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ANATOMICAL AND SYSTEMATIC REVIEW OF THE PACHYCORMIDAE, A FAMILY OF MESOZOIC FOSSIL FISHES

by

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ABSTRACT

A detailed account of the anatomy of Pachycormus macropterus (Blainville) 1818, the type species of the type genus of the family Pachycormidae is given, with special reference to the neurocranium, visceral arch skeleton and pectoral girdle.

The genera and species ascribed to the family Pachycormidae by various authors are reviewed with the result that:- three genera, Leedsichthys (Woodward) 1889, Eugnathides Gregory, 1923, and Ohmdenia Hauff, 1953, are removed; three other genera, Asthenocormus (Wagner) 1863, Prosauropsis Sauvage 1895, and Orthocormus Weitzel, 1930 are found to be ill founded and their species redistributed within the family; and the number of species in several of the remaining genera is reduced.

A revised diagnosis of the family is given and a list of characters drawn up, on the basis of which the Pachycormidae sensu stricto is considered to be monophyletic; the interrelationships of the genera within the family are considered. Finally the relationships of the pachycormids to other major groups of fishes are reviewed and a new systematic position assigned.

To

L. B. and R. J. Mainwaring

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CONTENTS

INTRODUCTION

The Pachycormidae Woodward, 1895 is a family of Mesozoic fishes within the Halecostomi, a division of the Neopterygii (Patterson, 1973). In Part III of his *Catalogue of fossil fishes* Woodward (1895) assigned seven genera, *Sauropsis* Agassiz, 1832, *Prosauropsis* Sauvage, 1894, *Euthynotus* Wagner, 1860, *Asthenocormus* (Wagner) 1863, *Pachycormus* Agassiz, 1833, *Hypsocormus* Wagner, 1860 and *Protosphyraena* Leidy, 1857 to the family and suggested that an eighth, poorly known genus, *Leedsichthys* (Woodward) 1890, might also be provisionally included. In 1896 Woodward re-established the genus *Saurostomus* Agassiz, 1833 which he had previously considered to be a junior synonym of *Pachycormus*.

Since 1896 three further genera, *Eugnathides* Gregory, 1923, *Orthocormus* Weitzel, 1930 and *Ohmdenia* Hauff, 1953, have been attributed to the Pachycormidae. Of all these genera only *Sauropsis*, *Pachycormus*, *Saurostomus*, *Euthynotus*, *Hypsocormus* and *Protosphyraena* are retained in the present work.

The family spans most of the Jurassic and Cretaceous Periods but individual genera are more restricted. *Pachycormus* and *Saurostomus* are known only from the Upper Lias (Lower Jurassic), *Sauropsis* and *Euthynotus* from the Upper Lias and from the Kimmeridgian (Upper Jurassic), *Hypsocormus* from the Oxfordian (Upper Jurassic) and the Kimmeridgian. *Protosphyraena* has the longest time-range, from the Oxfordian to the Senonian (Upper Cretaceous); it also has the widest geographical distribution, Cretaceous species of this genus having been recroded from England, N. America and Russia. Apart from one record of *Sauropsis* from Cuba, none of the Jurassic members of the family have been found outside Western Europe.

Interest was recently focused on the family *Pachycormidae* when Patterson (1973) identified them as the most primitive teleostean group, and stated that they appeared to be the sister-group of all succeeding teleosts, a conclusion which has been confirmed by extra studies (Patterson, 1977, Patterson & Rosen, 1977). Therefore it is important that there should be a comprehensive description of *Pachycormus macropterus* the type species of the type genus of the family, supplementing the accounts of Lehman (1949) and Wenz (1968), both of which were limited by the preparation methods employed. A detailed anatomical description of *Pachycormus macropterus* comprises the major part of this work, where special emphasis has been given to the structure of the meurocranium, to the visceral arch skeleton and to the pectoral girdle. Where possible comparisons has been made between *Pachycormus*, and the caturids and parasemionotids on the one hand (the groups with which the pachycormids were formally aligned (Rayner, 1941, 1948; Lehman, 1966; Gardiner, 1967 and Wenz, 1968)) and the pholidophorids and leptolepids on the other. In these comparisons special consideration has been given to the primitive status of *Pachycormus* within the Teleostei. However, before any consideration of the relationships of the family as a whole is possible, it is essential to estimate whether or not they are a monophyletic assemblage. To that end, a systematic review of the family has been carried out, and this constitutes the second major part of this study. The review is based on Woodward's 1895 *Catalogue of fossil fishes* and the criteria upon which certain genera and species were founded has been re-examined. From this reorganization a list of derived character-states has been drawn up for the Pachycormidae to provide information on both the inter-relationships of the genera within the family, and the relationships of the pachycormids to other teleostean groups.

