devonian dipnoans, the quadrate is completely fused to the neurocranium. Undoubtedly the bony tissue lying immediately dorsal to the posterolateral process of the pterygoid (Arratia & Schultze 1991, p. 27) constitutes part of the quadrate of *H.* (*Holodipteroides*). However, mesial and dorsal edges of the quadrate are not defined.

The dorsal surface of the posterior neurocranium bears paired lateral and dorsolateral cristae (figures 43 and 45*a*) and a single median crista which is completely broken away in the holotype, but well preserved in WAM86.9.649 (figure 46). As in *H.* (*Holodipterus*) *gogoensis* there are no adlateral cristae. In the shapes of the posterior termination of the median crista, the lateral wings of neurocranium, and the slightly diverging dorsolateral cristae, this species is similar to *H.* (*Holodipterus*) *gogoensis*.

The lateral walls of the occipital part of the neurocranium bear two pairs of processes. Ventral to the lateral crista on each side is the posteroventral eminence of Miles (1977) (see figures 45*c* and 48*a*,*b*). Ventral and anterior to this on each side is an approximately horizontally aligned adotic process (figures 45*a*,*c* and 47*a*). In the holotype these processes are very prominent. Indeed a comparison of the processes in this specimen with those in ANU49102, the specimen of *H.* (*Holodipterus*) *gogoensis* in which they are best displayed, suggests that they were considerably better developed in *H.* (*Holodipteroides*) *elderae*.

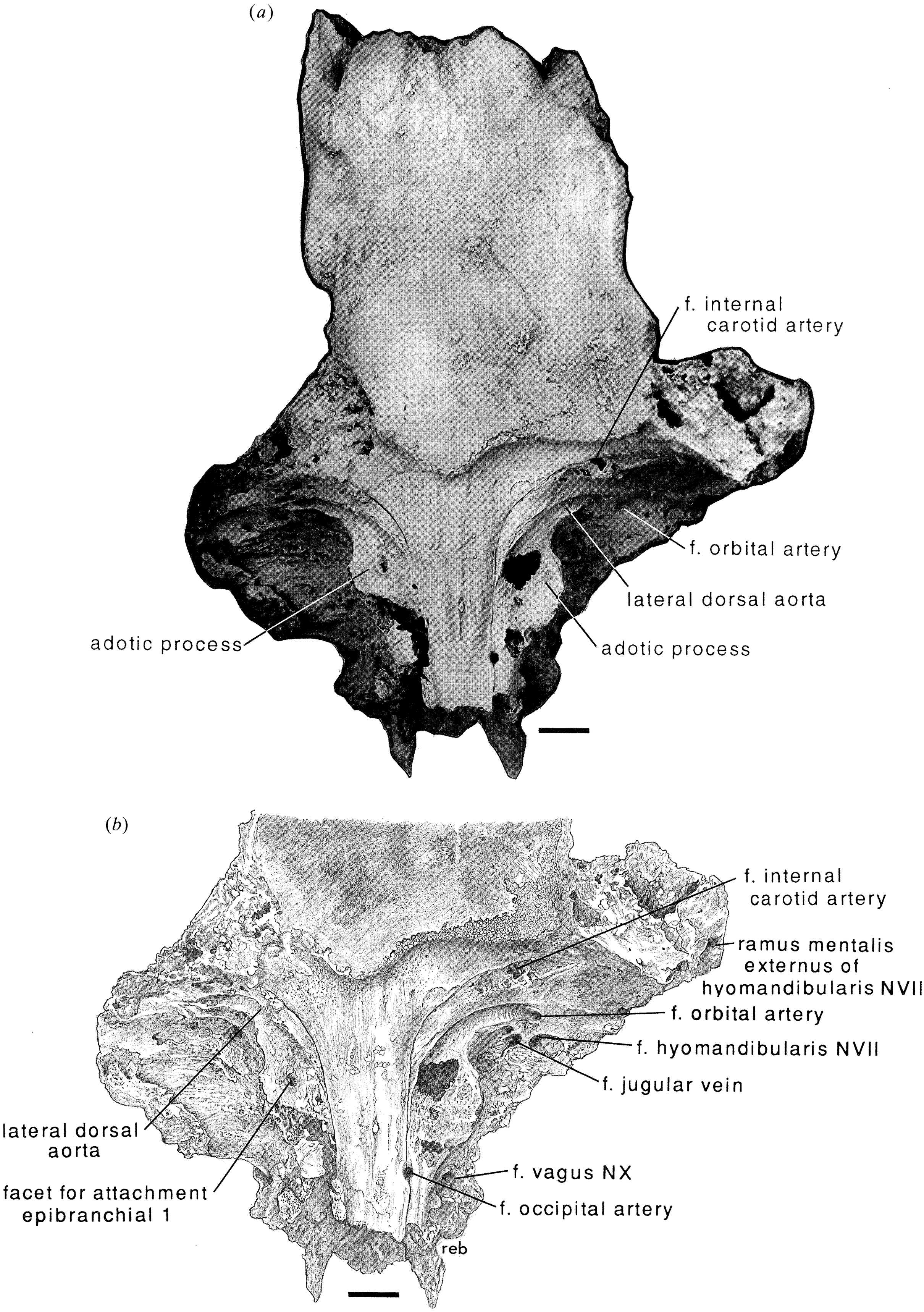


Figure 47. *H.* (*Holodipteroides*) *elderae*. (*a*) Ventral view of the holotype. (*b*) Drawing of posterior of same. Scale bars = 10 mm.

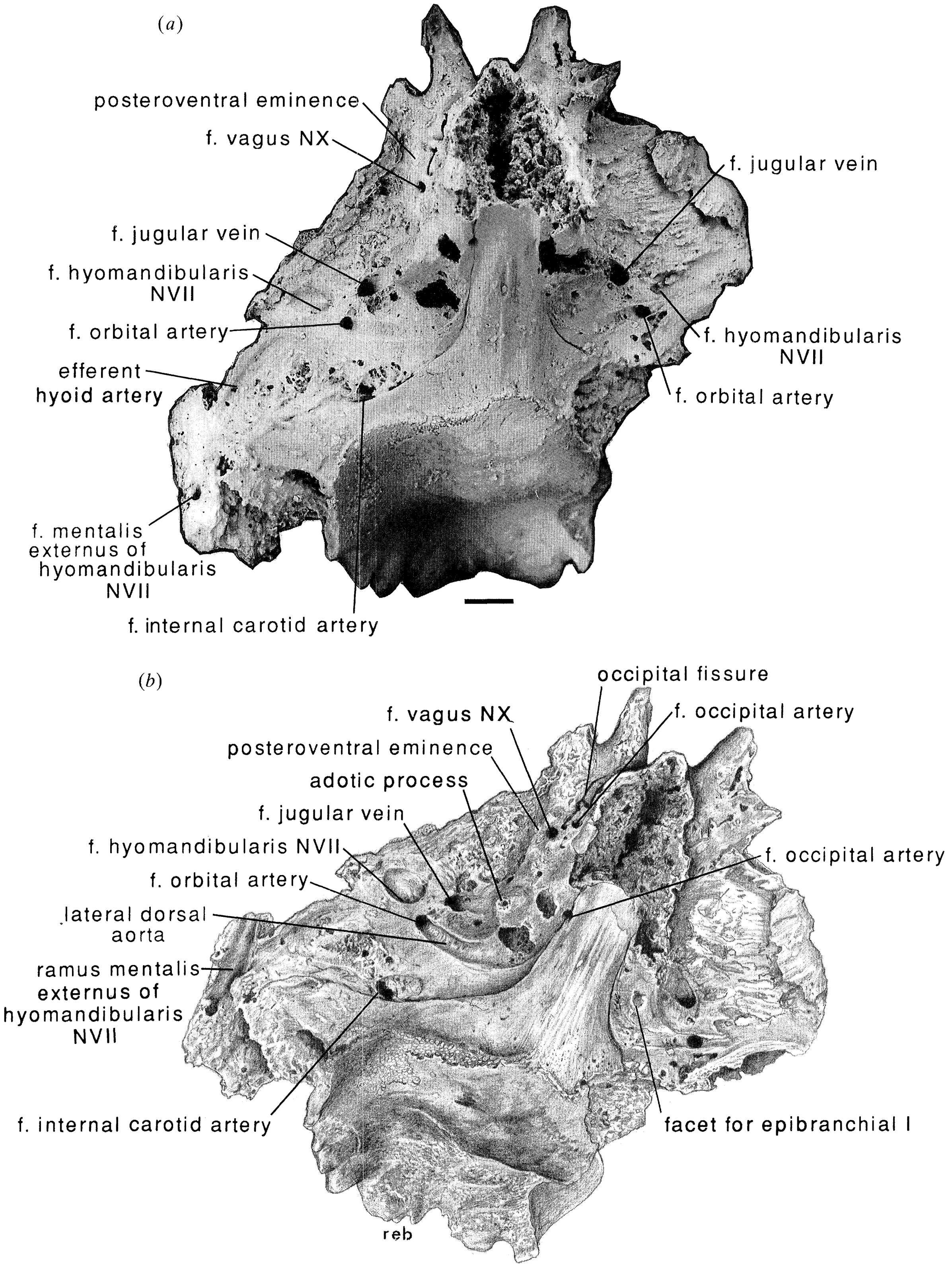


Figure 48. *H.* (*Holodipteroides*) *elderae*. (*a*) Posteroventral view of holotype, ANU49101. (*b*) Drawing of same. Scale bar = 10 mm.

As in *H.* (*Holodipterus*) *gogoensis* six major foramina or groups of foramina can be recognized on the posterior surface of the broad plate of bone making up of the lateral wing of the neurocranium and the quadrate (figures 44 and 48*a,b*). A large foramen on the posterior face of the ventral extremity of the quadrate connects by a short anteroventrally directed canal to a foramen located on the anterior face of the ventral extremity of that bone. This carried the major branch of the ramus mentalis externus of the hyomandibularis VII, the course of which can be traced down the posterior edge of the lateral margin of the quadrate as a broad vertical groove (figures 45b and 48*a*,*b*). Merging into this well-developed near vertical groove along its anterior margin are two much smaller horizontal grooves which run across the outer face of the quadrate 1.0 and 2.5 cm above the quadrate articulation (figure 45*b*,*c*). These open on to the anterior surface of the quadrate, and presumably carried minor branches of the same nerve.

In addition to these small anteriorly directed grooves the large main groove is approached by a third groove of intermediate size about 2.75 cm above the quadrate articulation. This intermediate groove which is less deeply incised than the others, runs from a mesial location outwards and increasingly downward in a smooth curve paralleling the margin of the lower facet for the articulation of the hyomandibular (figure 48*a*). In *H.* (*Holodipterus*) *gogoensis* the deeper groove in this position passes ventrally off the bone behind the articulation. The situation in *H.* (*Holodipteroides*) *elderae* is less clear but it is evidently the same. We interpret this separate groove as the passage for the efferent hyoid artery.

Three foramina make up a group on the mesial part of the posterior face of the lateral wing of the neurocranium. They are all large and essentially equal in diameter (figures 44 and 48*a*,*b*) and are arranged as in *H.* (*Holodipterus*) *gogoensis*. They are well exposed on the holotype, CPC30828 and CPC25739. On the last specimen they are totally exposed by fracture. Posteriorly each of these three foramina is continuous with one or more rounded grooves excavated into the posterior surface of the neurocranial wing.

The single groove extending from the most ventral foramen is especially well developed. It passes from this foramen mesially, ventrally and increasingly posteriorly in a smooth curve. The groove can be traced back along the neurocranial surface below and mesial to the adotic process and close to the lateral margin of the parasphenoid. As it passes backwards along the side of the stalk of the parasphenoid, the groove becomes increasingly shallow and ultimately indiscernible (figures 47*a*,*b* and 48*b*). We interpret this groove as marking part of the course followed by the lateral dorsal aorta which, having branched from the internal carotid artery, passed directly through the lateral wing as the orbital artery into the orbital chamber via a large foramen.

On the posterior surface the most mesial of the three foramina is confluent with two grooves, one from the mesial and the other from the lateral side. The mesial one is obvious and is a broad, relatively short groove which in the holotype passes posteriorly and slightly mesially along the side wall of the neurocranium some 7 to 12 mm above the anterior part of the adotic process, towards the foramen for nerve IX (see below). The lateral groove is much narrower, and not as well developed as in *H.* (*Holodipterus*) *gogoensis*. It passes almost directly laterally out of the mesial foramen over the posterior surface of the lateral wing towards the hyomandibular articulation. Before reaching this articulation it gives rise to a dorsal branch that turns through the bone to emerge at two foramina near the broken edge of the posterolateral margin of the commissure. In the holotype the connection of this small groove to the foramen is readily demonstrated with a probe, despite being almost completely obscured in posterior view by a broad thin plate of bone which lies at the lateral margin of the foramen (figures 47*b* and 48*a*,*b*). We interpret the mesial foramen as the point of exit of the jugular vein from the lateral wall of the neurocranium. The larger groove marks the further posteriorward path of this vein and the smaller branching lateral groove carried venules contributing to the jugular. As is well shown on CPC25739, the canal for the jugular splits within the neurocranial wall, one branch passing forwards to open with the orbital artery into the orbital chamber and the other passing along the cavum epiptericum to open through the foramen sphenoticum minus. The most lateral foramen of the three is continuous laterally with a broad shallow groove which passes distally over the posterior surface of the lateral wing of the neurocranium. We interpret this third foramen as carrying the hyomandibularis branch of nerve VII, and the large groove laterally continuous with it as the path taken by this nerve prior to its passage through the hyomandibular and its turning down along the lateral margin of the quadrate.

Ventral to this group of three foramina and located at the point of conjunction of the neurocranium, the pterygoids, and the parasphenoid is a large mesially and slightly anteriorly directed foramen. This foramen, which is clearly evident on the left side of both the holotype (figures 47*a*,*b* and 48*a*,*b*) and WAM86.9.649, occupies essentially the same position in all known Devonian dipnoans and is generally accepted to have transmitted the internal carotid artery. In CPC25739 in which the parasphenoid and pterygoids are separated from the neurocranium, the bony tube which is continuous with this foramen can be traced forward adjacent to the margin of the parasphenoid on each side.

On the left side of the holotype, above and anterior to the adotic process, is a group of four foramina, the anterior three being confluent and the fourth isolated behind. The most posterior of the group of three is of medium size, and the others smaller. On the right side of the specimen (figure 44), a single foramen occupies a similar position. In the holotype and WAM86.6.649, probing shows that the large external opening on each side passes into a tube that emerges at the back of the sacculus in the equivalent position to the internal opening for nerve IX in *Chirodipterus australis* (Miles 1977, figure 48; and personal observation). Thus all the evidence indicates that the large foramen in question carried nerve IX. By implication we consider that the smaller ones carried branches of that nerve.

In the holotype the group of three foramina located immediately anterior to the posteroventral eminence consists of one large and two smaller more dorsal foramina (figure 44). The large foramen is directed anteromesially, and can be shown to be continuous with a bony-walled tube extending into the bottom of the superior sinus of the otic cavity. The two smaller foramina of this group are also directed mesially and anteriorly. Their connections to the interior of the neurocranium are unknown. We accept the view of Miles that these foramina carried branches of the posterior cerebral vein.

Posterior to the posteroventral eminence is a cluster of foramina that vary considerably in size, the smallest being so fine that their exact number is difficult to determine. However, at least twelve seem to be present. On the right (figure 44), the largest and most anterior opening, which contains two confluent foramina, is at the ventral end of the lateral occipital fissure. The more posterior of these two of these joined foramina and another posteromedial to it, join within the bone, and pass mesially and then ventrally through a tube lateral to the notochordal chamber to emerge at the large foramen on the flank of the parasphenoid. These were for the occipital artery. It seems likely that several of the other foramina in this region also transmitted branches of this artery. The more anterior of the above-mentioned pair was for nerve X. On the left (figure 48*b*) a single large foramen for nerve X lies anterior and ventral to the end of the occipital fissure. Another large foramen for the occipital artery lies in a furrow 5–6 mm posteromesial to the foramen for nerve X.

On both sides, three smaller foramina lie on the lateral occipital fissure (figures 44 and 48). The largest of these probably transmitted other branches of nerve X or spino-occipital nerves.

The structure of the inner ear can be examined only in the holotype and WAM86.9.649. In the former (figure 43) the dorsal surface of the neurocranium is missing from the area anterior to the pores for the endolymphatic ducts, and although the semicircular canals and sacculus are incomplete, they are sufficiently preserved to allow us to outline their structure with considerable confidence. In WAM86.9.649 the inner and ventral walls of the sacculus are visible ventrally.

On the left of the holotype the horizontal (external) semicircular canal is largely intact (figure 43). The common point of attachment of the two vertical canals to the superior sinus of the sacculus is preserved on this side, as is much of the ampullary swelling of each of these two canals. On the right, less of the horizontal semicircular canal is present and what is preserved is partly obscured by neurocranial roof. However, the connections of this canal to the sacculus are present and the posterior portion of the posterior vertical semicircular canal is preserved to a considerable extent.

The outside dimensions of the horizontal semicircular canals are estimated to be *ca.* 2 cm longitudinally and *ca.* 2.2 cm transversely. The canal itself decreases in diameter laterally from 3 to 2 mm. The size of the anterior ampulla is proportionately as in other Gogo dipnoans. The portion of the canal common to the horizontal and posterior vertical canals is stout with a minimum outside diameter of *ca.* 7 mm. The posterior vertical is missing on the left and half preserved on the right where it is narrow (2 mm). Nothing remains of the anterior vertical canal other than its attachment to the other canals. The recessus utriculi is represented by a portion of roof on the left and a portion of anterolateral wall on the right. The utriculus is not clearly differentiated from the sacculus, but it seems to be more ventrally positioned with respect to the sacculus than in either *G. whitei* or *C. australis*.

The posterior margin of the sacculus seems to have lain at about the level of the junction between the posterior vertical and the horizontal semicircular canal and its anterior margin at least 3 mm forward of the anterior surface of the ampulla of the anterior vertical semicircular canal. The lateral wall of the sacculus extends laterally on a level with the middle of the ampulla of the anterior vertical semicircular canal.

The dorsal portions of the superior sinus and the superior otic cavity are completely missing. Ventral remnants of the former (figure 43) show that it lay antero-posteriorly at about the level of the middle of the horizontal semi-circular canal, and that its length was *ca.* 7 mm, which is about a third that of the horizontal semicircular canal.

In the holotype the pore for the endolymphatic duct is intact on the right side (figure 43). It apparently opened a little behind the posterior dorsal section of the superior sinus, and thus occupied a similar position to that in *Chirodipterus*, but one further forward than in *Griphognathus*. From the pore the endolymphatic duct runs antero-ventrally and mesially so that it approaches the midline. This suggests the presence of a common sac for the two sides. In WAM86.6.649 the endolymphatic pores, located in the base of the masseter chamber, are well preserved. They lie posterior to the extremity of the median crista, being similar in this respect to *H.* (*Holodipterus*) *gogoensis* (Miles 1977, figure 39).

A bone-bound duct ventrally contacts the anterior of the endolymphatic duct. This duct can be traced backwards curving around the posterior semi-circular canal where it appears to be joined by a series of smaller bone-walled canals. This canal is located in essentially the same position as in *Chirodipterus australis* (Miles 1977, figure 48); it may have carried the posterior cerebral vein, although it is difficult to verify this in so far as the posterior distribution of the smaller canals cannot be traced.

In general shape the palate of *H.* (*Holodipteroides*) *elderae* (figures 47*a*, 48*a* and 49*b*) is similar to that of H. *gogoensis*. It is broadly triangular anteriorly, shows a mildly waisted area (for the passage of the adductores mandibulae) with approximately parallel lateral margins immediately behind this, then expands laterally to its greatest breadth at the level of the quadrate rami.

Measurements (defined in the Appendix and figure 101) have been made on the palates of the available specimens of *H.* (*Holodipterus*) *gogoensis*, *H.* (*Holodipterus*) *longi*, *H.* (*Holodipteroides*) *elderae*, and *H.* (*Asthenorhynchus*) *meemannae* in an endeavour to clarify the differences between the three taxa. These data are presented in table 1. All measurements have some scatter, but we have found no palatal dimension that would enable us to discriminate the taxa.

The sectioned palate of CPC25739 provides interesting information on the thickness and internal structure of the pterygoids. These sections (Campbell & Smith 1987, figure 19) clearly show that the pterygoids thicken marginally but that immediately lateral to the sagittal dorsal ridge they are quite thin. Microscopic examination reveals that the dorsal and ventral surfaces of the pterygoids are composed of dense bone and that more open bone lies between the two.

In WAM86.9.649, which was collected in a weathered state, the pterygoids are eroded marginally and have split along the intermediate layer of open bone, behind the level of the antorbital wall and in front of the lateral commissure (arrows in figure 46*a*). Evidently water was able to penetrate the intermediate layer causing separation of the two outer, denser layers. A superficial examination of this specimen could lead to the conclusion that a separate palatoquadrate was present above the dentine-bearing pterygoid. Other better preserved specimens in which the pterygoidal margins are intact do not show this separation.

As in *H.* (*Holodipterus*) *gogoensis* the most obvious features of the dorsal surface of the palate of *H.* (*Holodipteroides*) are three raised ridges (figure 49*a*). All these ridges are completely obscured by the neurocranium in the holotype and in WAM86.9.649. However, in CPC30828 the posterior third of the sagittal ridge and much of the left oblique ridge can be seen. The sagittal ridge can be examined virtually in its entirety in the embedded and partly sectioned anterior palate of CPC25739 (Campbell & Smith 1987, figure 19). Natural and cut sections of the quadrate rami show them to be formed of a poorly ossified bony framework unlike the more densely ossified and lamellar bone of the more anterior parts of the pterygoids.

In comparison with *H.* (*Holodipterus*) *gogoensis* and *H.* (*Holodipterus*) *longi* the sagittal ridge and the quadrate rami in *H.* (*Holodipteroides*) are lower relative to the immediately adjacent dorsal surface of the palate.

In addition to these three pronounced ridges the dorsal surface of the palate bears two pairs of less obvious ridges on the pterygoids (arrows, figure 49*a*). The more posterior of these low ridges runs from below the optic nerve foramen posterolaterally towards the quadrate articulation. The anterior low ridge, which seems to mark the contact of the neurocranium with the palate, passes from below the optic nerve foramen anteriorly and slightly laterally. The angle between the anterior and posterior ridges is *ca.* 110–120°, whereas in the various species of *H.* (*Holodipterus*) and *H.* (*Asthenorhynchus*) it is 135° or greater.

The buccal surface of the palate is concave in all the available material, but the extent of this varies from specimen to specimen. The most extremely concave palate is that of the holotype (figures 41*a*, 44 and 48*a*). In this feature the range of variation is similar to that of *H.* (*Holodipterus*) *gogoensis*. Anterolaterally the buccal surface bears a series of broad radiating ridges. In WAM86.9.949 (figure 50) and CPC25739 a medial ridge extends backwards from near the anterior margin of the palate. Such a medial ridge is also present on some specimens of *H.* (*Holodipterus*) *gogoensis*. Around the lateral margins, from close to the midline to the adductor waisting, are three or four low, rounded, radial ridges. In general the more anterior of these flanking ridges are longer and broader than those located further back. Each ridge increases in breadth and depth anterolaterally. Large numbers of dark-coloured hypermineralized dentine units occur in these ridges, and less obviously in the valleys between them (figures 49*c* and 50). The interstices between the dark units are filled with white superficial dentine. This also occurs as a thick layer in some of the valleys.

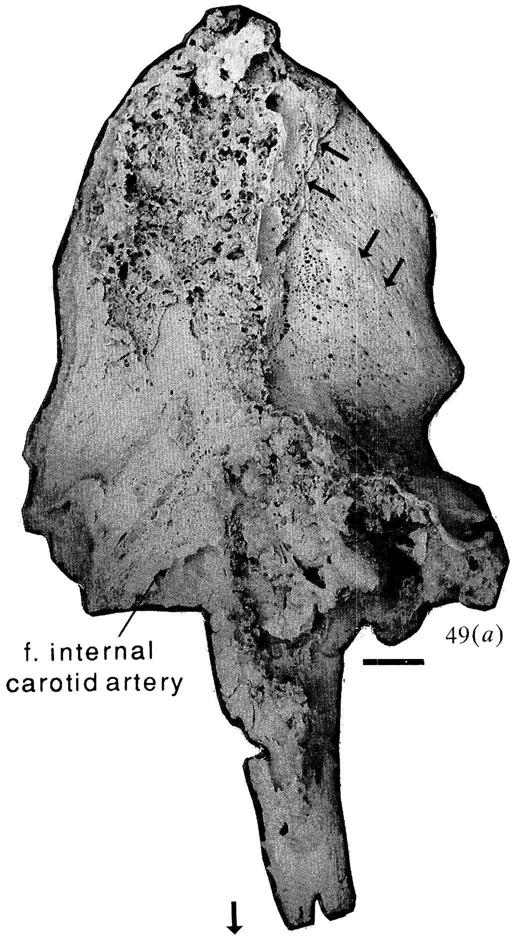
Posteromedially on the buccal surface is a large dark callus. This straddles the midline at about the level of the waisting for the adductores mandibulae, and sits proud of the surrounding buccal surface. The apex of the callosity is composed of a continuous mass of polished hypermineralized dentine (figure 50), and protrudes above the rest of the callus. The anterior surface of the callus slopes gently and displays two to four raised concentric bands representing the limits of successive resorption phases. The furrows separating the raised bands contain white superficial dentine. Unlike the similarly placed surface of *H.* (*Holodipterus*) *gogoensis*, the callus does not show anterolateral radial ridges. Anteriorly and posteriorly the callus is composed of discrete units of hypermineralized dentine set in less mineralized dentine.

Much of the surface of the buccal palate anterior and lateral to the callus also bears dark dentine units. These are less densely distributed than on the callus, and the interstices are filled by white superficial dentine (figures 49*c* and 50).

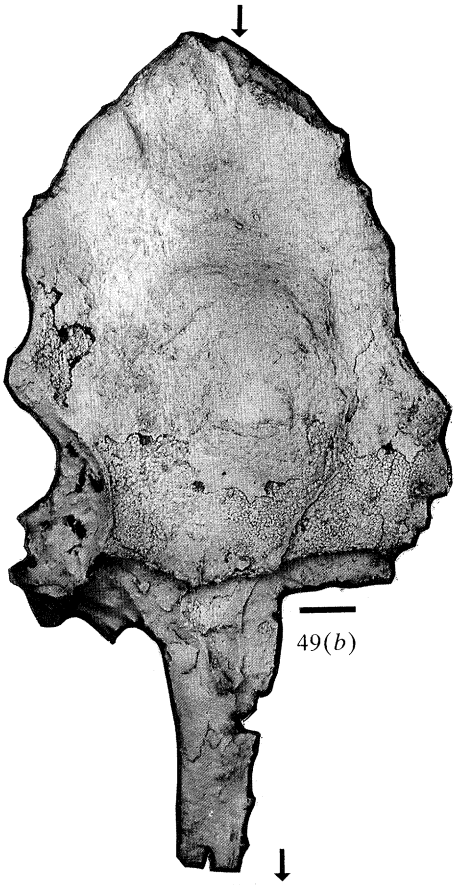
In a sub-rectangular area making up the posterior portion of the callus, dark dentine units stand proud of the surrounding white superficial dentine. The smallest of these units occur at a distance from the callus, but they show incomplete size-grading, some small ones lying between larger ones farther in. The areas of buccal palate lateral and posterior to the callus are covered with superficial shedding denticles and patches of continuous white superficial dentine.

As in *H.* (*Holodipterus*) *gogoensis* the anterolateral edges of the pterygoids carry a series of marginal denticles (figures 51*a*,*b* and 52*a*,*b*). These denticles are considerably larger than any superficial buccal dentine units or superficial denticles. They are always light-coloured, although they may have cores of dark dentine. Individually they are more-or-less conical in shape, have a rounded apex and smooth surface. They lie on the bone of the palate dorsal and slightly lateral to the margins of the palatal ridges and form a band which terminates on each side slightly posterior to the hindmost ridges. Within this band the denticles appear to be arranged in indefinite lines. Up to three lines of denticles are evident locally within the band.

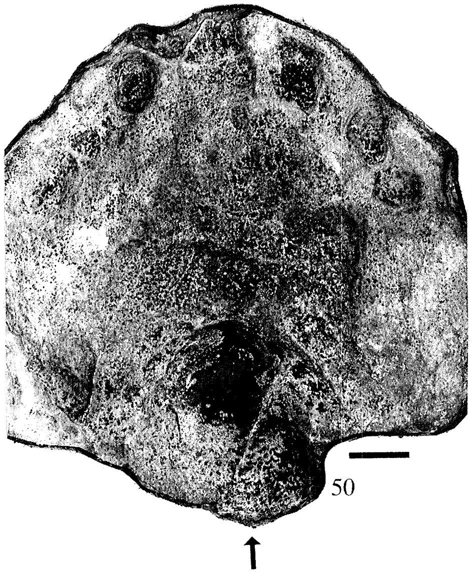
The pattern of distribution of hypermineralized units and white superficial dentine over the buccal palate reflects the history of deposition and resorption across this surface. Successive resorptive phases apparently reached progressively less further in towards the callosity. By themselves, the available



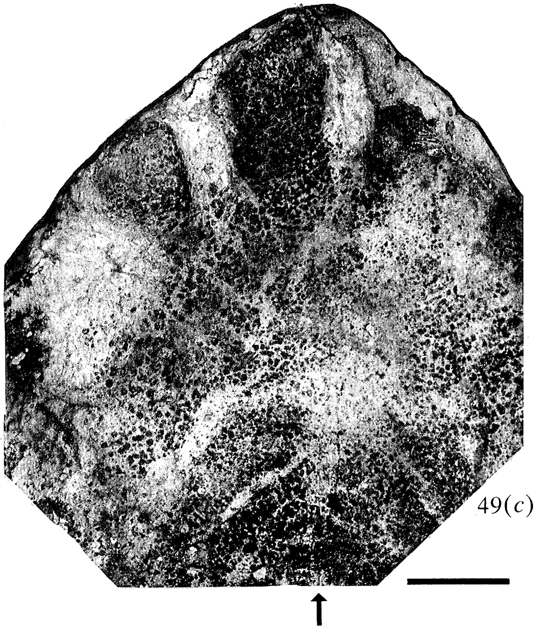
49(*a*)



49(*b*)



50

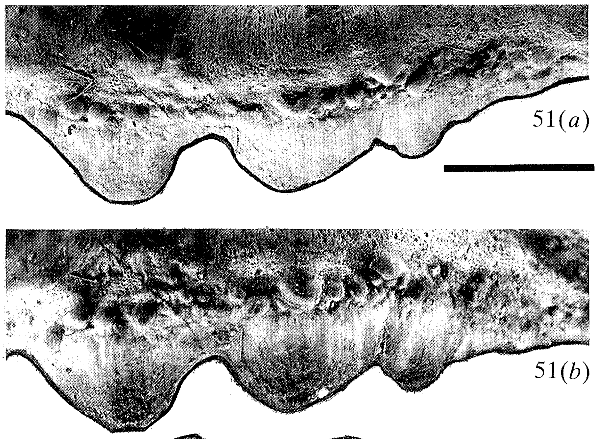


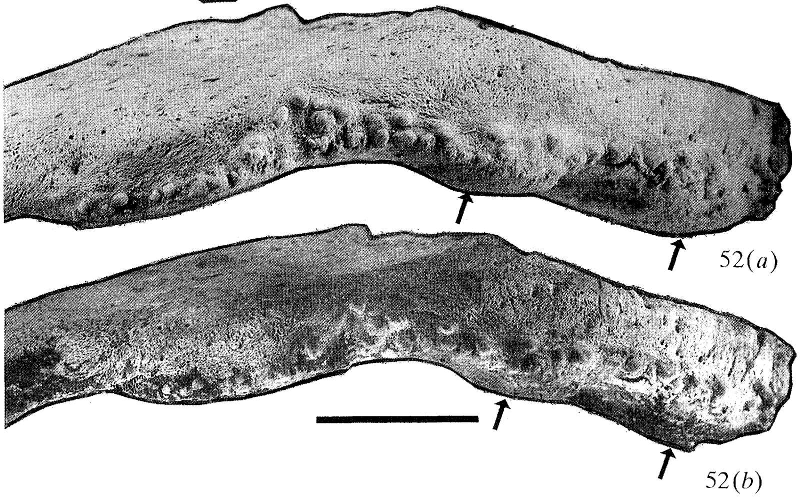
49(*c*)

Figures 49 and 50. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

Figure 49. Palate of CPC30828 in (*a*) dorsal, and (*b*) ventral view. An enlargement of the anterior portion of the ventral palate which has not been whitened with NH_4Cl is shown in (*c*). Arrows in (*a*) indicate minor ridges on the dorsal surface of the pterygoids. Arrows in (*b*) and (*c*) indicate the midline. Note that most of the palatal surface has numerous columns of black hypermineralized dentine which are most closely spaced on the radial ridges and the callus. Between these dark elements are white areas of superficial dentine.

Figure 50. Ventral view of the anterior palate of WAM86.9.949. Note the polished anterior surface of the callus. Arrows indicate the midline. The specimen is not whitened with NH_4Cl.





Figures 51 and 52. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

Figure 51. (*a,b*) Lateral views of the left side of the palate of the holotype, ANU49101, showing marginal denticles and enamel-covered ends of the palatal ridges. In (*a*) the specimen is whitened; in (*b*) unwhitened.

Figure 52. (*a,b*) Lateral views of right side of the palate of CPC30838 showing marginal denticles. In (*a*) the specimen is whitened; in (*b*) unwhitened. Arrows indicate the ends of palatal ridges.

specimens do not provide enough information to elucidate the pattern of change that took place across the buccal surface of the palate in *H.* (*Holodipteroides*) *elderae*. However, what is known is consistent with the pattern of deposition and resorption of *H. gogoensis* (Campbell & Smith 1987).

Marginal growth of the palate appears to have been a cyclic phenomenon. The marginal denticles which lie on the supporting bone of the palate immediately dorsal to the zone of contact of this bone with the dentine surface, were overgrown by the lateral advance of this bone. Such overgrowth is clearly evident in a thin section of CPC25739 (Campbell & Smith 1987, figure 19E). Apparently at the same time as this occurred the radial ridges and adjoining valleys were marginally expanded by the lateral addition of dentine.

During the later part of depositional phases, white dentine was deposited over the light coloured denticles and the dark units of hypermineralized dentine. During resorptive phases this material was completely removed along with any underlying denticles. The latter were replaced early in the next depositional phase by a new generation of well-formed denticles whose margins were often crenulated.

Although the material available is too limited to allow us to determine the details of the processes involved in the lateral addition of dentine to the palatal ridges, comparison between the ends of the ridges in CPC30828 (figure 52*a,b*) and ANU49101 (figure 51*a,b*) provides important clues. In the former these ends are simply undulations on the basal bone and the dentine, with an armour of marginal denticles. In ANU49101 they are thicker and each of the ridges 2–4 terminates in a vertically fluted layer of enamel. These enamel surfaces show no sign of turning inwards to surround the dentine forming the end of the ridge, nor can we detect buried enamel within the ridge at points where it ought to be if subconical teeth had been present. Marginal denticles cover the surface dorsal to the enamel. We interpret this to mean that the radial ridges were based on folds in the basal bone and that they were extended laterally, first by the deposition of pallial dentine under a layer of enamel and then by the growth beneath the pallial dentine of trabecular dentine, which firmly anchored the new structure to the end of the ridge. Within this trabecular dentine, pleromic growth of hypermineralized dentine then took place. Finally, new marginal denticles grew along the edge of the exposed bone and marked the beginning of a resting phase. A new growth phase began by the lateral growth of bone over the marginal denticles, followed by the formation of new denticles on the new bone. Accompanying this, resorption of the end enamel from the ridges took place, followed by the lateral growth of the bony ridge and deposition of a new layer of enamel backed by pallial dentine. As described above, pleromic growth then occurred.

We regard these ridges as homologous with the tooth-bearing ridges that occupy equivalent positions on the palate of *H.* (*Holodipterus*) *gogoensis*. However, we believe it important to distinguish the enamel-surfaced cones of this latter species from the dentine slabs of *H.* (*Holodipteroides*) *elderae* which have enamel only on their outer sides. These latter do not conform with any definition of teeth of which we are aware. Accordingly we regard it as inappropriate to refer to the structures making up the ends of the ridges in *H.* (*Holodipteroides*) *elderae* as teeth. We are unable to determine which of these two conditions is primitive, but, given the fact that real teeth are present in *H.* (*Asthenorhynchus*) as well as in *H.* (*Holodipterus*), we tentatively suggest that true teeth are more likely to fulfil this role.

In *H.* (*Holodipterus*) *gogoensis* Miles (1977, figures 4b, 88 and 89) has figured a number of isolated plates that he refers to as palatal tooth-plates, or possible dermopalatines. In the holotype of *H.* (*Holodipteroides*) *elderae* we have found one flat slightly arcuate plate (figure 54*a–c*) carrying denticles and some white superficial dentine which is possibly a dermopalatine, in addition to two other types. One of these is smaller with somewhat enlarged denticles (figure 63*a–c*), and the other type is flatter and carries denticles and white superficial dentine (figures 60, 61 and 64). Both of these could be palatal tooth-plates of the kind described by Miles. Unlike *H.* (*Holodipterus*) *gogoensis* no median plate has been found.

The parasphenoid is known from three of the four specimens referred to *H.* (*Holodipteroides*) *elderae*. Anteriorly the bone consists of a short broad corpus. It continues posteriorly as a narrowing elongate caudal process or stalk which in the holotype (figure 47*a*) and CPC30828 (figure 49*a*,*b*) is relatively broader than the stalk of either *H.* (*Holodipterus*) *gogoensis* or *H.* (*Asthenorhynchus*) *meemannae*. The stalk is composed of thin dorsal and ventral layers separated by a space in which there are struts of supporting bone. The dorsal surface of the corpus is formed of a distinctive layer of bone which is applied to the top of the stalk as in *H.* (*Holodipterus*) *gogoensis*. The interior of the corpus is an open meshwork (Campbell & Smith 1987, figure 19A) of stout vertical columns of bone (figure 53). This pattern of struts gives the appearance of endochondral bone which is unlikely given that the parasphenoid is dermal. Moreover the strutted pattern continues laterally into the interior of the quadrate rami of the pterygoids. This matter will be given further treatment in a subsequent paper.

Whereas the boundary between the stalk of the parasphenoid and the neurocranium is clear, that between the parasphenoid and the pterygoids is not, because all three elements are strongly fused. In specimen CPC30828 (figure 49*a*) there is a narrow zone of open vesicular bone on the dorsal surface of the palate immediately mesial to the left internal carotid foramen. We take this vesicular bone to indicate the area of contact of the parasphenoid and left pterygoid. This narrow zone of vesicular bone passes in a straight line forward and medially, but a little short of the midline it turns anteriorly. At the midline it is continuous with a zone of similar bone which runs forward along the mid-dorsal surface of the palate until obscured by an overlying portion of the neurocranium. We interpret this mid-dorsal zone of vesicular bone as indicating the position of the suture between the left and right pterygoids. Although the right suture is completely obscured by neurocranial bone in this specimen, the configuration of the left suture as it approaches the midline makes it clear that the anterior part of the parasphenoid corpus protruded acutely between the pterygoids.

The stalk of the parasphenoid is depressed and bears a pair of longitudinal ridges along its dorsal surface (figure 49*a*). These ridges, which are separated by a rounded groove, coalesce anteriorly and form a single broad median ridge on the corpus. The ventral surface is essentially flat in two of the specimens, and is smooth except for some fine but irregular longitudinal ridges and a few nutritive foramina. In the holotype (ANU49101) the anterior portion of the ventral surface of the stalk bears a broad low ridge medially (figure 47*a*,*b*). However, in other respects its ventral surface is in conformity with those of other specimens. Posteriorly the lateral margin is indented by the edge of the foramen for the occipital artery which passed dorsally through the neurocranium. In *H.* (*Holodipterus*) *gogoensis* this artery passed lateral to the suture between the stalk and the neurocranium, and on the flank of the neurocranium rather than through it.

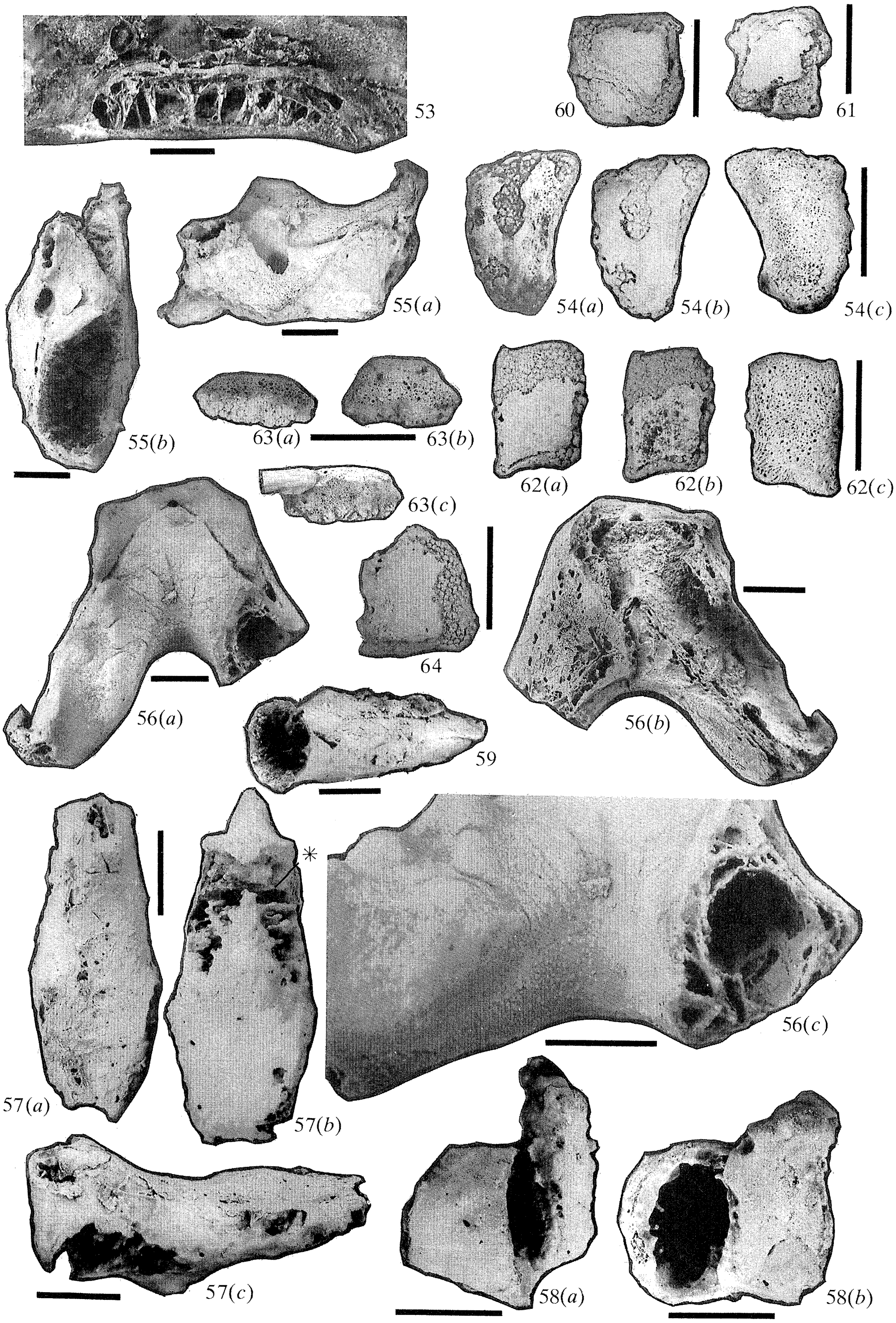
Although most of the ventral surface of the parasphenoid is naked in *H.* (*Holodipteroides*) *elderae*, it should be noted that, as in *H. gogoensis*, the corpus carries hypermineralized dentine units and white dentine of the same type as occurs on adjacent areas of the pterygoids and denticles posteriorly.

Only the posterior of one ramus of the mandible of *H.* (*Holodipteroides*) *elderae* is known with certainty (figure 55*a*,*b*). However, an isolated small specimen, WAM86.9.685, has features that indicate that it might be referred to this taxon (figure 56*a–c*).

The holotype includes the posterior third of a left ramus. In all features that are preserved, we cannot distinguish between this specimen and large specimens of *H.* (*Holodipterus*) *gogoensis*, although it is possible that the glenoid fossa is relatively broader. We add a couple of points of functional interest.

The anterior, lateral and posterior margins of the glenoid are indicated by finished edges on the articular. The mesial edge is not complete, but seems to have been formed by a thin edge of articular lying against the posterodorsal margin of the prearticular which has a finished edge. This suggests, in conjunction with the preserved margins, a single articular surface as in *H.* (*Holodipterus*) *gogoensis*, perhaps with a small mesial flattening as in that species. This is quite unlike the broadly doubled surface of *C. australis*. In lateral profile the fossa is open C-shaped, but not so deep as that of *G. whitei*. These points together suggest that movement of the jaw was primarily vertical and almost completely 'restricted' in the sense of Bemis (1987), although a little lateral movement would have been possible. Such an interpretation is consistent with the nature of the palatal surface on which the marginal ridges do not seem to have acted as stops to minor lateral movement.

Nothing remains of the articular surface of the glenoid fossa, most of the endochondral bone that lay immediately beneath it having been lost prior to or during preparation. Deep to the margins of the fossa there are irregular columns of endochondral bone (figure 55*b*). Miles (1977, p. 211) has conjectured that in life the surface of the glenoid fossa in *H.*



Figures 53–64. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

(*Holodipterus*) *gogoensis* was finished with a thick pad of cartilage. Such an arrangement probably occurred also in *H.* (*Holodipteroides*) *elderae*.

A small incomplete mandible (WAM 86.9.685) is tentatively assigned to this species. This specimen consists of much of the mandibular symphysis, and the anterior part of the left prearticular, together with the extreme anterior part of the right external dermal bones. It can be distinguished from specimens of *H.* (*Holodipterus*) *gogoensis* in the following respects: (i) the lack of a groove on the posterior face of the prearticular ventral to the heel and below the surface bearing superficial denticles (figure 56*c*); (ii) the absence of real teeth (i.e. enamel covered cones); (iii) a shallow rather than a deep anterior furrow (the ventral surface is shown in figure 56*b*); (iv) the failure of the surangular to reach as far forward as the lateral extremity of the anterior dental ridge on the prearticular; and (v) the less posterior extent of the deep ventral furrow of the posterior labial pouch.

Character (ii) suggests that this specimen is probably a member of *H.* (*Holodipteroides*).

This specimen is significant in that it shows the distribution of lateral line canals on the right side; the extent of the hypermineralized dentine on the prearticulars in the lingual furrow; a strong heel from which a pair of toothless ridges runs anterolaterally; at the posterior end of the dentary marginal denticles which continue along the edge of the prearticular to the end of the second radial ridge; and flat scattered denticles on the posterior surface of the lingual furrow. In many respects it is like the much larger specimen figured as *Holodipterus gogoensis* by Campbell & Smith (1987, figure 7).

The hyomandibular is unknown. Judging from the extent of the ossification of the other parts of the hyoid arch, and our knowledge of the relative strengths of the hyomandibular and the other elements in *Chirodipterus* and *Griphognathus*, we conclude that in *H.* (*Holodipteroides*) it must have been almost entirely cartilagenous.

As in *G. whitei* and *C. australis* (Miles 1977), the basihyal and the anterior basibranchial were co-ossified. No posterior basibranchial is known. A well-preserved basihyal/basibranchial is known from the holotype.

The known basihyal/basibranchial (figure 57*a–c*) has a well-developed, narrow and pointed anterodorsal projection and a steep vertical anterior keel. The dorsal surface is flattened and slightly concave over the posterior half and attains maximum width about two-thirds of its length from the front, at the level of the attachment surfaces for the first ceratobranchials. The curvature of this surface is such that it fits precisely over the palatal callus. Anteriorly, large facets exist for the articulation of the hypohyals (asterisk, figure 57*b*). These articulating surfaces, which lack endochondral bone except for a few struts that may have reached the surface, join in the midline towards their anterior ends. They are placed much farther forwards and ventrally than the equivalent structures of *G. whitei*. Surfaces for the articulation of two ceratobranchials are preserved. The anterior one has no perichondral bone on its surface and must have been similar in character to the hypohyal articulation. The more posteroventrally situated one has a perichondral covering.

The ventral surface of the basihyal/basibranchial is flat over its posterior half, but bears a large ventral projection below the posterior end of the hypohyal articulation. The posterior end of the bone is not well preserved, but in comparison with *G. whitei* it is very

Figure 53. Anterior view into the partly prepared corpus of the parasphenoid and the edge of the quadrate ridge of the left pterygoid of CPC25739 showing bony struts.

Figure 54. Presumed right dermopalatine of the holotype. (*a*) Unwhitened and (*b*) whitened views of buccal surface, and (*c*) visceral surface. Note the dark hypermineralized dentine set in white superficial dentine in (*a*).

Figure 55. (*a*) Lateral and (*b*) dorsal views of a posterior fragment of the left ramus of the mandible of the holotype, ANU49101.

Figure 56. (*a*) Dorsal, (*b*) ventral and (*c*) posterior views of a small mandible, WAM86.9.685, referred to *H.* (*Holodipteroides*) *elderae.* In (*b*) the external dermal bones have not been preserved on the left side, and the superficial layer has been ground away on the right to expose the lateral line canals. In (*c*) the denticles in the lingual furrow and the Meckelian space of the right ramus are evident.

Figure 57. (*a*) Dorsal, (*b*) ventral and (*c*) lateral views of the basihyal/basibranchial of the holotype, ANU49101. The anterodorsal tip is broken away.

Figure 58. (*a*) Lateral and (*b*) anterior views of the hypohyal and attached denticulated tooth plate of the holotype, ANU49101.

Figure 59. Anterodorsal view of the fragmentary ceratohyal of the holotype, ANU49101.

Figures 60 and 61. Buccal surfaces of two denticulate tooth plates of the holotype. Patches of smooth superficial dentine form the central part of each plate.

Figure 62. (a–c) A denticulated tooth plate from the holotype, possibly originally attached to the dorsal surface of the basihyal/basibranchial. In (*a*) and (*b*) the buccal surface of the plate is shown whitened and unwhitened respectively. A visceral view of the plate is given in (*c*). Note the dark hypermineralized dentine set in white superficial dentine in (*b*).

Figure 63. Three views (*a–c*) of a small isolated denticulated plate from the holotype. Part of the mounting match stick can be seen on the left side in (*c*).

Figure 64. Isolated denticulated tooth plate from the holotype.

depressed. Endochondral ossification of the whole bone is slight, and consists of a number of struts and a few sheets of bone.

The four robust denticulated dental plates of the flatter type mentioned above (figures 60, 61, 62*a–c* and 64) cannot be confused with denticulated roofing bones because they are too thick and have both denticles and sheets of white superficial dentine on their buccal surfaces. The individual plates are approximately square or rectangular in outline, and roughly symmetrical, although one tapers towards one end. It is possible that they are all dermopalatines or isolated palatal dental plates (see Miles (1977, figure 72) where similar entities are labelled tooth plates), but comparison with the dermopalatines of *H.* (*Holodipterus*) *gogoensis* suggests that they are not appropriately shaped (Miles 1977, figure 72). We assume that four plates were attached to the flattened dorsal surface of the basihyal/basibranchial, which would make the arrangement comparable with that of *G. whitei*. However, in that species the denticulated plates extend forwards to the anterior end of the supporting bone, whereas in the present species the narrow upturned anterior part would not be covered unless more as yet undiscovered plates were present. Given the size of the polished surface of the median palatal callus, we consider the existence of an additional plate probable. The denticles on the surface of these bones seem to have been replaced shortly before death, because they have unworn highly sculpted surfaces. The remaining surfaces are covered by white superficial dentine which has the usual characters of that substance on the palate and prearticulars.

Given the remarkable fit of the basihyal/basibranchial over the polished palatal callus, we are confident that this species, and by implication other holodipterans, reduced their food by working the hyoid dental plates against the callus.

As in *G. whitei* and *C. australis* the hypohyal (figure 58*a*,*b*) is cuneiform in outline and is composed of a thin shell of perichondral bone supported internally by weakly developed endochondral struts. Both articulating surfaces were presumably made entirely of cartilage supported by a few endochondral struts.

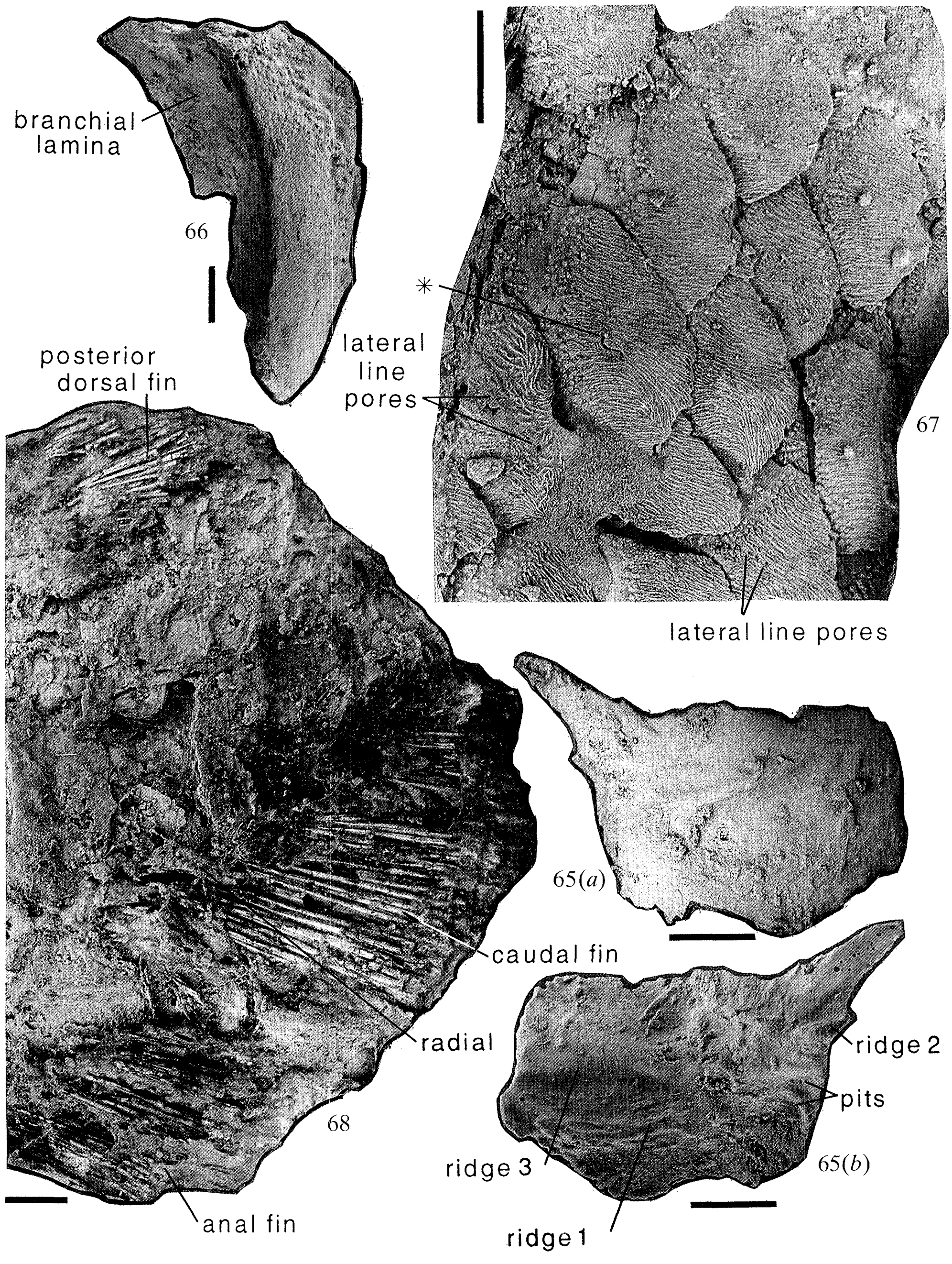
Only the anterodorsal half of the left ceratohyal is known (figure 59). This has a flared end where it articulated with the hypohyal, the flaring being particularly strong on the mesial side. This articular surface is approximately circular and open unlike both *G. whitei* and *C. australis* which have closely packed endochondral blisters forming their ends. The lateral surface of the ceratohyal is strongly convex and shows no sign of the deep groove which, according to Miles (1977 figure 150, gr. Chy) is found on *H. gogoensis*. Such a groove does not occur in *G. whitei*, but is known on many Devonian dipnoans including *Sorbitorhynchus* (Wang *et al.* 1993) and *Pillararhynchus* (Campbell & Barwick 1994) in both of which it is buried in the bone for part of its course. A similar groove occurs in *C. australis* also, and is referred to by Miles (1977) as a groove on the lateral crest. As is normal for dipnoans, the mesial surface of the ceratohyal is smooth. Overall it is wide in comparison with *G. whitei*. Insufficient of it is preserved to allow description of the shape of the lateral ridge.

The pectoral girdle (figures 65*a*,*b* and 66) is known only from a large part of a clavicle and an almost complete anocleithrum, both obtained from the holotype. The only other bones of comparable size we have available are from *Chirodipterus australis* and these together with Jarvik's reconstruction of *Scaumenacia curta* (Jarvik 1980, figure 335) have been used as a basis for comparison.

The external lamina of the clavicle (figure 66) is thick and only slightly convex overall on its outer face, which is strongly rugose posteriorly but granulose anteriorly. Its ventral end is incomplete, but the growth pattern indicates it must have been rounded rather than acutely angular in outline. It shows no evidence of an interclavicular articulation. A thickened dorsal edge indicates a long articulation with the cleithrum. The branchial lamina is extensive and remarkably thick. Its dorsal edge, which has a marked groove for the articulation of the cleithrum, is *ca.* 30 mm long in comparison with a total bone length of *ca.* 63 mm. It extends ventrally to within 8 mm of the end of the bone.

The anocleithrum (figure 65*a*,*b*) is a large bone with a broad body and a short anterodorsal process. It was not found in position, and so it was necessary to infer its orientation. If we take Jarvik's reconstruction of *Scaumenacia curta* as a standard, the strongly ridged concave surface (figure 65*b*) would have to be interpreted as lateral and the relatively smooth convex one as mesial (figure 65*a*). The preserved bone would then be from the right side of the specimen, and the anterodorsal process would be turned inwards. Allowing that this orientation is correct, we will now describe the bone. In vertical view it is distinctly sigmoid in outline with the anterior process deflected mesially. In lateral aspect, a short anterior ridge (ridge 2 of Jarvik 1980) runs forwards into a short blunt process. A strong arcuate ridge runs from the posterior edge of the bone forwards and upwards towards the posterior end of ridge 2. This is a more elongate representative of Jarvik's ridge 1. A third short slightly arcuate ridge, herein designated ridge 3 (figure 65*b*), is situated dorsal to ridge 1. Anterior to ridge 1 and ventral to ridge 2 are two pits (figure 65*b*) instead of the single linear one shown by Jarvik. There is no ridge along the anterodorsal process like the one shown by Jarvik in *Scaumenacia curta*. The mesial surface (figure 65*a*) has less relief, although a distinct ridge runs forwards from the posterodorsal extremity to end a little short of a point opposite the earlier mentioned pits, and a thickening runs ventrally parallel to the anterior margin. There are only minor differences between this bone and the equivalent in *H.* (*Asthenorhynchus*) *meemannae* (see below), but obvious differences from those of *Chirodipterus australis* (Campbell & Barwick 1987, figure 11), *Scaumenacia curta* (Jarvik 1980, figure 335) and *Sagenodus* (Watson & Gill 1923, figure 17).

A large block of scales (figure 67) is known from CPC30828. The cranial material of this specimen was extracted from a block of limestone which seems to



Figures 65–68. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

Figure 65. (*a*) Mesial and (*b*) lateral views of the left anocleithrum of the holotype.

Figure 66. Anterolateral view of the the left clavicle of the holotype.

Figure 67. Block of scales of CPC30828, anterior to the left. Pit line asterisked.

Figure 68. Posterior fins of CPC30828 showing rays of caudal, posterior dorsal and anal fins.

have formed one extremity of an elongate nodule originally found in six pieces. Two adjoining pieces which made up the middle of this nodule have been acid etched, yielding a section of body wall which provides information on the structure and disposition of the scales. Another piece, which evidently made up the other extremity of the original nodule, has revealed what we interpret as the remains of the second dorsal, caudal and anal fins.

As figure 67 shows, some post-mortem rearrangement of the scales of this section is evident. Each lateral scale lay at the intersection of two diagonal rows of scales. In the preserved (and flattened) section of body wall the diagonal scale rows intersect at *ca.* 60–65°. With respect to the lateral line the posterodorsally directed row makes an angle of between 70–75°, and the posteroventrally directed row an angle of 35–45°.

Anteriorly each lateral scale was covered on its outer side by three others belonging to the immediately anterior pair of diagonal rows. We estimate that somewhat in excess of 60% of the total external surface of each lateral scale was overlapped by these three.

Individual lateral scales are cycloid in form and the surface features differ greatly on their exposed and unexposed portions (figure 67). The exposed portion has the appearance of the keystone of an arch which has been turned through 90°. The surface of this exposed area is richly sculptured with elongate and slightly wavy raised ridges which are arranged in aligned segments traversing 10–40% of the diameter of a scale. Dorsally the ridges are linear and longitudinal, but ventrally they assume an increasingly vertical alignment. Overall the ridges have the appearance of whorls not unlike those of human fingertips. On the posterior margins of some scales the ridges are continued as fine spines. Such spines are uncommon, but this rarity seems to reflect the ease with which the scale margins are broken away rather than their low original abundance. Approaching the area of overlap the raised ridges break down into broad flat pustules, which have a smooth rim on all but the anterior margin. Beneath the overlap the scale surface is composed of highly porous bone with the pores arranged in linear series. Fine bony projections are arrayed in regular fashion around these pores. None of these scales shows evidence of cosmine.

A series of lateral line scales can be identified which apparently lay on a longitudinal line at about mid-body depth. The exteriors of many of these scales are damaged to an extent that makes it impossible to determine the number of pores that opened onto their surfaces. However, the outer layers are relatively intact in two scales and these indicate that the main canal opened to the exterior of each scale via six to twelve pores (figure 67). As in other bony fishes the main lateral line canal approached the covered portion of each lateral line scale from the anterior, penetrated the exterior of the scale at a low angle and, after giving off a number of finer secondary canals to the surface, exited the interior surface of the scale at a low angle.

The specimen provides no evidence of additional longitudinal lateral lines. However, in view of the poor condition of all scales at the margins of the section, their presence cannot be ruled out.

Pit lines can be identified on three scales. These (figure 67, asterisk) bear very obvious short deep grooves on their outer surfaces similar to the pit-line grooves found on the gulars of *Griphognathus whitei* and *Chirodipterus australis*. Two of these grooved scales lie dorsal to the main lateral line described above and the other one ventral to it. The three scales show no connection to one another or to the scales of the longitudinal row.

Three posterior fins can be recognized on CPC30828 (figure 68). None of these is complete distally and two of them are clearly broken off near the ends of the proximal rays. Scales of both sides of the caudal trunk are present, but these are all damaged to such an extent that the pattern of scalation on the tail is unclear.

The fin we identify as the posterior dorsal is represented by approximately 20 undivided proximal rays up to 2 cm long. No distal segmented rays or radials are preserved.

The most posterior of the preserved fins, which we identify as the caudal, is separated from the posterior dorsal by a gap of some 4 cm. It is composed of at least 35 undivided proximal rays. In the lower part of the fin these rays are broad distally and up to 4 cm in length; in the upper part the undivided proximal rays are finer and only attain a length of 2 cm. Two radials are clearly present.

The anal fin is separated from the caudal by about 1 cm. It includes at least 20 undivided proximal rays which are up to 3.5 cm long. Groups of distal divided rays are clearly evident on the posterodorsal portion of the fin where they lie ventral to the proximal undivided rays of the caudal fin. This is a valuable clue to the identification of these fins (cf. Forster-Cooper 1937, Plate 3, figure 5; Schultze 1969, figures 30–32). A single poorly preserved radial is evident half way along this fin proximal to the proximal undivided rays.

9. HOLODIPTERUS (ASTHENORHYNCHUS) (subgen. nov.)

Type species. H. (*Asthenorhynchus*) *meemannae* sp. nov. from the Gogo Formation.

Etymology. asthenos = weak; *rhynchos* = beak or snout; referring to the poor ossification of the snout.

Diagnosis. A subgenus of *Holodipterus* characterized by a weakly ossified or unossified snout and braincase; cheek bone 9 high and short and separated from the bones in front by a gap; bone 10 long, forming the ventral edge of the cheek; bone 4 not excluded from the orbit; prearticulars with a long and thick median symphysis, and carrying on the heel a callus joined anteriorly to the strong first (mesial) row of teeth; second, third and fourth tooth rows greatly reduced; dentary consisting only of a rim unsupported by dermal bone joining with the infradentaries; infradentaries with straight, slightly overlapping sutures, and surfaces of the central parts of the bones covered with pustules; surangular terminating behind the anterior end of the angular; dentary with deep depressions beneath the external nares, and a row of prominent teeth with hypermineralized cores and basal pulp cavities along its crest laterally and mesially.

10. HOLODIPTERUS (ASTHENORHYNCHUS) MEEMANNAE (sp. nov.)

Etymology. In honour of Chang Mee-mann, formerly Director of the Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, who has contributed significantly to our understanding of Devonian crossopterygians and dipnoans.

Holotype. ANU49103 from the northwest edge of the fossiliferous outcrop in Paddy's Valley, Gogo. The holotype is the only known specimen. It is represented by a crushed head, the roof of which has been largely reassembled, an almost complete palate, operculars and shoulder girdle, and parts of the scales from both sides of the body.

Diagnosis. As for the subgenus.

Description. The roof and cheek can be reconstructed to a greater extent than those of any other known holodipteran (figures 69, 70, 75, 76 and 78). Bone B is elongate and tapered towards the rear where it is only half the maximum width, as opposed to 0.75 in *H.* (*Holodipterus*) *gogoensis* (Miles 1977, figure 122). It is embayed anterolaterally for the reception of bone C. Along its posterior edge it has a short flange for the overlap of bone A, and laterally it is slightly overlapped by bones I and J. Mesially it has a pair of short pitlines forming a V at about its midlength. On its ventral surface, the attachment of the median crista, which is double, extends back about one-third the length of the bone.

Bone I does not reach as far forward as the middle of B, is narrower than long, and has a long posterior projection. J reaches the level of the anterior end of B. The lateral line in bone J is clear on the X-radiographs (figures 75 and 76), which show that it approaches the longitudinal canal in bone X, but the walls of the two canals do not impinge on each other. There is a clear indication that a flat open space exists between them, but this cannot be confirmed from the available material.

The specimen is asymmetrical in the Y positions. Y_1 is preserved on both sides, and although the left bone is much larger than the right, both are almost equidimensional. Y_2 is known from a large fragment in position on the left side, and the original part of the same bone was present on the right but has been lost during preparation. On both sides the bone must have been large judging from the space available. However, the projection on the side of I indicates that Y_2 did not reach more than half way back along that bone. Z is preserved on the left side. It is triangular, wider than long, and carries the trifid lateral line canal. Its position is fixed by matching the commissural lateral line canal with that of I, and in this position it abuts the end of Y_2. Bone H from the left side is preserved, but is incomplete. It is a thin subtriangular bone lacking any part of the lateral line commissure. Bone A is represented by a large fragment whose anterior margin is preserved almost in its entirety. Laterally it extensively overlapped the posterior process on bone I. The commissural lateral line canal forms a broad arc 15 mm wide across its anterior half.

On the anterior part of the roof L_1 and L_2 are as in *H.* (*Holodipterus*) *gogoensis* and the paired E's are long and narrow. The rear of the left E is missing. Bone D is small and lozenge-shaped.

The circumorbitals and cheek bones have many distinctive features (figures 69–70 and 75–76). They are known completely from the left and incompletely from the right of the specimen. As is apparent on both sides of the specimen, bone 4 extends from the opercular to the orbit, unlike *H.* (*Holodipterus*) *gogoensis* as represented by Miles (1977, figure 125). Bone 5 is preserved only on the left side, where it is also large and forms part of the orbital margin. It is bordered posteriorly by 8 and a small rounded entity. Ventral to 5 and the small rounded bone is a large elongate bone that forms the posteroventral edge of the cheek. It carries a pit line which is aligned with the pit line on the small rounded bone. Because of its form, position and the presence of the pit line, we recognize this elongate bone as 10 (Forster-Cooper 1937, figure 3). On the right cheek, bone 10 is shorter but deeper, its posterodorsal corner occupying the same space as the small rounded bone on the left cheek. For this reason we interpret the latter bone as a supernumerary, and label it as 10a in figures 69 and 78. The posterior edge of 10 is bevelled and was clearly not sutured against the bones behind. Bones 8 and 9 are short and carry the lateral line to the mandible. Bone 9 is separated from the bone in front by a considerable gap. Both 8 and 9 carry pit lines. These features are all different from those of *H.* (*Holodipterus*) *gogoensis* as figured by Miles (1977, figure 125).

Bones 1 and 7 form the ventral edge of the cheek in front of 10, 6 being excluded on both sides. Bones 6, 7 and 2 make the anterior and ventral orbital margins, but 1 is excluded. Bone 1 on both sides of the specimen has a distinctive paddle-like shape with the handle, which carries the infraorbital canal, directed forwards. The situation with respect to bones 2 and O is less clear. There is certainly one large bone 2 forming the anterior margin of the orbit above bone 7, but between this and bone 3 on the left side is a small gap. This could have been occupied by a small bone 2a. Such a bone was present on the right side attached to the top of bone 3 when the photographs were prepared. It was subsequently found to have an orbital margin and to fit precisely to the front edge of bone 3 on the right side. Between bone 2a and bone L is another gap which would have been occupied by bone O_1. Bone O_2 is still in position. A reconstruction of the roof and cheek is given in figure 78.

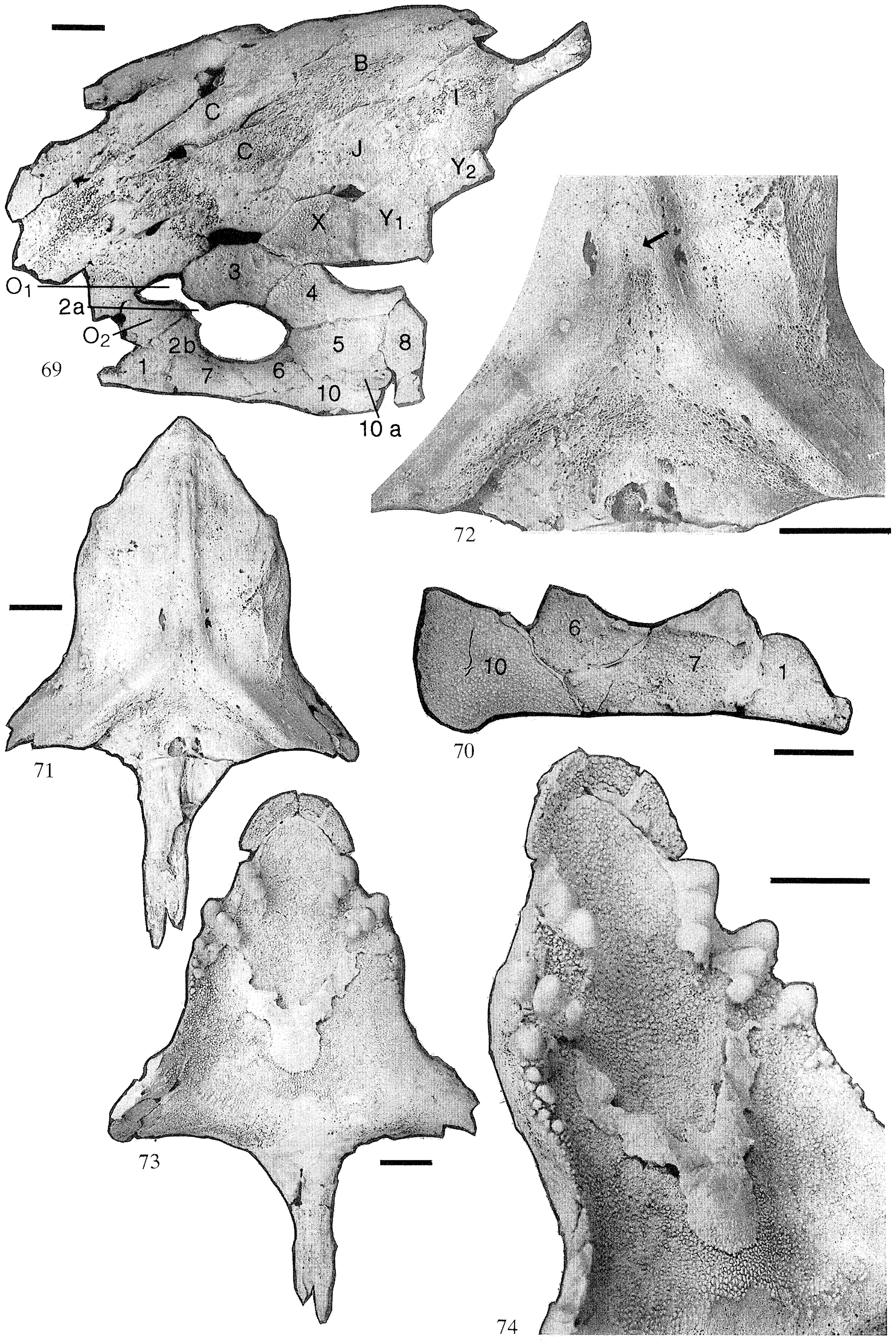
The neurocranium is not preserved. This appears not to be the result of crushing, because we find no evidence of broken edges or of isolated fragments. Rather it seems to indicate that the whole neurocranium was unossified.

In outline and in dorsal view the palate (figures 71–74) is almost identical with that of *H.* (*Holodipterus*) *gogoensis* figured by Campbell & Smith (1987, figure 3C). The pterygoids join at a median ridge which lacks a distinct suture. X-radiographs reveal that their growth centres abut the mid-line, indicating that growth was restricted to the free margins of the bones. Genera with distinct median sutures, such as *Chirodipterus* and the Carboniferous tooth-plated forms, increased their size along all margins.

The parasphenoid rises to the front in the same way as in *H.* (*Holodipterus*) *gogoensis*, and dorsally its body is seen to be composed of a layer of distinctive bone tissue (figure 72). Its stalk is not well preserved, but is narrow like that of *H.* (*Holodipterus*) *gogoensis* rather than broad like that of *H.* (*Holodipteroides*) *elderae*.

The buccal surface has four easily discriminated rows of teeth (figures 73 and 74). Two additional rows might be recognized posteriorly, depending on how one interprets small eminences at the posterolateral margin. Each tooth consists of a cone covered with enamel. The four tooth rows have respectively 2 or 3, 3, 3, 2, and 1 or 2 teeth. Along the palatal margin behind the fourth row are two or three small teeth so identified because they have cores of hypermineralized dentine. These may represent incipient rows. The first three rows all terminate sharply at their medial ends because the teeth and their supporting bone have been resorbed. They are replaced admedially by denticle-covered bone at a much deeper level, and without any vestige of the former tooth ridges.

Denticles also occupy most of the space between the tooth rows, although the resorption patterns show that they were connected by white superficial dentine in a previous growth phase producing a palate that must



Figures 69–74. *H.* (*Asthenorhynchus*) *meemannae*. Scale bars = 10 mm.

have been like that of the specimen of *H. gogoensis* figured by Campbell & Smith (1987, figure 3c). The most labial teeth of the first three rows extend laterally beyond the edge of the palatal bone, indicating that they were added shortly before death, a point corroborated by their unworn tips. Shedding denticles lie lateral to the hinder tooth rows on the right side, but there are no large marginal denticles armouring the lateral face of the palate as is common in holodipterans. This is not surprising, because as Campbell & Smith (1987, p. 160) pointed out, marginal denticles were developed during the growth phase after the addition of new distal teeth, and subsequently they were overgrown by laterally accreting bone.

A strong posteromedian callus is present as in most holodipterans. Running anterolaterally from it towards the gap between tooth rows 2 and 3 are extensions composed mainly of white superficial dentine, but with two or three patches of hypermineralized dentine giving the appearance of old worn teeth (figures 73 and 74). This they cannot be. The callus itself has a core of hypermineralized dentine, surrounded by white superficial dentine which at its lateral and posterior margins incorporated denticles, but at its anterior and anterolateral margins was being resorbed. Furthermore, the greater concentration of hypermineralized dentine in the proximal ends of the anterolateral extensions, indicates that this dentine was being added distally and is thus not relict from pre-existing teeth.

Two arcuate dermopalatines with denticles of the same type as occur on the palate, were preserved isolated, but they fit back against the front of the pterygoids precisely, meeting in the midline (figure 73 and 74). These correspond with the Dpl_1 in *Griphognathus whitei* (Miles 1977) and *Uranolophus wyomingensis* (Campbell & Barwick 1988).

An isolated small plate with a deep lateral embayment and a mesial articulatory edge, is covered on the buccal surface by denticles and a patch of white superficial dentine. It must have been one of another series of dermopalatines or palatal tooth plates. As we have discussed under *H.* (*Holodipterus*) *gogoensis*, it is comparable in shape and in the position of the denticles to the plate identified as Dpl_1 by Miles (1977, figure 72), but it bears a relatively longer lateral anterior process. This is the bone we identified as Dpl_3 in *H.* (*Holodipterus*) *gogoensis* (figure 10*c*).

Several other pieces of denticulate bone that could be interpreted as palatal tooth plates have been recovered, but these are of irregular shapes and do not lend themselves to accurate interpretation.

Four smaller thicker plates carrying larger denticles (or perhaps teeth) which are hypermineralized, were found loose in the matrix around the front end of the palate. Two of these can be fitted together (figure 79*a*,*b*), but the others show no obvious relationships. One of these is illustrated in figure 80*a*,*b*. They could be isolated plates from the skin of the solum nasi. The fact that the bone forming the bulk of the plates gives evidence that they were not attached to other bone, tends to support this view. Alternatively, given the fact that the snout was not ossified, they could be pieces of the upper lip such as have been figured by Miles (1977, figure 72) on the subnasal ridge of *H.* (*Holodipterus*) *gogoensis*, and observed by us to be more highly developed on CPC25740 of the same species. Either option would allow them to be opposed by teeth on the dentary as described below.

Among the other debris left after etching were two long narrow straight-edged plates 11 mm × 4.5 mm (figures 90 and 91). These have overlap articulations at the widest end. Their shape indicates that they do not belong to the dermopalatine series. It seems most likely that they were basihyal/basibranchial dental plates.

An almost complete left and parts of the right shoulder girdle (figures 81*a*–83) are preserved. The right anocleithrum (figure 81*a*,*b*) is more complete than the left and in conjunction with the left cleithrum greatly extends our knowledge of Devonian dipnoans. The anocleithrum does not lie in the one vertical plane, but is strongly sigmoid. Its anterodorsal process is short, only about 0.25 the total length of the bone, and is deflected anteromesially. Ventral to the process there is a pronounced angle from which a number of short spines project. In dorsoventral section, the lateral face of the main body of the bone is convex, and the mesial face is complementary. In longitudinal section, however, the lateral face is concave and the mesial face convex. In comparison with the figure of *Scaumenacia curta* given by Jarvik (1980, figure 335) this specimen has a weak ridge 2 extending forwards to the spinose ridge mentioned above, and an equivalent ridge 1 which is situated lower on the bone than in *S. curta*.

The cleithrum (figures 82*a*,*b*) has a short external part with a raised sharp leading edge, separated from the remainder by a deep furrow. This furrow fades rapidly as it approaches the clavicle and becomes increasingly distant from the leading edge, the ventral end of which is flattened. This flattened edge and the surface behind the furrow carry low granules like those on the roofing bones. The ventral end of the

Figure 69. Dorsolateral and slightly anterior view of the skull roof of the holotype ANU49103.

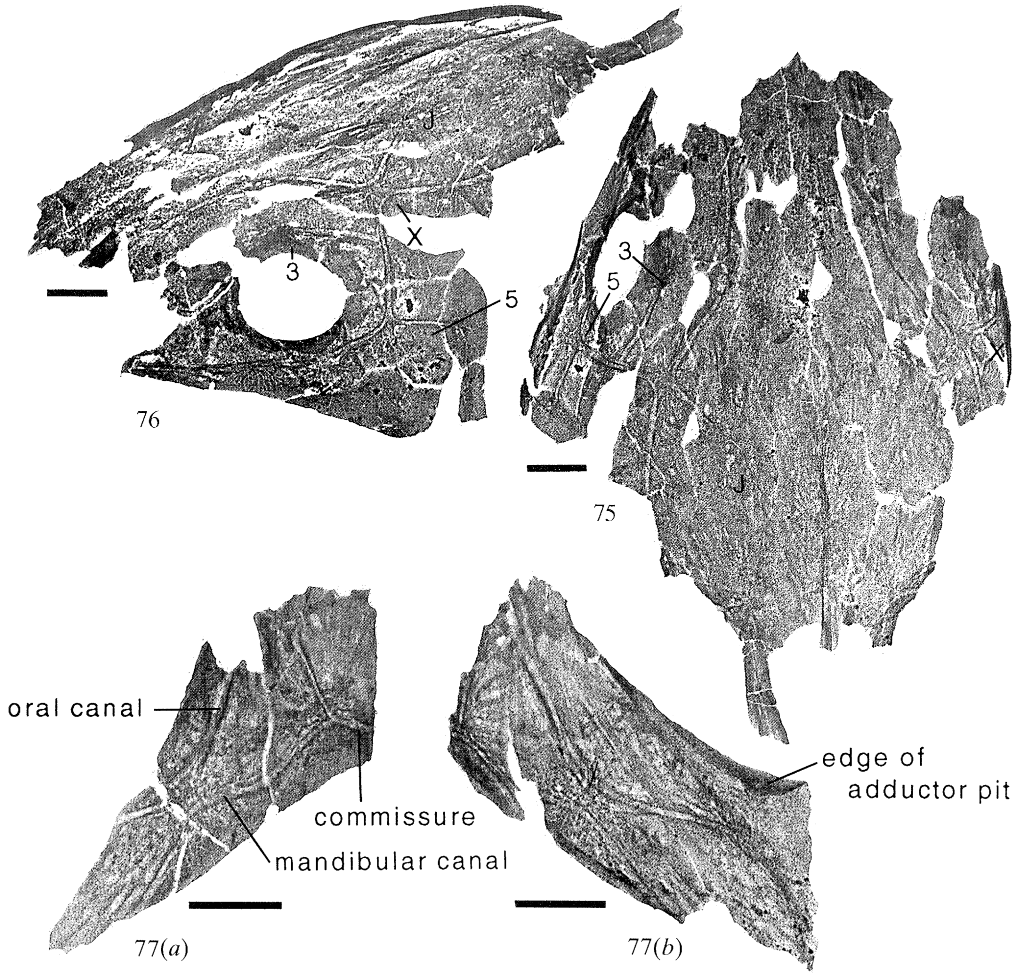
Figure 70. Isolated right cheek of the holotype showing pitlines on bone 10. The ventral margin of the orbit is preserved on bones 6 and 7.

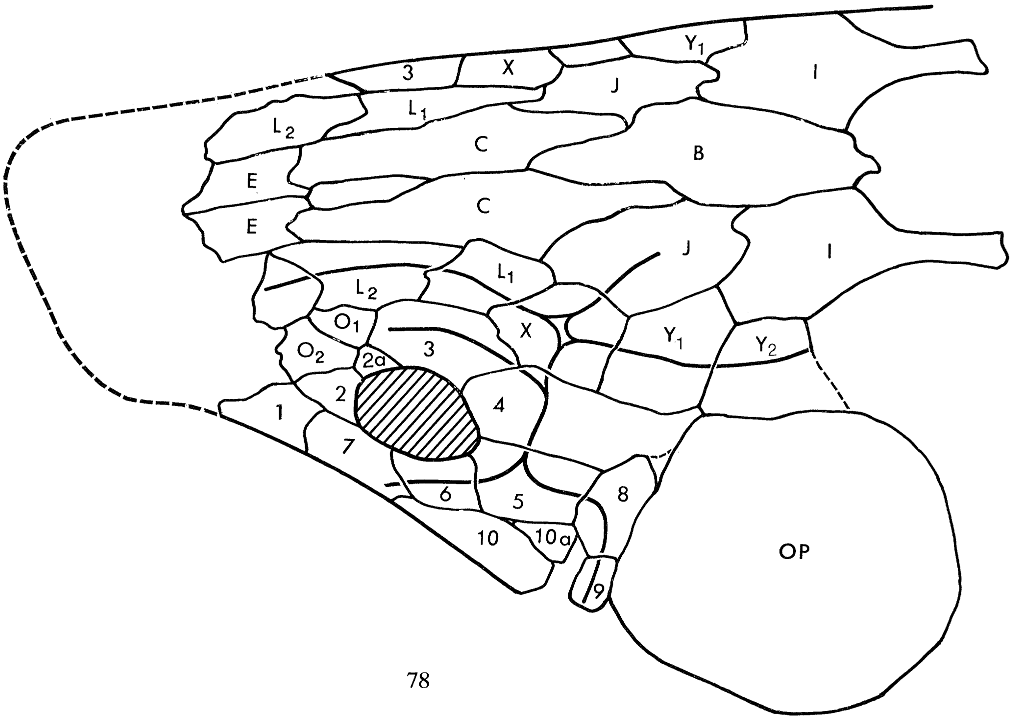
Figure 71. Dorsal view of the palate of the holotype.

Figure 72. Enlargement of the parasphenoid of same in dorsal view showing the bone texture and the foramina for the vascular canals. Arrow indicates anterior extremity.

Figure 73. Ventral view of the palate of holotype with paired dermopalatines attached.

Figure 74. Ventrolateral view of same showing patches of hypermineralized dentine. Note the posterior extension of the callus dentine over the old denticles the tops of which can just be discriminated.





78

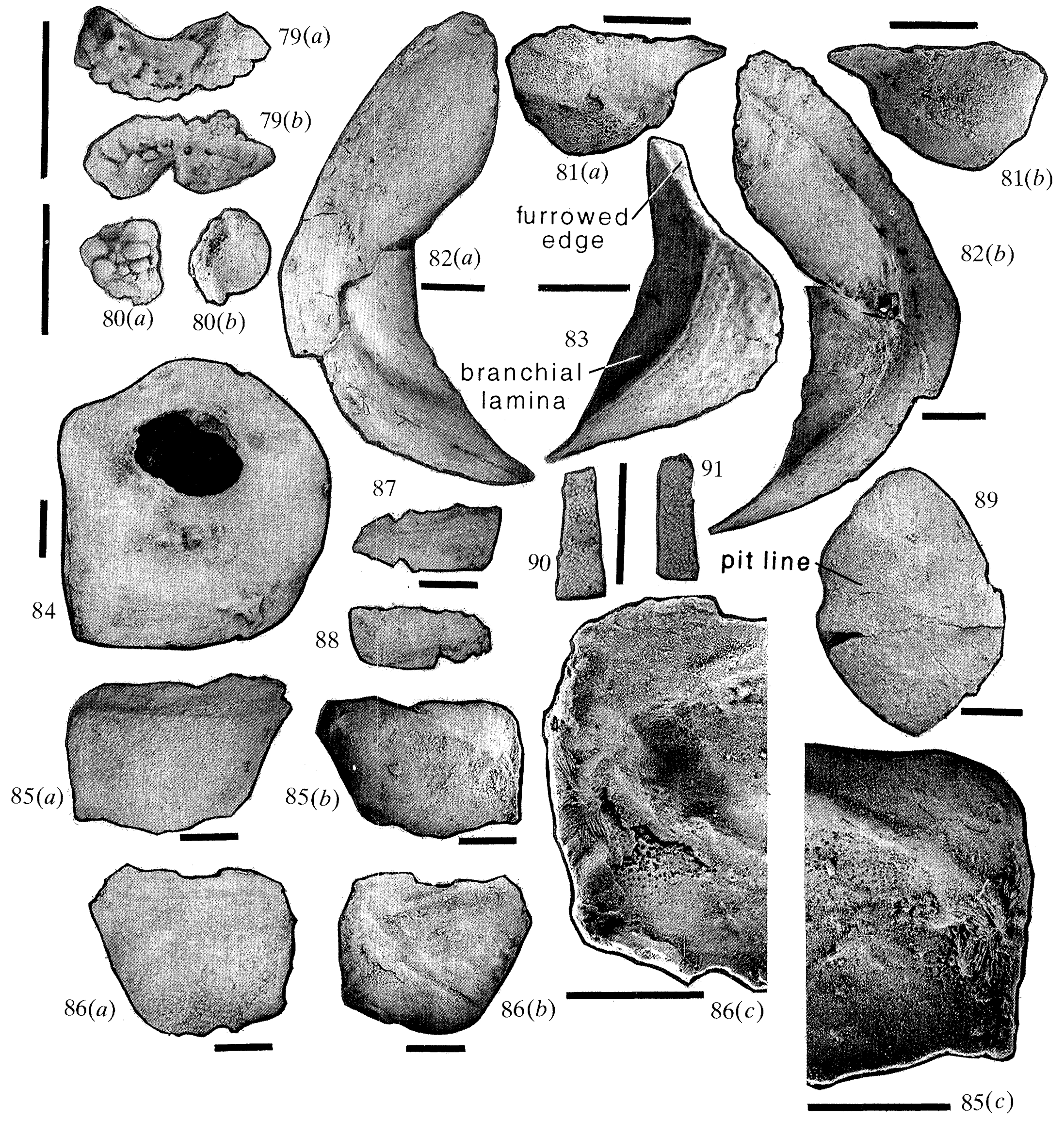
Figures 75–78. *H.* (*Asthenorhynchus*) *meemannae*. Scale bars = 10 mm.

Figure 75. Dorsal X-radiograph of skull roof of the holotype showing the radiation centres and lateral lines in bones X, J, 3 and 5.

Figure 76. Lateral X-radiograph of same. Compare with figure 69.

Figures 77. (*a,b*) X-radiographs of the known external dermal bones of the right and left sides of the mandible of the holotype. Note the approach of the oral and mandibular canals in the angular bone on each side of the specimen.

Figure 78. Reconstruction of the roof, cheek and operculum in anterodorsolateral view. Based on the holotype.



Figures 79–91. *H.* (*Asthenorhynchus*) *meemannae*. Scale bars = 10 mm.

Figure 79. (*a,b*) Two isolated dental plates from the snout region of the holotype here glued together and shown in (*a*) oblique, and (*b*) buccal views. These dental plates, and the one shown in figure 80, carry teeth with hypermineralized dentine cores.

Figure 80. (*a,b*) Isolated dental plate from the holotype in (*a*) buccal and (*b*) visceral views.

Figure 81. (*a*) Lateral, and (*b*) mesial views of the right anocleithrum of the holotype.

Figure 82. (*a*) Mesial, and (*b*) lateral views of the articulated left cleithrum and clavicle of the holotype.

Figure 83. Lateral and slightly anterior view of the separated clavicle of the holotype showing the external ornament and articular surface for reception of the branchial lamina of the cleithrum.

Figure 84. Lateral view of the left opercular of the holotype. The specimen was collected with the large hole eroded in it dorsally.

Figure 85. (*a*) Lateral, and (*b*) mesial views of the left subopercular 1 of the holotype. The anterior portion of the mesial surface is shown enlarged in (*c*) to illustrate portions of the ridges and an attachment scar.

Figure 86. (*a*) Lateral, and (*b*) mesial views of the right subopercular 1 of the holotype. An enlargement of the anterior part of the mesial surface is shown in (*c*).

Figures 87 and 88. Lateral views of the left and right suboperculars 2 of the holotype.

Figure 89. Ventral view of left principal gular of the holotype, showing a transverse pit line near its mesial edge.

Figures 90 and 91. Isolated denticulated plates from the holotype; in life possibly attached to the basihyal/basibranchial.

cleithrum is incomplete, but carries a flange on its anterior edge to articulate with the inner face of the clavicle. The clavicular articulation indicates that the cleithrum was acutely terminated ventrally. Most of the external surface lies in one plane, but the ventral end is turned inwards and forwards rather abruptly. The branchial lamina is extensive and on its inner surface merges imperceptibly with the external lamina. The two parts meet at *ca.* 130°. The ventral edge of the branchial lamina is slightly deflected outwards to make a rim that articulates with a pronounced groove on the dorsal edge of the lamina of the clavicle.

The external surface of the clavicle (figures 82*b* and 83) is longer than that of the cleithrum. Its dorsal and ventral terminations are acute. Along its anterior edge is an exposed band covered with low granules, behind which is a groove shallower than the one on the cleithrum, and becoming increasingly shallow ventrally. The posterior surface consists of smooth unornamented bone that was probably buried in soft tissues in life. When fitted to the cleithrum, the clavicle is seen to turn forwards at a high angle and inwards at a lower angle. Its branchial lamina is extensive where it meets that of the cleithrum, but tapers rapidly ventrally to stop well short of the ventral end of the bone. The dorsal edge of the lamina is furrowed for the reception of the edge of the cleithral lamina. It shows no evidence of an articulation for an interclavicle.

The opercular series is well-preserved, and consists of an opercular and two suboperculars. The opercular (figure 84) is a broadly convex bone with a straight leading edge on the ventral half of which is a slight flange that tucked under the bones of the cheek. Its dorsal edge is concave anteriorly and convex posteriorly, passing round into a broadly convex posterior edge. The ventral edge is almost straight. The external surface of the bone is covered with low pustules like those of the roof. A hole eroded through the only bone available has probably obliterated any internal scars.

Subopercular 1 (figures 85*a,b* and 86*a,b*) is about half the size of the opercular, has a large dorsal overlapped edge that curves around to a slight articulatory flange on the anterodorsal corner. It has a straight anterior edge, an acute but truncated posterodorsal angle, and an almost straight posterior edge that curves around to the gently convex venter. It also is pustule covered. On the inner surface the bone has three distinctive features (figures 85*b,c* and 86*b,c*). A low rounded ridge runs anteroventrally from a point in front of the posterodorsal corner to the anterior edge of the bone. This is not related to the articulation of the bone with the opercular, and its function is unknown. Below this ridge and towards the front of the right bone is a depression (figure 86*c*) that has the appearance of a muscle attachment; this is poorly developed on the left. A well-developed knot of textured bone (figures 85*c* and 86*c*) lies anterior to this depression, as was noted by Miles in *H.* (*Holodipterus*) *gogoensis*.

Subopercular 2 (figures 87 and 88) is an elongated bone somewhat less than a third the size of subopercular 1. It has extensively overlapped dorsal and ventral surfaces. These overlaps taper away before reaching the posterior end of the bone, so that the central, raised, pustulose exposed surface expands posteriorly. The anterior edge is not well preserved, but shows evidence that the overlaps continued around it as in *H.* (*Holodipterus*) *gogoensis* (Miles 1977, figure 131d).

The gular series is represented by two bones, one complete and the other broken. They appear to be a pair of principal gulars. The large left principal gular (figure 89) is thin, and carries the standard pustules and a short transverse pitline towards the mesial edge. The fragmentary right plate is similar in thickness. The better plate is elongate-ovate in outline, and all its edges are finished except a short segment on one side which has a narrow overlap. By analogy with *G. whitei* we take this edge to be mesial. No matter how the bone is oriented there is a considerable obliquity to the anteromesial edge, and this implies the presence of a moderate-sized median gular overlapped by the principal gular. Such a bone would be much larger than any equivalent described for other Devonian dipnoan genera (Miles 1977, figure 126; Schultze & Campbell 1987, figure 5). The oblique anterolateral edge suggests the presence of large submandibulars. Apart from these deductions we cannot comment further on the gular/submandibular series.

The preserved parts of the mandible consist of two almost complete but separated prearticulars, a pair of separated dentary crests, an adsymphysial, one complete and one incomplete surangular, two angulars, one complete and one incomplete splenial/postsplenial. The length at the symphysis is *ca.* half the total jaw length (table 3).

The ossified dentary is much reduced, consisting only of a crescent of bone in two parts, without any external bone connecting these with the infradentaries (figures 92*a* and 93*a*). The absence of signs of erosion or fracture along the edges of the dentary crescent, indicates that a bony connection was not lost during preservation. We do not consider the paired nature of the dentary as primitive for two reasons. First, all the Early and Middle Devonian dipnoan genera described to date, and most of the Late Devonian genera (Campbell & Barwick 1987), have a single dentary that is firmly joined to the infradentaries. Second, the other holodipterid species have dentaries like those of other Devonian dipnoans. The unique structure in *H.* (*Asthenorhynchus*) is therefore most probably derived.

The two parts of the dentary make a weak suture in the midline leaving a gap between them and the adsymphysial plate, as is normal for holodipterans.

The lateral and mesial crests of the dentary carry a single discontinuous row of dark-coloured teeth composed of hypermineralized dentine. In addition there are one or two isolated teeth behind this row at the mesial end of each half of the dentary. There is a gap in the row anterolaterally (figure 92*a*) where the crest is depressed; this depression presumably gave water access to the anterior naris while the mouth was closed. The teeth on the crest increase in size towards the lateral extremities of the bone. The tooth at the left extremity was accidentally removed during preparation, but has since been replaced. It has a distinct basal cavity beneath the dentine.

We use the term tooth rather than denticle for these structures because, although they are smaller than most teeth, they consist of hypermineralized dentine and have a basal pulp cavity (Campbell & Smith 1987). In such primitive genera as *Speonesydrion* there are slight thickenings of the dentine or denticles along the crest of the dentary but, to our knowledge, teeth have never been reported in this position in tooth- or dentine-plated genera. The presence of teeth in this position in *H.* (*Asthenorhynchus*) therefore supports the view that teeth, like denticles, can arise during development in any place where they are functionally necessary. Thus we see no reason to accept the view of Smith (1985, 1988) that dipnoan teeth, as defined above, require the presence of dental laminae that are unique structures.

Along the inner side of the tooth row (figure 92*a*), the teeth are bounded by a band of white superficial dentine with a sharp resorption edge. Inside this again is a broader band with small denticles.