Unless otherwise stated all the specimens referred to are housed in the collection of the British Museum (Natural History), and are referred to in the text by their registered numbers (with or without the prefix P).

In addition type material of the family was examined from the following museums: Muséum d'Histoire Naturelle, Paris; Sedgwick Museum, Cambridge; Bath Museum (Moore collection); Staatsammlung für Historisches Geologie und Paläontologie, Munich; and Naturhistoriska Riksmuseet, Stockholm. Where possible the registered number of each type specimen is given before its diagnosis (for brevity the Museums of Paris, Munich and Stockholm will be indicated just by those cities' names before the registered number).

Individual specimens were prepared for this study by repeated immersion in dilute formic acid. Between treatments each specimen was dried and any newly exposed bone was coated with Polybutyl-methacrylate, this both strengthens and protects the bone (Methly-ethyl-ketone was used as solvent).

ANATOMY OF *PACHYCORMUS MACROPTERUS* (BLAINVILLE) 1818

(a) Previous work

In 1949 Lehman published the first comprehensive anatomical account of a species of *Pachycormus*. He confirmed the arrangement of dermal bones illustrated by Woodward (1908, fig. 1, A&B), and presented new information about the palate and suspensorium, the visceral arch skeleton, and the neurocranium. A year earlier Rayner (1948), in her paper "The structure of certain Jurassic holostean fishes", had included a brief account of the brain cases of both *Pachycormus curtus* and of a specimen identified as *Hypsocormus sp.* (Here described as *Protosphyraena obtusirostris* sp. nov.). Wenz (1968) reviewed the Jurassic actinopterygian fishes of Normandy, including *Pachycormus* and certain other members of the Pachycormidae. In her account Wenz expanded Lehman's description and wrote extensively on the structure of the paired and median fins.

Patterson (1973) identified and described a large median rostrodermethmoid, a reduced quadratojugal, and uroneurals in the caudal fin in *Pachycormus curtus*. More recently he commented on the structure of the neurocranium and on some of the associated dermal bones of this same species (Patterson, 1975). It was this 1975 paper that forms the starting point for this research.

(b) The dermal bones of the ethmoid region and skull roof

These are illustrated in dorsal and lateral views in Figs 1 and 2 and Plates 1 and 2. As usual in the family Pachycormidae, the rostrodermethmoid is large and pointed, and in lateral view the skull roof is almost straight and set at an acute angle to the upper jaw. At the highest point of the skull roof there is a median projection, the cranial boss, formed by the parietals and part of the frontals.

Figure 1. *Pachycormus macropterus*. Reconstruction of head in dorsal view. Based on 32433 and P10146.

Figure 2. *Pachycormus macropterus*. Reconstruction of head in lateral view. Based on 32433 and P10146.