The prearticulars (figures 92*a*,*b* and 93*a*,*b*) are thick bones that meet along a deep zigzag median suture. Each buccal surface is divided into two parts by the heel and the first (mesial) tooth row. The anterior (inner) part slopes steeply (almost vertically) down and then flattens towards the midline. The posterior (outer) part is shallowly inclined downwards towards the rear. At the posterior end of the lingual furrow the bone slopes steeply, and ventrally it is slightly recurved forwards. Most of the surface is covered with denticles, but white superficial dentine occurs along the mesial side of the first tooth row and between adjacent tooth rows. The number of denticles decreases posteriorly in the lingual furrow, and they disappear entirely on the posterior face of the bone. The four rows of teeth are very unequal in length. The first row is by far the longest and bears 5 or 6 teeth which clearly retain their identity back almost to the callus on the heel, with which that row is clearly connected. The teeth on the second, third, and fourth rows number 2 or 3, 2, and 1 or 2 respectively. White superficial dentine encroaches on the callus, filling embayments and showing signs of later resorption. Several teeth are undercut by resorption and the resorbed areas carry younger well-formed denticles. In the more posterior parts of the lingual furrow the denticles become increasingly sparse and finally disappear, leaving smooth bone. As on the pterygoids there are no marginal denticles.

The adsymphysial plate is broad and crescentic (figures 92*a* and 93*a*), and fits closely to the dentary. Its buccal surface is covered with small denticles except towards the midline where white superficial dentine forms a pair of eminences.

There are three infradentaries which are not sutured together, but narrowly overlap except in the midline where the margin of the right plate shows that they simply abutted each other (figure 94*a*). As in other holodipterans, we identify a surangular; an angular which is recognized by the entry of the mandibular canal towards its posterodorsal corner and the branching of the commissure from it (figures 77*a*,*b* and 94*a*,*b*); and a large mesial bone, the splenial/postsplenial, that extends from the angular to the midline. All three bones are thickest in their mesial parts where they carry low pustules. Elsewhere they thin out and are naked. Anteriorly all bones are thin and have zigzag margins. It is not known if any bone articulated with these margins. We consider it improbable that such a bone existed, because we have found no evidence of a thin bone of appropriate shape, and because the well-ossified dentary crest shows no evidence of a ventral continuation.

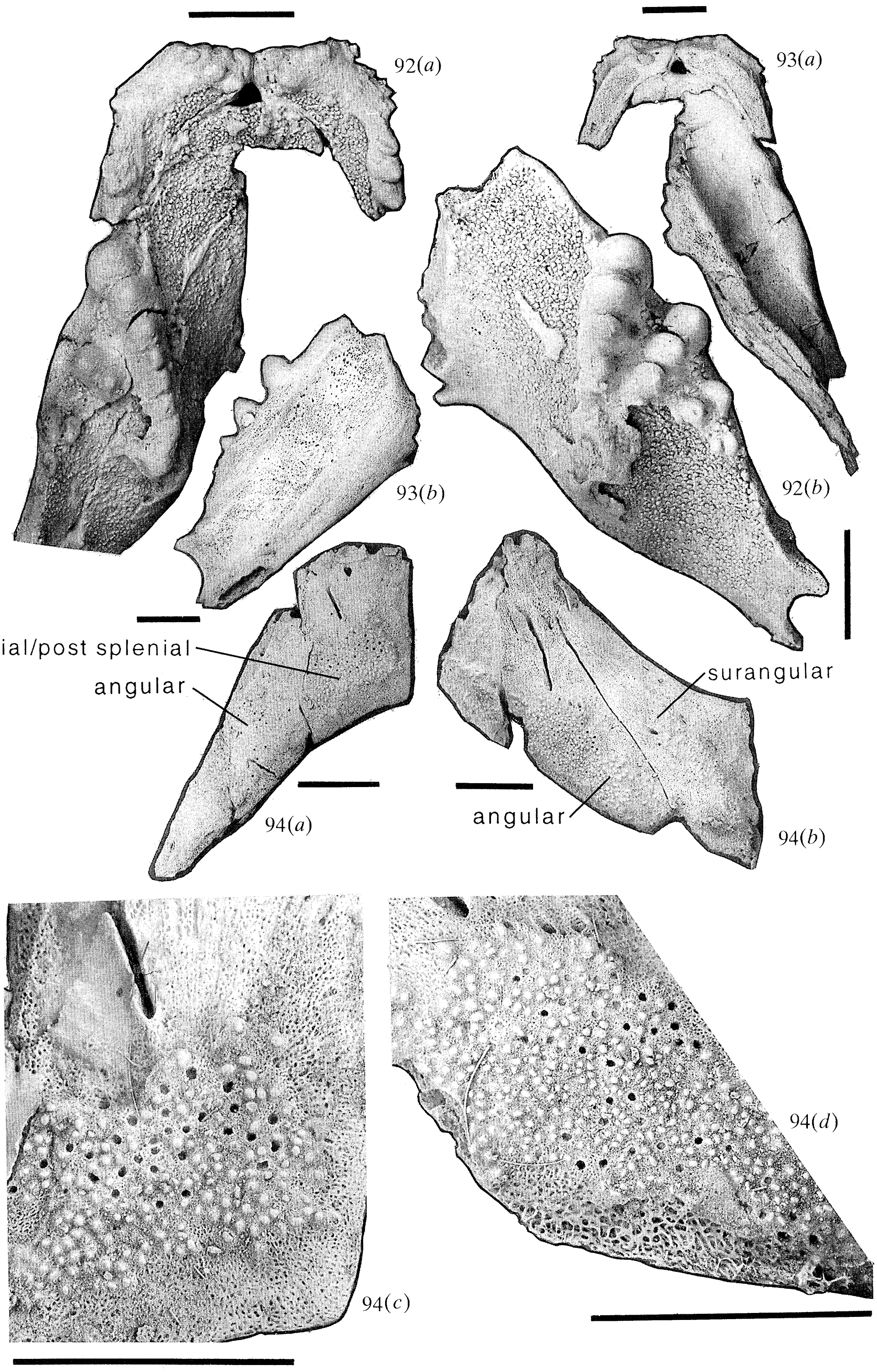
The surangular has a high naked dorsal blade with a concave edge for the adductor pit. At the anterior and posterior ends of this, the inner edge has flanges for articulation with the prearticular (figures 77*b* and 94*b*). By placing these in position it is possible to show that the surangular extends forwards only to the depression between the distal teeth of the first and second rows, whereas in *H.* (*Holodipterus*) *gogoensis* the surangular runs forwards into the labial pit anterior to the first row of teeth.

The angular is in the form of an attenuated triangle that extends back almost as far as the surangular, and much farther forwards than that bone. A narrow posterior band, and the entire anterior half of the bone are unornamented.

The splenial/postsplenial (figure 94*a*) has an overall rectangular outline, but its lateral margin is distinctly sinuous. The naked band on its posterior edge is wider than that on the angular. The anterior half is also naked, so that only about one-third of the surface is ornamented. Both this bone and the angular show the fine porous bone structure that we regard as common to all holodipterans (figure 94*c*,*d*).

The lateral lines have been studied in X-radiographs (figure 77*a*,*b*), which clarify a pattern that is suggested by specimens of the other subgenera. (See the discussion of *H.* (*Holodipterus*) *gogoensis*.) The oral canal reaches back on to the posterior third of the surangular. It runs anteroventrally from the ossification centre of this bone towards the ossification centre of the angular where it approaches, but does not meet, the mandibular canal. Anterior to this it is directed as a groove towards the anterior edge of the angular. The mandibular canal enters the jaw about 12 mm from the rear end of the angular, runs to the ossification centre of that bone, and then on to the centre of the splenial/postsplenial. There it gives rise to the anterior branch which runs into the anterolateral corner of that bone, as well as to the mesially directed commissural branch. On the anterior naked parts of the angular and splenial/postsplenial, the lateral lines form grooves with slit-like openings on the outer surface of the bone as in other holodipterans. Anterior to this the canal must have been embedded in soft tissue.

The scales of the flanks are well shown on the holotype, although a great deal of fracturing has occurred (figure 95). The scale pattern is very similar to that of *H.* (*Holodipteroides*), and that description may be consulted for details. Individual scales also



Figures 92–94. *H.* (*Asthenorhynchus*) *meemannae*. Scale bars = 10 mm.

Figure 92. Dorsal views of (*a*) much of the left ramus and the complete symphysis, and (*b*) the right prearticular of the holotype.

Figure 93. Ventral views of (*a*) much of the left ramus and the complete symphysis, and (*b*) the right prearticular of the holotype.

Figure 94. Infradentaries of the holotype in external view. The right splenial/postsplenial and angular are shown in (*a*), and the left angular and surangular with a fragment of the splenial/postsplenial are shown in (*b*). Details of bone structure are shown in (*c*) for the right splenial/postsplenial and in (*d*) for the left angular.

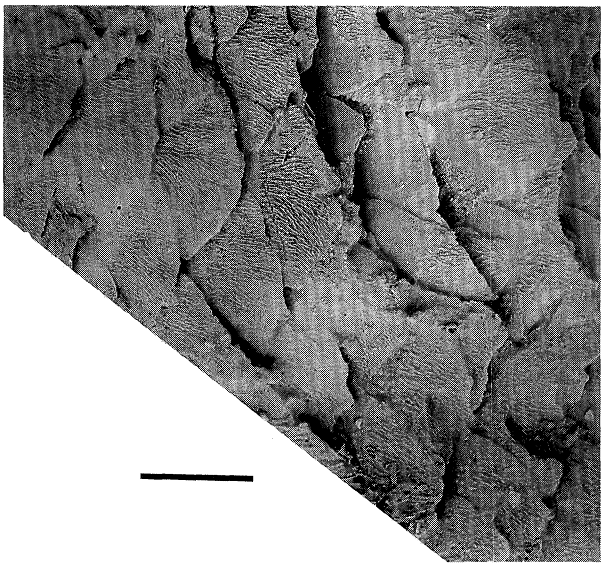


Figure 95. *H.* (*Asthenorhynchus*) *meemannae*. Block of scales of the holotype. Scale bar = 10 mm.

have the characteristic ornament of thin raised ridges on the exposed parts.

11. HOLODONTID (gen. et sp. indet.)

Material. ANU49107. A single specimen consisting of a small isolated palate complete anteriorly and truncated posteriorly through the corpus of the parasphenoid; a detached snout, and several dermal plates, all obtained from one small nodule.

Description. The snout is 24 mm across the lateral nasal ridges. It is relatively flattened, and its ventral surface is recurved (figure 96). As in other holodipterans the front of the snout is covered with dentine within which pores of two sizes can be seen. The largest are single or composite; the smaller ones are clumped. Posterior to this dentine-covered zone is a narrow band of cosmine that also has pores of the same types, together with cosmine pores. More posteriorly on paired roofing bones, the cosmine breaks down into fingers of enamel-covered dentine lacking pores for flask chambers. Internally the snout shows details of the rostral tubules and the openings into the pores of various kinds. This individual shows the arrangement of such pores as clearly as any dipnoan specimen with which we are acquainted.

An irregular group of four to six hypermineralized teeth is symmetrically placed on each of the paired preoral eminences. Four similar but flatter teeth lie at the extremity of the left lateral nasal ridge.

Several isolated dermal plates probably all came from the same individual, as they occurred in the same nodule. Most of these cannot be identified, but they have surfaces with multitudinous shiny pustules lying on bone showing the usual holodipteran pore system. Two plates which we judge to be from the edge of the skull in front of bone 1 have small patches of cosmine.

The palate is only 27 mm across the waist behind the tooth rows, making it the smallest holodipteran in the collection (figure 97). Its anterior angle is 30°, which is within the range of the smallest specimens of *H.* (*Holodipterus*) *gogoensis*. The margins bear a dense array of marginal denticles (figures 98 and 99) which anteriorly form three rows as in some specimens of *H.* (*Holodipterus*) *gogoensis* (Campbell & Smith 1987, figure 2B), but laterally only a single row is present. Where the tips of these are slightly worn, the ends of several pulp canals are visible. Some of these marginal denticles are almost totally embedded in bone, but others are virtually unworn and have high relief. This disposition of denticles indicates that the animal died just before a period of rapid lateral bone growth.

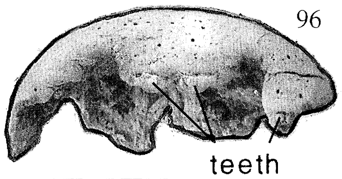
Within the array of marginal denticles, on each side of the specimen, are three enlarged 'denticles' which lie at the ends of radial rows of worn teeth (figures 97 and 98, arrows in figure 99). The largest is at the end of the most anterior row and is *ca.* three times the diameter of the neighboring denticles. The most anterior one on the left side has small denticles between it and the remainder of the row. Hypermineralized dentine forms the cores of these structures, which we therefore refer to as real teeth.

The posterior part of the palate is covered with a thick callus of hypermineralized dentine out of all proportion to the size of the specimen. It is *ca.* 3 mm thick on the exposed right lateral flank. Posteriorly the thick callus extends almost the whole width of the palate as a continuous sheet. Anteriorly it extends forwards as three projections: a narrow medial flanked on each side by a much broader lateral, which buttresses the inner ends of the second and third tooth rows. The laterals are cut by transverse resorption bands, two on the right and one on the left. The bulk of the callus consists of smooth continuous dentine, but its margins have a roughened surface formed from isolated columns of hypermineralized dentine which had not been completely incorporated into the main callus when the animal died.

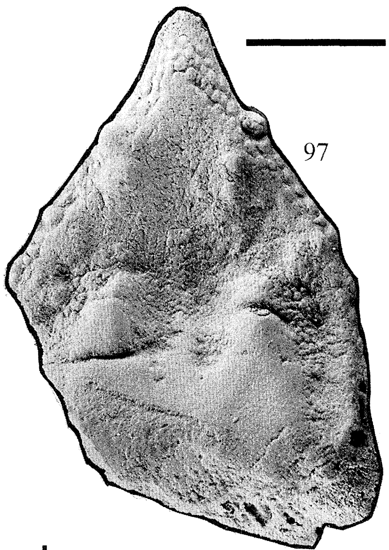
The anterior and most lateral parts of the palate are covered with white superficial dentine within which lie overgrown denticles and columns of dark coloured dentine. White dentine also occurs between the tooth rows and even between the individual teeth in a row in some places. This confirms that the animal died at the end of a stabilization phase and immediately prior to a major growth phase.

As is usual for holodipterans, the median ridge on the visceral surface shows no sign of a suture between the pterygoids. The quadrate ridge of the pterygoid is pronounced. Bone spaces within it are oriented parallel with the ridge length. In the junction between these ridges the anterior tip of the parasphenoid is clearly outlined by the orientation of its bone spaces. As in other holodipterans, this tip is acute. The internal structure of the parasphenoid is well shown in the naturally eroded section on the rear of the specimen (figure 100). In the middle of the interior there are well-spaced bony struts, but marginal to these is a layer of more finely vesicular bone. We can find no sharp boundary between the quadrate ridge of

96

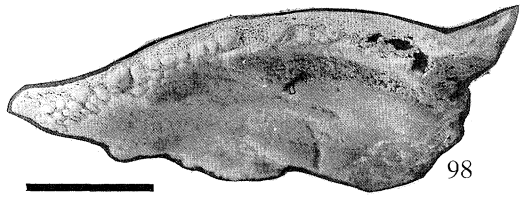


97

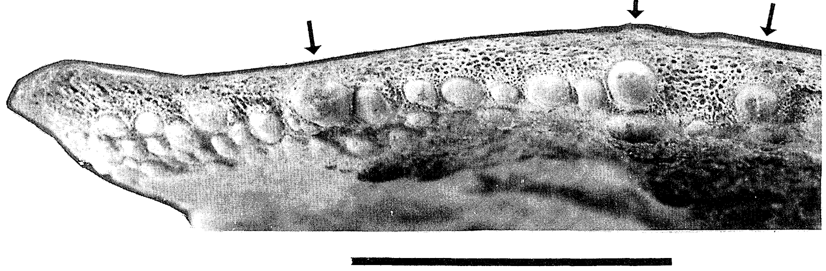


100

98



99



Figures 96–100. Holodontid gen. et sp. indet. Scale bars = 10 mm.

Figure 96. Anteroventral view of snout of ANU49107.

Figure 97. Ventral view of palate of same.

Figure 98. Lateral view of palate of same showing the position of the teeth at the ends of the rows lying within the group of marginal denticles.

Figure 99. Enlargement of lateral part of the palate of same. The arrows indicate the positions of the ends of the tooth rows.

Figure 100. Posterior view of palate of same, showing the bony struts within the corpus of the parasphenoid.

the pterygoid and the parasphenoid, but it is obvious that the vesicular structure extends well forwards to the anterodorsal tip of the bone. The front wall of the parasphenoid must therefore be high, and it probably slopes steeply anteroventrally. The preserved portion of the ventral surface of the parasphenoid is covered with the thick layer of hypermineralized callus dentine.

Remarks. The significance of this specimen is threefold. Firstly, the massive callus in such a small specimen shows that age is not the only controlling factor in the development of callus thickness, as might be concluded from an examination of *H.* (*Holodipterus*) *gogoensis* alone; accordingly it is valid to use the absence of a callus for the diagnosis of *H.* (*Holodipterus*) *longi*. Secondly, the position and size of the marginal teeth lend support to the contention that teeth may be formed from enlarged marginal denticles and are not necessarily the result of the presence of a complex dental lamina. Thirdly, it confirms previous conclusions about the nature of the corpus of the parasphenoid.

12. COMPARISON OF GOGO HOLODIPTERANS

Recently the concept of two evolving lineages (denticle shedding and dental plated) based on the mode of food reduction within Devonian Dipnoi (Campbell & Barwick 1990) has been contested by Schultze (1992). By using a number of non-dental characters, he concluded that his new genus *Iowadipterus* is a close relative of *Holodipterus*. Unfortunately the palate and prearticular tooth plates of *Iowadipterus* remain unknown, and he was forced to use external dermal bone characters to make his assignment. Of course the only way to be sure of the position of *Iowadipterus* is to etch the specimen and examine the buccal surfaces, but this option was not open to Schultze because etching was not permitted. Meanwhile he concluded that '*Iowadipterus* and *Holodipterus* are long-headed dipnoans with a short lower jaw, in contrast to long-headed forms with a long snout (*Griphognathus*, *Soederberghia*, *Rhynchodipterus* and *Fleurantia* with elongated rami, and *Rhinodipterus* with an elongated symphysis)'.

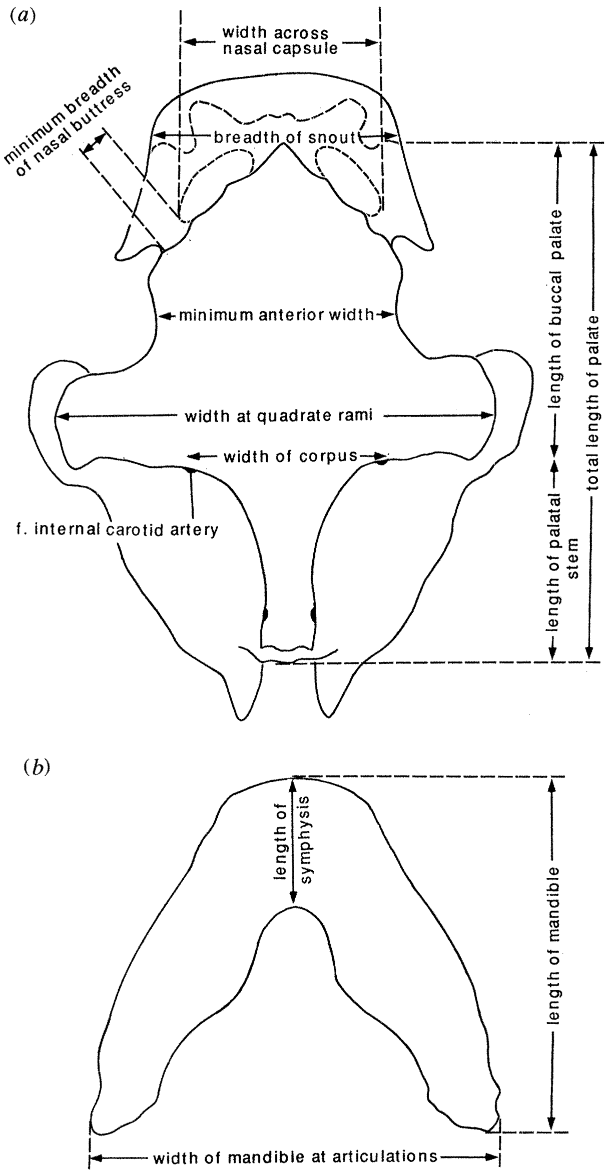


Figure 101. Diagrams illustrating dimensions measured on (*a*) the skulls and (*b*) the mandibles of Gogo holodipterans.

In making this statement he put the tooth plated genus *Rhinodipterus* together with a group of denticulated genera, and he omitted *Uranolophus* from the long-snouted denticulated group. Although *Uranolophus* is not as long-snouted as the other genera listed, it is longer snouted than Schultze indicated, because he misinterpreted the position of the eye in that genus (Schultze, figure 5C). A much better representation of the skull roof of the genus was given by Denison (1968, figure 3A), which is a reconstruction based on a single relatively complete specimen, and not on a composite as was that of Schultze. In our view, *Uranolophus* is the earliest known member of the denticle-shedding lineage which developed along two lines: one to *Griphognathus* with a very long snout and weak marginal structures on the palate, and one to *Holodipterus* with stronger marginal structures on the palate and a shorter snout. The functional reasons for this are now discussed.

We maintain our view that *Holodipterus* is a member of the denticle-shedding lineage which has secondarily developed a peculiar set of marginal and submarginal teeth which, unlike the teeth in normal tooth-plated genera, were subject to episodic shedding. It certainly does not fall into the long-snouted class, but we see no reason to believe that all denticle shedders should be of that type. On the contrary, all denticle shedders from *Uranolophus* onwards, used marginal structures to break down food to some degree, and such marginal structures ranged from ridges as in *Uranolophus*, to isolated protuberances as in *Griphognathus*, to teeth as in *Holodipterus*. As would be expected, the more efficient the initial breakdown mechanism, the less would be the emphasis on rasping. Consequently the length of the snout, which is related directly to the length of the basihyal/basibranchial and hence the length of the rasping device, would be decreased. Increased emphasis on the marginal palatal bite would require a strengthening of the mandibular symphysis. Such a scenario would account for the peculiarities of *Holodipterus* relative to the other members of the denticulate lineage, but strong morphological and stratigraphic evidence is needed to strengthen this interpretation of the affinities of holodipterans. Our reasons for retaining this view are adumbrated below.

In parenthesis we note that although the distinction between long-headed and long-snouted dipnoans is a valuable one, we see no evidence to support the view that it provides a basis for dismissing a phylogenetic scheme based on a variety of characters related to two independent means of breaking down food on the palate without the use of maxillary and premaxillary dentitions.

(*a*) ***Features in common with denticulated genera***

Cheek bones. The cheek of holodipterans has a long bone 10 extending forwards below 6 and 7 in the same manner as in *Griphognathus*, but not as in the dental-plated genera *Dipterus*, *Scaumenacia* and *Chirodipterus*. Bone 9, which carries the mandibular lateral line canal down from 8, is isolated from the bones in front. Specimens of *Griphognathus* from our collection, do not have this phenomenon preserved, but it is clear that the posterior edge of 10 is attached to the quadrate and that the bone behind it, labelled 9a by Miles (1977, figure 112), either is not firmly sutured or is entirely separated. The situation in *Soederberghia* is not clear because Lehman (1959) did not recognize the presence of the mandibular canal coming out of bone 5. We tentatively suggest that this is a feature of the denticulated group, and recommend that the position in *Soederberghia* be used as a test of the hypothesis that in this group bone 9 is separated from the bones anterior to it.

Lateral profile of the skull. Genera such as *Griphognathus* and *Soederberghia* have a characteristic depression in the skull roof anterior to the orbits. The lateral profile of the skull is thus concave. Although no known specimen of *H.* (*Holodipterus*) *gogoensis* has a complete skull roof, enough is preserved on some to show that it also had a concavity anterior to the orbits, but of course it lacked the elongated snout of the other genera. No dental-plated genera have such a characteristic. We also note that the snout, in lateral profile, is recurved ventrally in a manner similar to that of *Griphognathus*, rather than the high and upright profile characteristic of *Chirodipterus* and its allies.

Antorbital cheek pouches. As has been pointed out previously, the ventral edge of the anterior part of the cheek (the labial lamina of Miles 1977, figure 40) of *Holodipterus* is highly arched (Campbell & Smith 1987; Campbell & Barwick 1990). This arch lies above a deep pouch in the flank of the mandible. These two features indicate the presence of a large thick (muscular?) antorbital cheek which could collect food that had moved laterally from the buccal grinding surfaces, and could then recycle it by contracting the cheek. Dental-plated genera tend to have a straighter ventral edge on the cheek bones; evidently their mode of feeding did not require such lateral food recycling. We consider that extinct dental-plated genera, like the living ones, pulverized their food and extruded it through the mouth before sucking it in again for further processing. From what we know of the buccal space occupied by the basihyal/basibranchial in *Griphognathus*, there could have been no tongue pad to assist with the extrusion of food. This suggests that extrusion was not used by genera that rasped their food to break it down prior to swallowing.

Anterior end of the soft cheek. In *G. whitei* the area for the attachment of the soft cheek to the end of the subnasal ridge has the inner margin more posteriorly extended than the lateral margin. In the dental- and tooth-plated genera such as *Chirodipterus* the opposite arrangement occurs. Holodipterans (figures 3, 5 and 96) have the same pattern as *G. whitei.*

Number and type of dermopalatines and tooth plates. H. (*Holodipterus*) *gogoensis* has a number of loosely attached denticulated plates like those of *Griphognathus* (Miles 1977, figure 72), rather than a pair of narrow dermopalatines and a median anterior plate, as is found in *Dipnorhynchus*, *Chirodipterus* and *Dipterus*. *H.* (*Asthenorhynchus*) has at least one pair of denticulated dermopalatines that meet in the midline as in *G. whitei* and *Uranolophus wyomingensis*. These carry shedding denticles of the same type as those on the palate. A second dermopalatine, the Dpl_3 of Miles, with a deep lateral embayment to accommodate the anterior naris, is known only from *Griphognathus whitei* and holodipterans. In addition both have a number of small isolated denticulated tooth plates, some of which have hypermineralized teeth.

The significance of these dermopalatines and tooth plates is not difficult to discover. As Campbell & Barwick (1984) pointed out, on complete occlusion the dentary in *Griphognathus whitei* passed up above the edges of the pterygoids, and the plates in question would have prevented it obtruding into the base of the already shallow nasal capsule. As we have already noted, the dermopalatines 1 in *H.* (*Holodipterus*) *gogoensis* lie above the level of the pterygoids as in *G. whitei*, and the dermopalatines 3 lie still higher and form the inner margin of the external naris. Campbell & Smith (1987, figure 3D) have figured an articulated mandible and palate in which the dorsal edge of the mandible passes up beside the pterygoids exactly as in *G. whitei*. Hence we conclude that the dermopalatines served the same functions in the two species, namely protection of the base of the nasal capsule and the provision of an occlusal surface for the dentary. This is quite unlike the situation in the dental-plated genera.

Denticles inside the external naris. H. (*Holodipterus*) and *H.* (*Holodipteroides*) have *Griphognathus*-like denticles situated immediately inside the external naris, a feature not found in *Speonesydrion*, *Dipnorhynchus* or *Chirodipterus*. *H.* (*Asthenorhynchus*) has no ossified snout and so this feature would not have been preserved. In other characters this subgenus is a typical holodipteran, and failure to ossify should not disqualify it from membership of the group; nor should it influence discussions of relationships (Campbell & Barwick 1990, p. 14).

Teeth on the subnasal ridge and preoral eminence. Hypermineralized teeth occur on the subnasal ridges and the preoral eminences of some specimens of *G. whitei*. Our specimens of *H.* (*Holodipterus*) *gogoensis* and the Holodontid sp. indet. have teeth in the same positions. None of the dental-plated (dentine- or tooth-plated) species to which we have access have teeth in these positions.

Teeth and the plates of Holodontid sp. indet. One of our main concerns is the origin of dipnoan teeth. Whereas Smith (1985, 1988) has maintained that a special structure, the dental lamina, of complex derivation is required to produce dipnoan teeth, Campbell (in Campbell & Smith 1987), and Campbell & Barwick 1991 have maintained that dipnoan teeth may be just enlarged denticles that have developed in radial arrays. One of the problems in this discussion is a matter of definition. If teeth are defined solely on the basis of structure and position in a specimen, i.e. solely on morphological grounds, we have no difficulty in recognizing them. However, if in addition, the definition includes a concept of mode of formation, such as 'programmed to form in a pattern determined by the position of a dental lamina', it becomes impossible to identify teeth with certainty in a fossil.

The specimen described herein that cannot be assigned to a species or subgenus, has structures that have all the characteristics of enlarged marginal denticles; that is, they lie in the array of marginal denticles that are of the same kind and disposition as the marginal denticles of species of *Holodipterus* and they have the same shape and hypermineralized cores. The only difference is that they are somewhat larger. It seems likely that at certain points along the margin, denticles were programmed to grow larger than their fellows and that these continued to grow above the level of the palate when those adjacent to them were overgrown by the laterally expanding palate. This is unlike the way teeth are added in genera such as *Dipterus* or such Carboniferous genera as *Sagenodus*. In our opinion, it confirms the view that teeth, defined as enlarged conical or semiconical structures covered with enamel and having hypermineralized cores, are not so unusual that they must have evolved only once in dipnoan history.

The foramen for the intermandibularis V. In *G. whitei* this foramen lies near the end of the surangular and is continuous internally with a long anteriorly directed tube. In the dental-plated genera *Dipnorhynchus*, *Speonesydrion* and *Chirodipterus* the tube is more dorsally oriented and the foramen is on the ventral side of the articular. *Holodipterus* conforms to the *G. whitei* pattern. Their pattern suggests that the intermandibularis muscles extended farther back than on the dental-plated genera. This has implications for the role of this muscle in feeding in the two groups.

Bone structure. The surface of the dermal head bones of holodipterans is covered by pustules of shiny dentine-covered material. These pustules vary in size and density and lie on a thin layer of relatively dense bone, which is perforated by regularly spaced pores, each with a rim around its edge. These pores are not connected with the lateral line canals and, in fact, do not seem to join any tube system in the underlying bone. Where such pustules are not developed, particularly on the anterior parts of the head, cosmine occurs in patches. Beneath the dense bone is a basal layer of the usual strongly vesicular type found in other Devonian dipnoans. The scales have a similar arrangement of bone layers and, in addition, have a fine bone mesh forming the surface layer of the overlapped part found in most Devonian dipnoans of which we are aware. However, the edge of the overlap adjacent to the exposed surface has pustules that have a ring of hard tissue around all except the posterior edges. All these features can be matched precisely with those of *Griphognathus whitei* juveniles, although adults tend to be smooth, at least on the skull.

In the holodipterans the cranial dermal bones have strongly zigzag sutures in some areas. This is not a primitive feature, and it is not found in Devonian members of the dental-plated genera although it does occur in many Carboniferous forms with tooth plates, such as *Sagenodus*. *Griphognathus*, *Soderberghia* and *Jarvikia*, all of which have denticulated palates, and occur in Upper Devonian sediments, have zigzag sutures over part or whole of the head.

The hyoid system. This is not well known in holodipterans, but in *H.* (*Holodipteroides*) a well-preserved basihyal/basibranchial and fragments of the ceratohyal and hypohyal provide enough information to permit us to make definite reconstructions. The basihyal/basibranchial has a flat posterodorsal surface on which four denticulated plates were situated. These plates have white superficial dentine between the denticles like that of the palate during certain phases of development. When placed in position, these plates match almost precisely the curvature of the large, polished median callus on the palate, a fact that we interpret as indicative of the means of reducing food after it had been partly crushed by the marginal dental apparatus.

H. (*Holodipterus*) *gogoensis* and *H.* (*Holodipterus*) *longi* also have denticulated plates on the basihyal/basibranchial, but they are not as well preserved as those of *H.* (*Holodipteroides*) *elderae*. Nevertheless we regard their very presence as vitally significant, indicating that such plates are of general occurrence among holodipterans. This is a clinching argument in favour of the view that holodipterids are related to *Griphognathus*, a genus that has a more elongated snout and a less well-developed marginal dental apparatus, and consequently a longer basihyal and longer attached denticulated plates.

The pectoral girdle. As was indicated by Campbell & Barwick (1987), *Griphognathus* has a cleithrum on which the branchial lamina merges gradually with the external lamina and the two are set at a very obtuse angle. The branchial lamina runs from the dorsal extremity to the articulation with the clavicular branchial lamina, which also is long. Dental-plated genera such as *Chirodipterus*, *Sagenodus* and *Ctenodus* have branchial laminae that stand almost at right angles to the external lamina and do not reach to the dorsal end of the cleithrum. *H.* (*Asthenorhynchus*) is entirely comparable with *Griphognathus* in these features and is easily distinguishable from *Chirodipterus*. Our specimens of the girdles of the other subgenera of *Holodipterus* are not sufficiently well preserved to verify that this is a general holodipteran feature.

We assume that the branchial lamina defined the back of the gill chamber, and that the differences in shape and orientation reflect differences in the flows of water through these chambers as would be expected if our hypotheses about the two different modes of feeding are correct. This issue needs further investigation.

The anocleithrum is known from both *H.* (*Holodipteroides*) and *H.* (*Asthenorhynchus*). In both genera it is deep-bodied, sinuous in dorsal view, and has a short anterodorsal process. In these respects it is quite unlike that of *Chirodipterus australis*, *Pillararhynchus longi* and *Scaumenacia curta*, but we have no adequate specimens of *Griphognathus whitei* with which to compare it. Hence though we cannot claim a similarity with the denticulate lineage, we can show a difference from both dentine- and tooth-plated types.

The similarities between H. (Holodipterus) longi *and* Griphognathus whitei. As discussed above, in such characters as the number of tooth-like structures along the palatal margins, the lightness of ossification, the absence of calluses, and the shortness of the mandibular median symphysis, *H.* (*Holodipterus*) *longi* is unlike other species of *Holodipterus*, but similar to *Griphognathus whitei*. Despite this, it has the defining characters of the genus *Holodipterus*. These indicate that *H.* (*Holodipterus*) *longi* should not be regarded as phylogenetically closer to *Griphognathus* than it is to the species of *Holodipterus* that have been placed in the subgenera *Holodipteroides* or *Asthenorhynchus*. We prefer to conclude that *Holodipterus* and *Griphognathus* shared the genetic capacity to permit a number of morphological novelties, given the appropriate environmental stimuli. Several features shared by *H.* (*Holodipterus*) *longi* and *G. whitei* may be the consequence of a diet of soft foods.

(*b*) *Features in common with tooth-plated genera*

Of the features that holodipterans share with tooth-plated genera, some seem to be primitive for dipnoans and others convergent. Some of the primitive features that might be taken as indicative of a relationship with tooth-plated genera are the relatively short and truncated snout, the relatively well-developed pit for the adductor mandibulae, and the strengthening of the palate to carry marginal dentition. These features are present in all the Early Devonian dipnoan genera known. In the convergent category are the teeth which are known in a variety of types in the subgenera of *Holodipterus*. *H.* (*Holodipterus*) *gogoensis* has radial teeth that are restricted to the lateral parts of the tooth plates, but *H.* (*Holodipterus*) *longi* has teeth that are more like the isolated enamel-covered structures forming the marginal ridges of *Griphognathus*. *H.* (*Holodipteroides*) develops radial marginal ridges without invoking teeth of any kind. Thus not all holodipterans have teeth, and those that do include some that are not developed in the same way as those of the tooth-plated genera. Consequently, the teeth in *H.* (*Holodipterus*) *gogoensis* are regarded as convergent on those of the tooth-plated genera, a point that is supported by the sustantially different histology of teeth in normal tooth plates and in *H.* (*Holodipterus*) *gogoensis* (Campbell & Smith 1987, figures 15–18).

13. THE PHYLOGENETIC POSITION OF HOLODIPTERANS

We have shown that holodipterans have distinctive derived characters in common with *Griphognathus*. In addition, we have shown that conical enamel-covered teeth are not present in all members of the genus *Holodipterus*, and therefore they cannot be regarded as of primary significance in its definition. We have also shown that teeth in holodipterans were formed in a manner different from that of teeth in tooth-plated genera. The contention that conical enamel-covered teeth in dipnoans imply the presence of a dental lamina that is so complex a structure that it is likely to have evolved only once, is considered incorrect. Consequently, the view expressed by Smith (1985, 1988) and Smith & Chang (1990) that the presence of teeth requires that holodipterans be regarded as having been derived from a primitive tooth-plated form such as *Speonesydrion*, is without force.

We consider holodipterans to have the following primitive dipnoan characters:

1. Lateral line canal in J.
2. Lateral line canal in 3.
3. Lateral lines deeply buried in or beneath skull bones.
4. Both Y_1 and Y_2 present.
5. Snout short.
6. Strengthened palatal margins.
7. Relatively well-developed pit in the mandible for the adductores mandibulae.

The following characters are shared with the advanced members of the denticulated lineage of Campbell & Barwick:

8. Reduced cosmine on the external dermal bones.
9. Bone K not present as an isolated entity.
10. Concave lateral profile of skull roof.
11. Anterior furrow of mandible covered.
12. Moderately well-developed preglenoid process for the attachment of the adductores mandibulae.
13. Mandibular articulation semi-restricted.
14. Patterns of extensive remodelling of the dental surfaces.

Of these characters, numbers 8 and 9 are not unique to the denticulated lineage, but are found in Palaeozoic members of both dental-plated lineages also.

The following characters, which are advanced with respect to the primitive denticulated genus *Uranolophus*, appear to be restricted to the holodipterans within the denticulated lineage:

15. Teeth with complex dentine present.
16. A callus on the posterior part of the palate.
17. Callus and palate intergrown with hypermineralized dentine columns that were not resorbed during successive growth phases.
18. Corpus of parasphenoid covered dorsally and ventrally by thin layers of bone which are joined by numerous vertical bony struts.
19. Infradentaries reduced to three.
20. A perforation in the symphysis of the mandible between the dentary and the adsymphysial plate, opening down into the covered anterior furrow.

Of these characters, number 15 is also found in both dental plated lineages, although *Holodipterus* has very distinctive complexities in its tooth dentine (Campbell & Smith 1987, figures 10–12). Apropos of number 19, so far as we are aware, apart from the unrelated *Sorbitorhynchus*, holodipterans are the only dipnoans in which three infradentaries are present. The more advanced denticulated rhynchodipterans apparently have two infradentaries (Miles 1977, p. 197).

In addition, holodipterans are characterized by the possession of the following advanced character:

21. Jugular vein entering the lateral wall of the neurocranium via the foramen sphenoticum minus and a foramen in the post temporal wall beside that for the orbital artery.

As *Uranolophus* does not have the lateral wing of the neurocranium preserved, we cannot confirm its absence in that most primitive member of the denticulated lineage, although we note that a similar condition has been acquired independently in the dental-plated genus *Pillararhynchus*.

In view of the lack of data on other members of the Holodontidae, we are unable to indicate how widespread these advanced characters might be.

In many respects *Holodipterus* is not so advanced as *Griphognathus*, but its unique characters as listed above clearly indicate that it was a highly specialized genus within the denticulated lineage. It is easy to see how *Griphognathus* could have evolved from a common ancestor of both genera by the elongation of the snout and the rami of the mandible, the flattening of the snout to make a shovel-shaped form, modification of the marginal ridge, the further restriction of the jaw articulation, the extension of the basihyal and its denticulated plates, and the restriction of the supra-meckelian vacuity. Developments of this sort were envisaged in the phylogenetic scheme of Campbell & Barwick (1990).

We thank John Long (Western Australian Museum), Gavin Young (Australian Geological Survey Organisation) and Peter Forey (British Museum (Natural History)), for making available specimens from the collections of their respective institutions. Moya Smith (Guy's & St Thomas's Hospitals) provided us with measurements of a number of specimens housed in the British Museum (Natural History) for which we are most grateful. We have benefited from discussions with Moya Smith and Chang Mee-mann on matters about which we continue to disagree. Val Elder, Claire Findlay and Melissa Fellows prepared many of the specimens. Keith Herbert and Chris Foudoulis assisted with the preparation of photographic negatives and Wal Ambrose prepared the X-radiographs. This work was supported by an A.R.C. Grant to K.S.W.C. and R.E.B.

REFERENCES

Arratia, G. & Schultze, H.-P. 1991 Palatoquadrate and its ossifications: development and homology in osteichthyans. *J. Morph.* **208**, 1–81.

Bemis, W.E. 1987 Feeding systems of living Dipnoi: anatomy and function. *J. Morph. Suppl.* **1**, 249–276.

Bertin, L. 1958 Appareil circulatoire. In *Traité de Zoologie – Anatomie Systématique, Biologie* (ed. P. P. Grassé), vol. 13(2), 1399–1458. Paris: Masson et Cie.

Bertmar, G. 1966 The development of skeleton, blood-vessels and nerves in the dipnoan snout, with a discussion on the homology of the dipnoan posterior nostrils. *Acta Zool.* **47**, 81–150.

Campbell, K.S.W. 1982 Lungfishes – alive and extinct. *Field Mus. nat. Hist. Bull.* **52**, 3–5.

Campbell, K.S.W. & Barwick, R.E. 1982 A new species of the lungfish *Dipnorhynchus* from New South Wales. *Palaeontology* **25**, 509–527.

Campbell, K.S.W. & Barwick, R.E. 1983 Early evolution of dipnoan dentitions and a new genus *Speonosydrion*. *Mem. Ass. Australas. Palaeontols.* **1**, 17–49.

Campbell, K.S.W. & Barwick, R.E. 1984 The choana, maxillae, premaxillae and anterior palatal bones of early dipnoans. *Proc. Linn. Soc. New South Wales* **107**, 147–170.

Campbell, K.S.W. & Barwick, R.E. 1987 Paleozoic lungfishes – a review. *J. Morph. Suppl.* **1**, 93–131.

Campbell, K.S.W. & Barwick, R.E. 1988 Geological and palaeontological information and phylogenetic hypotheses. *Geol. Mag.* **125**(3), 207–227.

Campbell, K.S.W. & Barwick, R.E. 1990 Paleozoic dipnoan phylogeny: functional complexes and evolution without parsimony. *Paleobiology* **16**(2), 143–169.

Campbell, K.S.W. & Barwick, R.E. 1991 Teeth and toothplates in primitive lungfish and a new species of *Holodipterus*. In *Early vertebrates and related problems of evolutionary biology* (ed. Chang Mee-mann, Liu Yu-Hai & Zhang Guo-rui), pp. 429–440. Beijing: Science Press.

Campbell, K.S.W. & Barwick, R.E. 1994 The Late Devonian dipnoan, *Pillararhynchus*, from Gogo, Western Australia, and its relationships. *Palaeontographica*. (In the press.)

Campbell, K.S.W. & Smith, M.M. 1987 The Devonian dipnoan *Holodipterus*: dental form variation and remodelling growth mechanisms. *Rec. Aust. Mus.* **39**(3), 131–167.

Cheng Hong 1989 On the tubuli in Devonian lungfish. *Alcheringa* **13**, 153–166.

Denison, R. H. 1968 Early Devonian lungfishes from Wyoming, Utah and Idaho. *Fieldiana Geol.* **17**(4), 353–413.

Forster-Cooper, C. 1937 The Middle Devonian fish fauna of Achanarras: *Dipterus*. *Trans. R. Soc. Edinb.* **59**, 223–240.

Fox, H.H. 1965 Early development of the head and pharynx of *Neoceratodus* with a consideration of its phylogeny. *J. Zool., Lond.* **146**, 470–554.

Goodrich, E.S. 1930 *Studies on the structure and development of vertebrates*. London: MacMillan & Co.

Gorizdro-Kulczycka, Z. 1950 Les Dipneustes dévoniens du Massif de Ste.-Croix. *Acta Geol. Polonica* **1**, 53–105.

Jarvik, E. 1980 *Basic structure and evolution of vertebrates*, vol. 1. New York: Academic Press.

Kesteven, H.L. 1945 The cranial nerves of *Neoceratodus*. *Proc. Linn. Soc. New South Wales* **70**, 25–33.

Lehman, J.-P. 1959 Les Dipneustes du Dévonien supérieur du Groenland. *Medd. Grønland* **160**, 3–58.

Long, J.A. 1992 *Gogodipterus paddyensis* (Miles), gen. nov., a new chirodipterid lungfish from the Late Devonian Gogo Formation, Western Australia. *The Beagle* **9**, 11–20.

Miles, R. S. 1977 Dipnoan (lungfish) skulls and the relationship of the group: a study based on new specimens from the Devonian of Western Australia. *Zool. J. Linn. Soc. Lond.* **61**, 1–328.

Moy-Thomas, J.A. & Miles, R.S. 1971 *Palaeozoic fishes*, 2nd edn. London: Chapman and Hall.

Northcutt, R.G. 1987 Lungfish neural characters and their bearing on sarcopterygian phylogeny. *J. Morph. Suppl.* **1**, 277–298.

Romer, A.S. 1937 The braincase of the Carboniferous crossopterygian *Megalichthys nitidus*. *Bull. Mus. Comp. Zool. Harvard* **82**(1), 1–73.

Rudebeck, B. 1945 Contributions to forebrain morphology in Dipnoi. *Acta Zool.* **26,** 9–156.

Schultze, H.-P. 1969 *Griphognathus* Gross, ein langschnauziger Dipnoer aus dem Oberdevon von Bergisch-Gladbach (Rheinisches Schiefergebirge) und von Lettland. *Geol. Palaont.* **3**, 21–79.

Schultze, H.-P. 1992 A new long-headed dipnoan (Osteichthyes) from the Middle Devonian of Iowa, USA. *J. Vert. Paleont.* **12**(1), 42–58.

Schultze, H.-P. & Campbell, K.S.W. 1987 Characterisation of the Dipnoi, a monophyletic group. *J. Morph.* **1**, (Suppl.), 25–37.

Smith, M.M. 1985 The pattern of histogenesis and growth of tooth plates in larval stages of extant lungfish. *J. Anat.* **140**, 627–643.

Smith, M.M. 1988 The dentition of Palaeozoic lungfishes: a consideration of the significance of teeth, denticles, and tooth plates for dipnoan phylogeny. In *Teeth revisited, Proceedings of the VIIth international symposium on dental morphology, Paris, 1986* (ed. D. E. Russell, J.-P. Santoro & D. Sigogneau-Russell) (*Mém. Mus. natn. Hist. nat., Paris* **C53**), pp. 179–194.

Smith, M.M. & Campbell, K.S.W. 1987 Comparative morphology, histology and growth of the dental plates of the Devonian dipnoan *Chirodipterus*. *Phil. Trans. R. Soc. Lond.* B **317**, 329–363.

Smith, M.M. & Chang Mee-mann 1990 The dentition of *Diabolepis speratus* Chang and Yu, with further consideration of its relationships and the primitive dipnoan dentition. *J. Vert. Paleont.* **10**(4), 420–433.

Thomson, K.S. & Campbell, K.S.W. 1971 The structure and relationships of the primitive Devonian lungfish – *Dipnorhynchus sussmilchi* (Etheridge). *Peabody Mus. nat. Hist., Yale Univ. Bull.* **38**, 1–109.

Wang Shitao, Drapala, V., Barwick, R.E. & Campbell, K.S.W. 1993 A new dipnoan genus, *Sorbitorhynchus*, from the Lower Devonian of Guangxi, China. *Phil. Trans. R. Soc. Lond.* B **340**, 1–24.

Watson, D.M.S. & Gill, E.L. 1923 The structure of certain Palaeozoic Dipnoi. *Zool. J. Linn. Soc. Lond.* **35**, 163–216.

White, E.I. & Moy-Thomas, J.A. 1940 Notes on the nomenclature of fossil fishes. Part II. Homonyms D.-L. *Ann. Mag. nat. Hist. Lond.* (11), **6**, 98–103.

Received 7 December 1992; revised 7 July 1993; accepted 1 December 1993

APPENDIX

Twelve measurements are listed for various specimens in tables 1–3. These measurements (figure 101) are defined as follows:

Total length of palate is the distance from the anterior tip of the palate to the posteriormost part of the stalk of the parasphenoid. This is the sum of the two immediately following measurements.

Length of buccal palate is the distance from the anterior tip of the palate to a line joining the back edges (ventrally viewed) of the pterygoids.

Length of palatal stem is the distance from a line joining the back edges of the pterygoids (ventrally viewed) to the posteriormost part of the stalk of the parasphenoid.

Width of palate at quadrate rami is the distance between the point of most lateral contact (ventrally) of the quadrate ramus of the pterygoid with the quadrate on one side and the equivalent point of contact on the other side.

Minimum width of anterior palate is a measure of the minimum breadth of the anterior portion of the palate in the area of 'waisting'. This is posterior to the marginal projections of the hindmost tooth rows and anterior to the quadrate rami.

Width of corpus of parasphenoid is an approximate measure of the maximum breadth of this bone obtained by determining the distance separating the internal carotid foramina on opposite sides of the skull.

Width across nasal capsules is the distance separating the most lateral margin of the nasal capsule on one side from the most lateral margin of its pair.

Breadth of snout at tip of palate is the distance separating the outer surfaces of the dermal bone on each side of the snout at the level of the tip of the palate.

Minimum breadth of nasal buttress is the narrowest thickness of the broad buttress of bone immediately postero-laterad of the nasal capsule.

Length of mandible is the distance from the medial anterior tip of the mandible to a point midway between the posteriormost portion of each ramus. It is measured in the plane of the mandible.

Length of mandibular symphysis is the distance between the medial anterior tip of the mandible and the posterior margin of the symphysis. It is measured in the plane of the mandible.

Width of mandible at articulations is the distance separating the most lateral point on the articulatory region of each ramus.

Figure 1. *H.* (*Holodipterus*) *gogoensis*. Dorsal view of ANU49102, showing the perichondral ossification of the inner and outer walls of the neurocranium, the dorsolateral and median cristae, the nerve canals in the snout and the remaining external dermal bone of the snout. Scale bar = 10 mm.

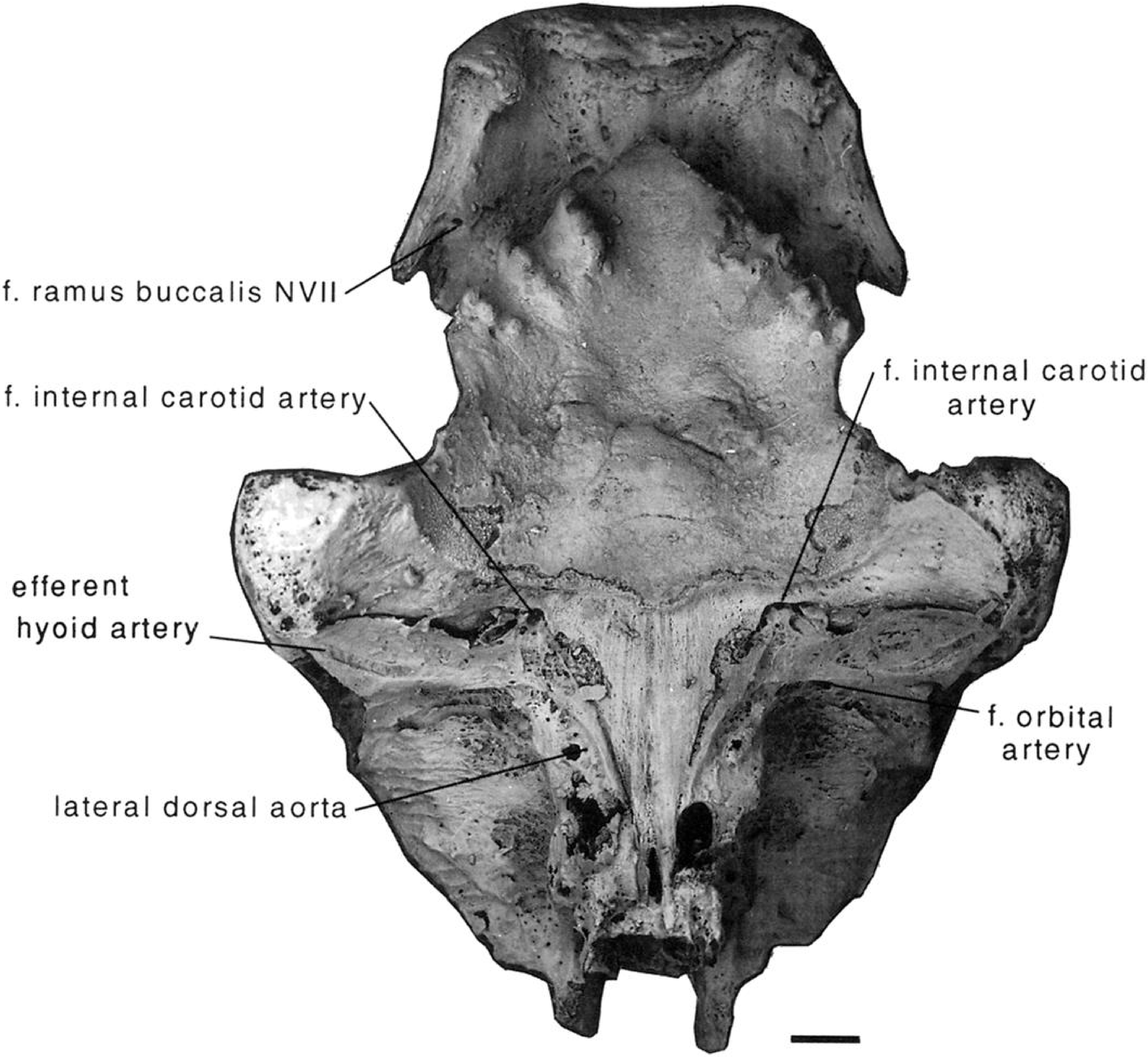
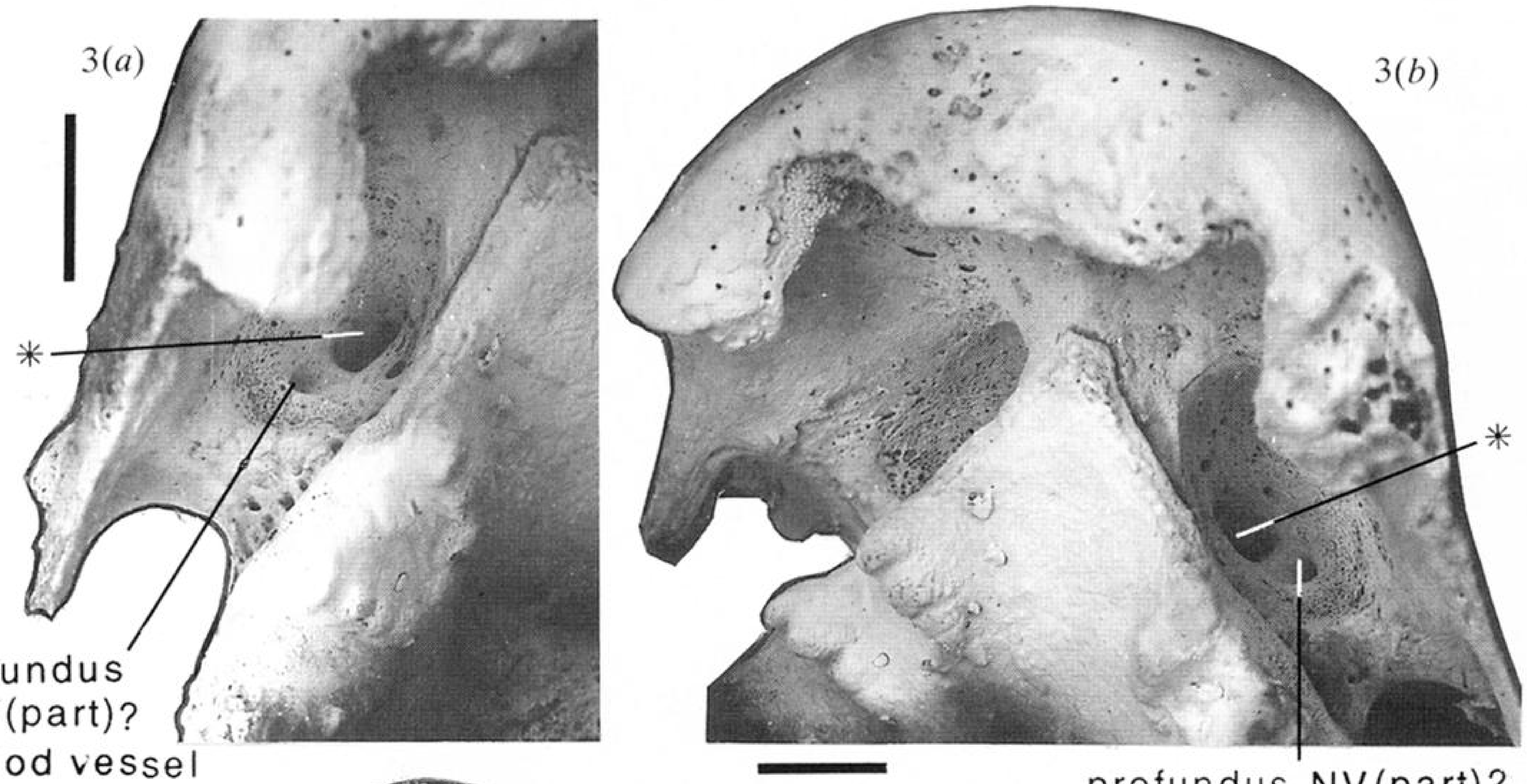
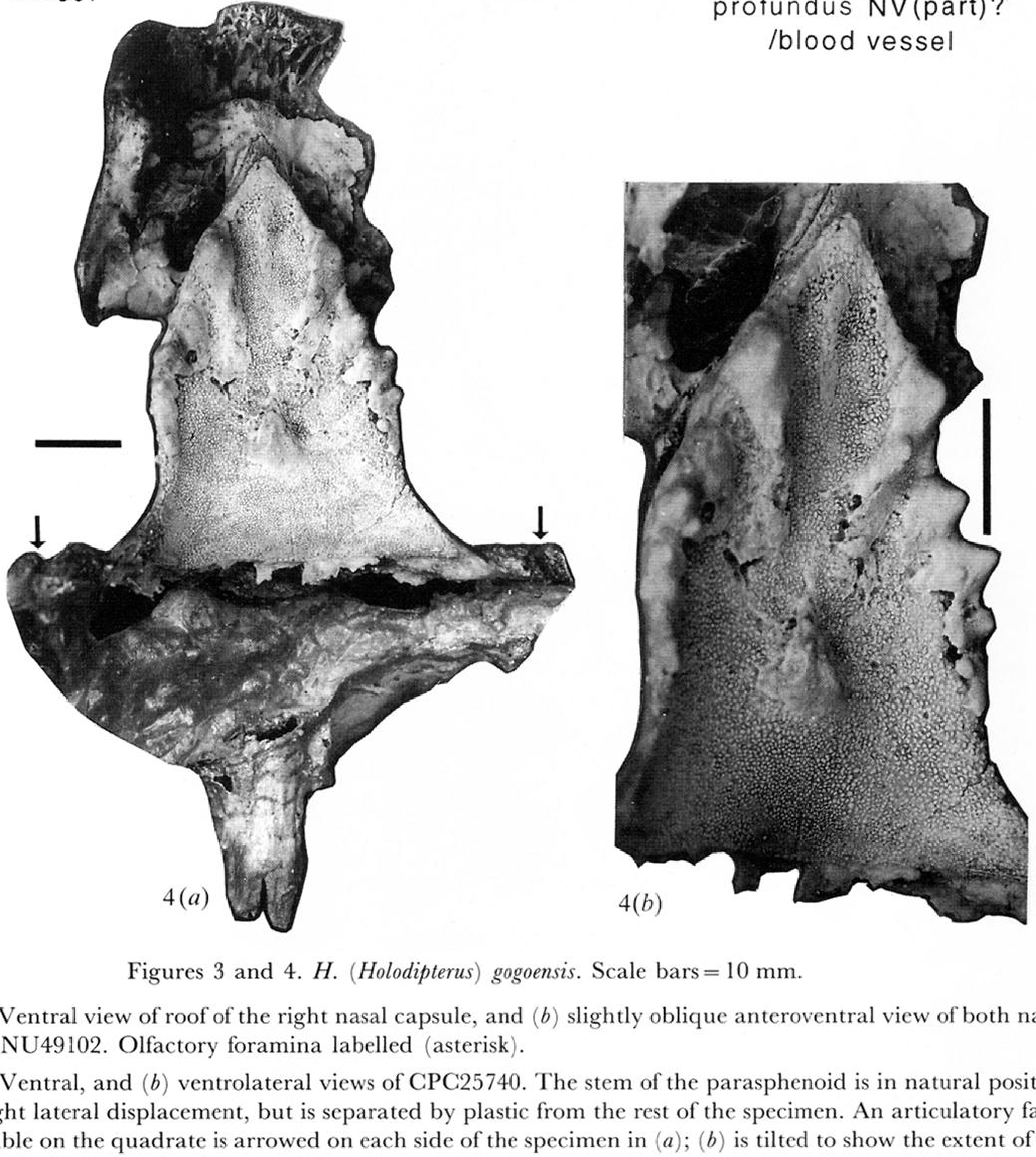


Figure 2. *H.* (*Holodipterus*) *gogoensis*. Ventral view of ANU49102 showing palate, roof of nasal capsules, parasphenoid and occipital area. Scale bar = 10 mm.

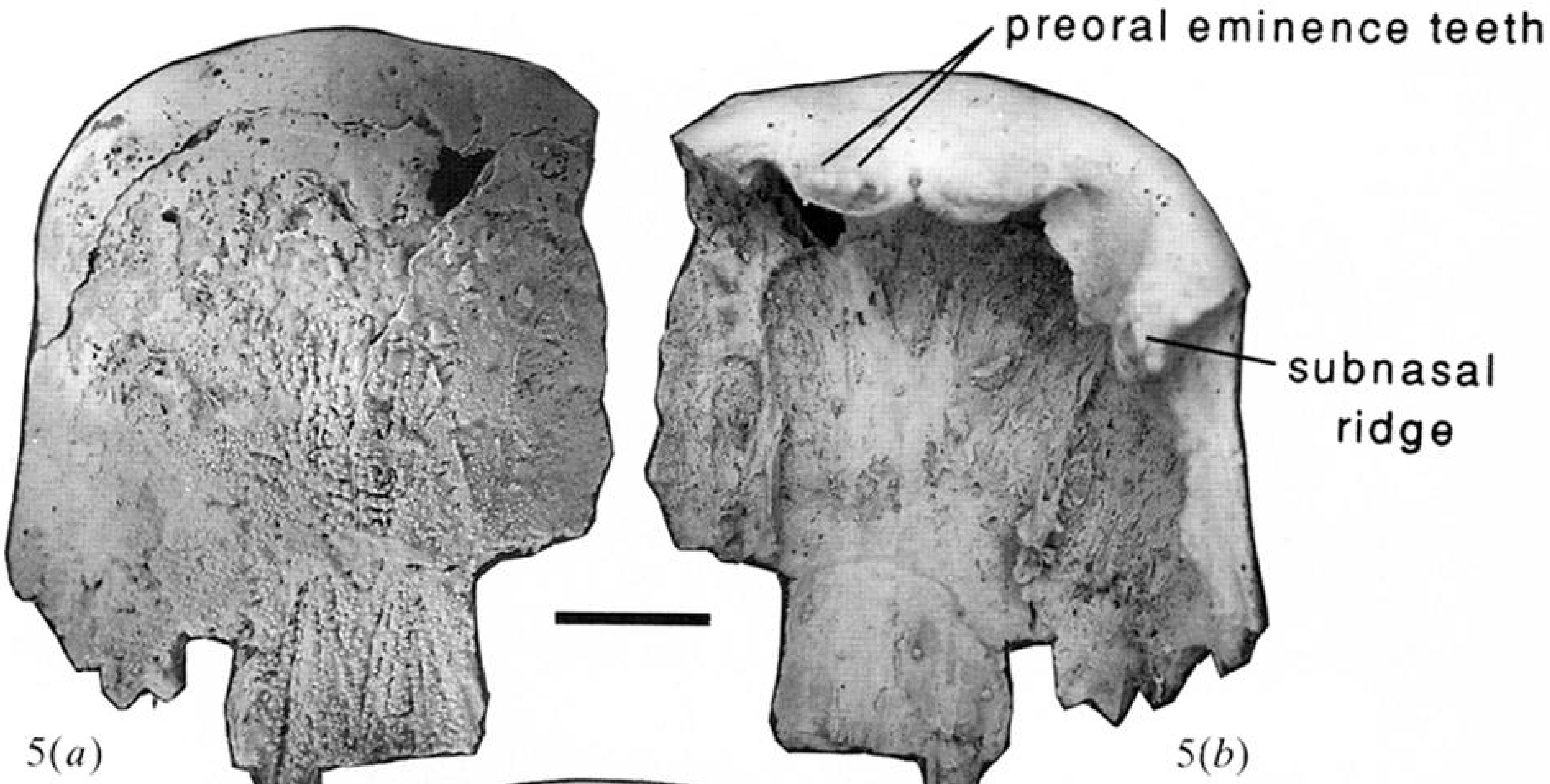


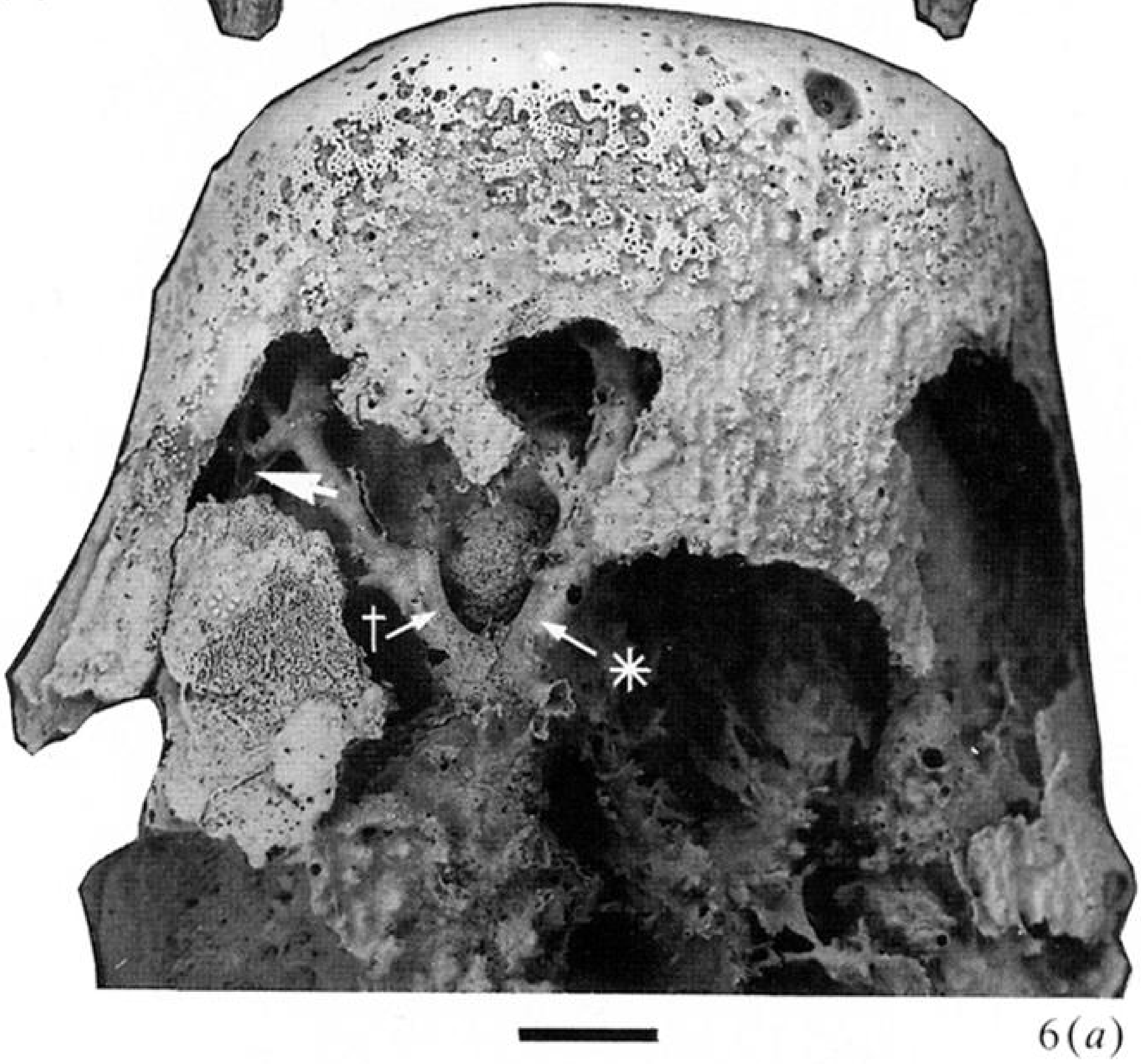


Figures 3 and 4. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figure 3. (*a*) Ventral view of roof of the right nasal capsule, and (*b*) slightly oblique anteroventral view of both nasal capsules of ANU49102. Olfactory foramina labelled (asterisk).

Figure 4. (*a*) Ventral, and (*b*) ventrolateral views of CPC25740. The stem of the parasphenoid is in natural position except for slight lateral displacement, but is separated by plastic from the rest of the specimen. An articulatory facet for the mandible on the quadrate is arrowed on each side of the specimen in (*a*); (*b*) is tilted to show the extent of the resorption at the lingual ends of the tooth rows.





Figures 5 and 6. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figure 5. (*a*) Dorsal view of snout of CPC25740 showing ossification centres. (*b*) Ventral view of same showing remnants of the lateral line canals, and teeth on the subnasal ridge and the preoral eminence.

Figure 6. (*a*) Dorsal view of snout of ANU49102, showing detail of surface of dermal bones and branching canals both for the ophthalmicus superficialis and a mesial ramus of the ophthalmicus profundus (asterisk), and for a lateral ramus of the ophthalmicus profundus (dagger) nerves. The large white arrow indicates a branch of the buccalis nerve. (*b*) Reconstruction of the orbit and snout in left dorsolateral view to show the positions of the major nerves and the orbital artery. The reconstruction is based mainly on ANU49102 in which the neurocranium has been weathered through dorsal to the perichondral bone investing the the brain. The fine bony tubules and struts joining the inner and outer perichondrial layers of the neurocranium have been omitted on the left side for clarity. Instead we have shown the passage of the nerves and artery between the inner and outer neurocranial walls as encased in a bony collar. Details of the inner ear are not well known in *H.* (*Holodipterus*) *gogoensis*, and for this figure data from *H.* (*Holodipteroides*) *elderae* has been used. The size of the eyeball is arbitrary.

6(*b*)


lateral dorsal cristae
eroded edge of neurocranium
fine bony trabeculae
ramus ophthalmicus superficialis NVII
ramus ophthalmicus profundus NV
sacculus dorsalis
anterior vertical canal
optic NII
median crista
posterior vertical canal
pineal foramen
superior sinus
inner perichondrium of neurocranium
ramus accousticus NVIII
olfactory tract
vagus NX
branches of ophthalmicus superficialis NVII & ophthalmicus profundus NV
horizontal canal of inner ear
glossopharyngeus NIX
left nasal capsule
ramus hyomandibularis NVII
lateral branch of opthalmicus profundus NV
orbital artery
orbital artery
buccal branch NV_2
ramus maxillaris NV_2
branch mandibularis NV_3
ramus buccalis NV_2 & NVII

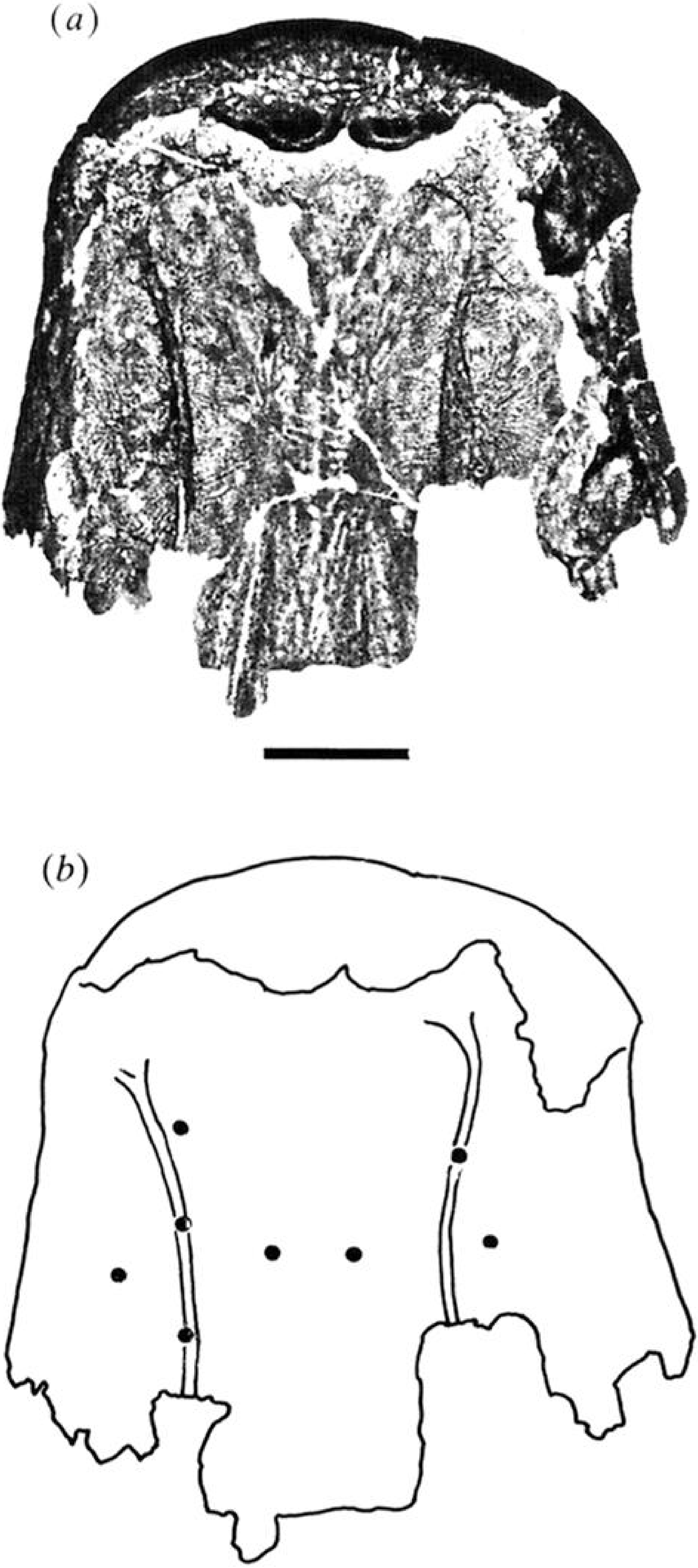
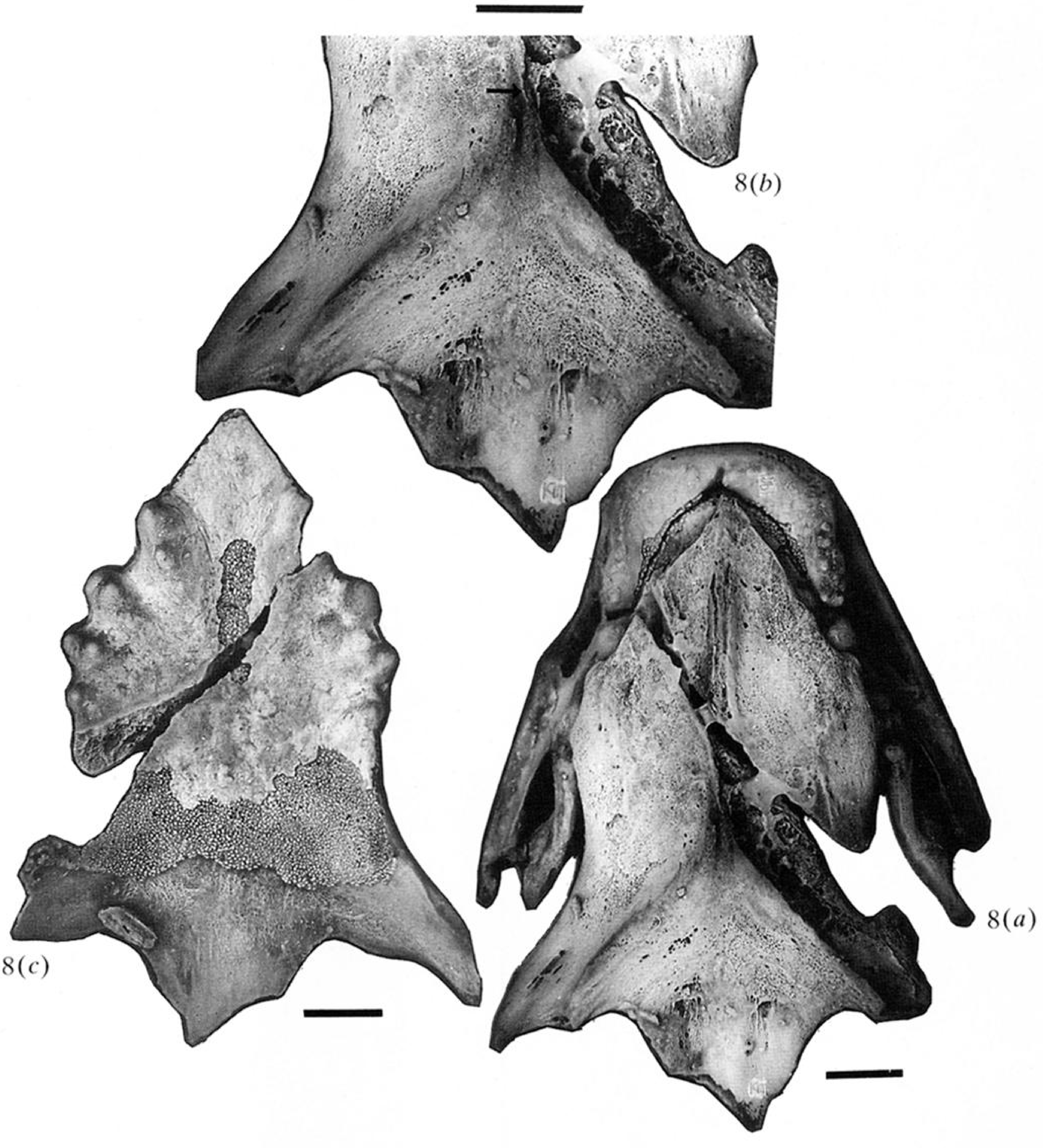


Figure 7. *H.* (*Holodipterus*) *gogoensis*. (*a*) X-radiograph of CPC25740 showing ossification centres and lateral line canals. (*b*) Diagram of same with ossification centres indicated by dots and the lateral lines shown. Note that bones were rejoined to the right side of the specimen between the time that the photographs for figures 5*a*,*b*, and the radiographs for this figure were made (cf. figures 5*a*,*b*). Scale bars = 10 mm.



Figures 8. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm. (*a*) Dorsal view of palate of CPC25738 with the mandible in position. Note the teeth on the dentary, and the three major ridges on the palate. (*b*) Enlargement of dorsal view of parasphenoid of same showing differences in bone texture between the corpus and the stalk. Note the foramina for the vascular canals at the posterior of the corpus, and the forward extension of the tip of the parasphenoid between the pterygoids (arrowed). (*c*) Ventral view of the same palate showing resorption of white superficial dentine and replacement by denticles.

Figure 9. *H.* (*Holodipterus*) *gogoensis*. Ventral view of the anterior part of the holotype showing the loose plates in the subnasal region. Scale bar = 10 mm.

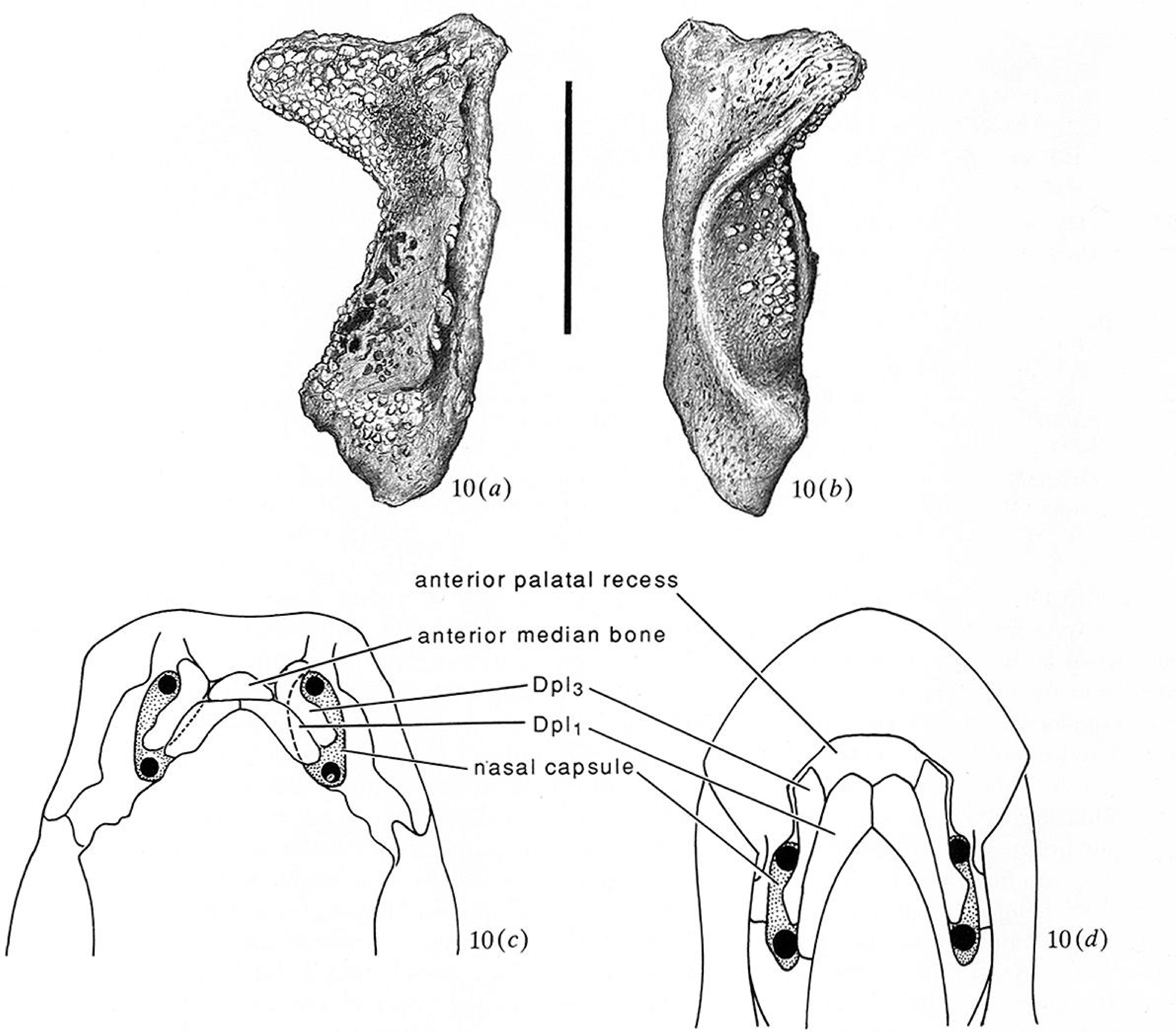
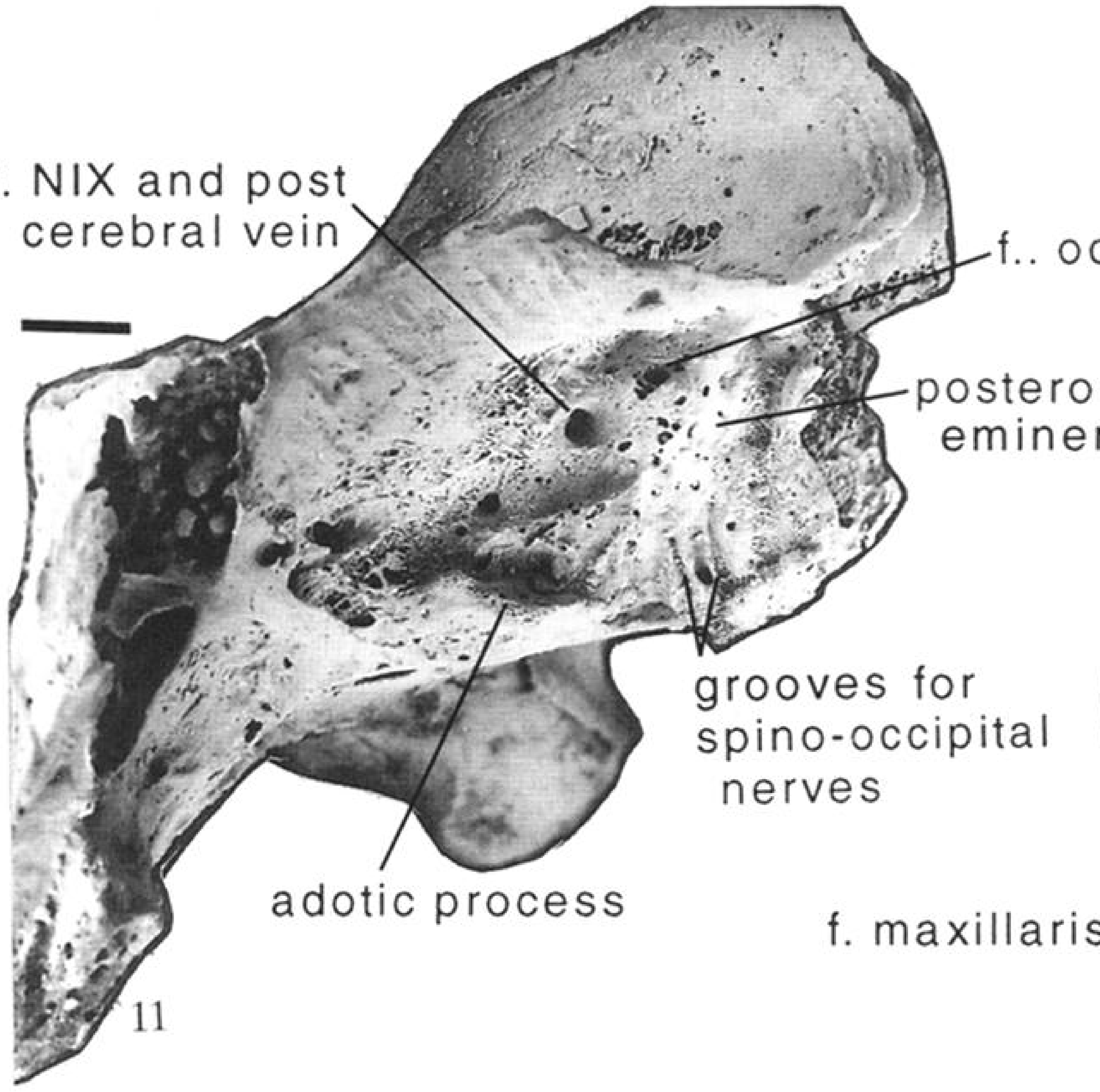
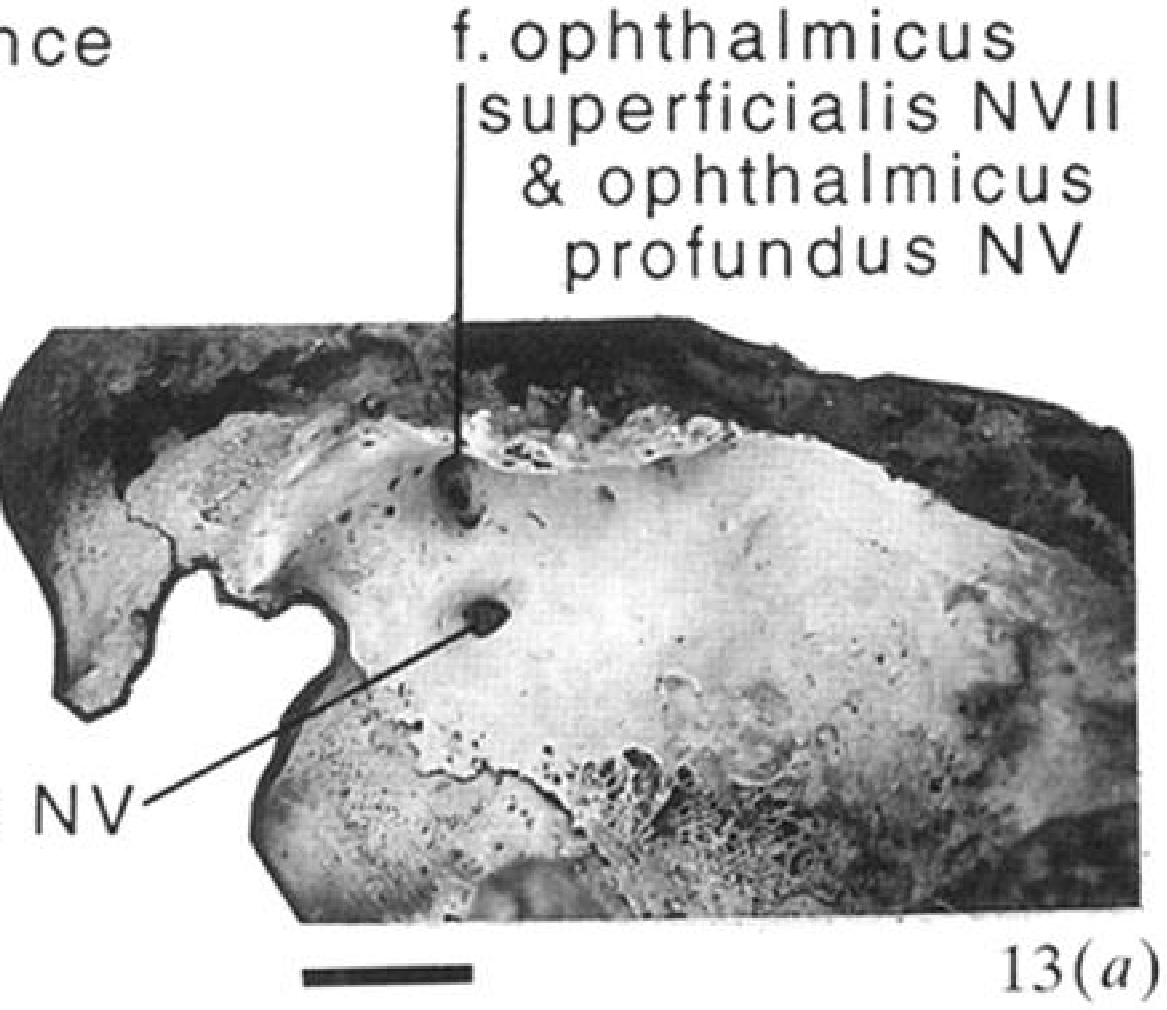


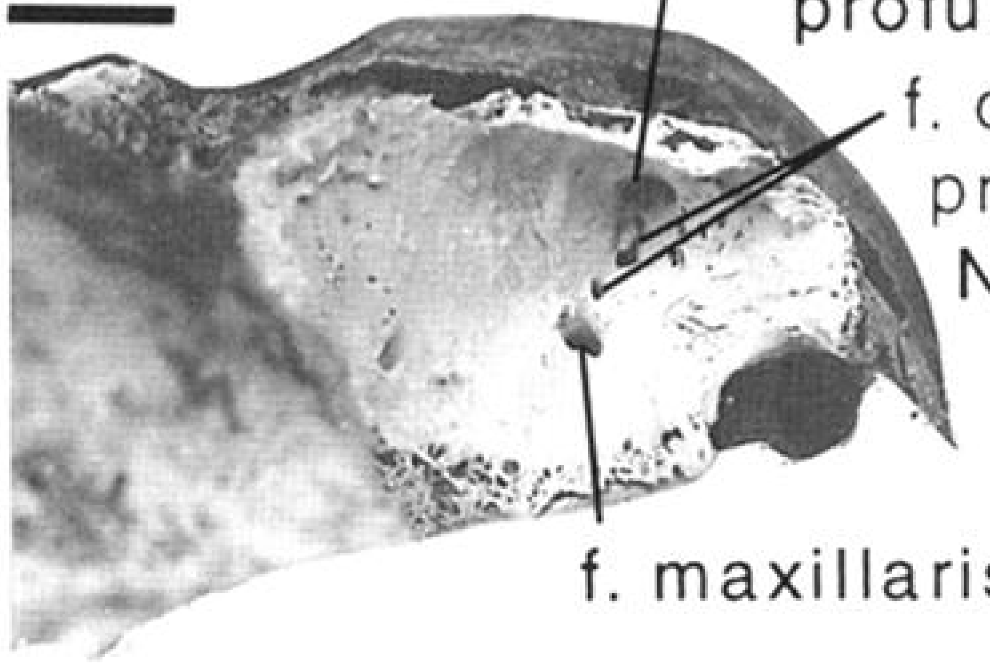
Figure 10. *H.* (*Holodipterus*) *gogoensis*. (*a,b*) Drawings of an isolated dermopalatine 3, ANU49179, from an unidentified specimen in ventral and ventrolateral views. (*c*) Reconstruction of the anterior half of the palate of the holotype showing the inferred relative positions of the dermopalatines. (*d*) Comparative diagram of *Griphognathus whitei* based on Campbell & Barwick (1984, figure 7E). Scale bar = 10 mm



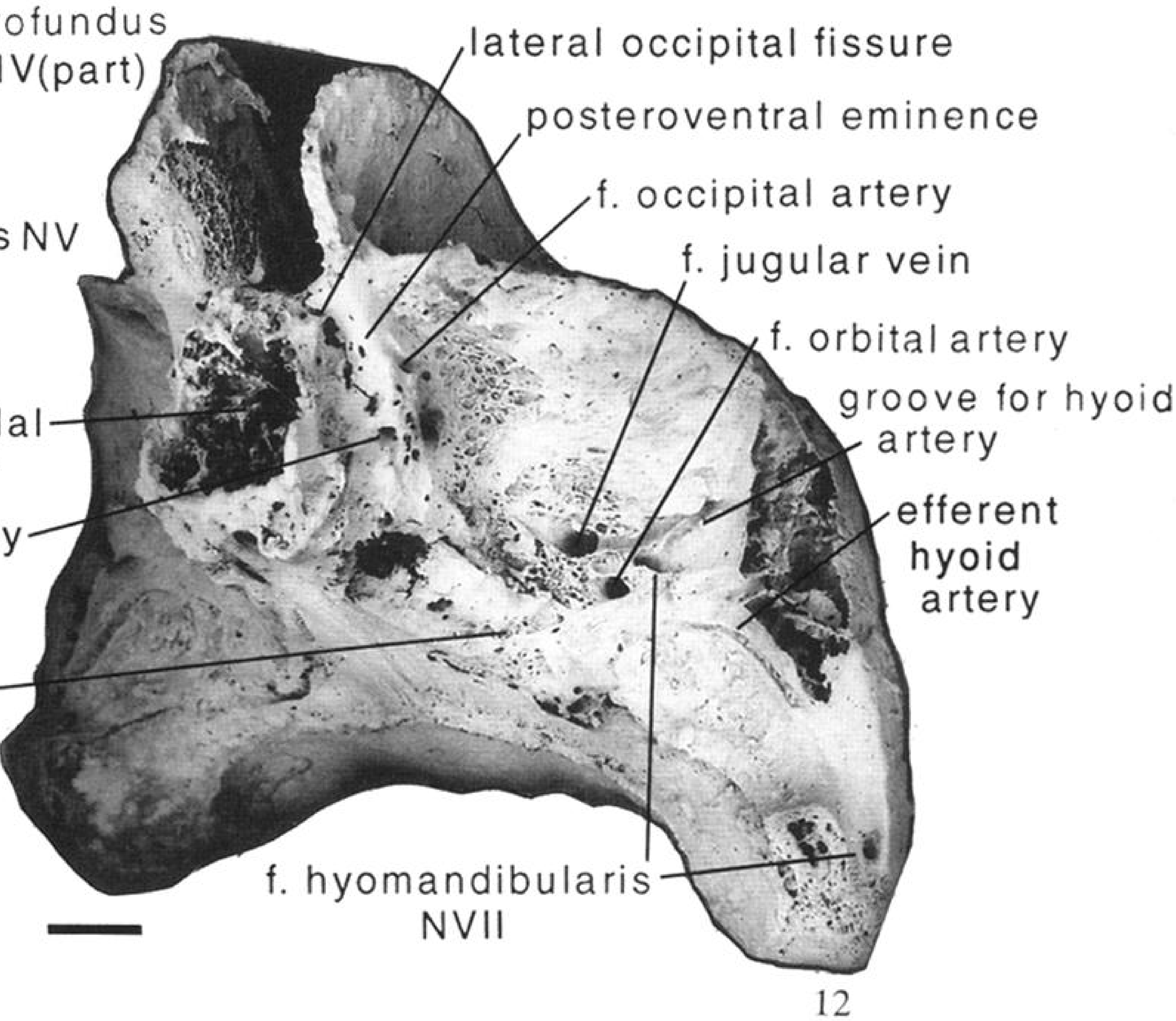
11



13(*a*)



13(*b*)



12

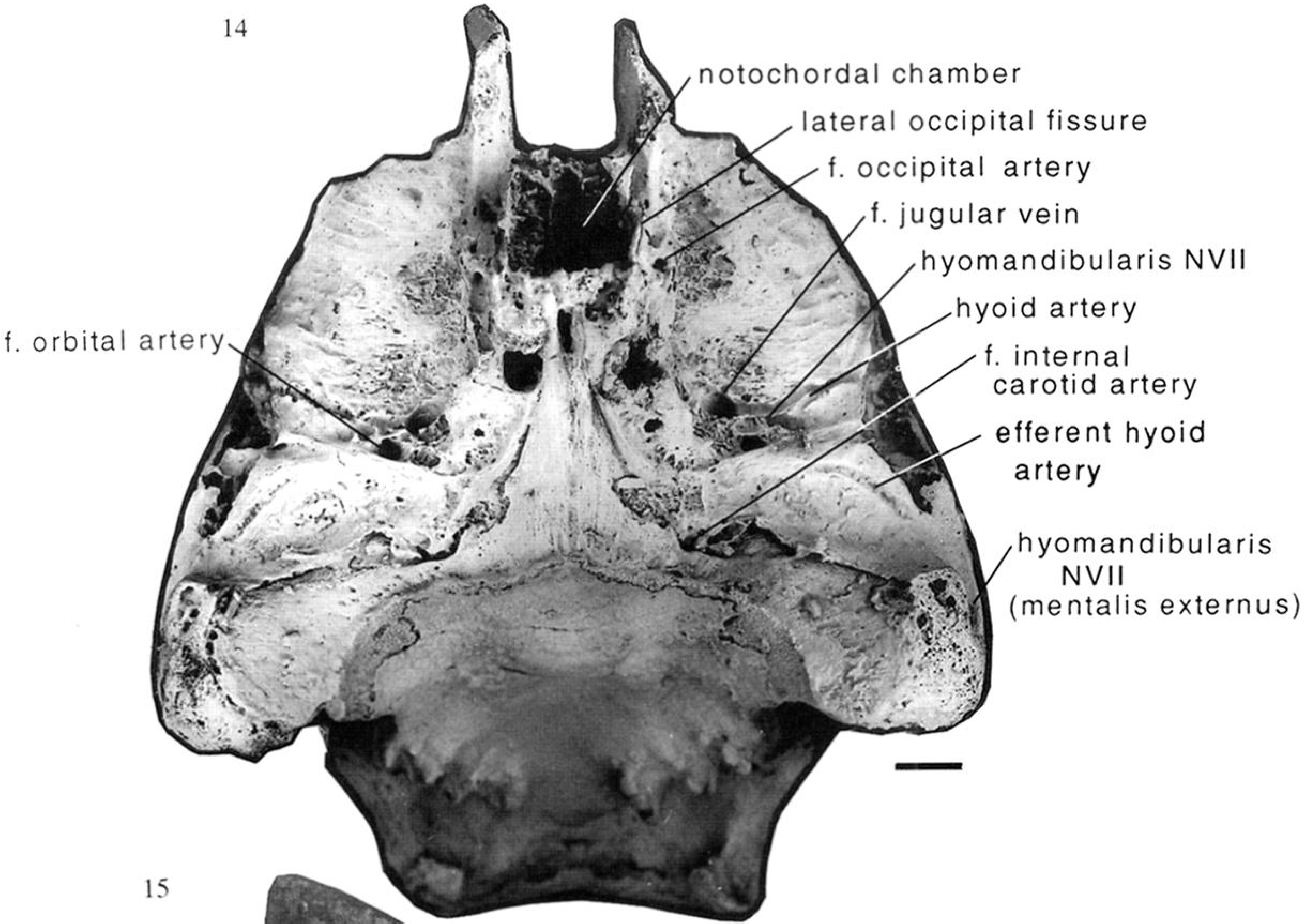
Figures 11–13. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figure 11. Posterolateral view of the left side of the occiput of ANU49102 (fNIX lies 10 mm anteroventrally to the indicated post-cerebral vein foramen).