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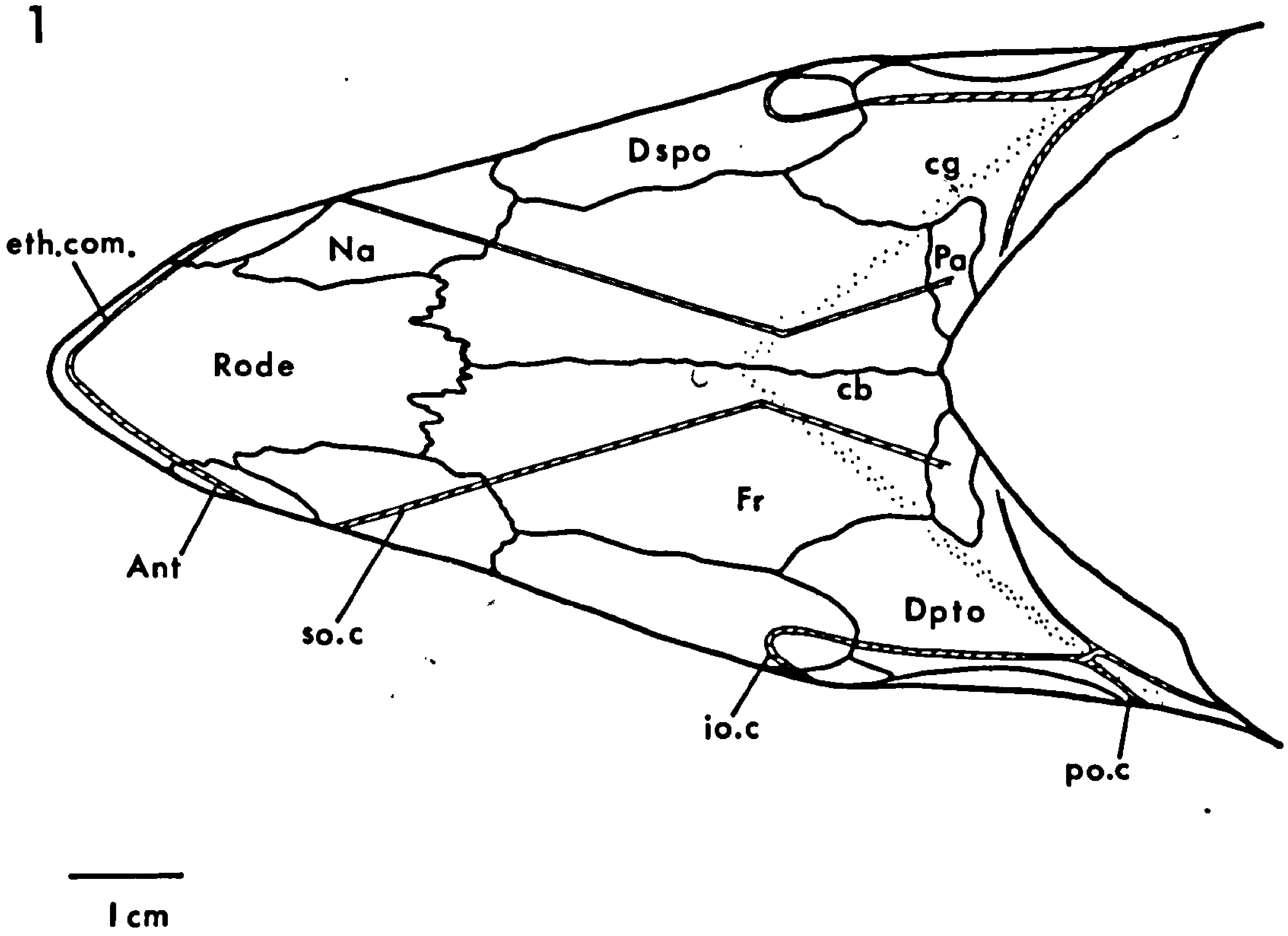
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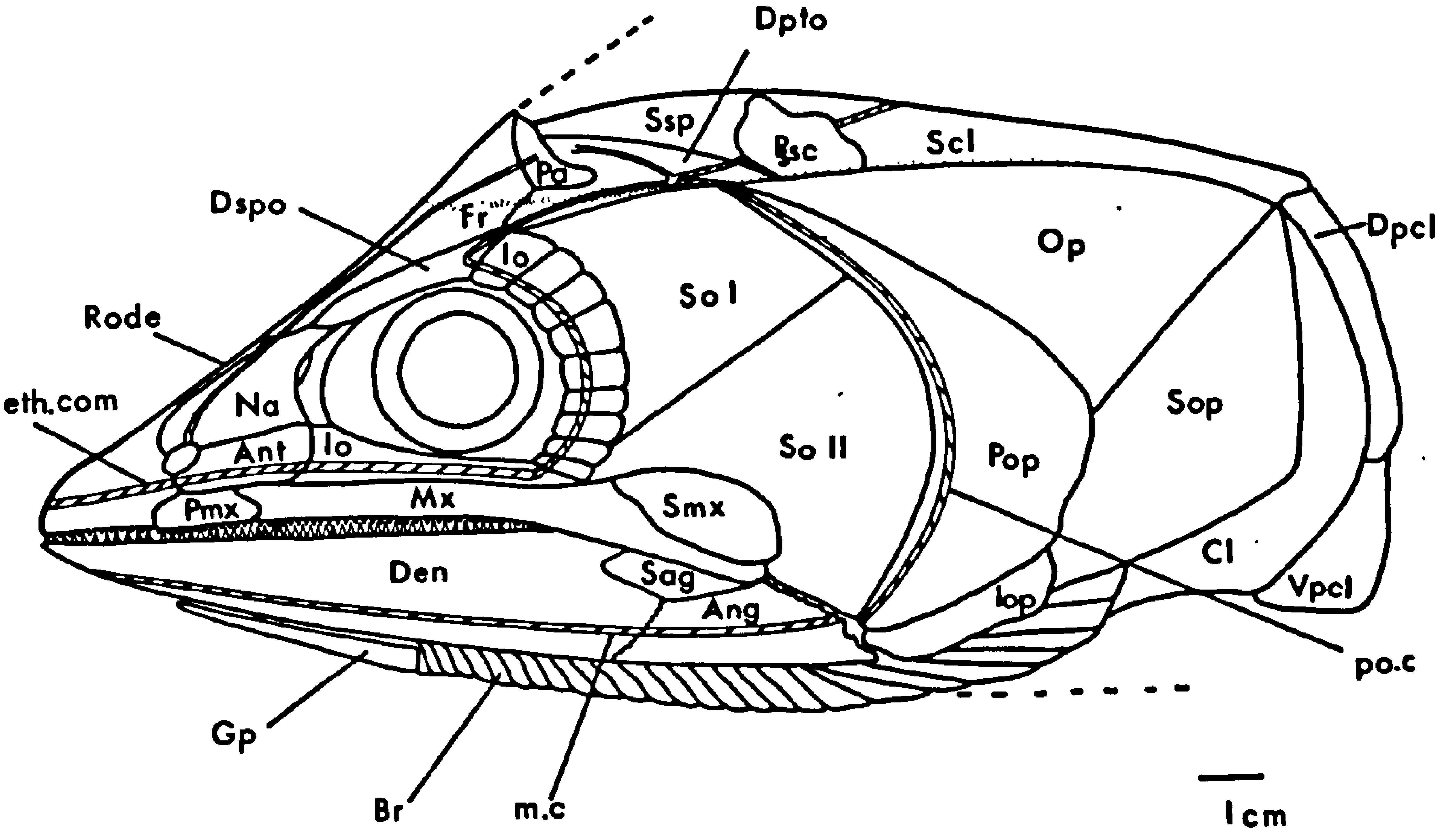
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The cranial boss is clearly marked off from the rest of the skull roof by a pair of conspicuous straight grooves. These cranial grooves begin anteriorly close to the mid-line and run the remaining length of the head, diverging at an angle of about 35° from the mid-line.

The compound rostro-dermethmoid (Fig. 3, Plates 3 and 4) was first described by Patterson (1973), and illustrated by him in 1975 (fig. 139). It comprises a large, median, shield-like rostral bone, and hidden behind this a pair of small, toothed lateral-dermethmoids. (For the origin of the term lateral-dermethmoid see Patterson 1975:481).

The rostral component contains the ethmoid commissural sensory canal, but is not dominated by it as are the rostrals of caturids, semionotids, pleuropholids and ichthyokentemids. The commissure runs parallel to the ventral edge of the bone passing anteriorly through its centre of growth, just as it does in the pholidophorids. Posteriorly the rostral component meets the frontals in an irregular, asymmetrical suture, and thus separates both the pre-maxillae and the nasals. It is significant that this rostral component possesses all those external characteristics associated with its pholidophorid counterpart (Patterson, 1975:497). It is quite unlike the rostral normally found in the amiids (Lehman, 1966); the group with which the Pachycormidae was formerly associated (Gardiner, 1960; 1967).

Hidden beneath the rostral component and lining the anterior wall of the nasal pit are the paired lateral-dermethmoids. Patterson (1973) first identified this pair of anamestic bones in the pholidophorids and leptolepids, and compared them with the "holostean" premaxillae with their well developed nasal (ascending) processes. He pointed out that the pholidophorid (and therefore the teleostean) lateral-dermethmoid bears the same relationships to the adjacent bones as does the holostean nasal process, and that the lateral plate-like premaxilla of the pholidophorids is the homologue of the toothed portion of the "holostean" bone. The significance of the development of paramedian, lateral-dermethmoids with independent, plate-like premaxillae lateral to them is that it marks a clear boundary between the Halecomorphi, in which these structures are not present, and the Teleostei (Patterson, 1973), while the precise arrangement of the lateral-dermethmoids and the rostral bone can indicate relationships within the Teleostei.

In Pachycormus the ventral edges of the lateral-dermethmoids are fused to the rostral as they are in the leptolepids but their dorsal edges are separated from that bone by a deep crevice. Internally their concave posterior faces form a pair of deep, open depressions that housed the endochondral pre-ethmoid bones (Plates 3 and 4). The ventral wall of each depression is thickened to form a distinct shelf, which bears a postero-laterally directed nasal process. The lateral-dermethmoids are toothed, as are the lateral-dermethmoids of Pholidophorus macrocephalus (Patterson, 1975), but this is the only respect in which they resemble the pholidophorid bone. In other respects ie. in being fused to the rostral, and in not meeting the frontals posteriorly, the lateral dermethmoids resemble those of the leptolepids (Patterson, 1975:497).

The paired frontals are long and wide and form the major portion of the skull roof. For about two-thirds of their length the frontals continue the gentle slope of the rostro-dermethmoid, until at the level of the

Figure 3. *Pachycormus curtus*. P10145 unrestored drawing of rostro-dermethmoid in posterior view.

Figure 4. *Pachycormus macropterus*. Reconstruction of left lower jaw in (a) lateral and (b) medial view. Based on P10146 and 32432.