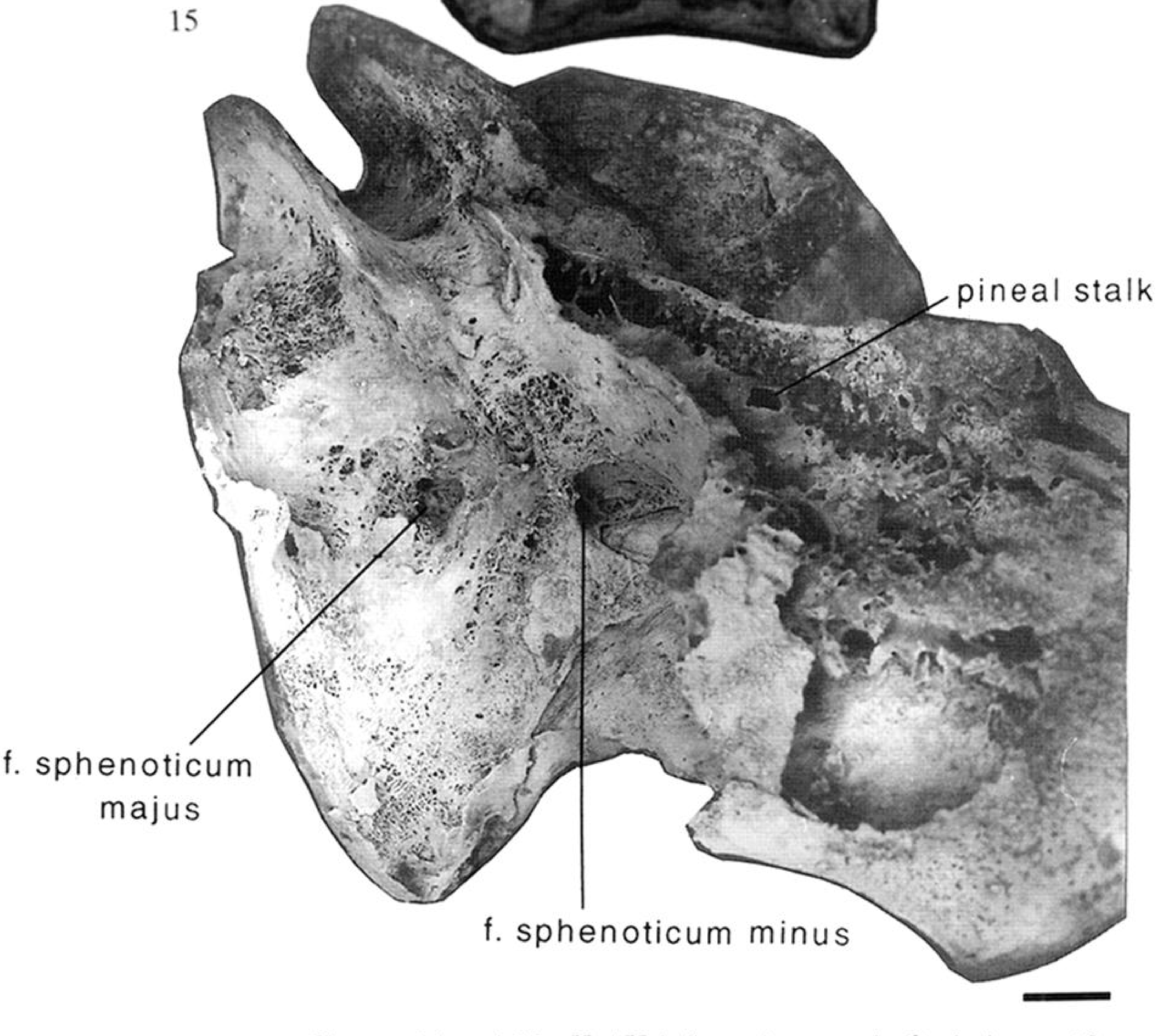
Figure 12. Posterolateral and slightly ventral of the rear of the skull of ANU49102.

Figure 13. Posterior views of the antorbital walls of (*a*) the left and (*b*) the right sides of ANU49102.

14



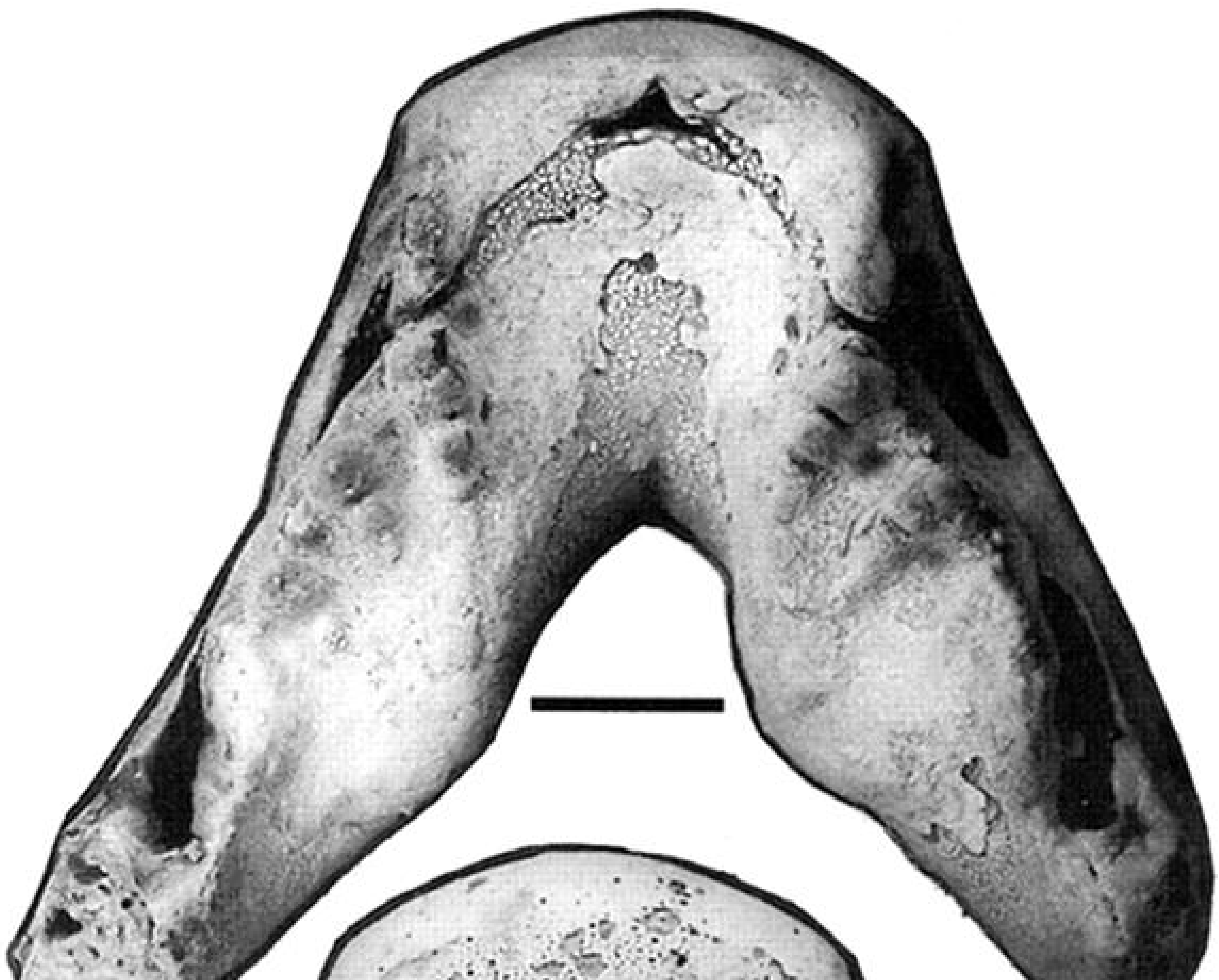
15



Figures 14 and 15. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

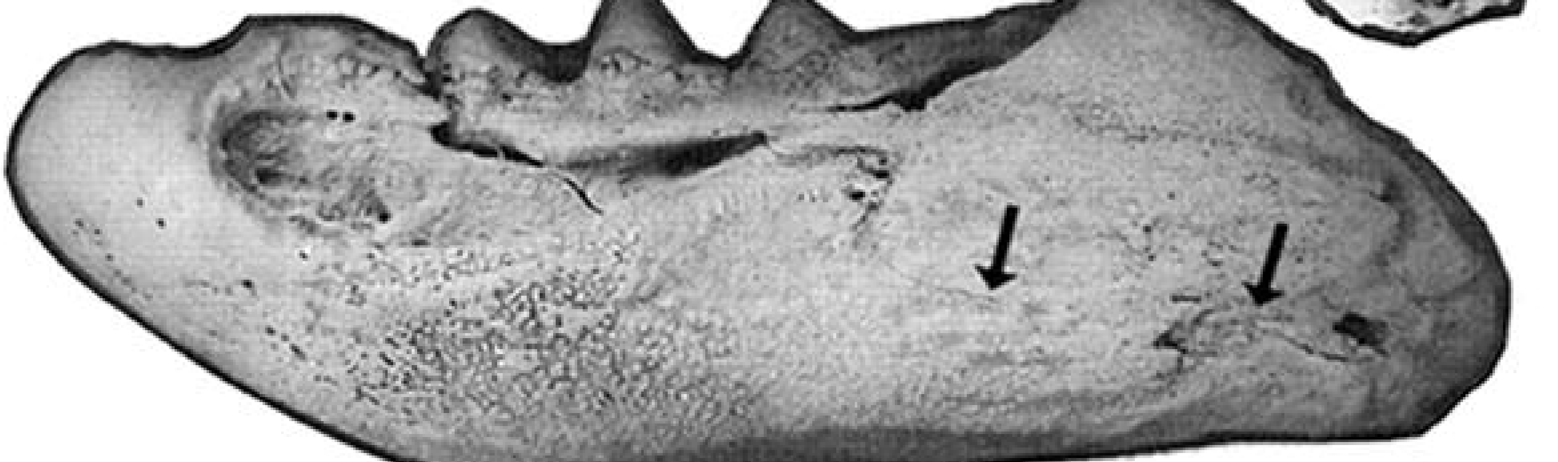
Figure 14. Posteroventral view of skull of ANU49102.

Figure 15. Antero-dorso-lateral view of same.

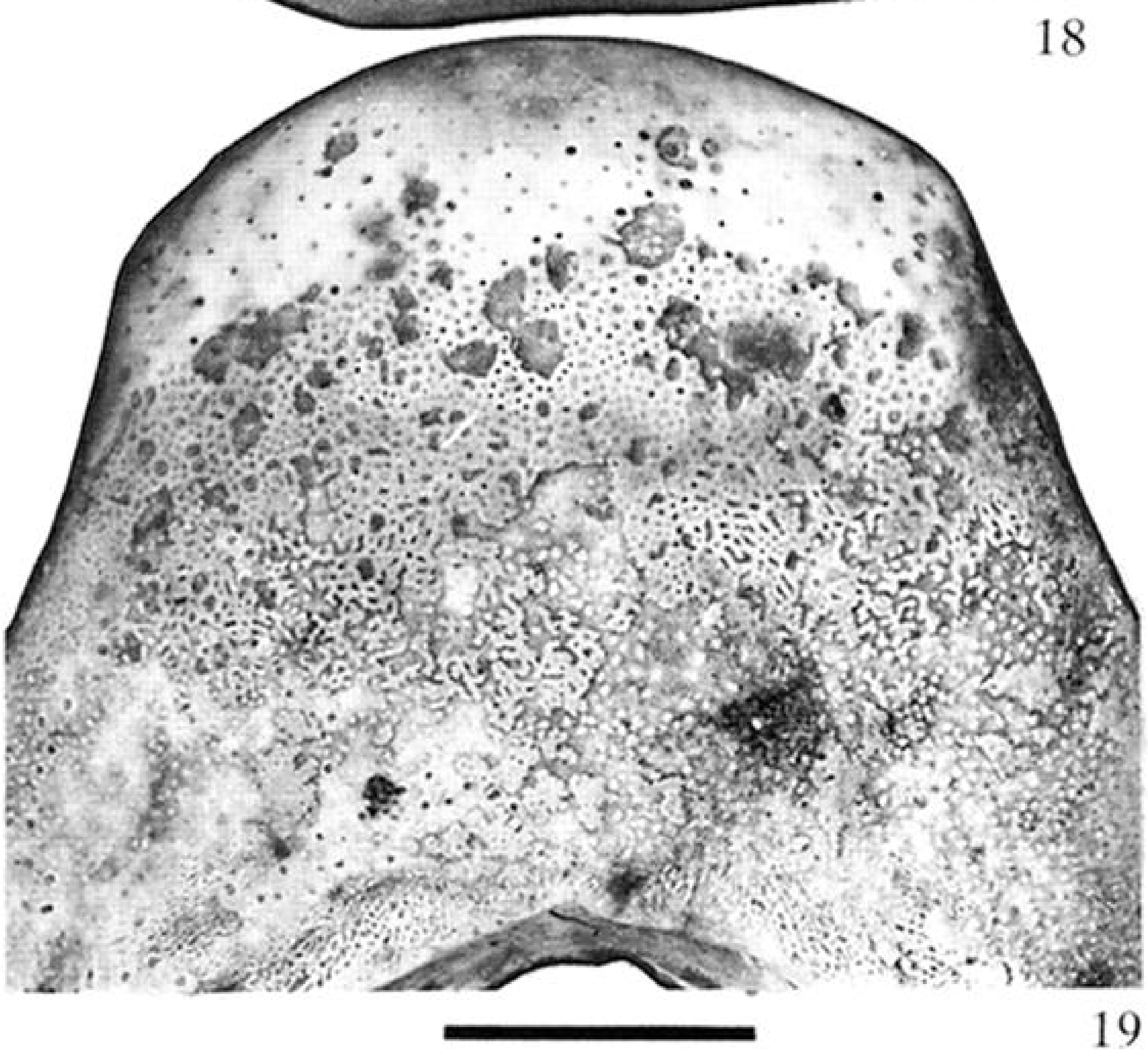


16

17



18



19

Figures 16–19. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figures 16–18. Dorsal, ventral and lateral views of the mandible ANU49104. Note the suture (arrowed) between angular and the splenial/postsplenial in figure 17, and between the surangular and the angular in figure 18.

Figure 19. Ventral view of the anterior of the mandible of ANU49104 showing variation in the dentine coating and in the shape and size of pores on different parts of the surface.

Figures 20–23. *H.* (*Holodipterus*) *gogoensis*. Scale bars = 10 mm.

Figures 20–22. Dorsal, ventral and dorsolateral views of the mandible of CPC25738. Note the resorption and replacement patterns of the dentine in figures 20 and 22.

Figure 23. Enlargement of anterior ventral surface of same. Note the absence of cosmine anteriorly and anterolaterally, and the variation in pore size and structure.

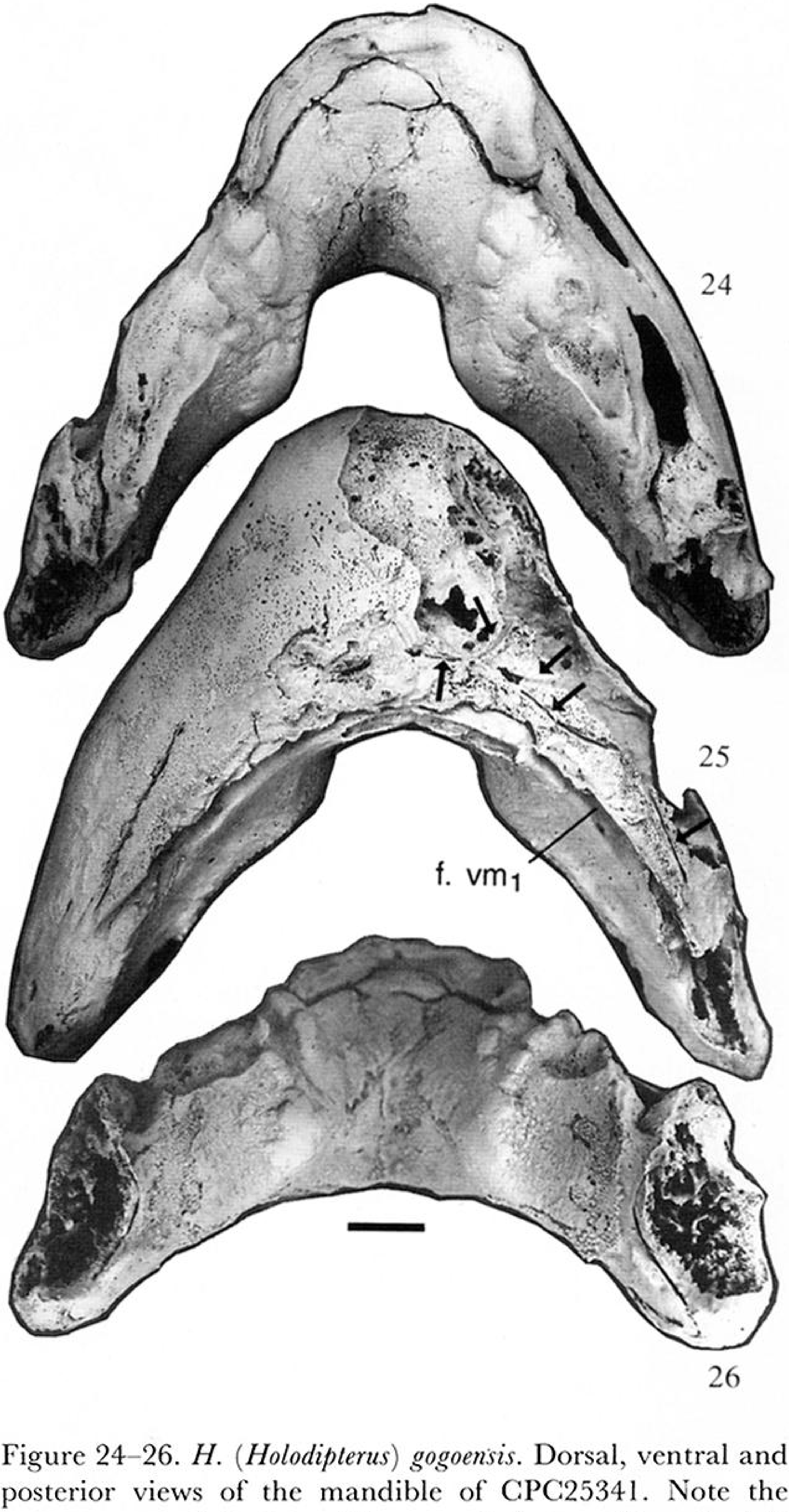
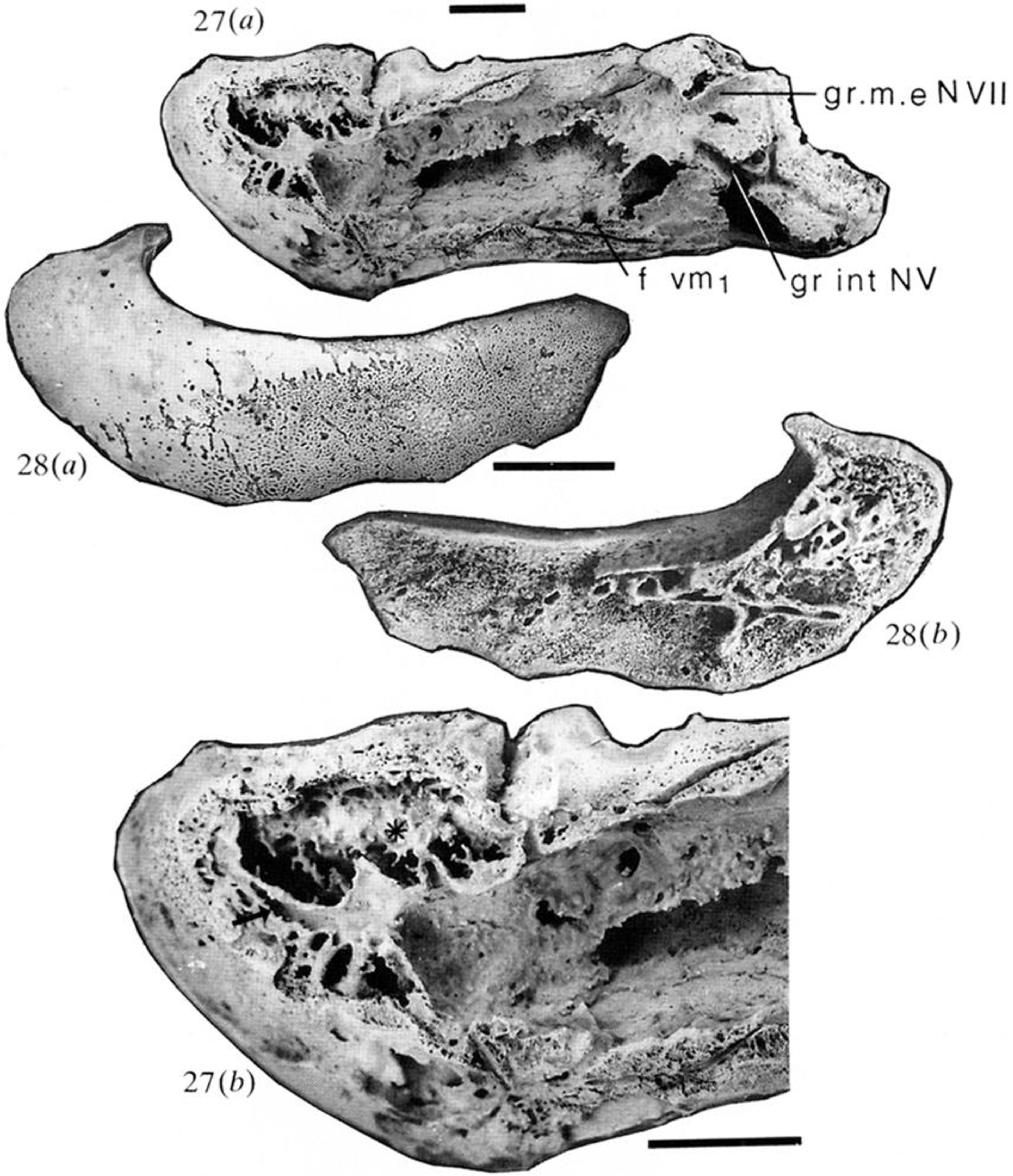


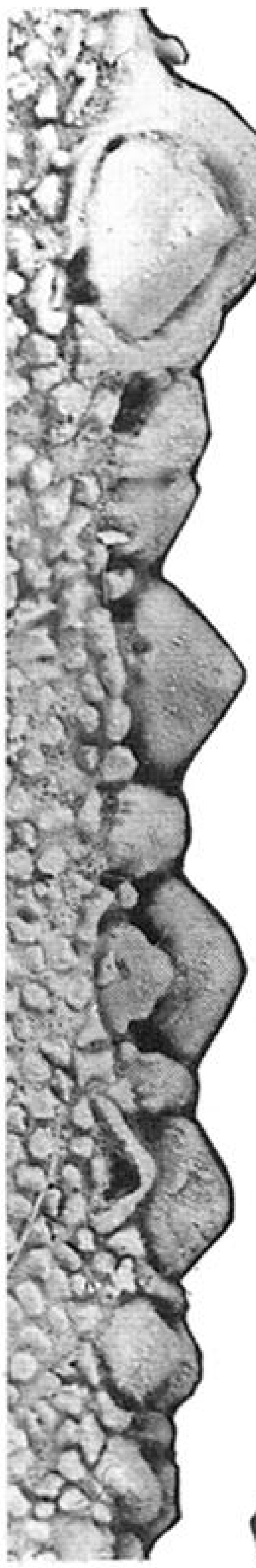
Figure 24–26. *H.* (*Holodipterus*) *gogoensis*. Dorsal, ventral and posterior views of the mandible of CPC25341. Note the arrangement of the lateral line canals (arrowed) on the left side of figure 25.



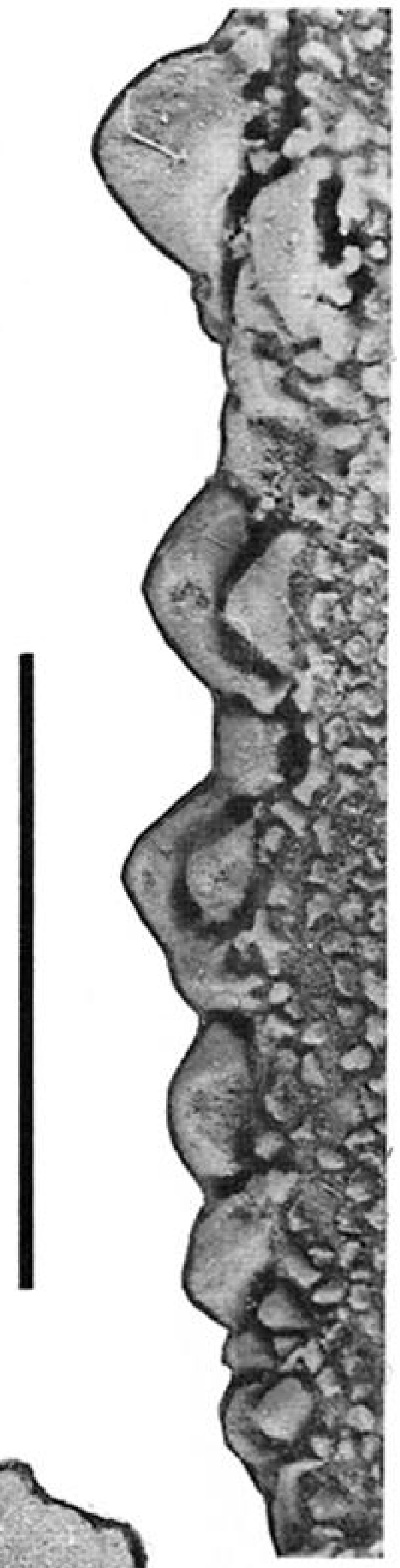
Figures 27 and 28. *H.* (*Holodipterus*) *gogoensis.* Scale bars = 10 mm.

Figure 27. (*a*) Left ramus of CPC25341 in lateral view, with the external dermal bones removed, and the mesial wall of the Meckelian cavity partly lost during preparation. (*b*) Enlargement of anterior of same showing the extension of the Meckelian cavity into a branching system of canals. Two major tubes at the anterior of the Meckelian cavity are indicated by an arrow and an asterisk.

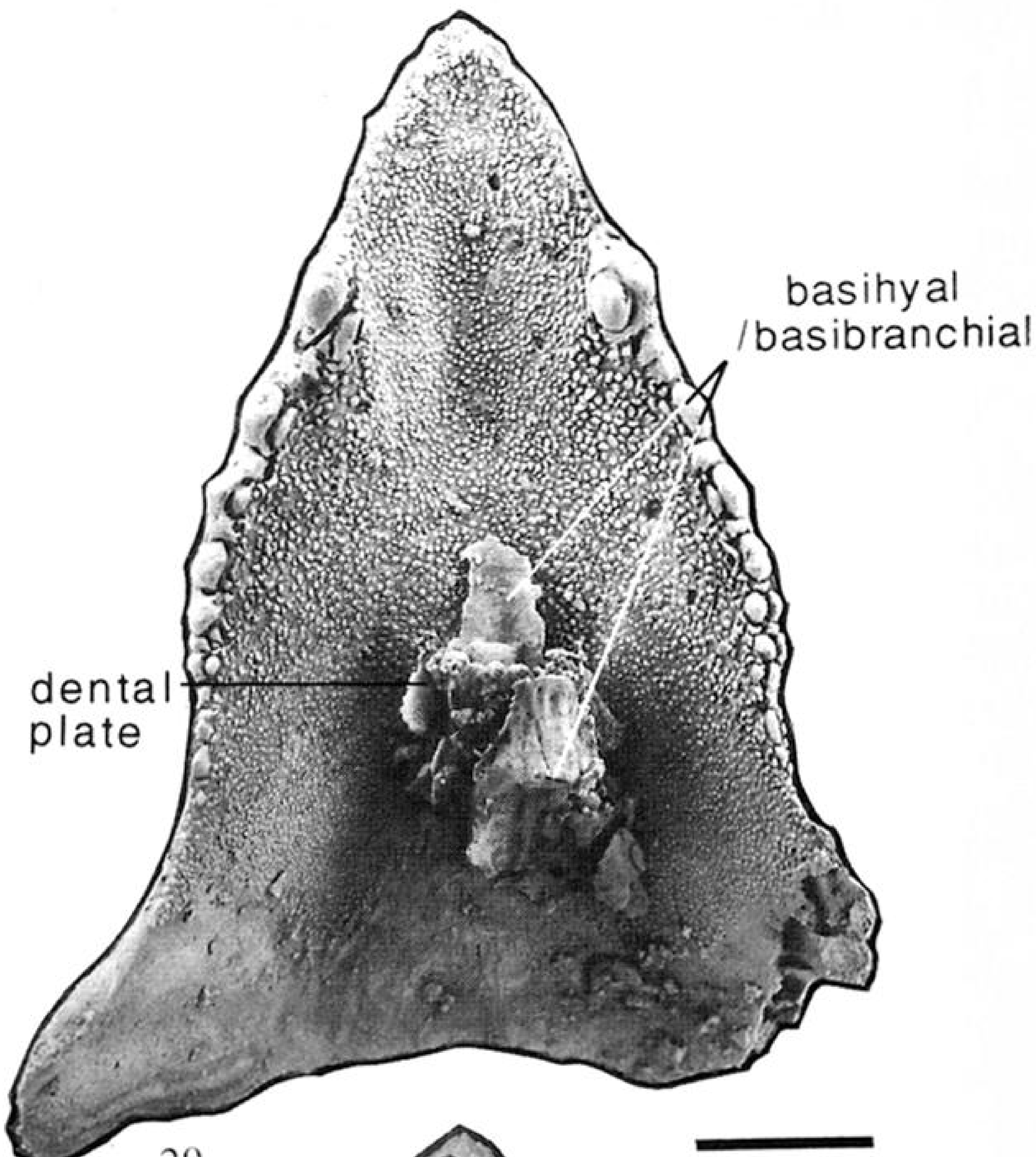
Figure 28. (*a*,*b*) External and internal views respectively of the dermal bone flaked from CPC25341. The depth of burial of the lateral line canals and the large tubules extending from them to the surface are shown in (*b*) as well as the tubules connected with the system from the front of the Meckelian cavity.



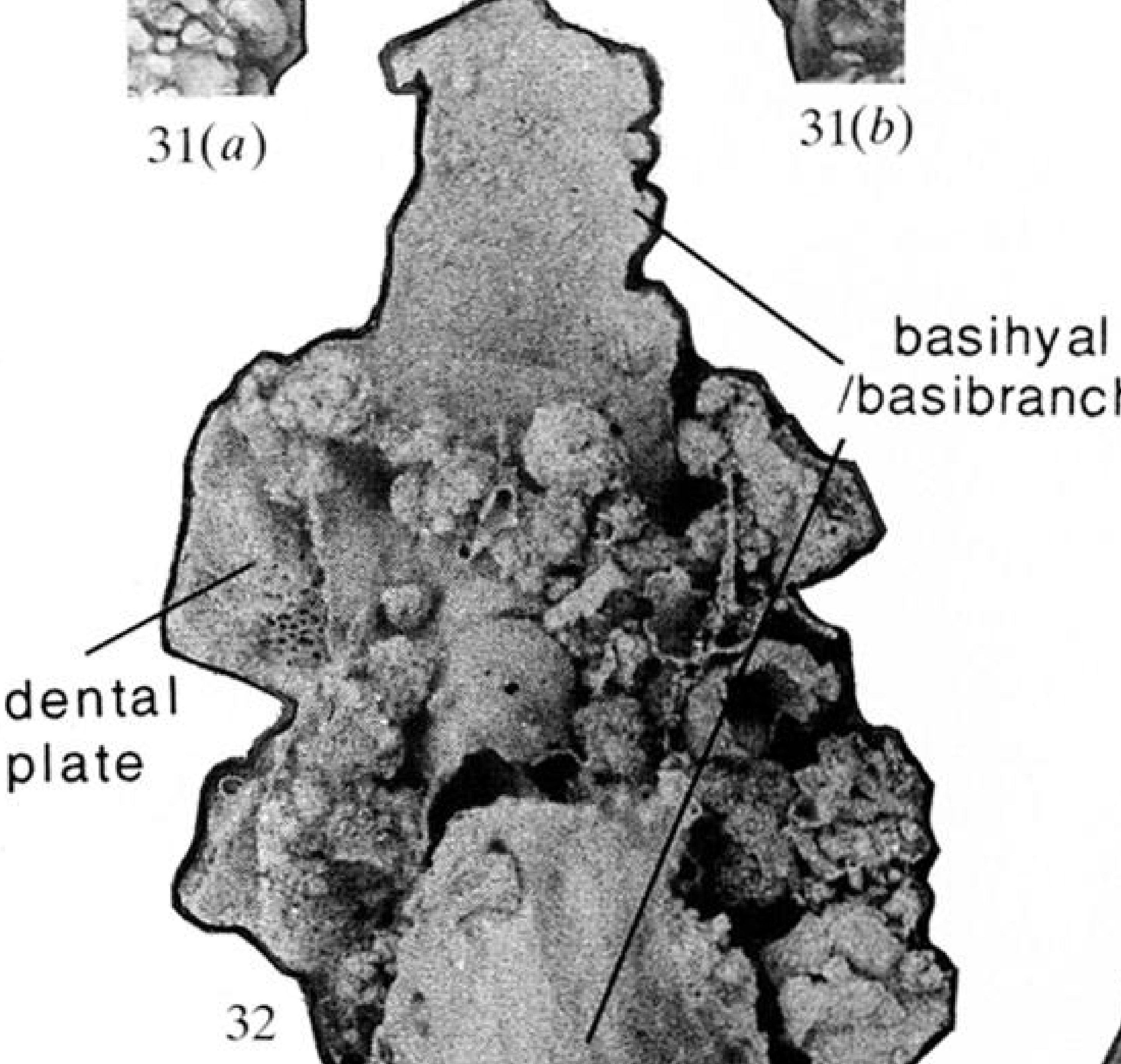
31(*a*)



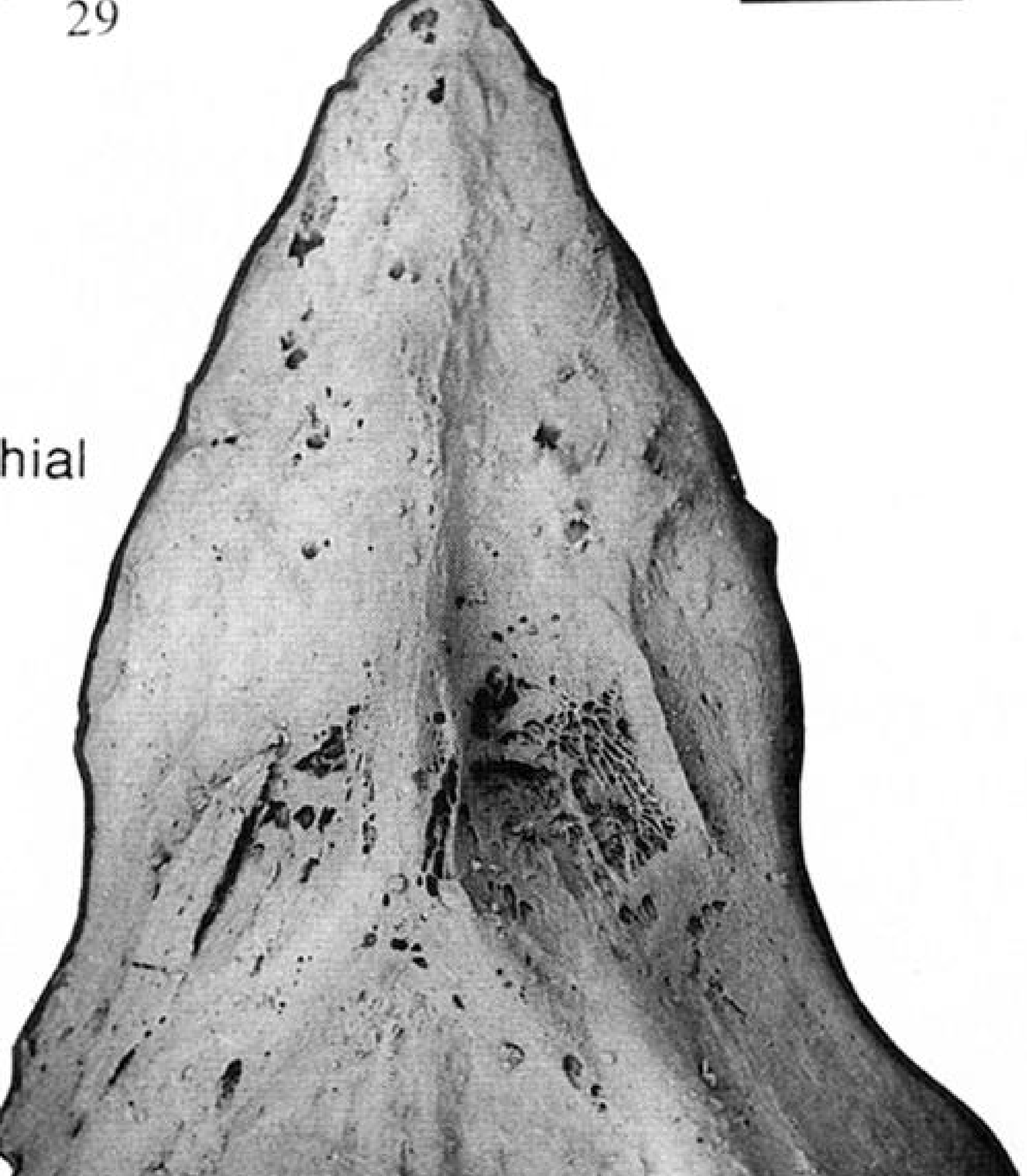
31(*b*)



29



32



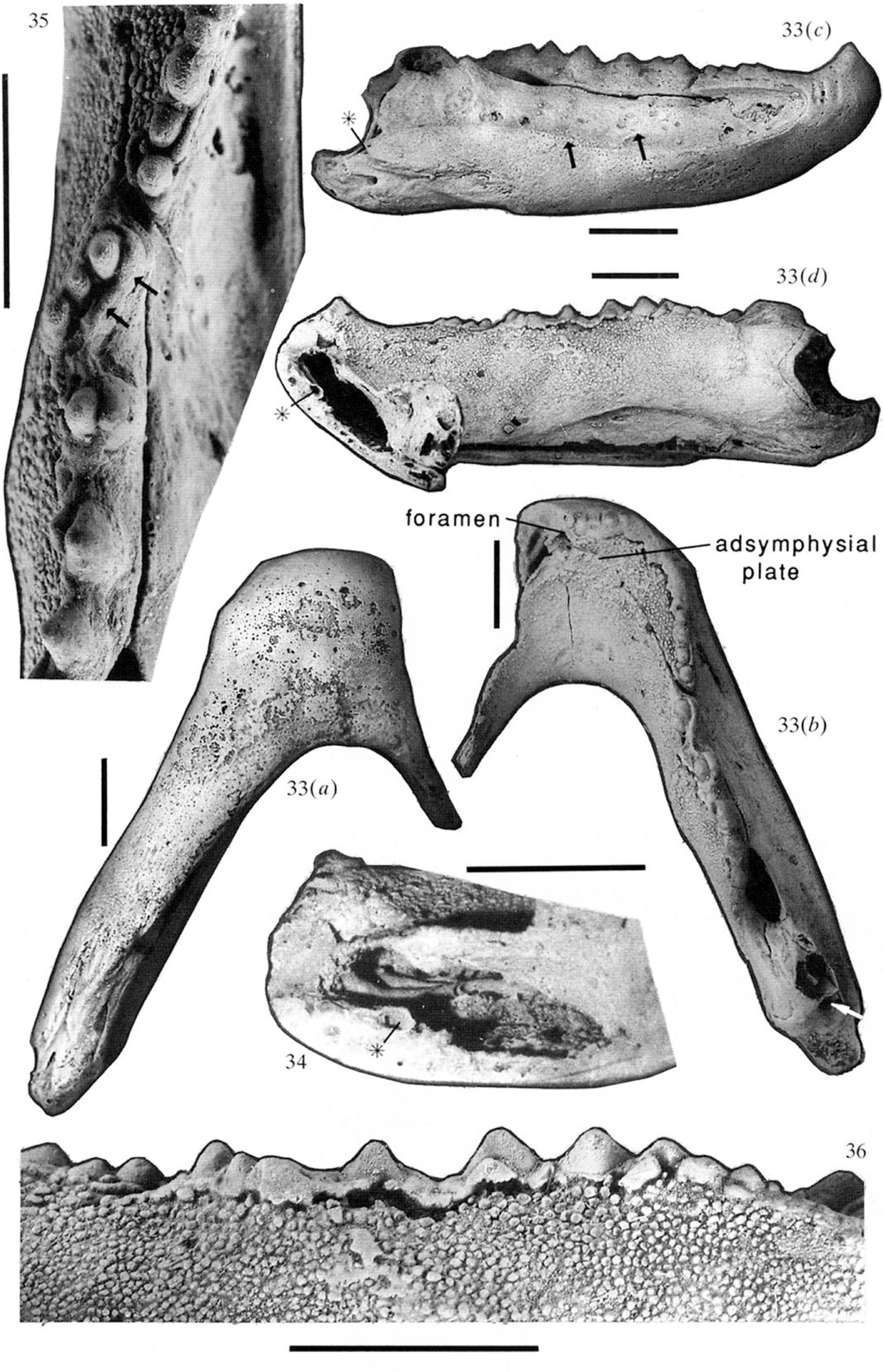
30

Figures 29–32. *H.* (*Holodipterus*) *longi*. Scale bars = 10 mm.

Figures 29 and 30. Ventral and dorsal views of the palate of WAM86.9.684.

Figure 31. (*a,b*) Enlargement of the left and right marginal teeth and adjacent denticles of the same palate showing the effects of resorption.

Figure 32. Enlargement of mesial part of the palate of same showing the remains of the basihyal/basibranchial and one of its denticle bearing plates, tilted to the left with respect to figure 29.

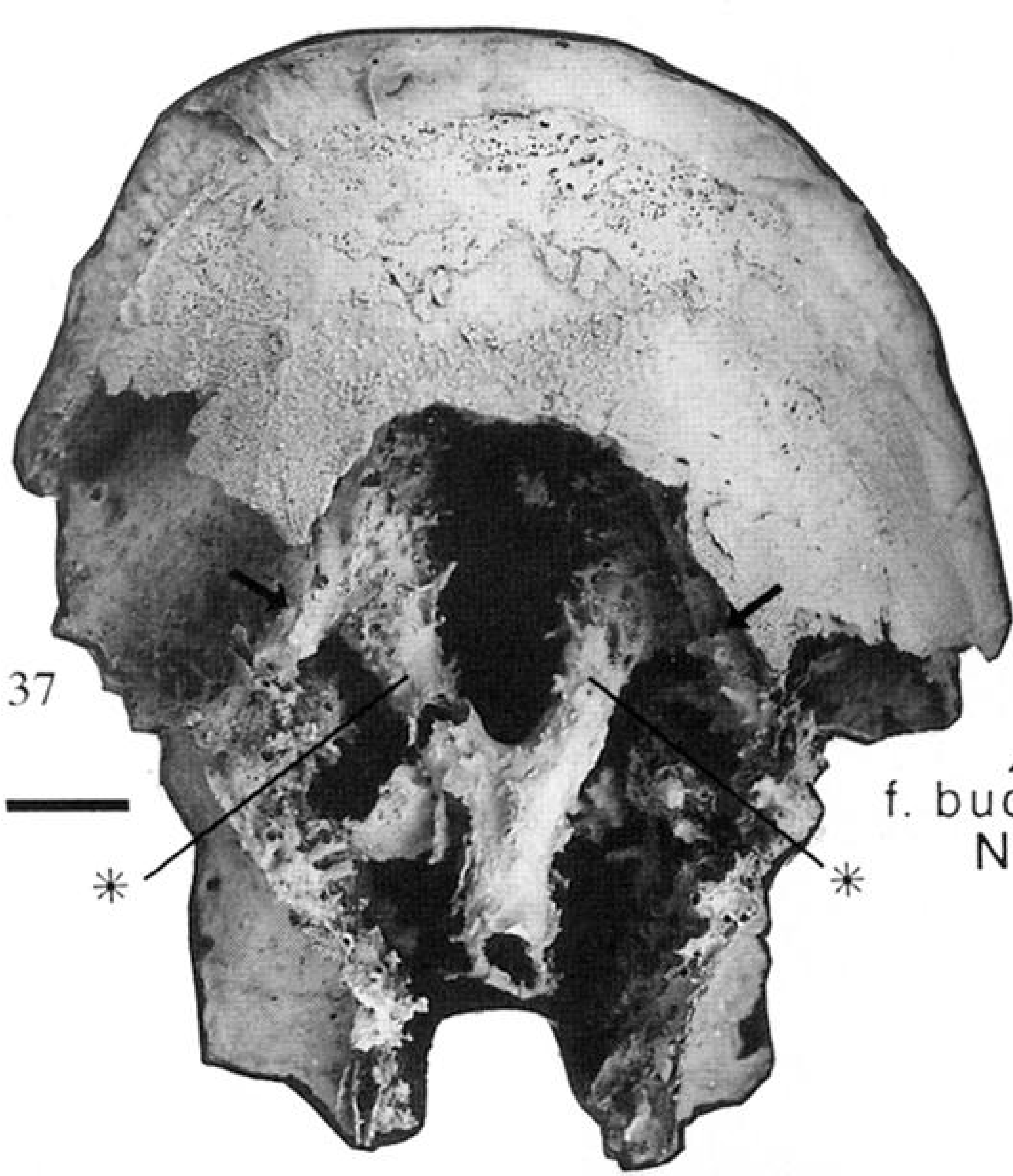


Figures 33–36. *H.* (*Holodipterus*) *longi*. Scale bars = 10 mm.