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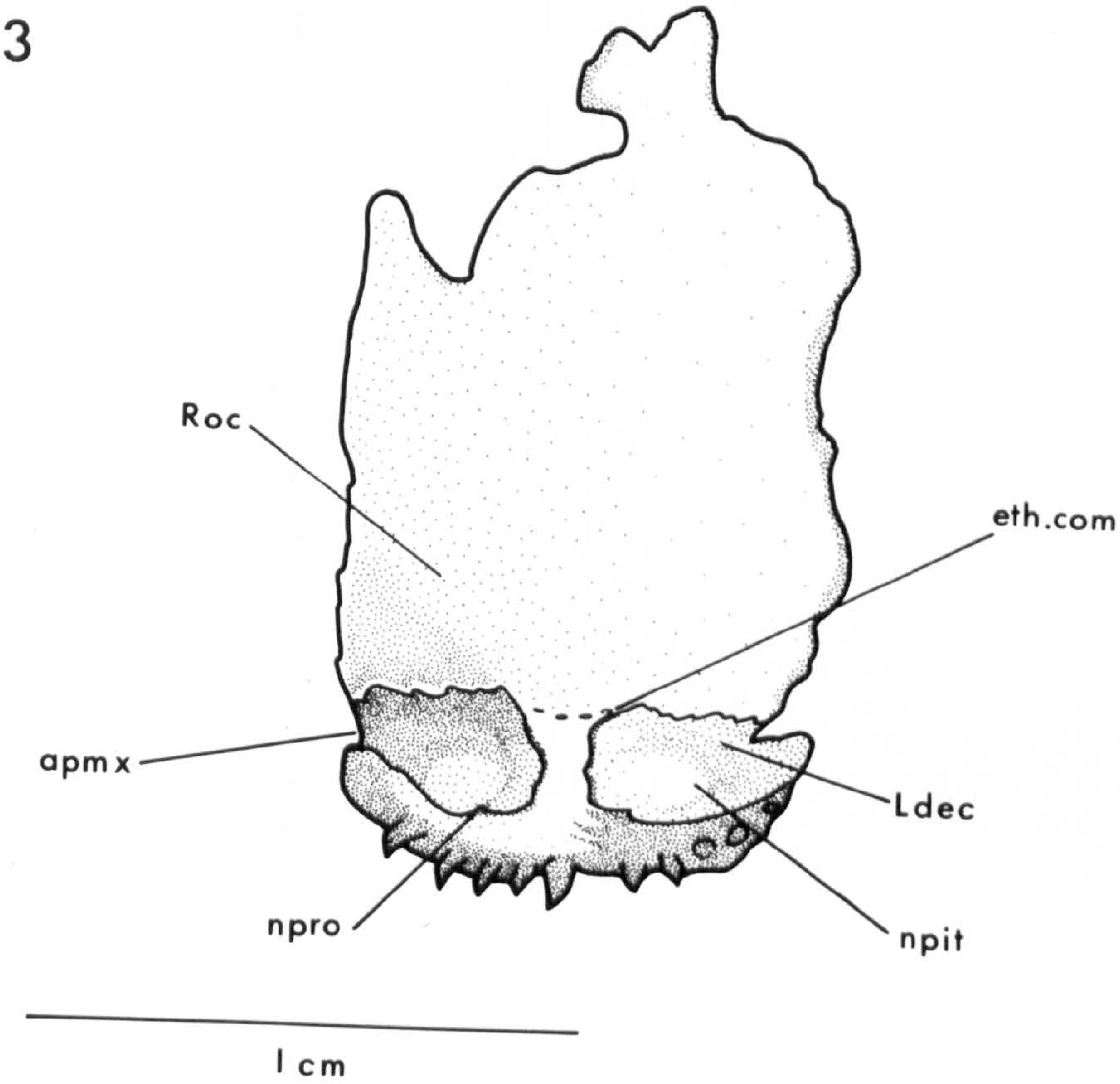
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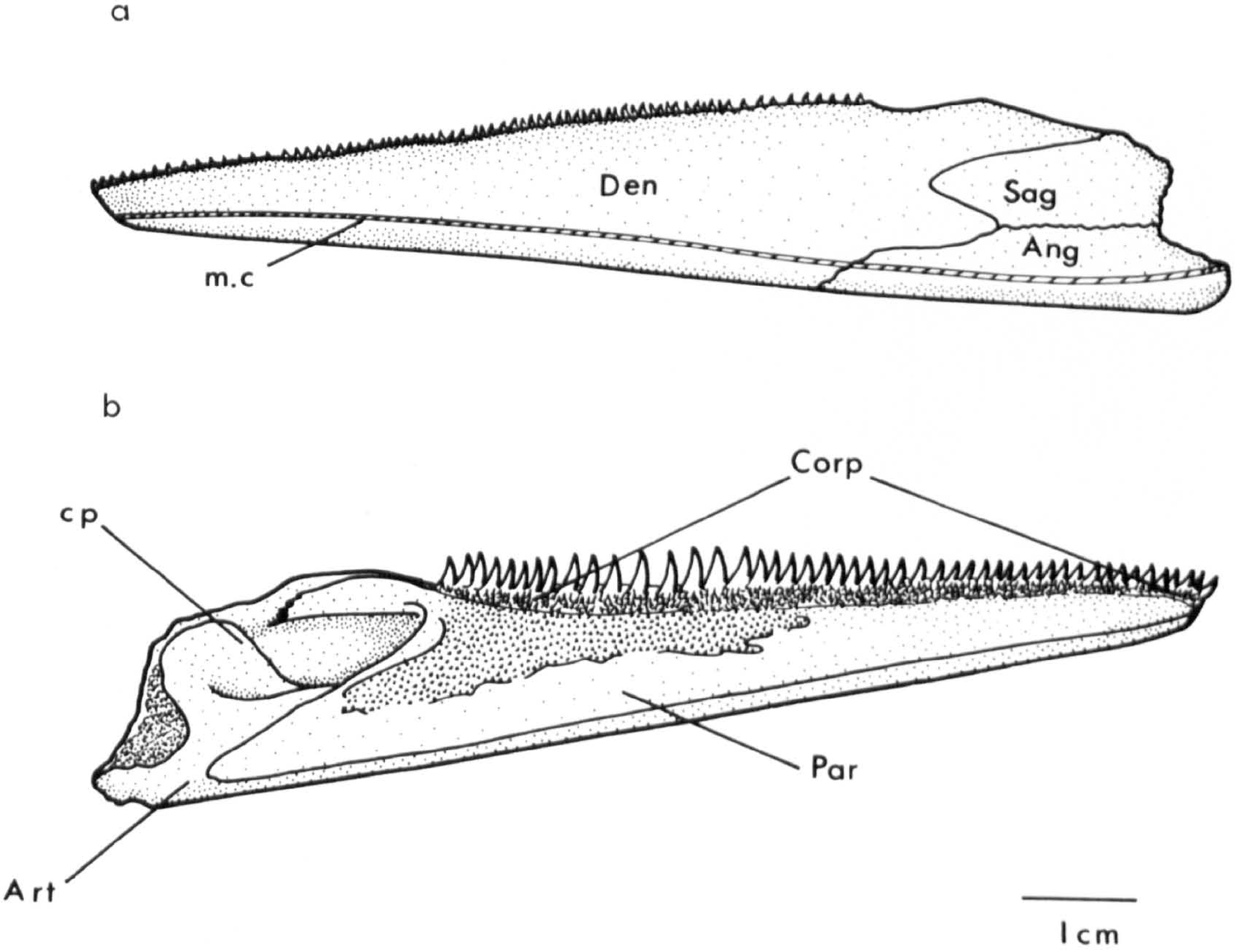
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cranial grooves they rise more steeply to form part of the characteristic cranial boss. Antero-laterally the frontals meet the nasals above the lateral-ethmoids, but the frontals have no antero-lateral tongue-like process as seen in the pholidophorids (Patterson, 1975); nor are the lateral edges of the frontals excavated above the orbits, as they are in so many fishes. Each frontal meets the dermosphenotic laterally in a long, straight suture. Posteriorly the frontals overlap the parietals and the dermopterotics.

In large, well ossified individuals (eg. P10146), the dermopterotics are bound to the frontals by a series of interlocking laminae that extend from the internal surfaces of both bones across the suture.

The supraorbital sensory canals are concealed within the thickness of the frontal bones, but can be traced by the series of pores that open onto their surfaces. Each canal enters the frontal from the nasal and runs postero-medially until it reaches the anterior end of the longitudinal cranial groove. Here it turns posteriorly and enters the parietal without meeting the infraorbital sensory canal. Again, in well ossified individuals, the route of the canal is marked by a descending lamina on the internal surface of the frontal bone, as described by Patterson (1975) in Pholidophorus germanicus. This lamina runs directly beneath the sensory canal until it reaches the anterior end of the cranial groove where it deserts the canal and turns postero-laterally to follow the course of the groove.

The parietals are small and asymmetrical. They are separated from each other medially by the frontals, behind which they form the posterior part of the cranial boss. Each parietal is overlapped anteriorly by the frontal and posteriorly by the dermopterotic, so that about half the true extent of the bone is hidden. The supraorbital sensory canal, which enters from the frontal, ends in the parietal.

The nasals lies one on each side of the rostro-dermethmoid. Posteriorly they meet the dermosphenotics and postero-medially the frontals. Each nasal can be divided into two portions: a large dorsal portion which occupies the antero-lateral part of the skull roof, and a smaller roughly triangular, vertical portion which covers the lateral ethmoid and contributes to the margins of the nasal openings. The supraorbital sensory canal begins postero-dorsal to the anterior nostril and passes across the nasal to enter the frontal.