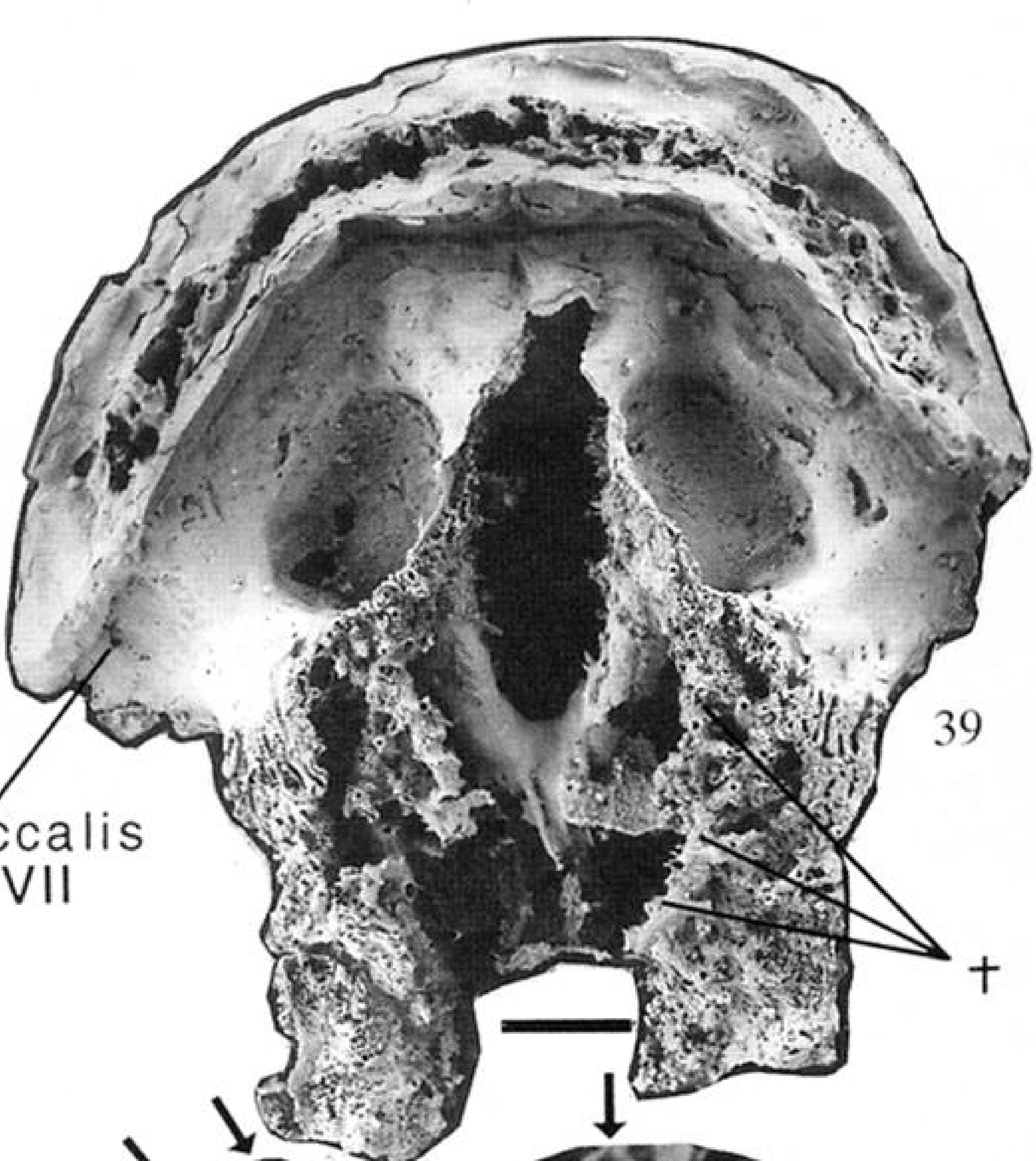
Figure 33. (*a*) Ventral, (*b*) dorsal, (*c*) lateral and (*d*) mesial views of the mandible of WAM86.9.684. The arrow in (*b*) marks the common foramen for the mentalis VII and the mandibularis V. The arrows in (*c*) mark the suture between the angular and the surangular. In (*d*) an asterisk indicates the tube of the oral lateral line canal.

Figure 34. Internal view of the symphysis of same. Note the ramifying tubules. An asterisk marks the tube of the oral lateral line canal.

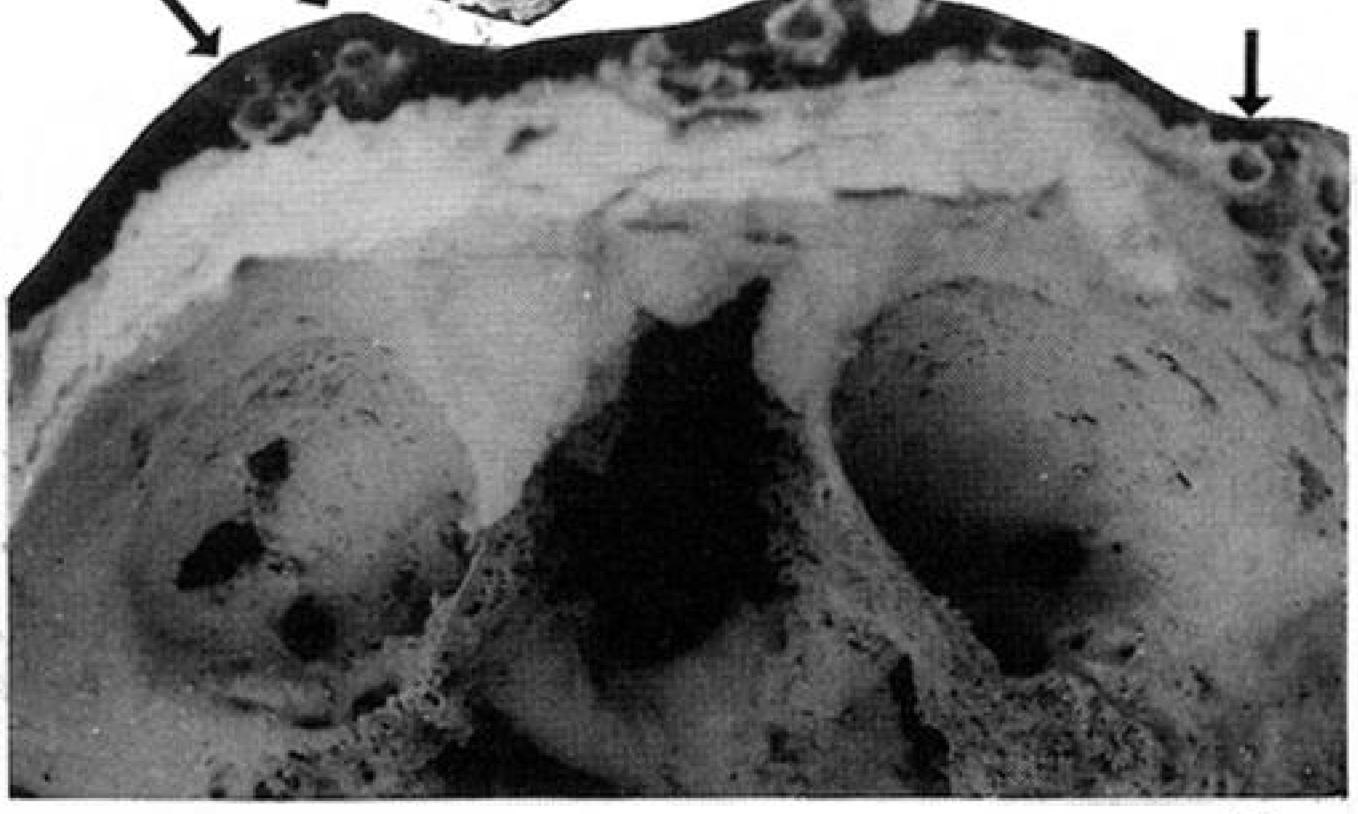
Figures 35 and 36. Enlargements of marginal tooth row of WAM86.9.684 in dorsal and medial view. The arrows in figure 35 indicate an enamel-covered rim of white superficial dentine. In figure 36 the anterior is to the left.



37

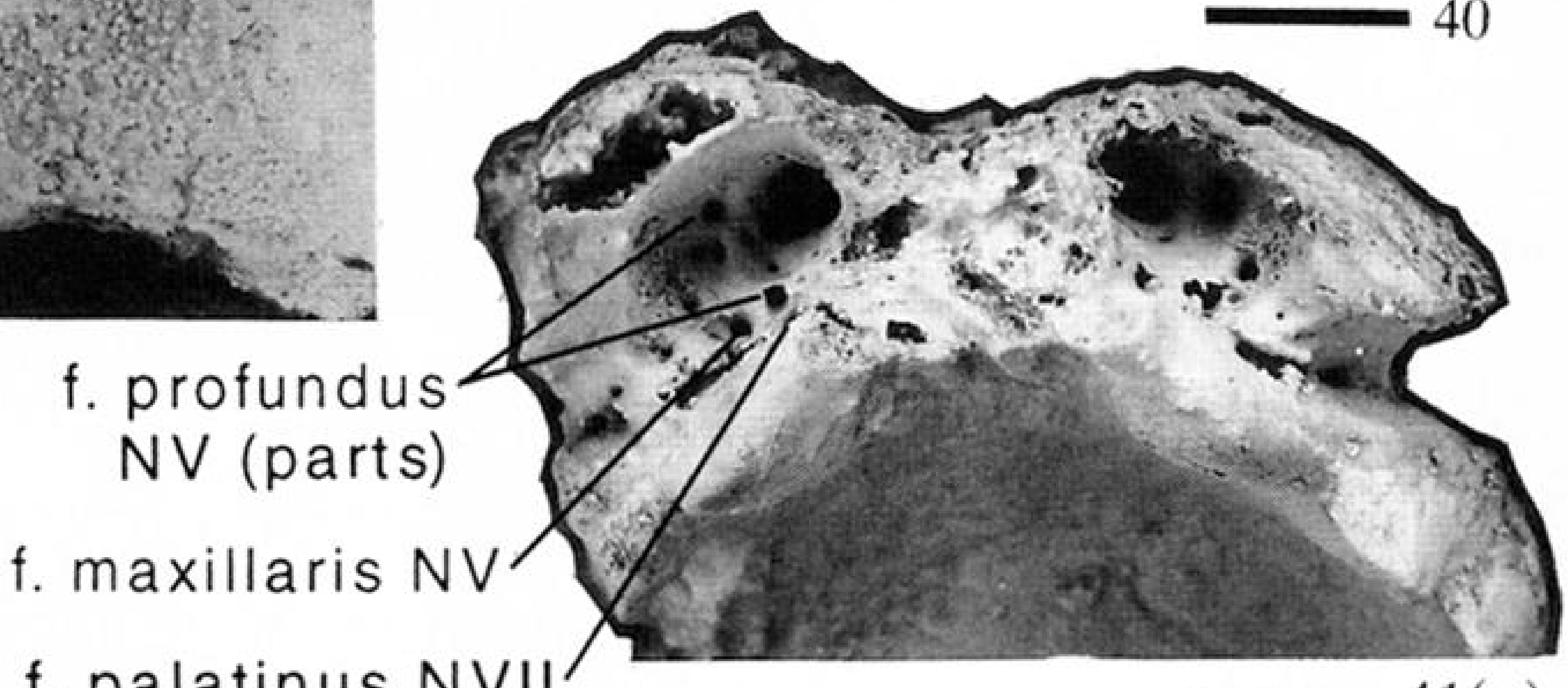


39

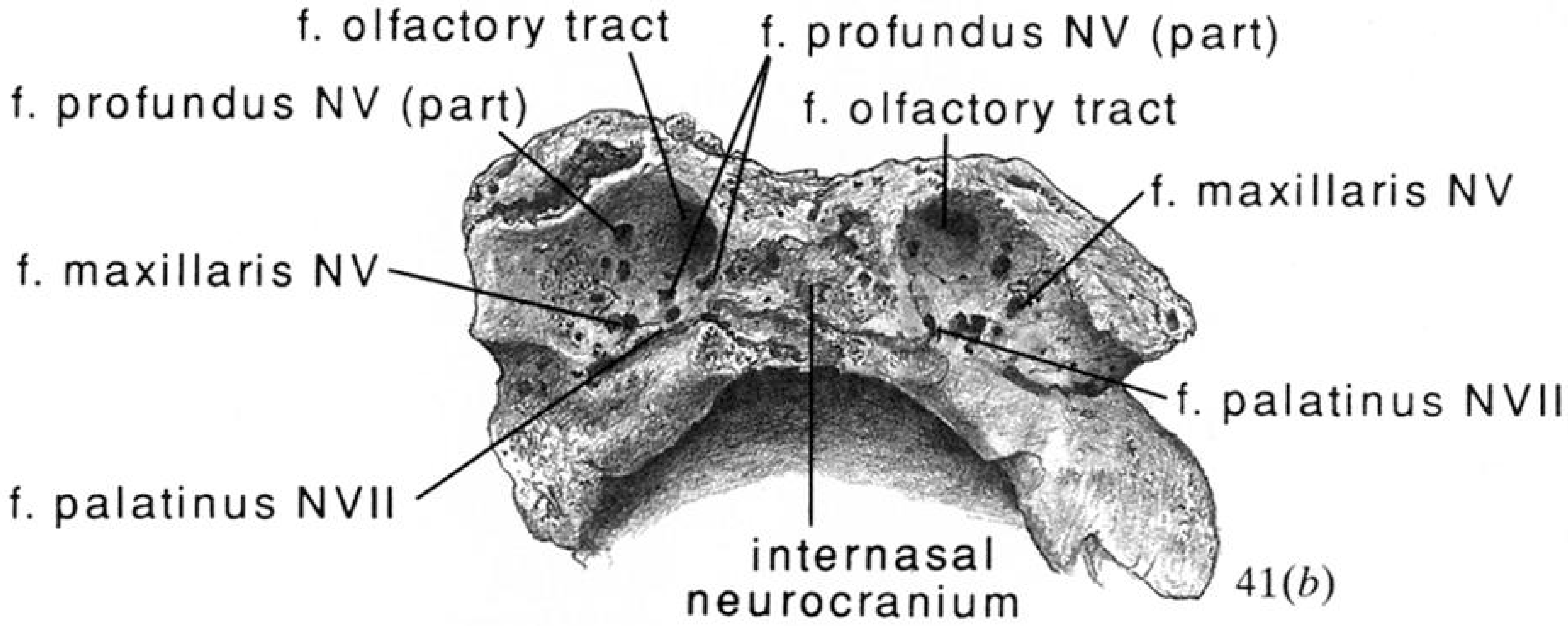


40

38



41(*a*)



41(*b*)

Figures 37–41. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

Figure 37. Dorsal view of the snout of CPC25739 showing the anterior of the braincase, the bony tubes for the olfactory tracts (asterisks) and the tubes for the ophthalmicus profundus (arrows) on each side of the specimen.

Figure 38. Enlargement of part of the dermal bone of the snout of same to emphasize the extent of the cosmine and the porous structure of the bone.

Figure 39. Ventral view into the roofs of the nasal capsules of CPC25739. The longitudinal tube for the palatinus nerve is indicated by daggers. The anterior rim of the specimen is plastic embedding material.

Figure 40. Anteroventral view into the nasal capsules of same to show the foramina in the posterior wall of the nasal capsule. The two anterolateral holes in the roof of the right capsule (tectum nasi) are artifacts. Rostral tubules are preserved (arrows).

Figure 41. (*a*) Anterior view into the nasal capsules of the holotype, ANU49101. (*b*) Drawing of same.

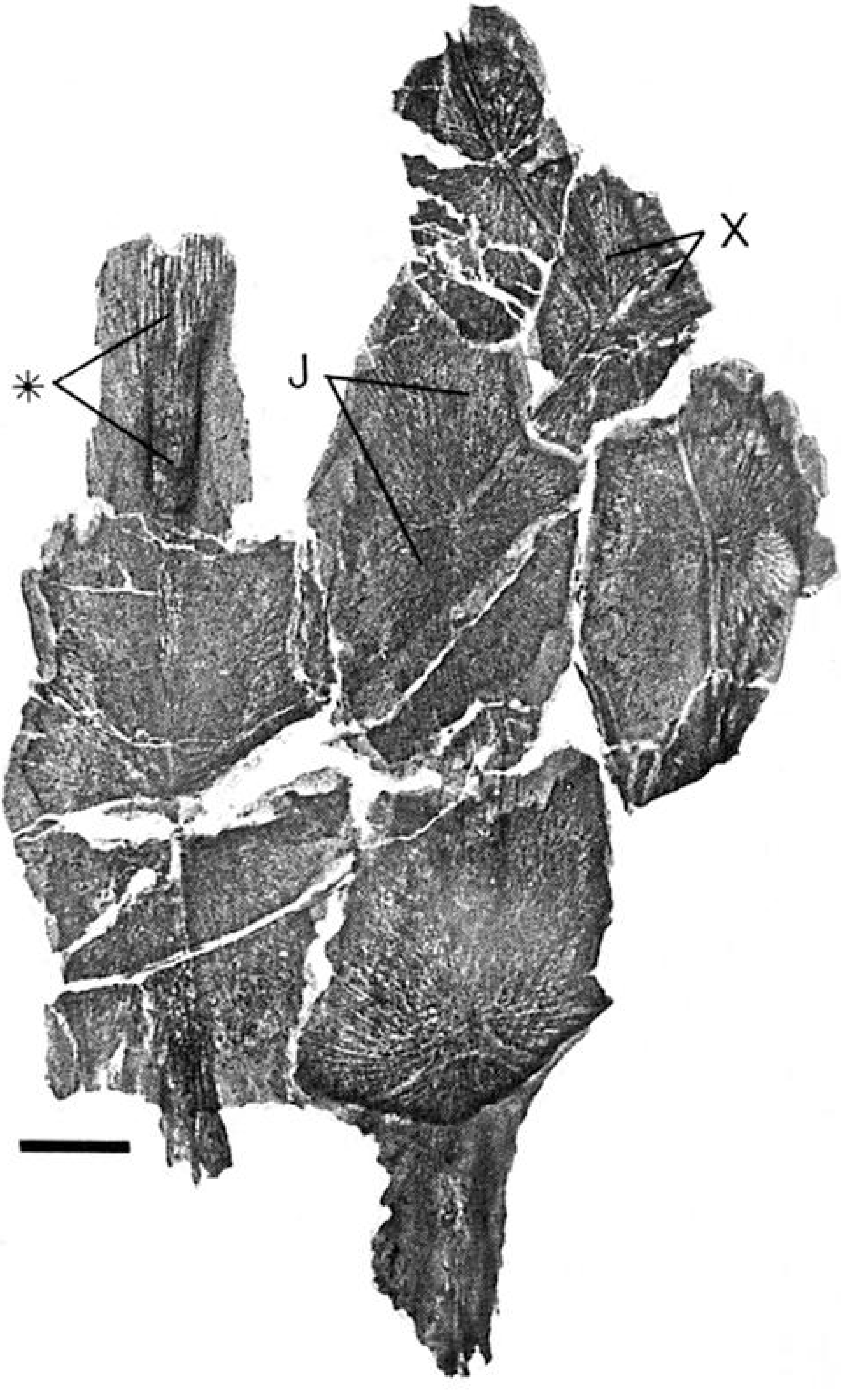


Figure 42. *H.* (*Holodipteroides*) *elderae*. X-radiograph of the right posterior roofing bones of CPC25739, showing radiation centres. Note the canal in bone J and the broad connection of the two canals in bone X. The anterior third of bone B (asterisk) carries the attachment for the median crista. Scale bar = 10 mm.

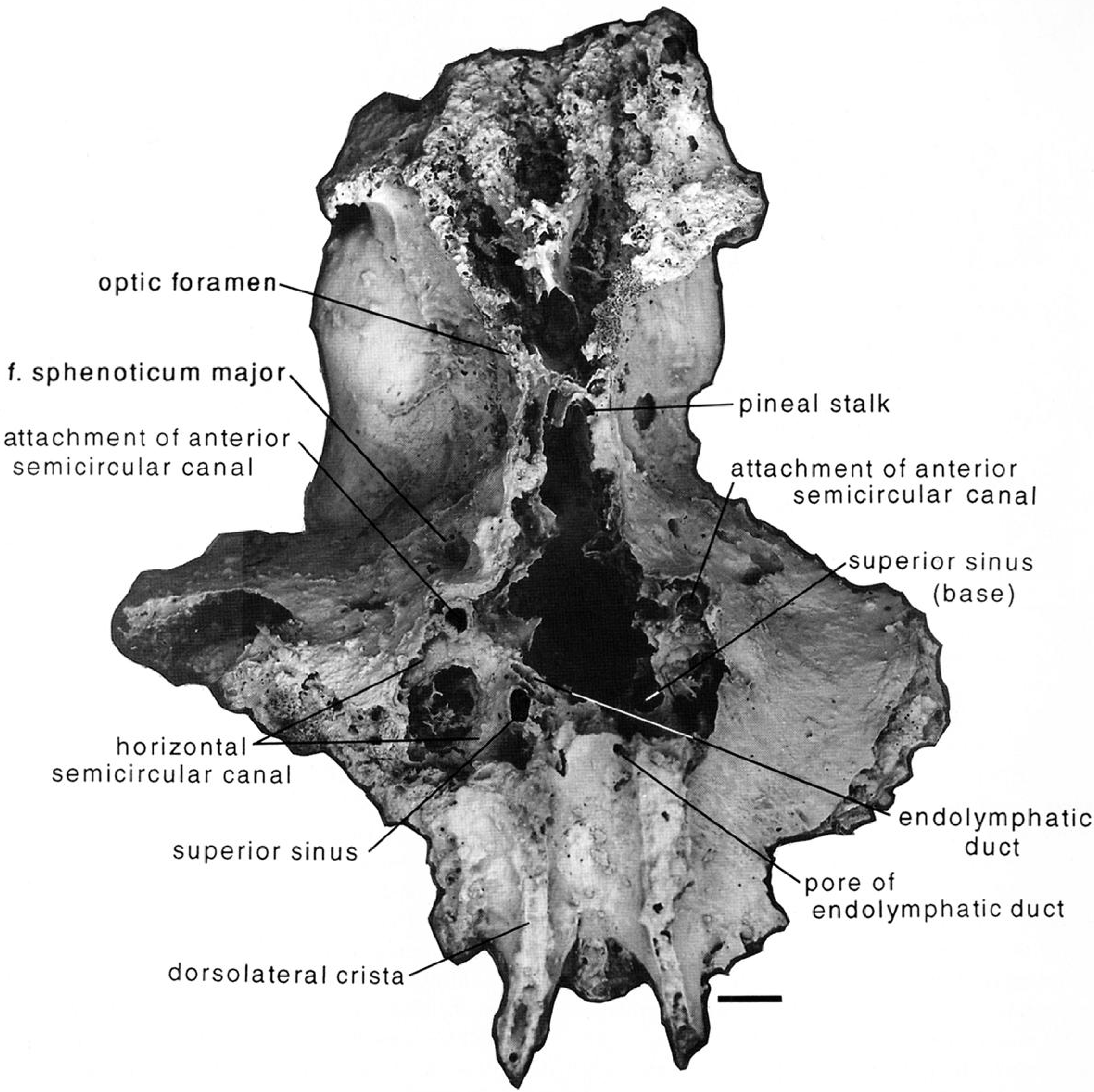


Figure 43. *H.* (*Holodipteroides*) *elderae*. Dorsal view of the holotype, ANU49101, showing the horizontal semicircular canal on the left, and sections through the verticals on the right. Scale bar = 10 mm.

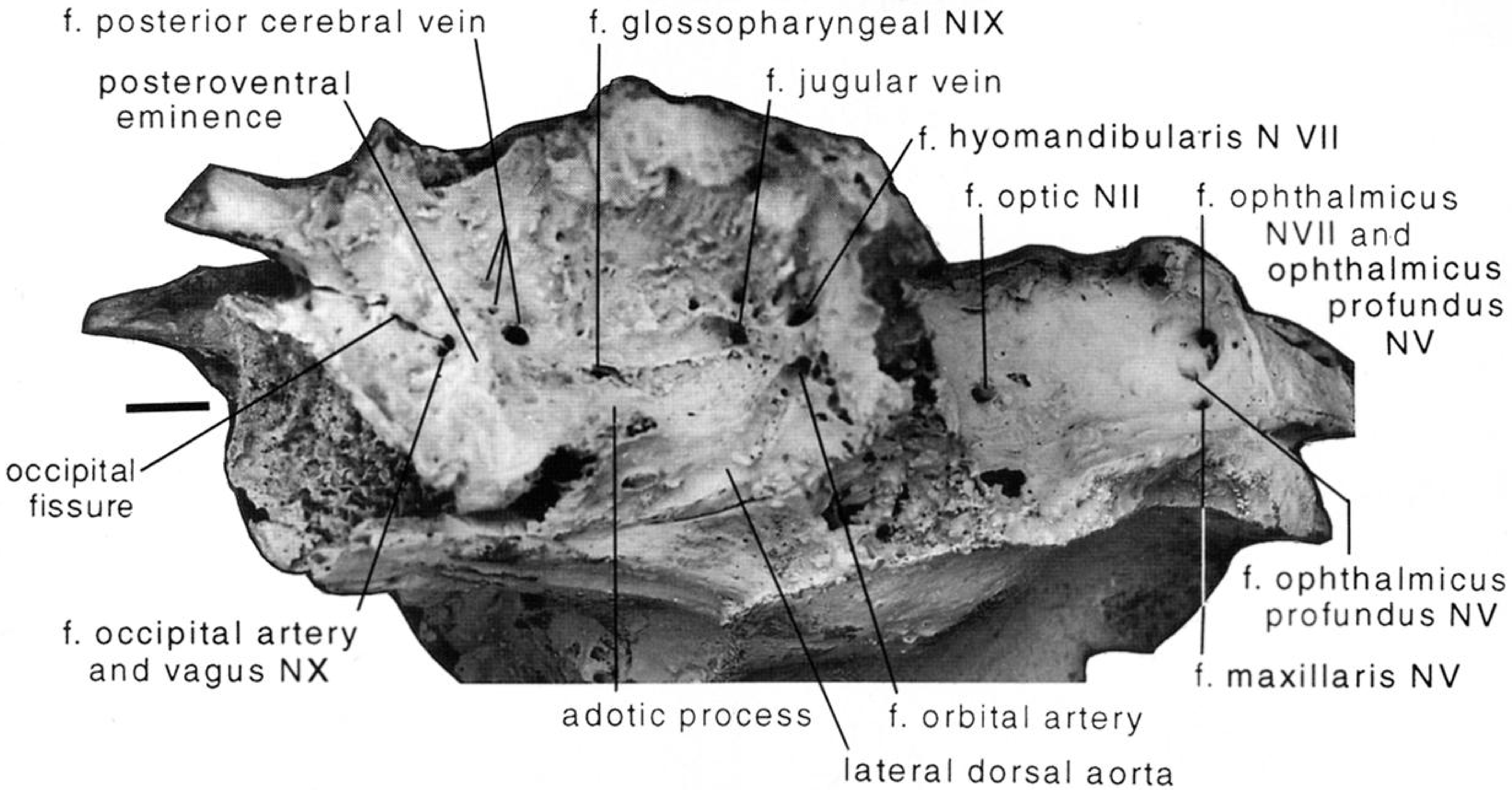


Figure 44. *H.* (*Holodipteroides*) *elderae*. Posterolateral and slightly ventral view of the holotype, ANU49101, showing the foramina in the antorbital wall and the posterior wing of the neurocranium. Scale bars = 10 mm.

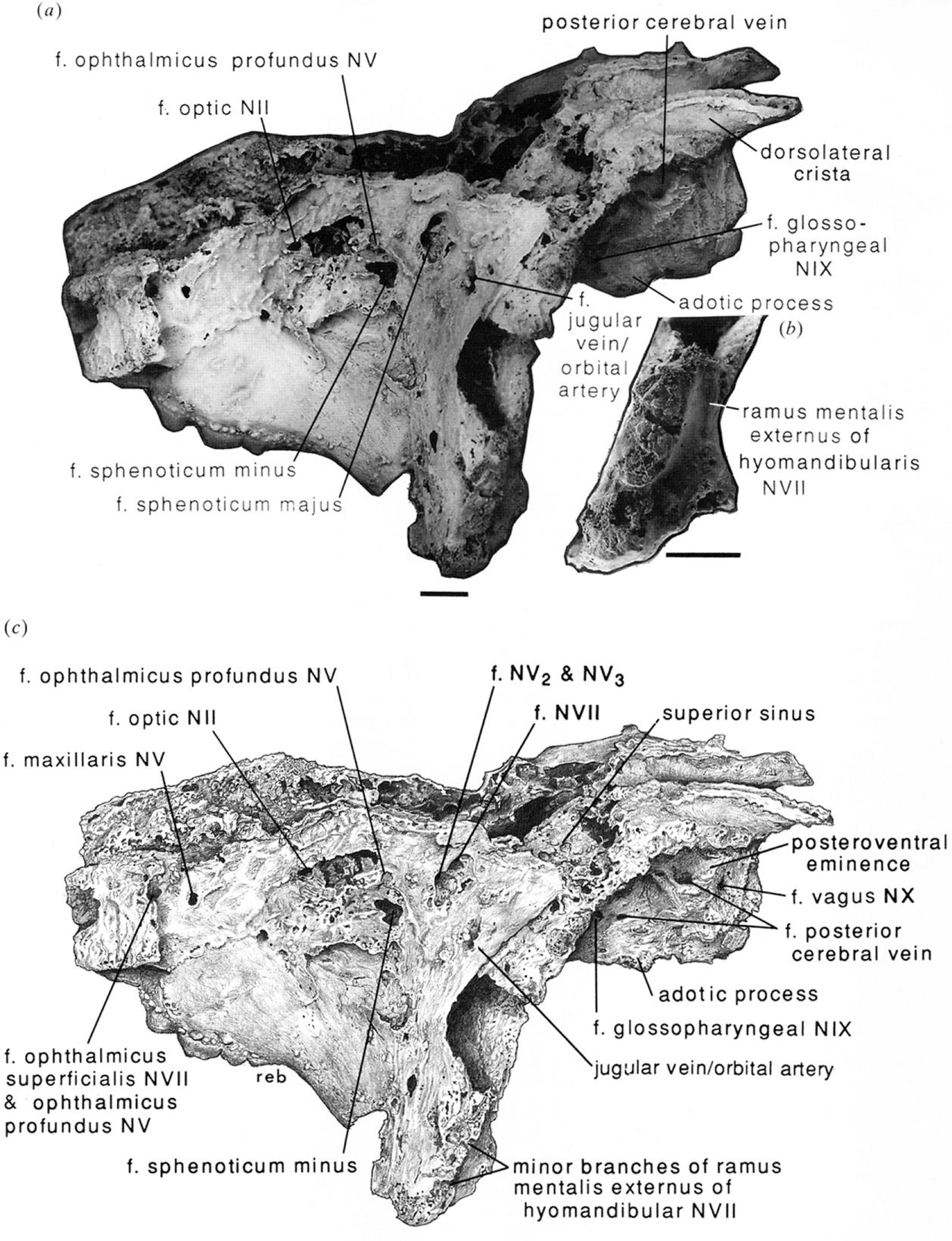


Figure 45. *H.* (*Holodipteroides*) *elderae*. (*a*) Dorsolateral view of the holotype. (*b*) Enlargement of the quadrate region of same. (*c*) Drawing of (*a*) to emphasize detail not shown by the photograph, particularly in the occipital region. Scale bars = 10 mm.

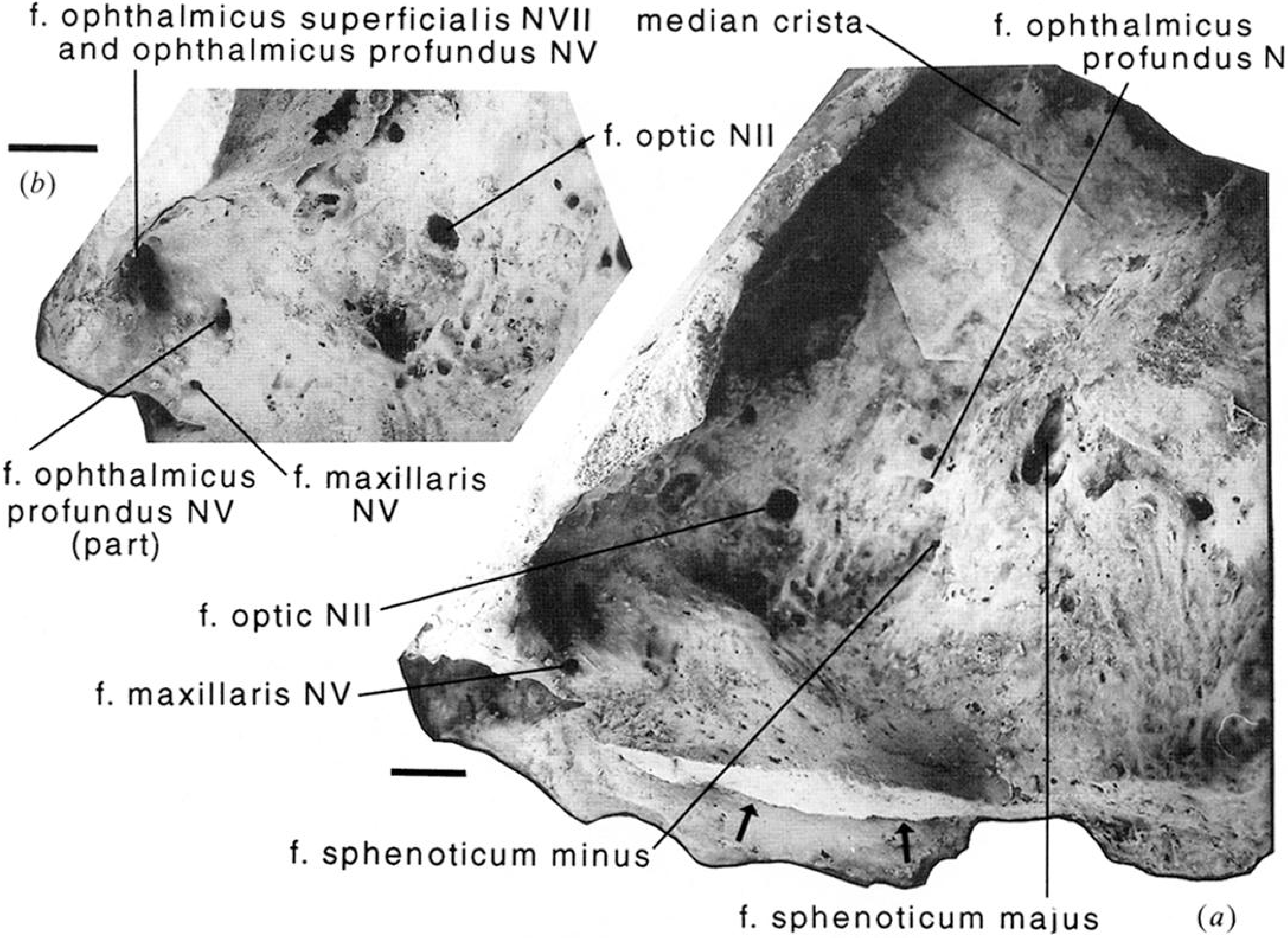


Figure 46. *H.* (*Holodipteroides*) *elderae*. (*a*) Lateral view of WAM86.9.949 showing the fracture (arrowed) within the pterygoid resulting from weathering. The external surface of the snout is covered with plastic used to consolidate the specimen before preparation. (*b*) Posterolateral view into antorbital wall showing foramina. Scale bars = 10 mm.

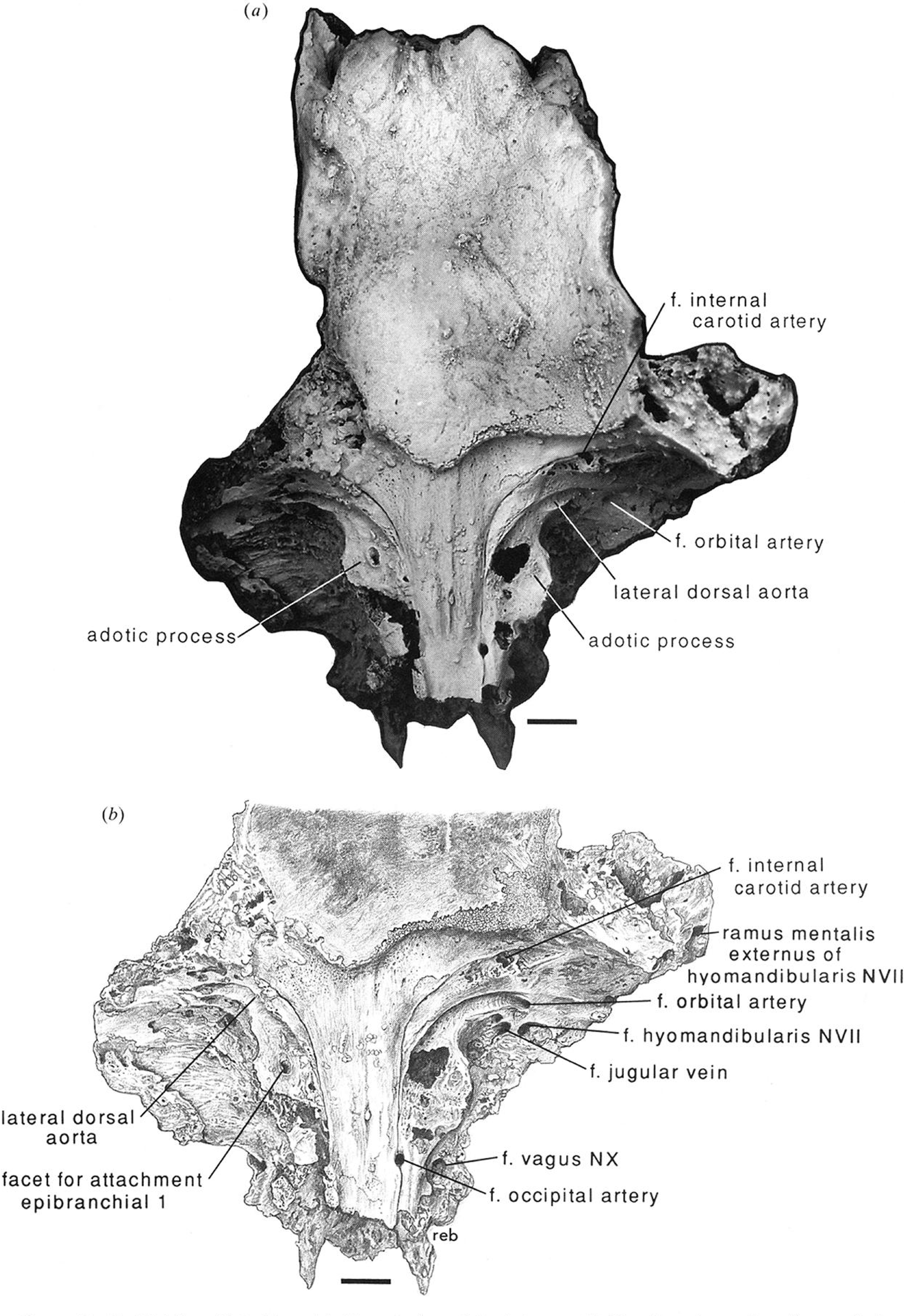


Figure 47. *H.* (*Holodipteroides*) *elderae*. (*a*) Ventral view of the holotype. (*b*) Drawing of posterior of same. Scale bars = 10 mm.

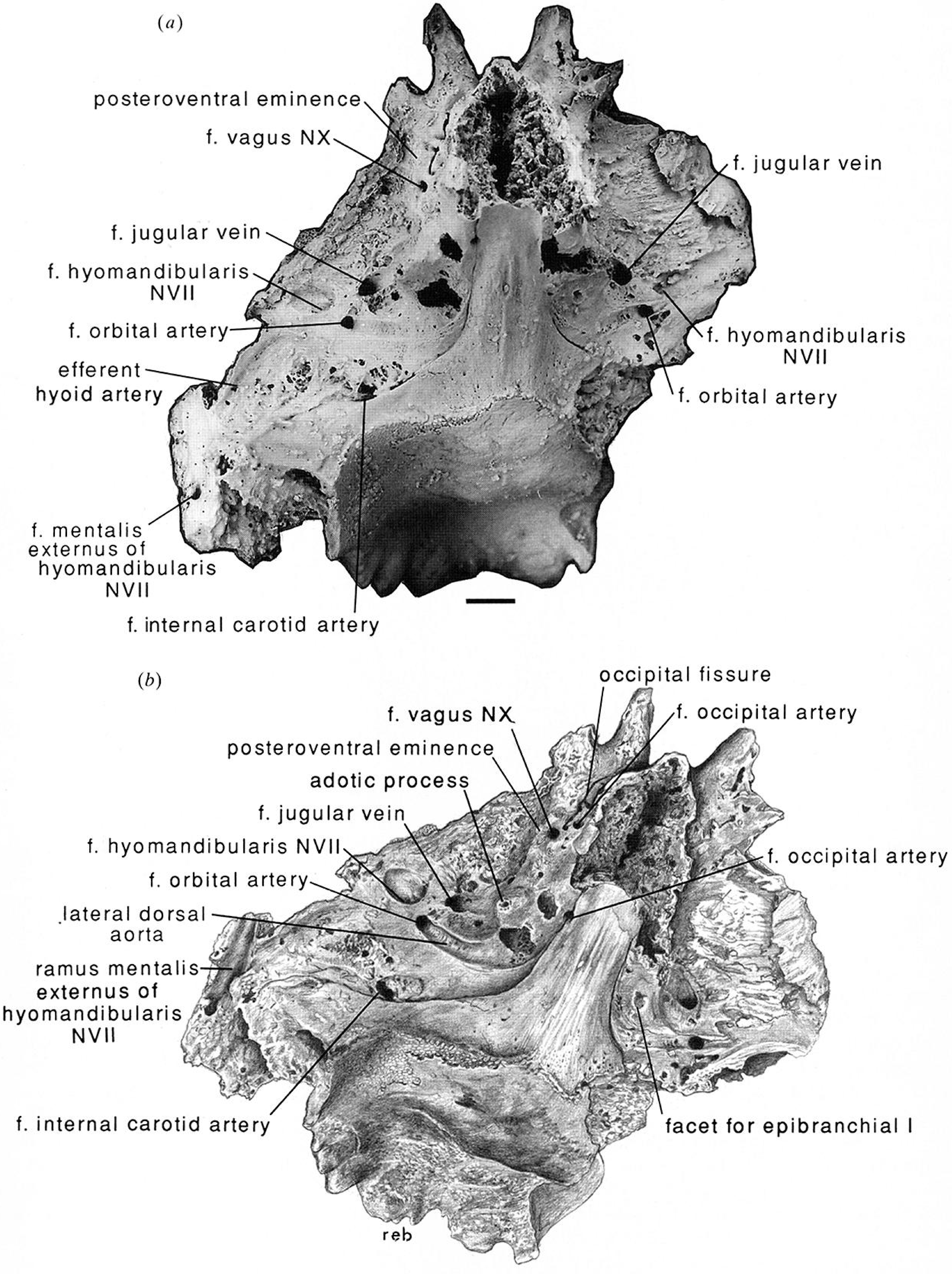
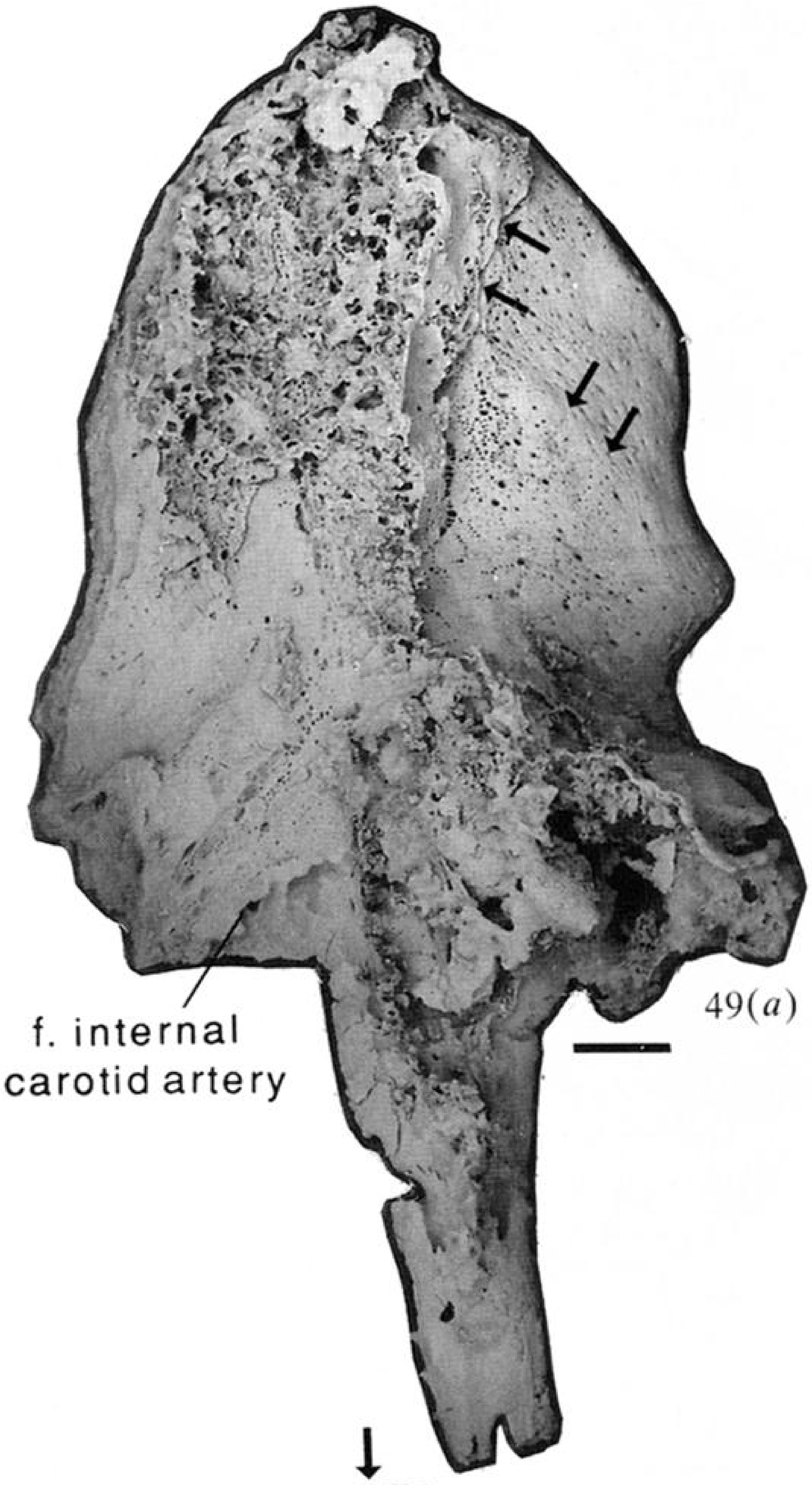
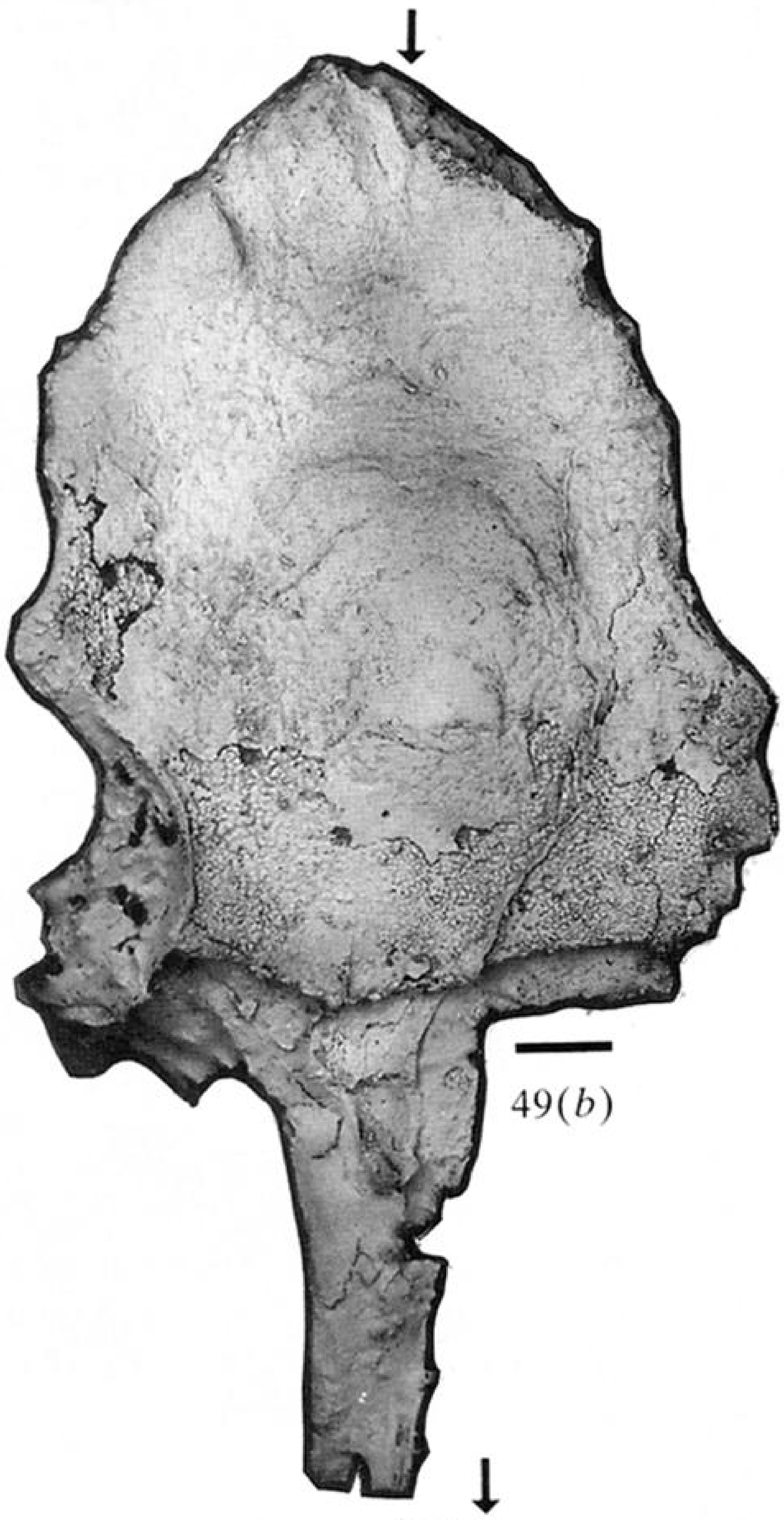


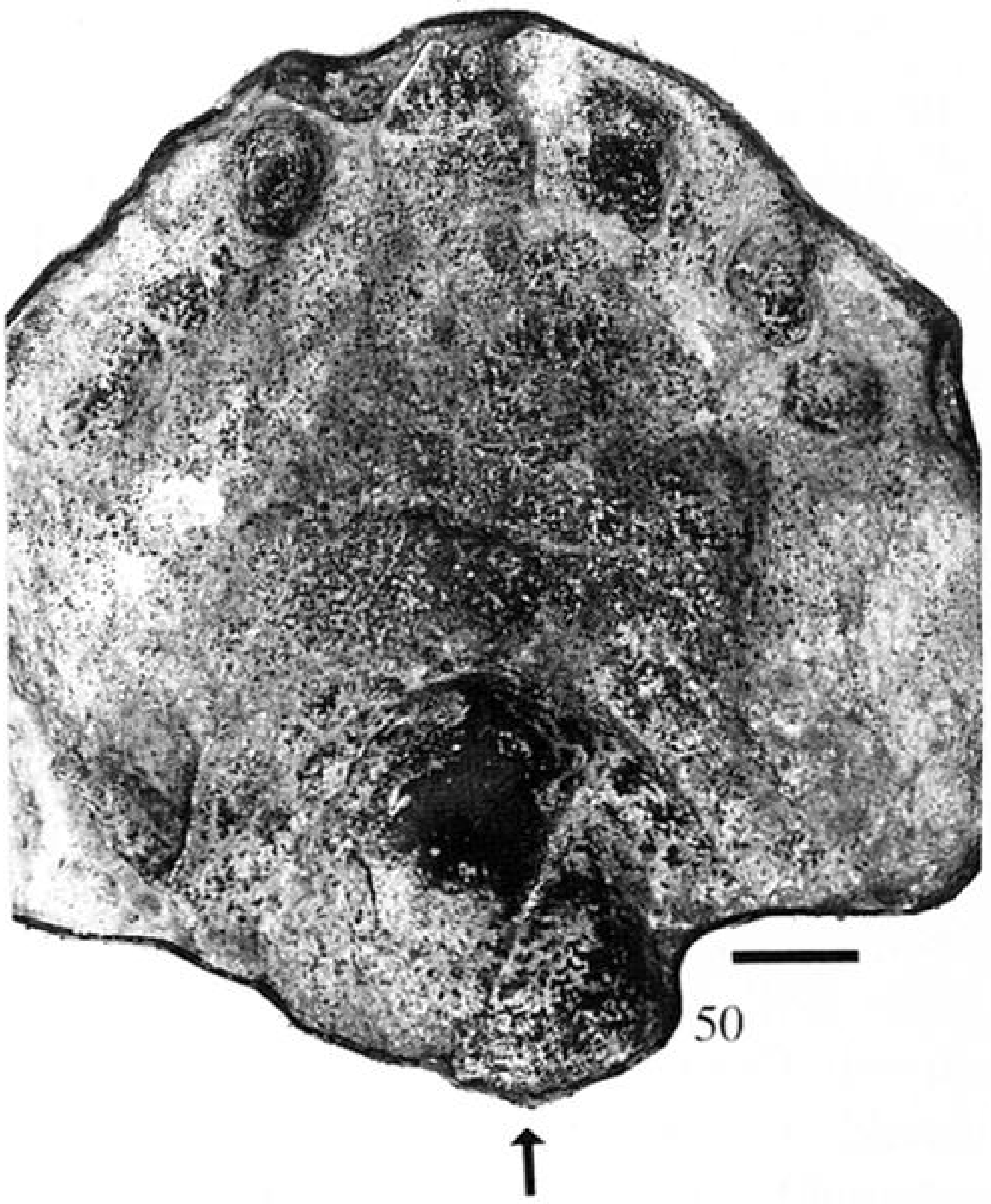
Figure 48. *H.* (*Holodipteroides*) *elderae*. (*a*) Posteroventral view of holotype, ANU49101. (*b*) Drawing of same. Scale bar = 10 mm.



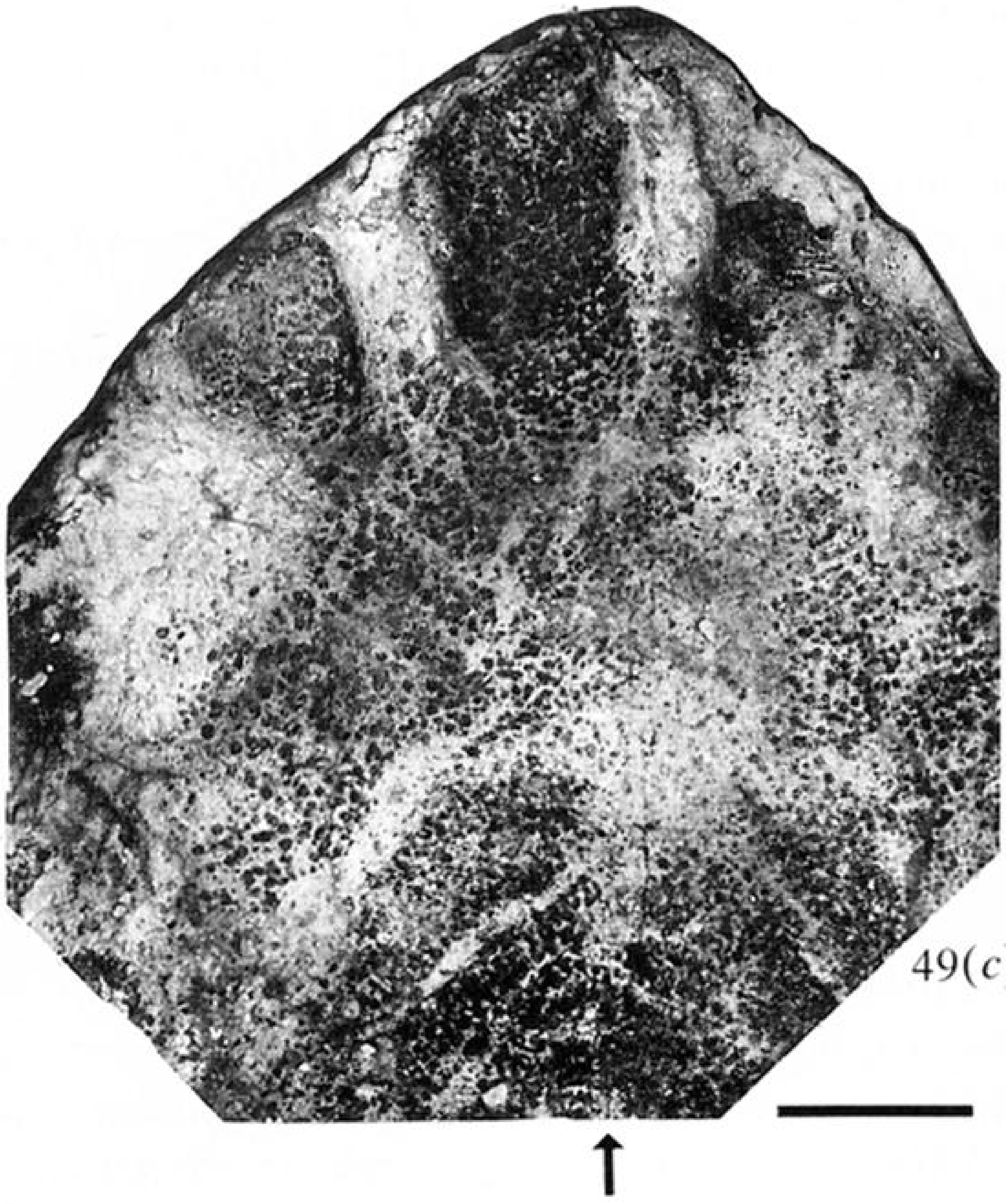
49(*a*)



49(*b*)



50

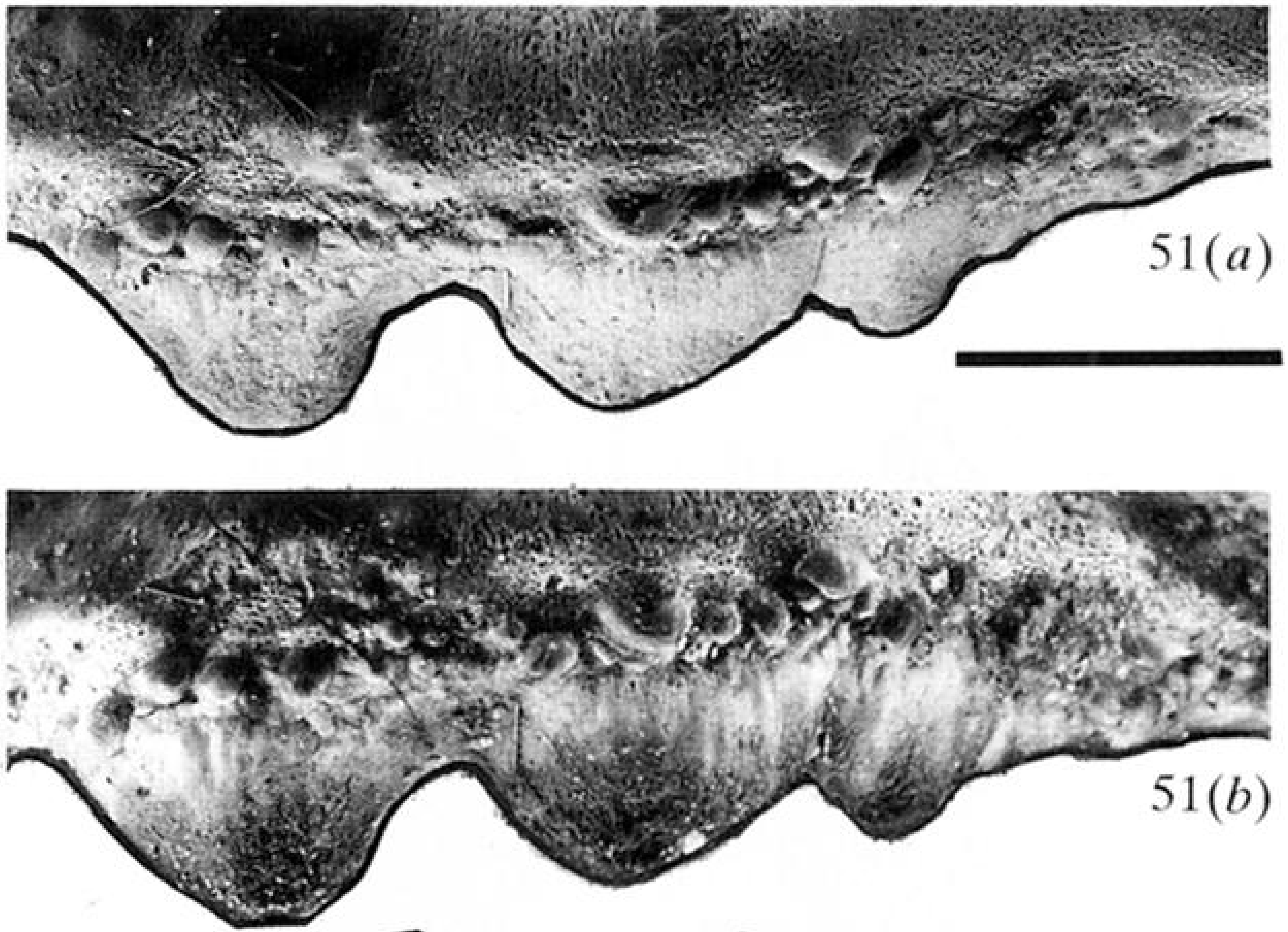


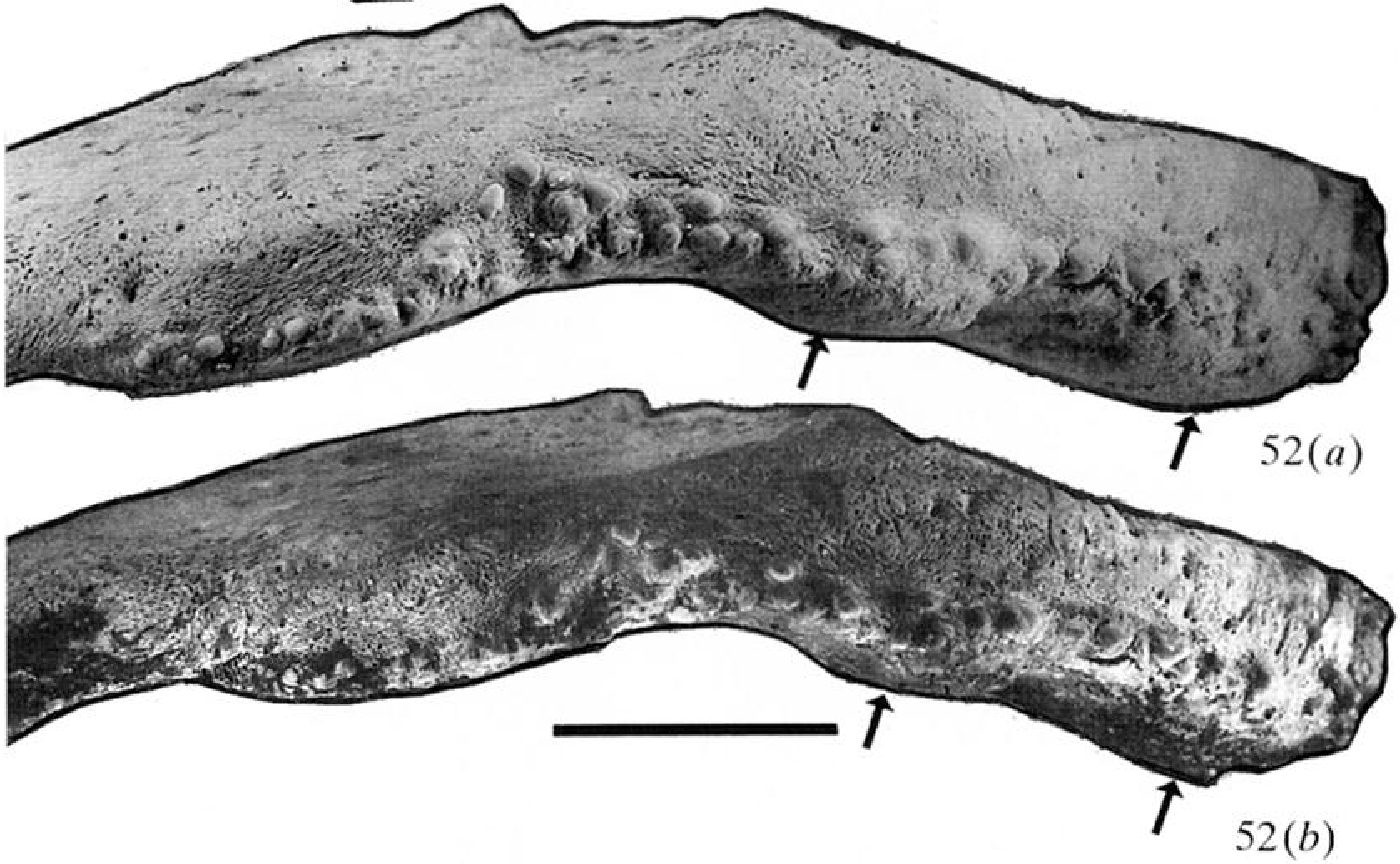
49(*c*)

Figures 49 and 50. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

Figure 49. Palate of CPC30828 in (*a*) dorsal, and (*b*) ventral view. An enlargement of the anterior portion of the ventral palate which has not been whitened with NH_4Cl is shown in (*c*). Arrows in (*a*) indicate minor ridges on the dorsal surface of the pterygoids. Arrows in (*b*) and (*c*) indicate the midline. Note that most of the palatal surface has numerous columns of black hypermineralized dentine which are most closely spaced on the radial ridges and the callus. Between these dark elements are white areas of superficial dentine.

Figure 50. Ventral view of the anterior palate of WAM86.9.949. Note the polished anterior surface of the callus. Arrows indicate the midline. The specimen is not whitened with NH_4Cl.

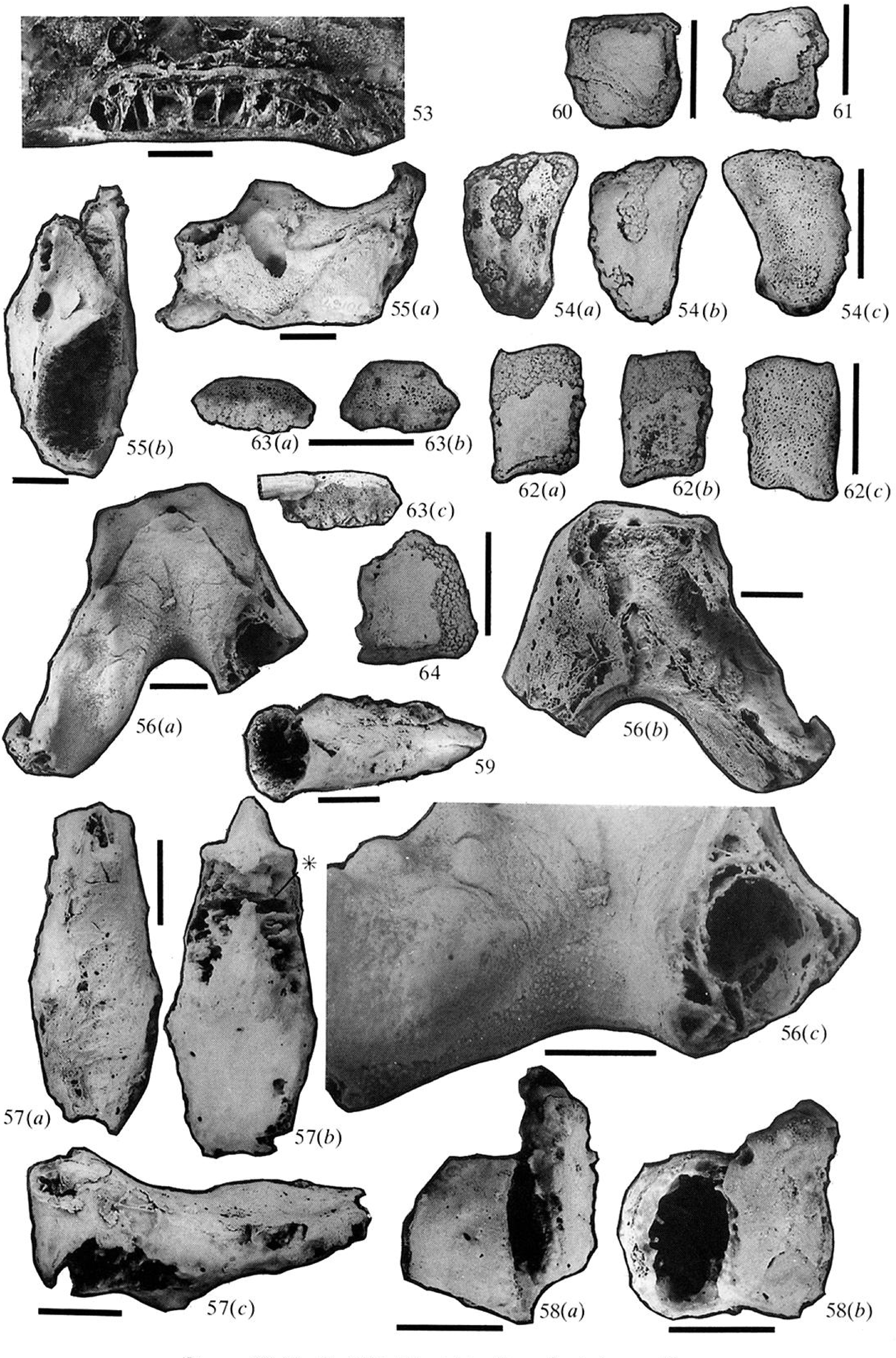




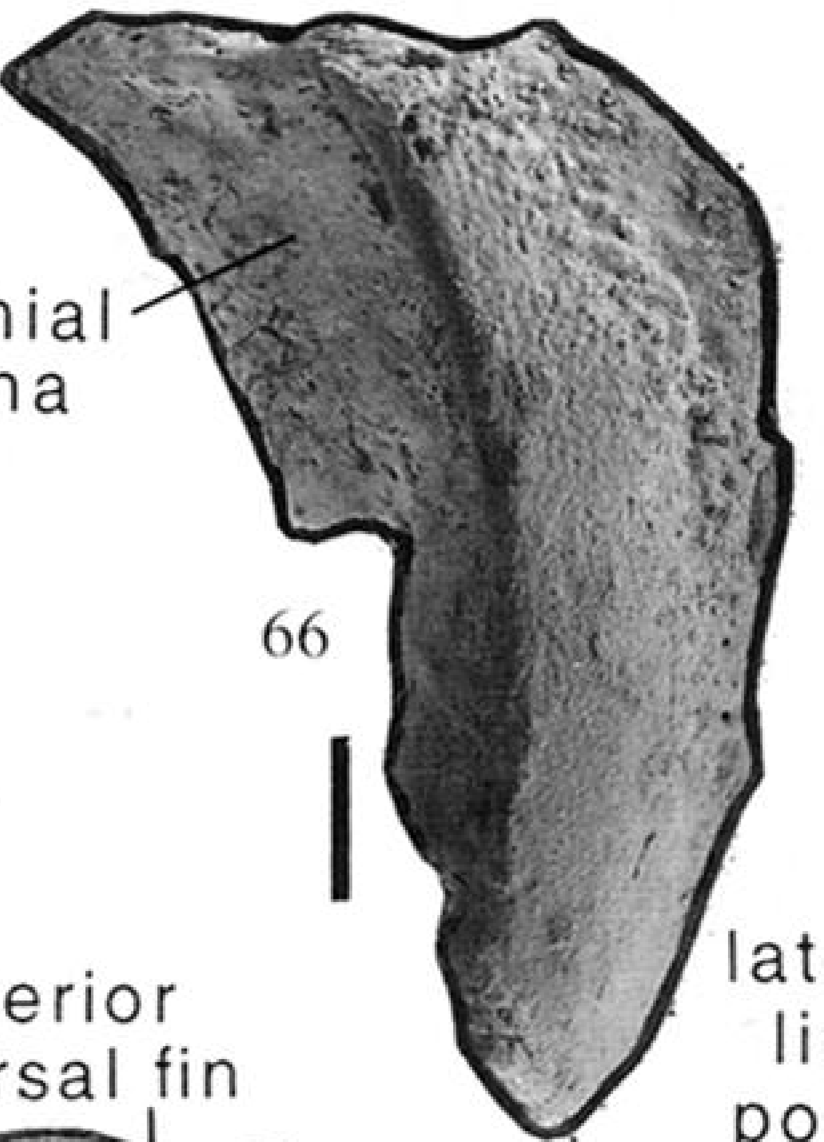
Figures 51 and 52. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

Figure 51. (*a*,*b*) Lateral views of the left side of the palate of the holotype, ANU49101, showing marginal denticles and enamel-covered ends of the palatal ridges. In (*a*) the specimen is whitened; in (*b*) unwhitened.

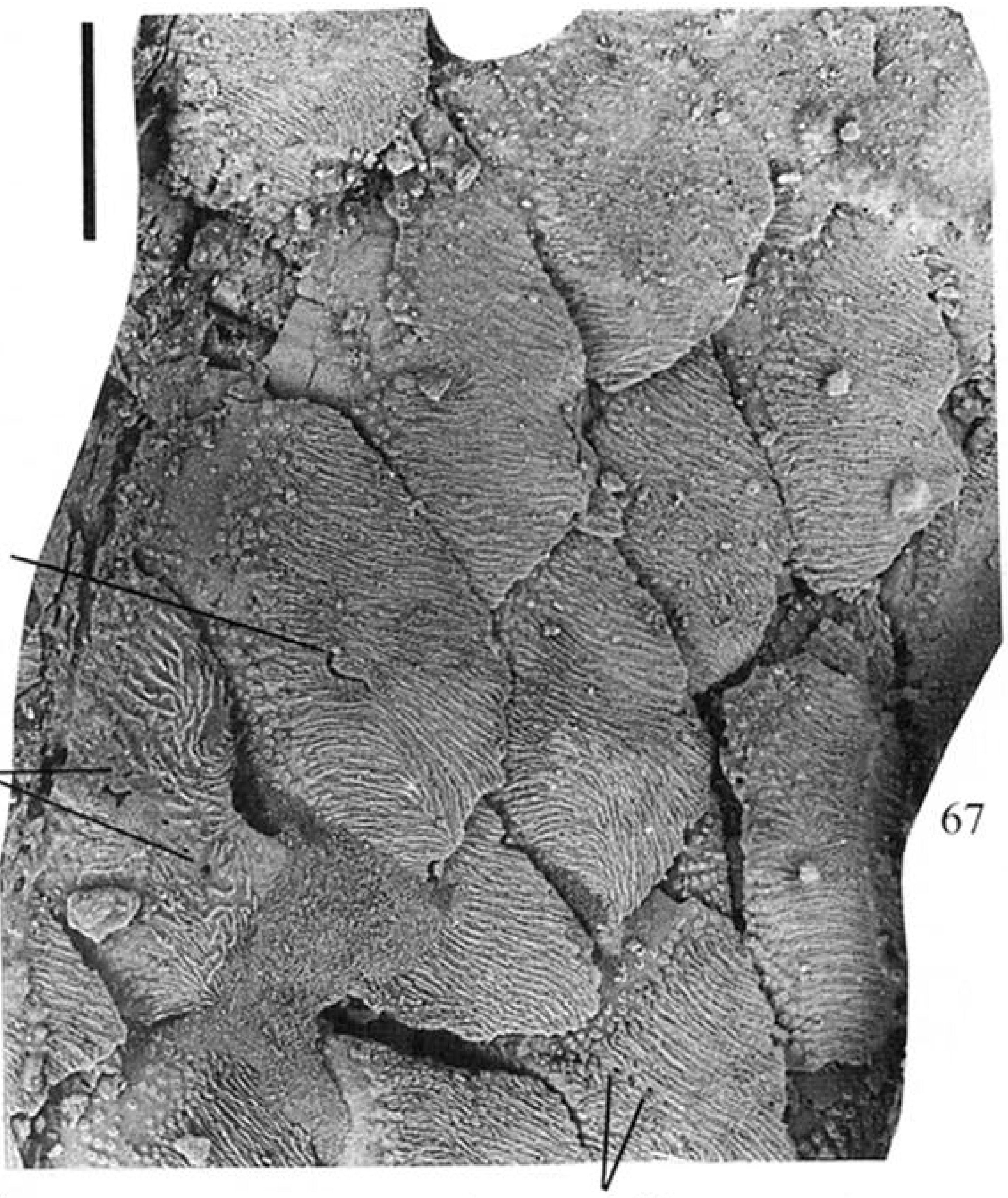
Figure 52. (*a*,*b*) Lateral views of right side of the palate of CPC30838 showing marginal denticles. In (*a*) the specimen is whitened; in (*b*) unwhitened. Arrows indicate the ends of palatal ridges.



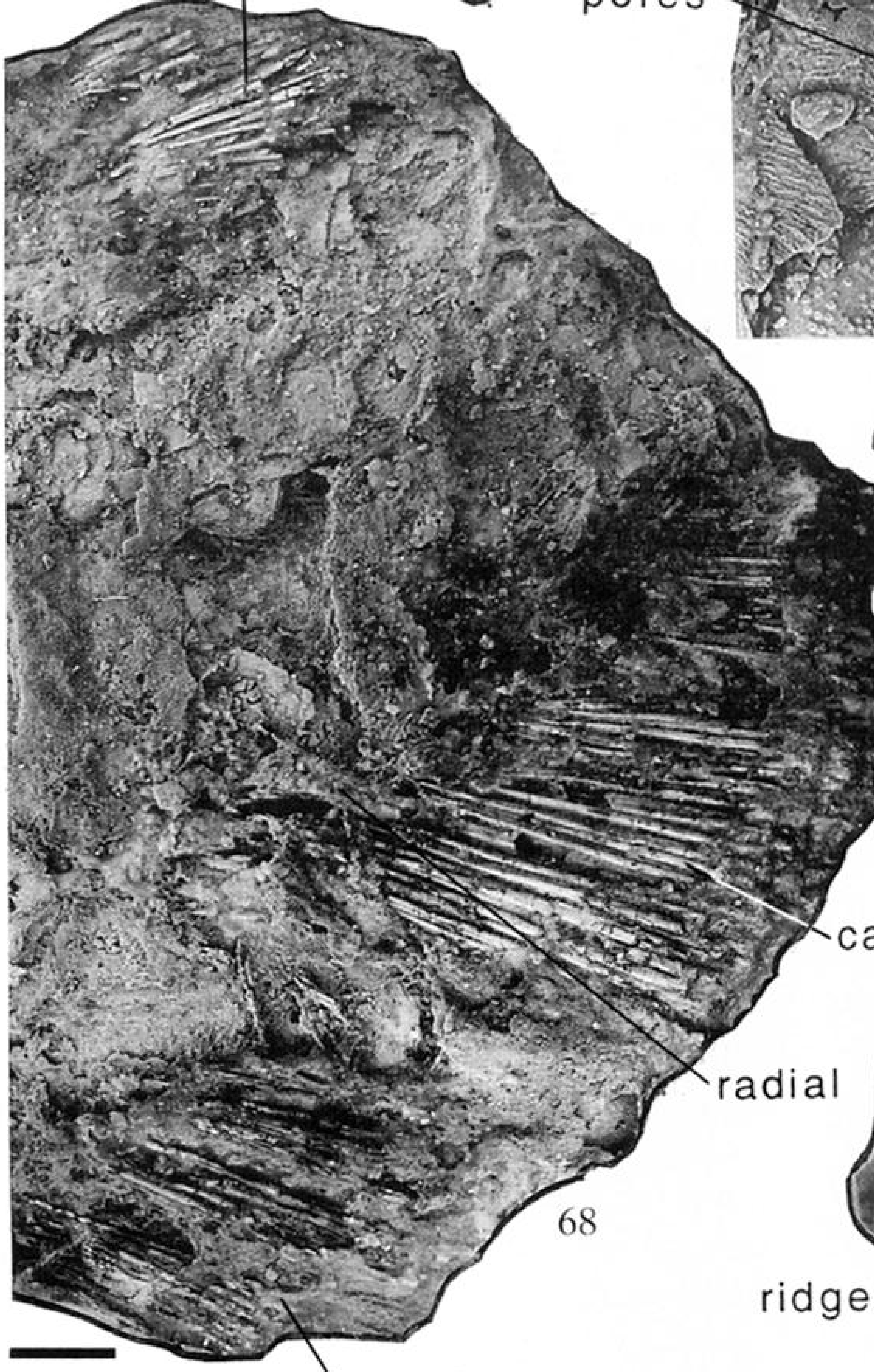
Figures 53–64. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.



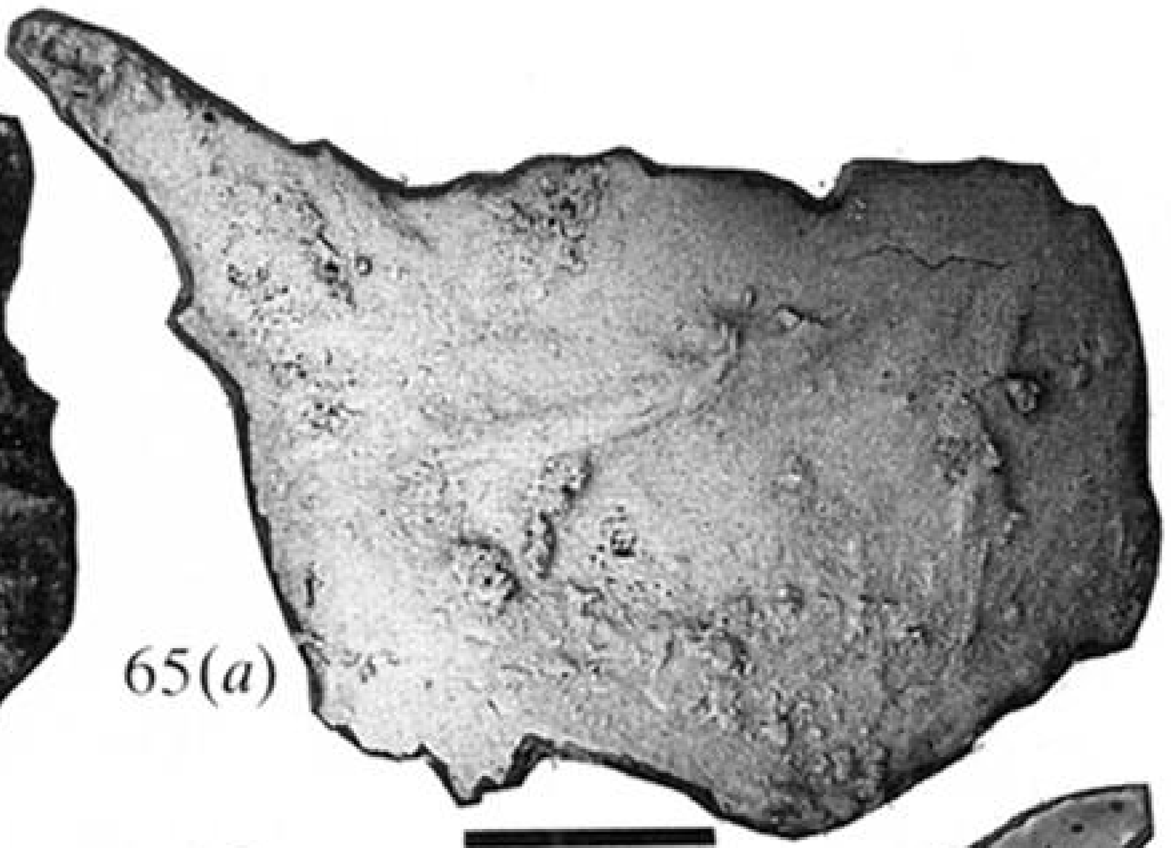
66



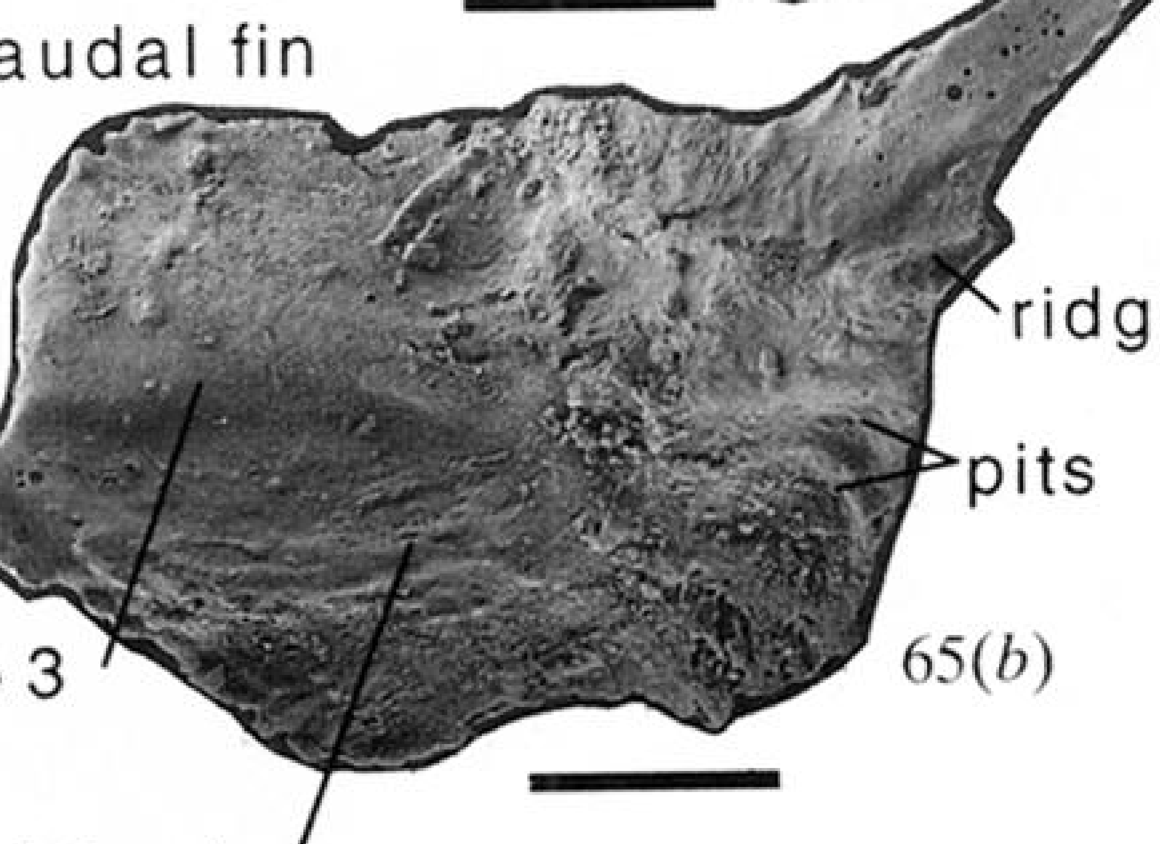
67



68



65(*a*)



65(*b*)

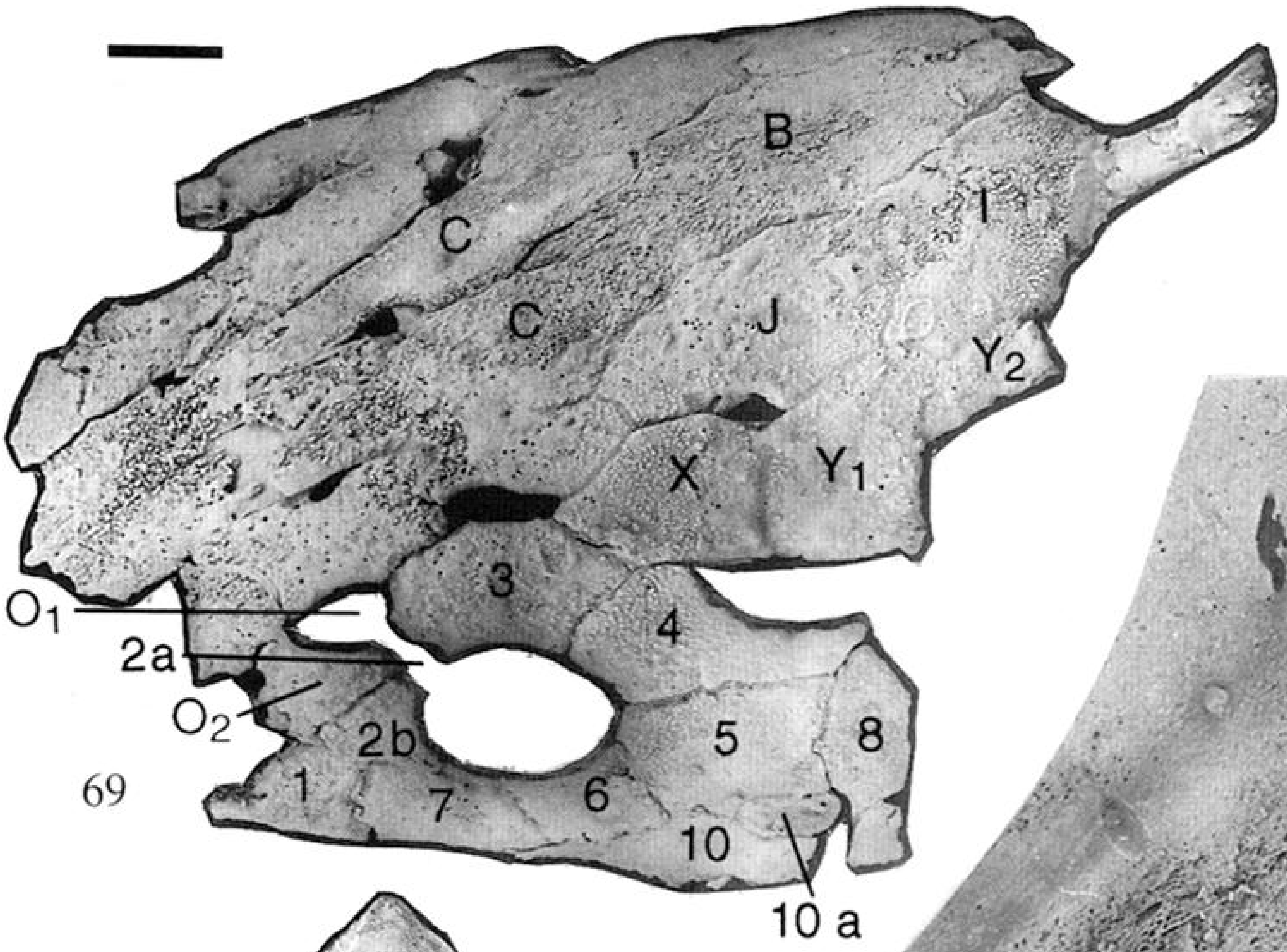
Figures 65–68. *H.* (*Holodipteroides*) *elderae*. Scale bars = 10 mm.

Figure 65. (*a*) Mesial and (*b*) lateral views of the left anocleithrum of the holotype.

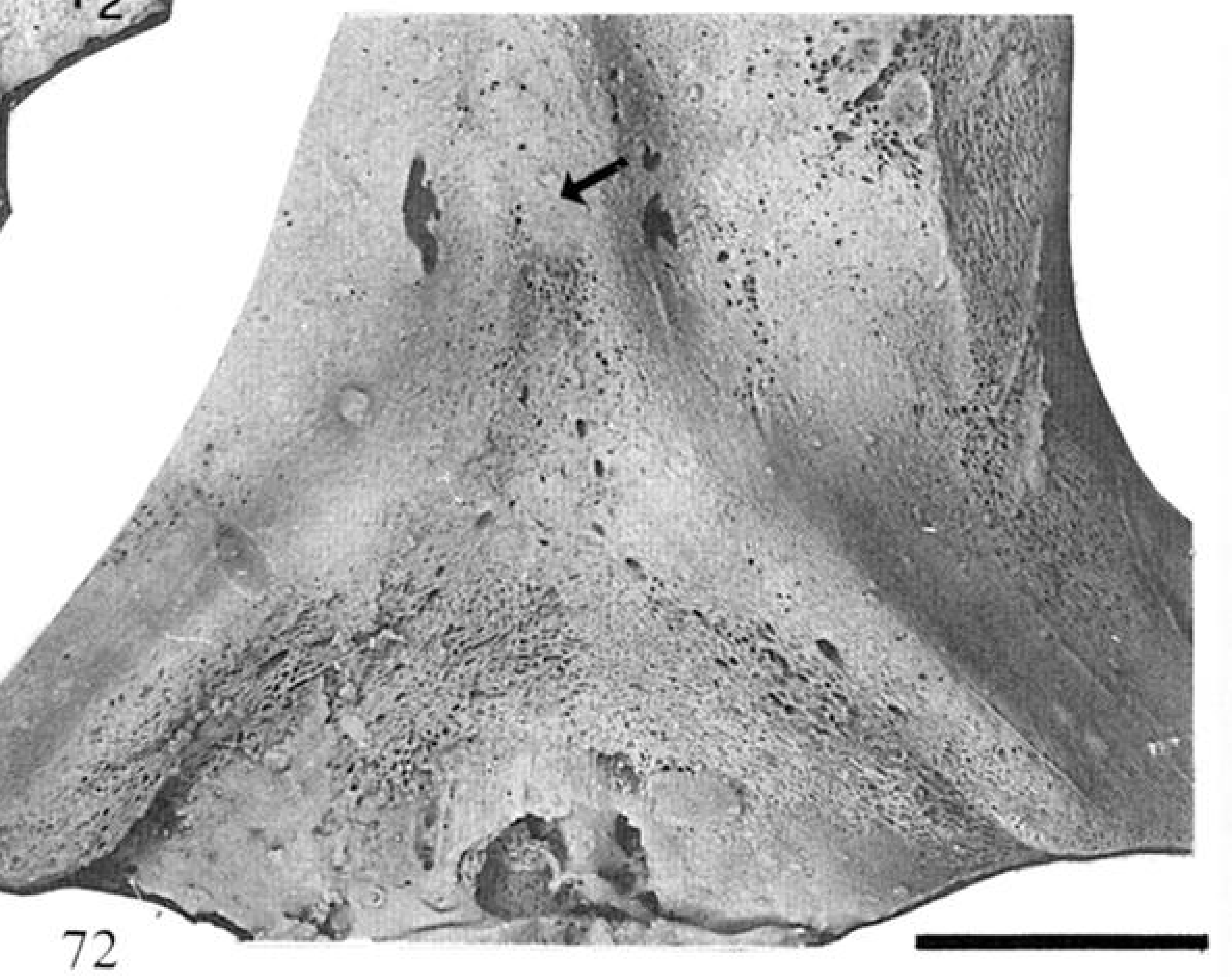
Figure 66. Anterolateral view of the the left clavicle of the holotype.

Figure 67. Block of scales of CPC30828, anterior to the left. Pit line asterisked.

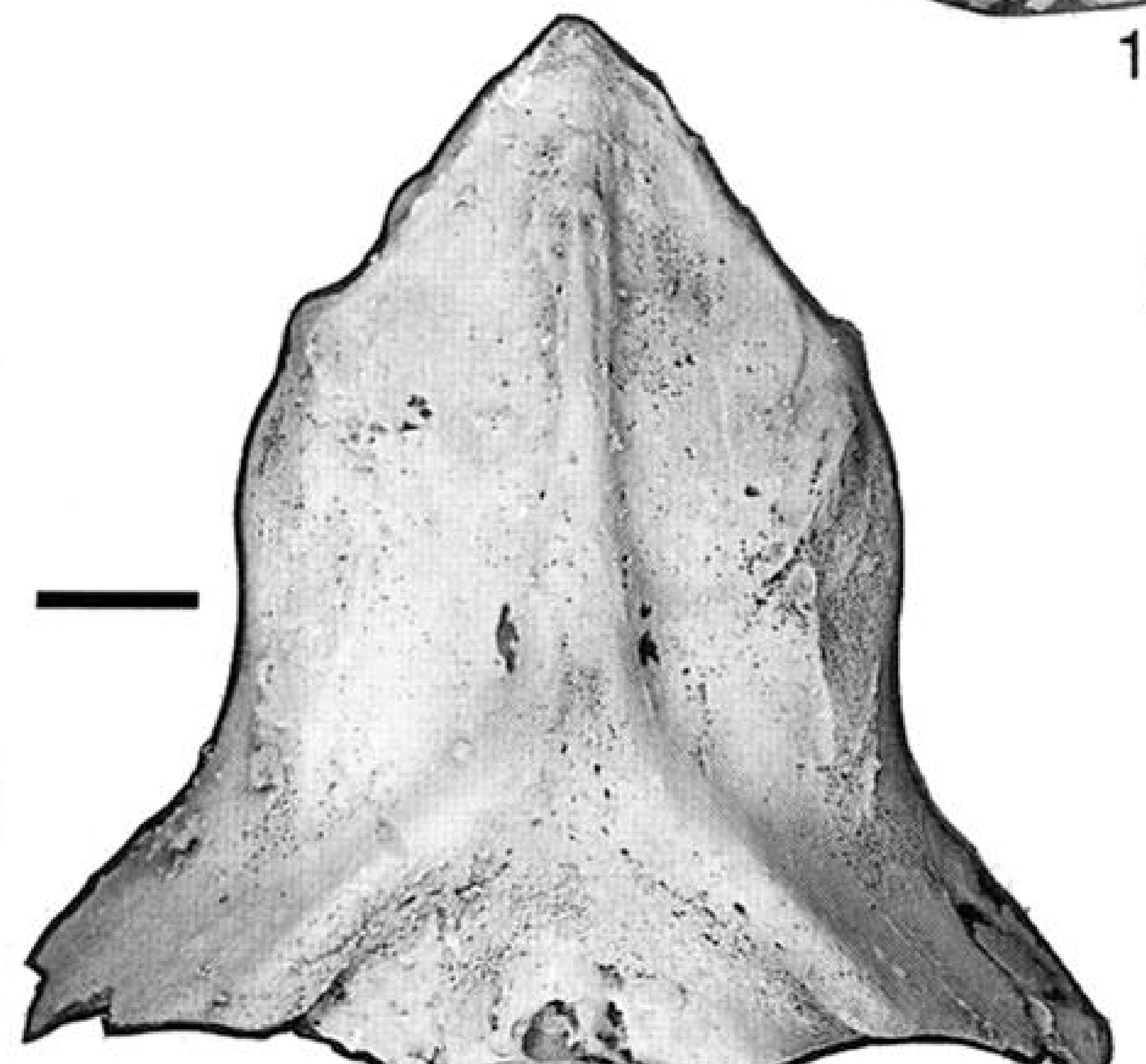
Figure 68. Posterior fins of CPC30828 showing rays of caudal, posterior dorsal and anal fins.