The paired dermosphenotics are rougly rectangular. As in Amia, they form an integral part of the skull roof and the greater part of each bone lies anterior to the endochondral sphenotic. In contrast to Amia, however, in Pachycormus the dermosphenotics are quite separate from the cartilage bone, and are produced forwards dorsal to the orbit to meet the nasals anteriorly. Consequently in Pachycormus there are no supraorbital bones, the lateral edges of the dermosphenotics alone form the entire dorsal margins of the orbits. The infraorbital sensory canal enters each dermosphenotic postero-laterally and makes its characteristic sharp turn to pass into the dermopterotic posteriorly.

The skull roof is completed posteriorly by a pair of Y-shaped bones, which occupy the position more normally filled by separate dermopterotics and extrascapulars. The stem of the 'Y' is short and extends obtusely backwards dorsal to suborbital 1 nearly as far as the opercular.

One arm runs anterio-medially and may make a narrow contact with its fellow in the mid-dorsal line, the other projects forwards between suborbital I and the parietal and frontal to meet the dermosphenotic. The main sensory canal of the head enters the bone posteriorly, gives rise to the supratemporal and preopercular canals, and continues forwards through the anterior arm of the bone into the dermosphenotic. The anteromedial arm of the bone carries the supratemporal commissure. The cranial groove bisects the two arms and this has been misinterpreted as a suture by other workers (Lehman, 1949; Wenz, 1968). Though the shape and position of the bone and the distribution of the sensory canals obviously suggest a compound structure there is no evidence of this in the shape of multiple centres of ossification. For convenience this bone is referred to hereafter as the dermopterotic though its possible compound nature is recognized.

(c) The dermal bones of the cheek and upper jaw

These are particularly well preserved in Pachycormus macropterus and are illustrated in Figure 2 and Plate 2.

The paired antorbitals are roughly rectangular. Antero-dorsally they form a part of the margin of the anterior nostril. The infraorbital sensory canal crosses the bone rostro-caudally, at about the same horizontal level as the ethmoid commissure. Posteriorly the antorbital is excluded from the orbital margin by infraorbital I.

There are at least 10 infraorbitals on each side. The most anterior, infraorbital I is an elongated, wedge-shaped bone widest anteriorly. Its dorsal edge is concave and forms a substantial part of the ventral margin of the orbit. The remaining infraorbitals form a series of small, rectangular bony plates along the posterior edge of the orbit. Each plate slightly overlaps the one ventral to it. The plates vary slightly in size, but are remarkably uniform compared to those of the Parasemionotidae and Amiidae (Lehman, 1966),

There are two suborbitals: the dorsal suborbital (SoI); and the larger, ventral suborbital (So II). They overlie the hyomandibular and meet the preopercular posteriorly. (The presence of a third suborbital, apparently divided off from the anterior dorsal margin of suborbital I, has been reported in one specimen of *Pachycormus curtus* (Wenz, 1968:fig. 33). This appears to be merely a rare, individual variation.)

Although the presence of two large suborbitals is a primitive actinopterygian character (Schaeffer (1973) includes it in his list of the character-states that might be expected in an ancestral chondrostean morphotype) nevertheless when combined with the arrangement of the infraorbitals it constitutes a highly distinctive feature of the family Pachycormidae.

The major portion of the cheek is occupied by the bones of the opercular series. The preopercular is roughly crescent-shaped and separated from the maxilla by the large suborbitals. Each preopercular is broadest ventrally, tapering dorsally into a narrow splint. The anterior edge of each bone is particularly well ossified and carried the preopercular sensory canal.

The operculars are large, about twice as long as they are deep, and in the form of an inverted triangle. Their dorsal edges lie adjacent to the posterior extensions of the cranial grooves. Antero-dorsally, on the internal surface of each bone there is an "ear-like" hyomandibular process.

The subopercular is roughly rectangular and about as large as the opercular. Its anterior and dorsal margins are more strongly ossified than the rest of the bone. The anterior margin gives off an antero-dorsally directed process that underlies the anterior border of the opercular for some distance.

The interopercular is the smallest but the most robust bone in this series. It too, is roughly rectangular in shape and meets and is overlain by the preopercular dorsally.

The interopercular is a relatively new recruit to the opercular series. Its appearance is linked with the freeing of the maxilla from the other cheek bones and the development of the supramaxilla. Patterson (1973) cites the presence of an interopercular in his list of halecostome characteristics.

The opercular series is completed ventrally by a series of branchiostegal rays which meet the interopercular posteriorly, and the large rectangular gular plate, anteriorly.

In ventral view, the upper jaw of Pachycormus is like an elongated, slightly rounded "V". The antero-medial portion is formed by the rostro-dermethmoid which separates the two premaxillae. The elongated maxillae have well developed articular heads. Posteriorly they are free from the cheek; each is surmounted by a single supramaxilla (Plate 2).

The dentition of these upper jaw elements is evenly developed and generally less robust than that of either of the lower jaw or the palate.