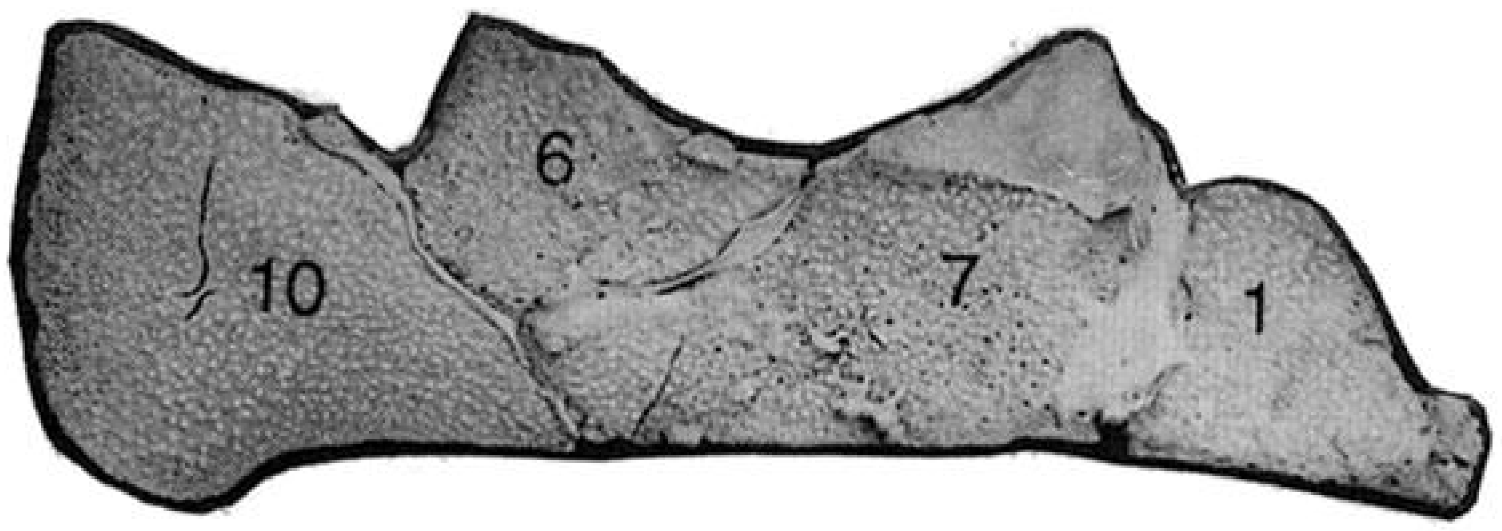
69



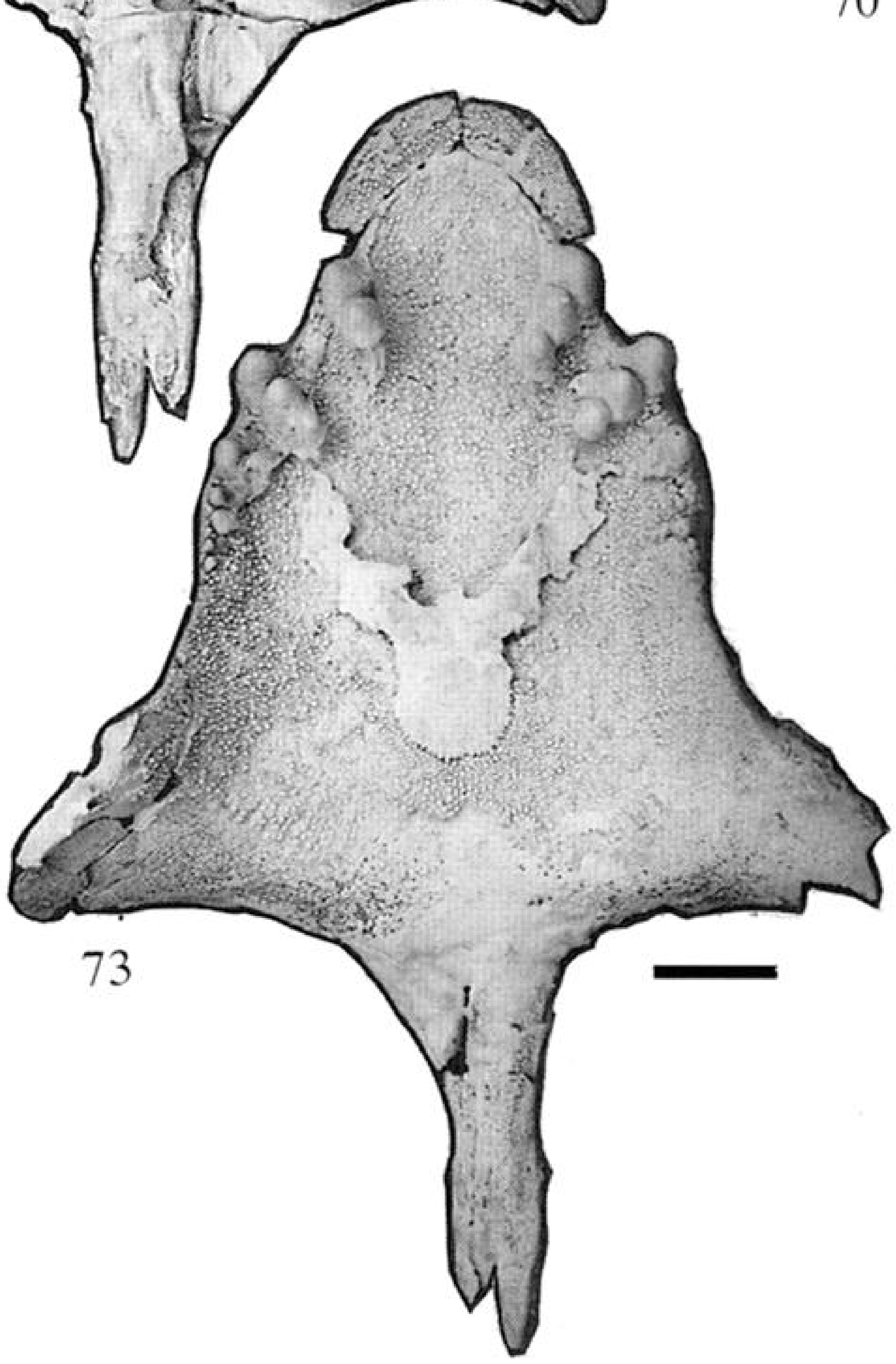
72



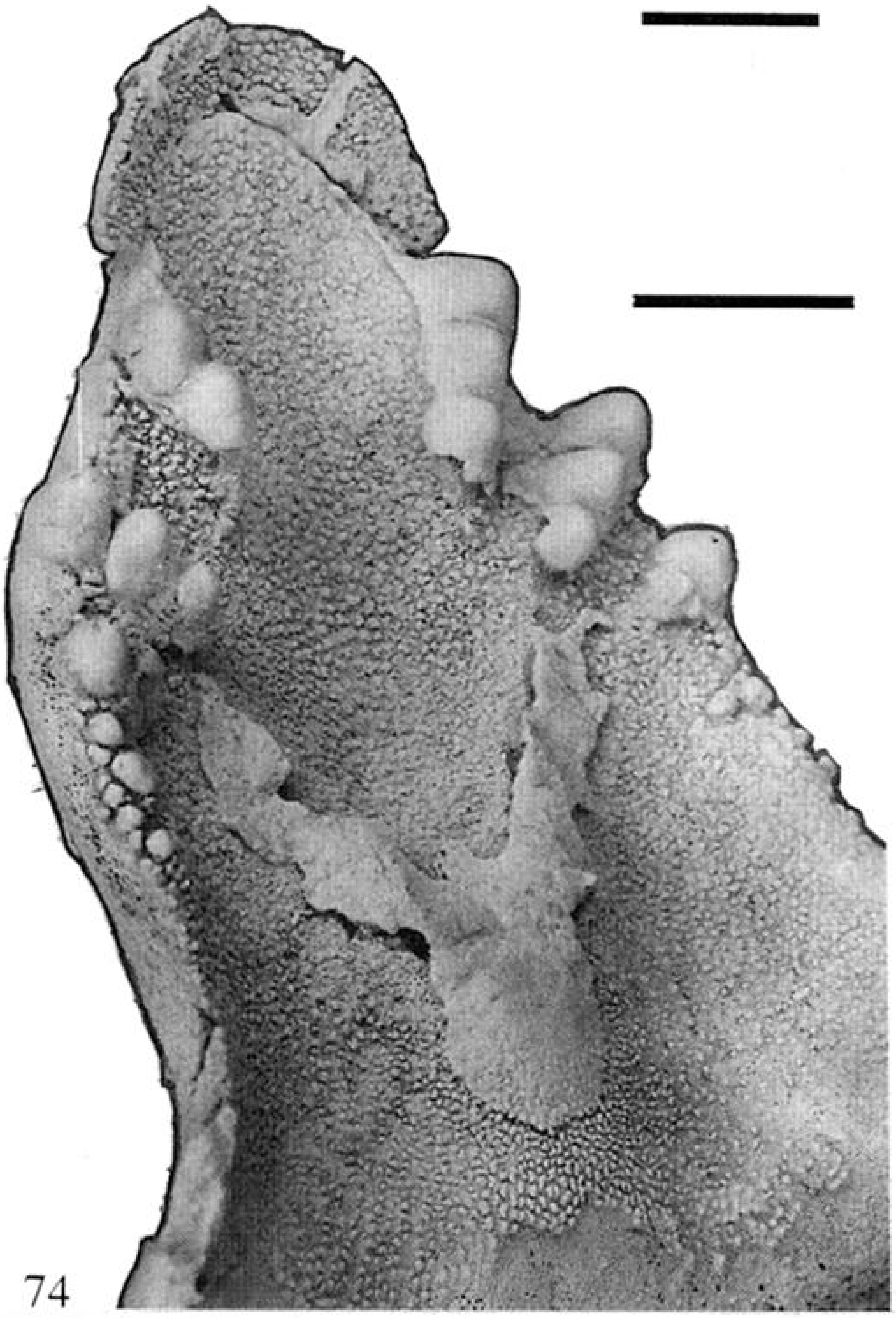
71



70

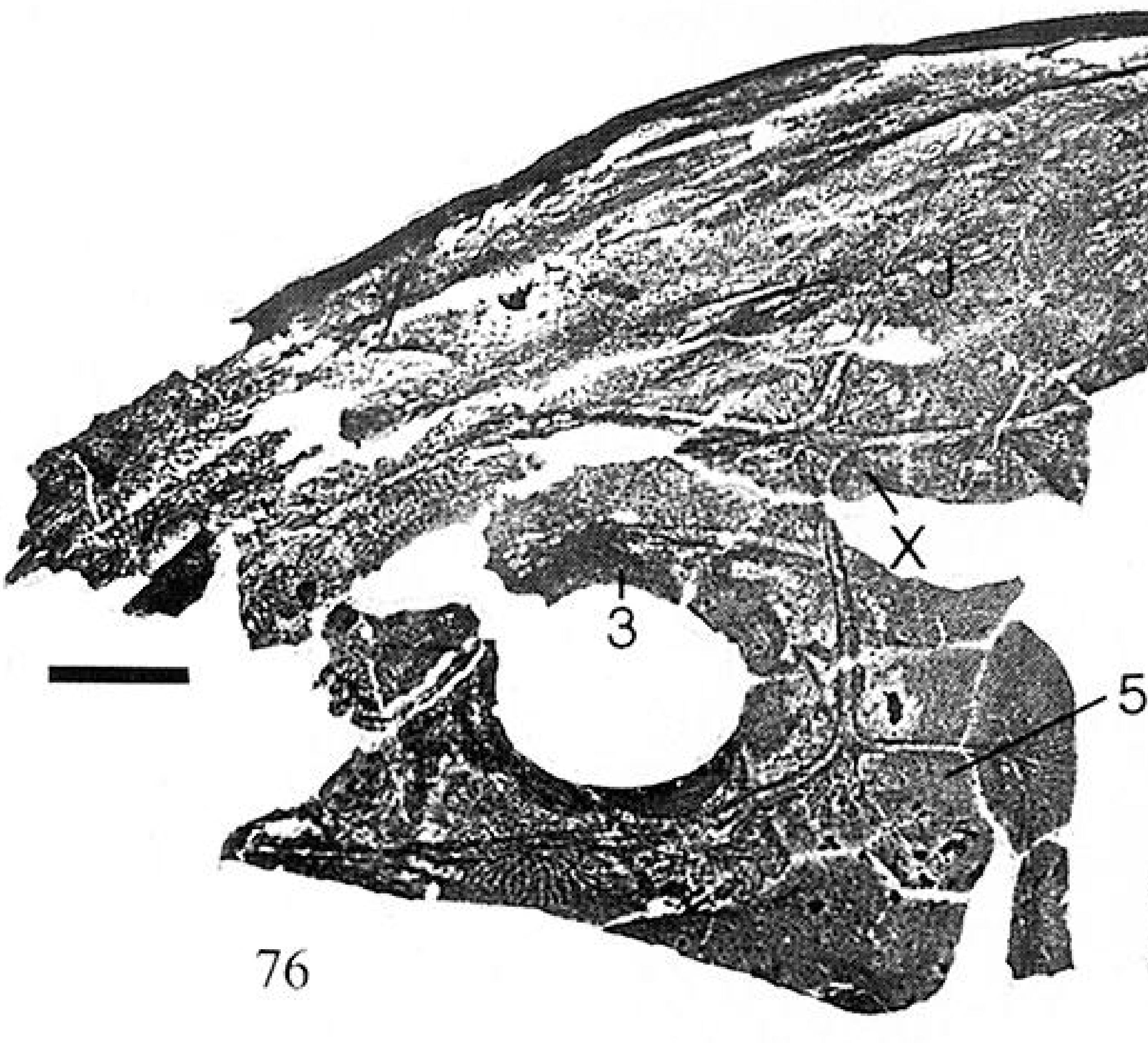


73

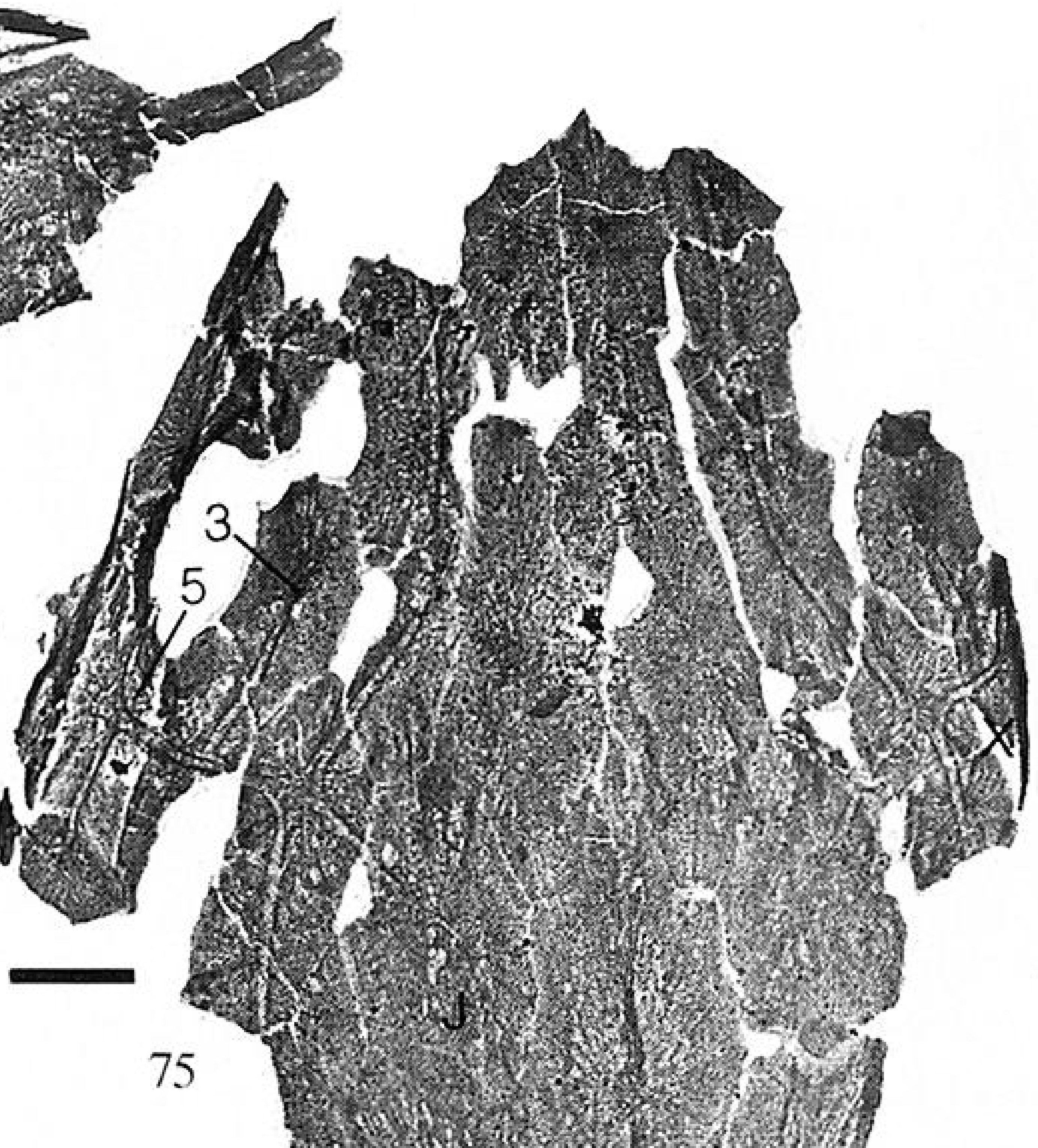


74

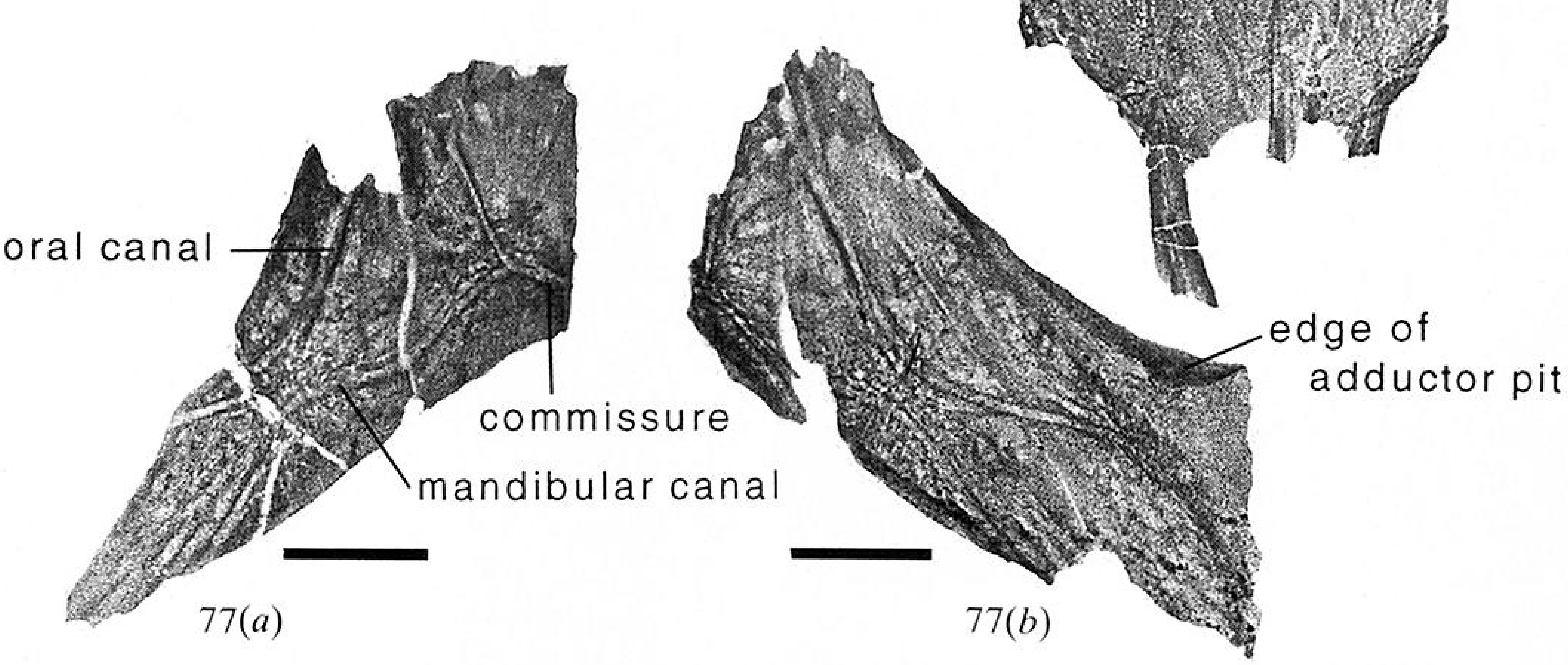
Figures 69–74. *H.* (*Asthenorhynchus*) *meemannae*. Scale bars = 10 mm.



76

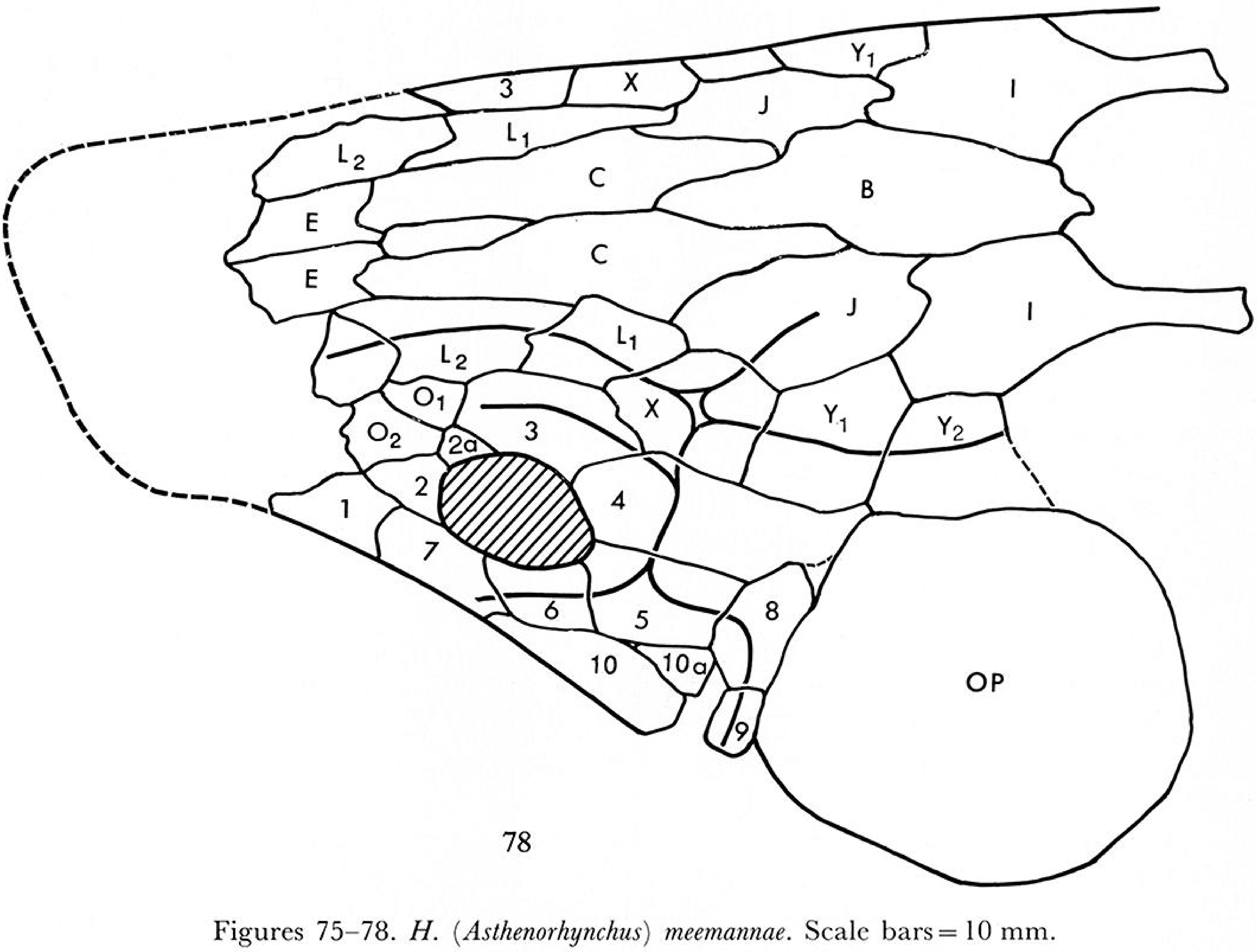


75



77(*a*)

77(*b*)



78

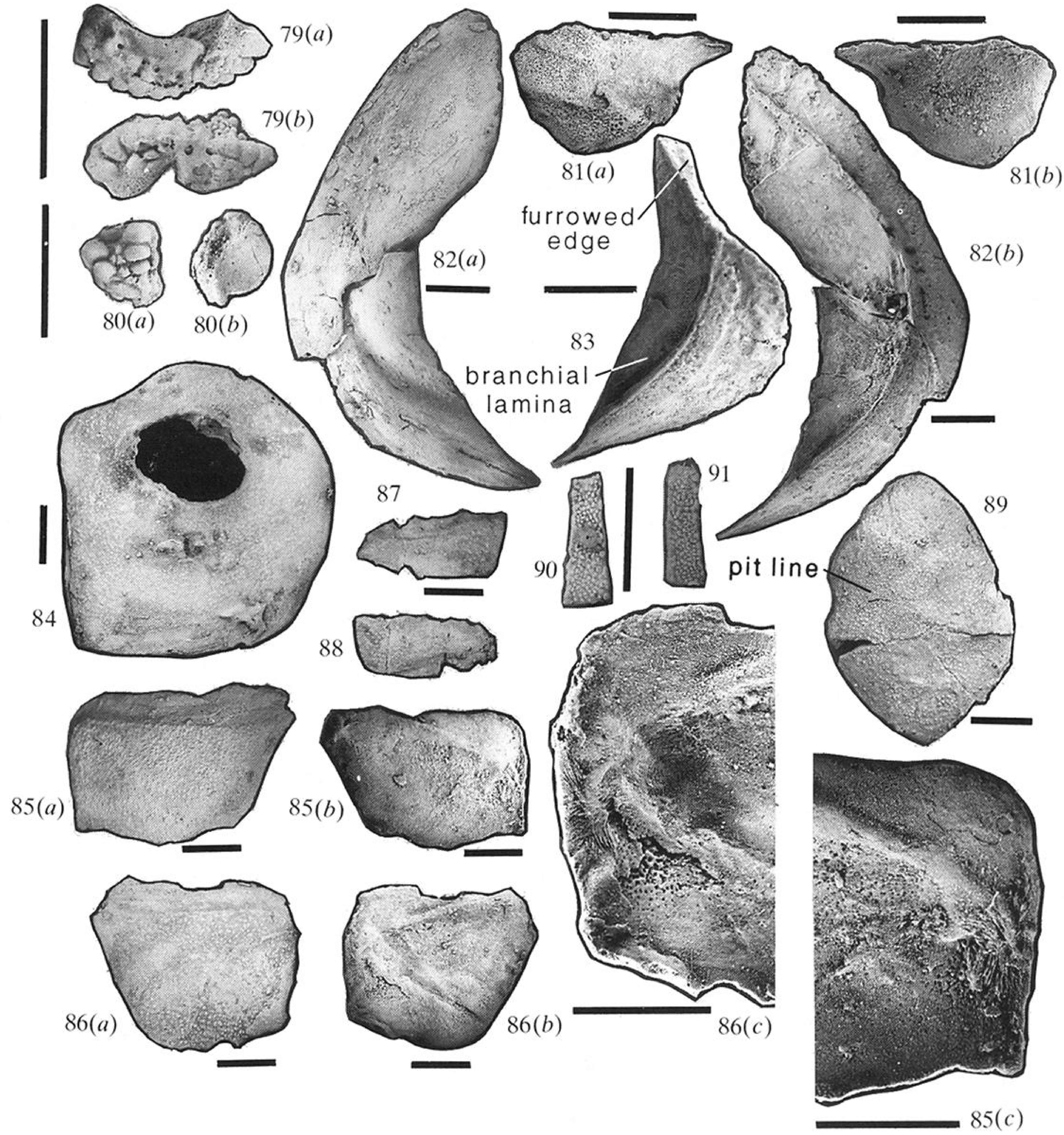
Figures 75–78. *H.* (*Asthenorhynchus*) *meemannae*. Scale bars = 10 mm.

Figure 75. Dorsal X-radiograph of skull roof of the holotype showing the radiation centres and lateral lines in bones X, J, 3 and 5.

Figure 76. Lateral X-radiograph of same. Compare with figure 69.

Figures 77. (*a*,*b*) X-radiographs of the known external dermal bones of the right and left sides of the mandible of the holotype. Note the approach of the oral and mandibular canals in the angular bone on each side of the specimen.

Figure 78. Reconstruction of the roof, cheek and operculum in anterodorsolateral view. Based on the holotype.



Figures 79–91. *H.* (*Asthenorhynchus*) *meemannae*. Scale bars = 10 mm.

Figure 79. (*a,b*) Two isolated dental plates from the snout region of the holotype here glued together and shown in (*a*) oblique, and (*b*) buccal views. These dental plates, and the one shown in figure 80, carry teeth with hypermineralized dentine cores.

Figure 80. (*a,b*) Isolated dental plate from the holotype in (*a*) buccal and (*b*) visceral views.

Figure 81. (*a*) Lateral, and (*b*) mesial views of the right anocleithrum of the holotype.

Figure 82. (*a*) Mesial, and (*b*) lateral views of the articulated left cleithrum and clavicle of the holotype.

Figure 83. Lateral and slightly anterior view of the separated clavicle of the holotype showing the external ornament and articular surface for reception of the branchial lamina of the cleithrum.

Figure 84. Lateral view of the left opercular of the holotype. The specimen was collected with the large hole eroded in it dorsally.

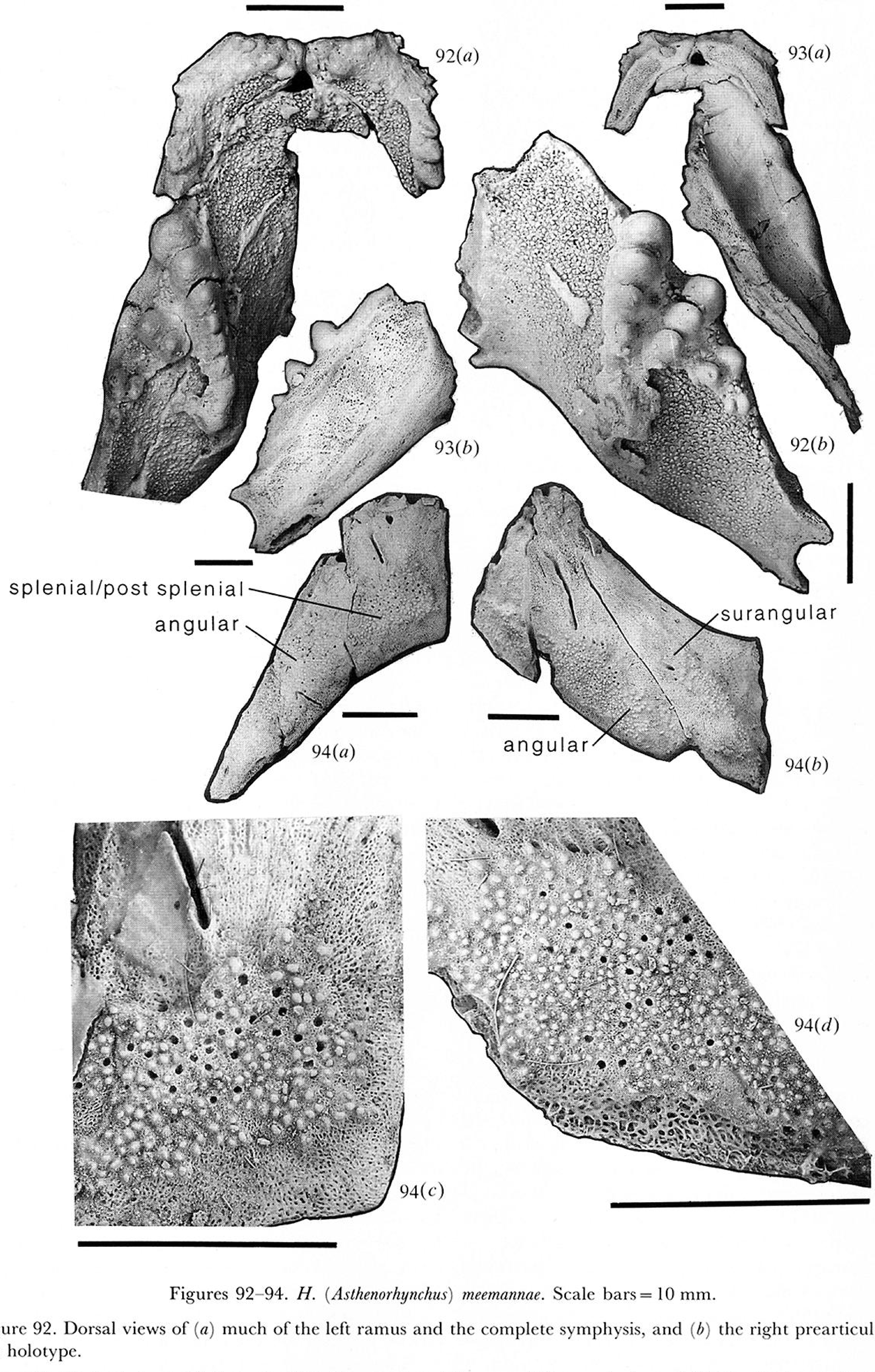
Figure 85. (*a*) Lateral, and (*b*) mesial views of the left subopercular 1 of the holotype. The anterior portion of the mesial surface is shown enlarged in (*c*) to illustrate portions of the ridges and an attachment scar.

Figure 86. (*a*) Lateral, and (*b*) mesial views of the right subopercular 1 of the holotype. An enlargement of the anterior part of the mesial surface is shown in (*c*).

Figures 87 and 88. Lateral views of the left and right suboperculars 2 of the holotype.

Figure 89. Ventral view of left principal gular of the holotype, showing a transverse pit line near its mesial edge.

Figures 90 and 91. Isolated denticulated plates from the holotype; in life possibly attached to the basihyal/basibranchial.



Figures 92–94. *H.* (*Asthenorhynchus*) *meemannae*. Scale bars = 10 mm.

Figure 92. Dorsal views of (*a*) much of the left ramus and the complete symphysis, and (*b*) the right prearticular of the holotype.

Figure 93. Ventral views of (*a*) much of the left ramus and the complete symphysis, and (*b*) the right prearticular of the holotype.

Figure 94. Infradentaries of the holotype in external view. The right splenial/postsplenial and angular are shown in (*a*), and the left angular and surangular with a fragment of the splenial/postsplenial are shown in (*b*). Details of bone structure are shown in (*c*) for the right splenial/postsplenial and in (*d*) for the left angular.

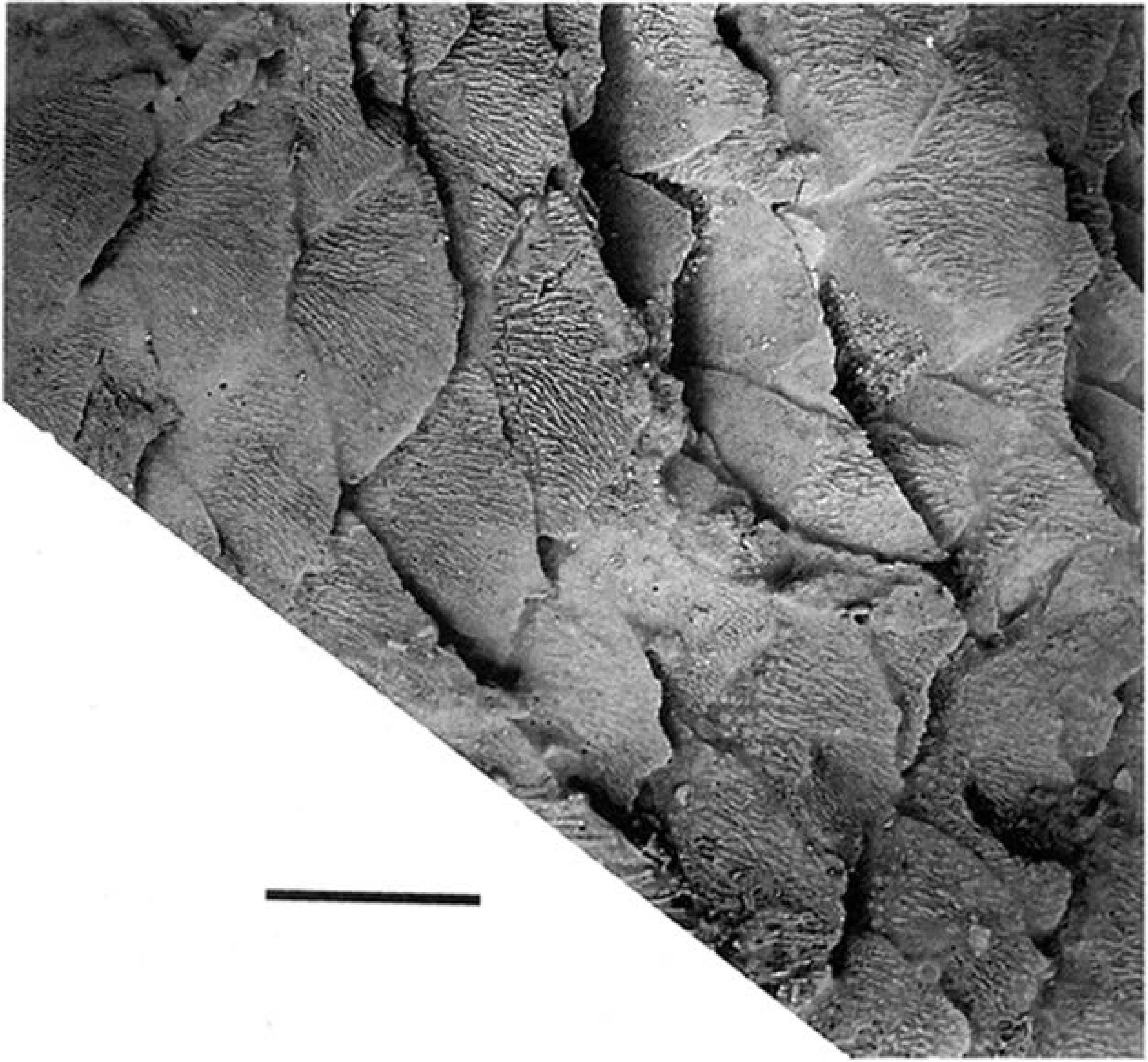
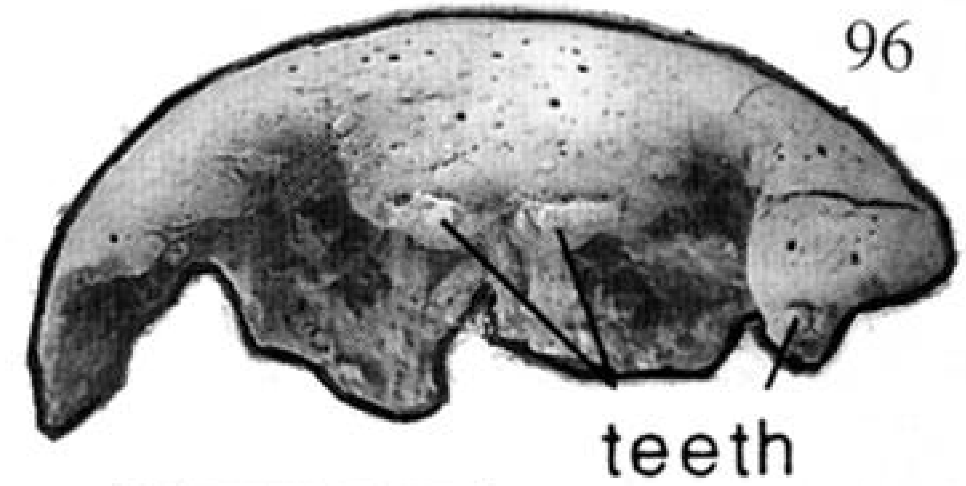
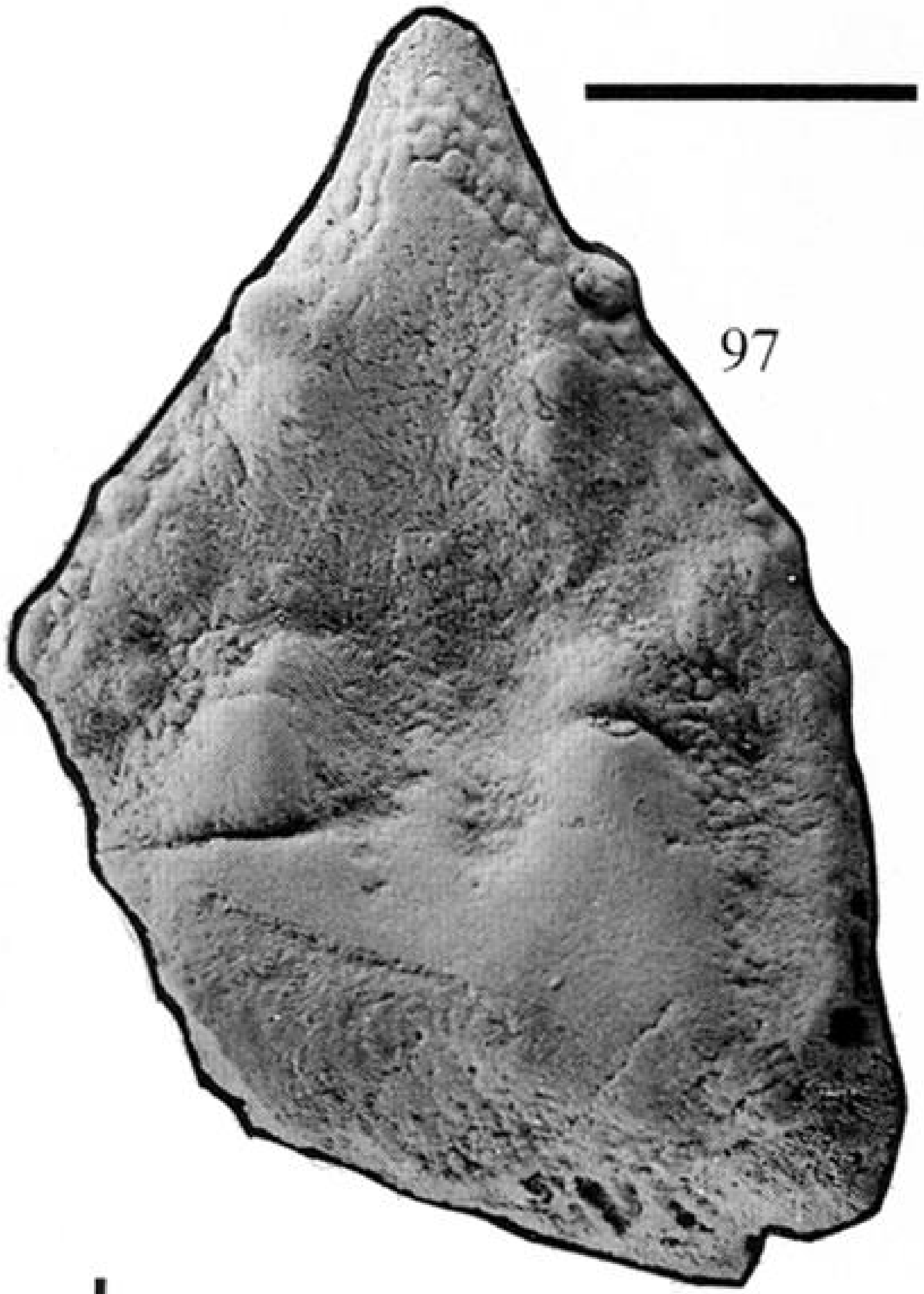


Figure 95. *H.* (*Asthenorhynchus*) *meemannae*. Block of scales of the holotype. Scale bar = 10 mm.

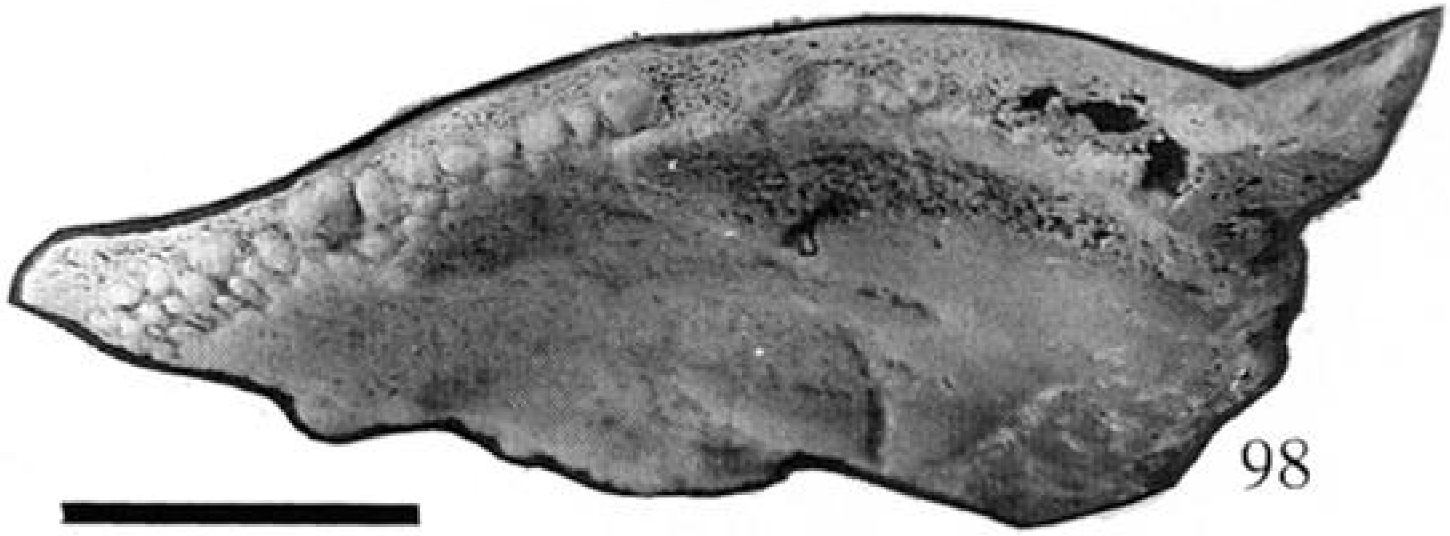


96

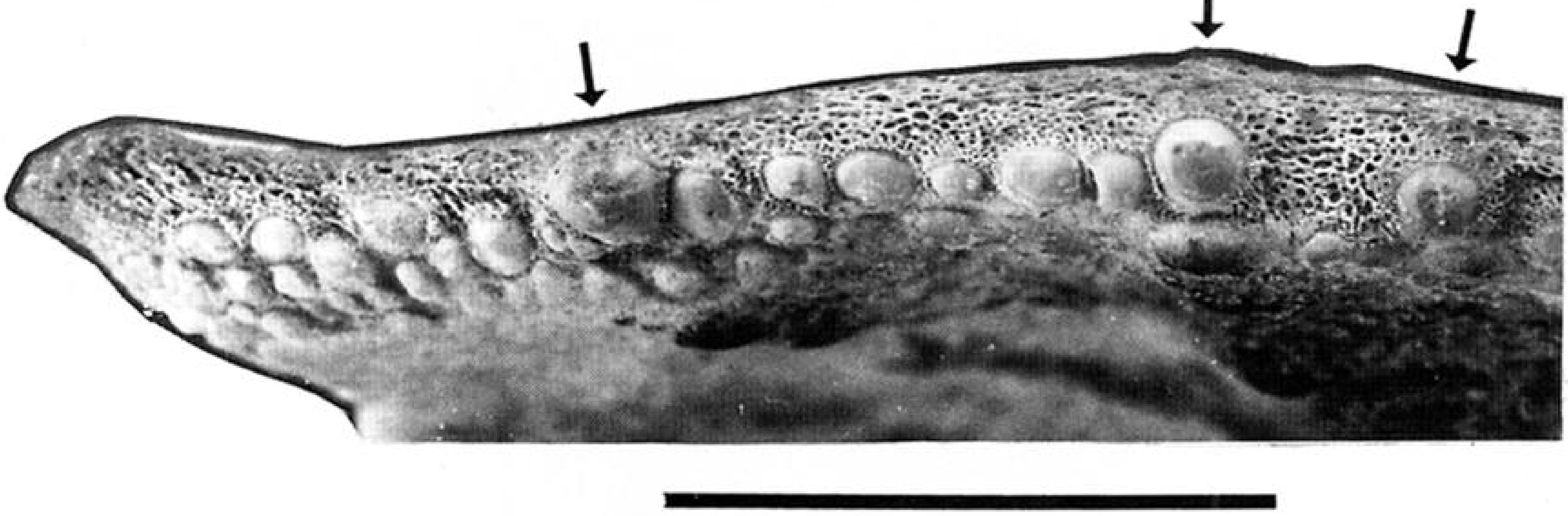


97

100



98



99

Figures 96–100. Holodontid gen. et sp. indet. Scale bars = 10 mm.

Figure 96. Anteroventral view of snout of ANU49107.

Figure 97. Ventral view of palate of same.

Figure 98. Lateral view of palate of same showing the position of the teeth at the ends of the rows lying within the group of marginal denticles.

Figure 99. Enlargement of lateral part of the palate of same. The arrows indicate the positions of the ends of the tooth rows.

Figure 100. Posterior view of palate of same, showing the bony struts within the corpus of the parasphenoid.