The existence of separate, independent premaxillae was first recognised by Patterson (1973). In that paper Patterson discussed the relationships of the "holostean" premaxilla with its nasal (ascending) process, to the pholidophorid premaxilla and lateral-dermethmoid. He concluded that the lateral-dermethmoids were the homologues of the holostean nasal processes, and that the tooth-bearing portion of the holostean bone was the counterpart of the pholidophorid premaxilla. In the earlier accounts of Lehman (1949:fig.2) and Wenz (1968:figs 50 & 51) the premaxillae were assumed to be incorporated in a complex median "postrostro-rostro-premaxillary" ossification.

Each premaxilla is roughly triangular in lateral view. Anteriorly it fits into a recess in the postero-ventral margin of the rostro-dermethmoid. The ventral, tooth-bearing part of the premaxilla is robust, but dorsal to this the bone is relatively fragile and this region is overlain by the antorbital. The posterior edge of each premaxilla is deeply notched where it meets the maxilla.

The maxilla is elongated and extends back well beyond the level of the orbit. It is deepest posteriorly and narrows as it arches forwards. Anteriorly, its simple, peg-like, articular head passes medial to the premaxilla and extends forwards, cradled in a groove on the dorsal surface of the anterior dermopalatine, to articulate with the pre-ethmoid bone and the rostro-dermethmoid. Ventrally the maxilla carries a single row of simple conical teeth. Postero-dorsally the border of the maxilla is deeply excavated to accommodate the single, plate-like supramaxilla.

(d) The mandible

In *Pachycormus macropterus* the mandible is extremely robust. It extends posteriorly beyond the maxilla; although, in dorsal view it has the same elongated, slightly rounded V-shape described for the upper jaw. It contains a number of dermal ossifications, in contrast to the mandibles of modern teleosts (Nelson, 1973). Each ramus is deepest posteriorly (Figs 2, 4). Its dorsal margin is almost horizontal. Its ventral margin slopes gradually upwards. Anteriorly the two rami meet in a long oblique symphysis.

The dentaries are the largest, and most anterior bones in the mandible. They form approximately three-quarters of its external surface, and meet each other anteriorly. Each dentary is roughly r-shaped in cross-section. Its horizontal dental lamina supports a single row of simple conical teeth, which are larger than those found on the maxilla. The mandibular sensory traverses the bone parallel and close to its ventral margin. Posteriorly the dentaries meet the angulars and surangulars in an uneven, zig-zag suture.

The external surface of the jaw is completed by the dorsal Surangular, and the larger, ventral angular. Each surangular is a roughly triangular bony plate, hardly visible when the jaw is closed as it is then overlain by the maxilla. The angular on the other hand forms the prominent postero-ventral corner of the lower jaw. Its lateral surface is crossed ventrally by the mandibular sensory canal running backwards from the dentary.

Internally, the surface of each mandibular ramus comprises two major bones, the articular and pre-articular, and a series of small coronoid plates.

The articular is an extremely robust endochondral bone sandwiched between the angular laterally, and the pre-articular medially; though the latter does not completely cover its medial surface. Postero-dorsally, each articular bone forms the whole of the facet for the articulation with the quadrate. Immediately in front of this lies the small coronoid process and this too, involves only the articular bone (Patterson, 1973). Anteriorly the medial surface of the articular is overlain by the lateral surface of the pre-articular.

The pre-articular is an elongated, plate-like bone that meets the dentary anteriorly and dorso-medially. Its posterior border has a large excavation to accommodate the adductor mandibulae muscles; dorsal to this the bone projects backwards as a horizontal splint parallel with, and medial to the postero-dorsal part of the dentary. Ventrally the bone extends to partly cover the medial surface of the articular. The medial surface of each pre-articular bears numerous, minute, closely spaced teeth. These appear to be inserted directly onto the surface of the bone, and not onto a separate pre-articular tooth-plate.

A series of about 8 small, toothed, rectangular coronoid plates completes the internal surface of the mandible. These lie along the jaw overlying the dorso-medial suture between the dentary and the pre-articular. Each plate is progressively smaller than the one anterior to it, the last and smallest plate lying at about the level of the anterior end of the coronoid process. Their dorsal surfaces are covered by small conical teeth, the largest of which are approximately one-fifth the size of those found on the dentary.

(e) The parasphenoid and vomers

The parasphenoid (Fig. 5, Plate 5) is long and moderately stout. It is widest at about two-thirds of its length where it gives rise to a single pair of processes - the ascending processes; as Rayner (1951) observed there are no basipterygoid processes in Pachycormus. The ascending processes separate the anterior, inter-and preorbital portion of the parasphenoid from the posterior, cranial portion underlying the brain case.

The anterior part of the parasphenoid has the form of an inverted "T" in cross section. The vertical limb is formed by a median bony ridge which is most prominent between the ascending processes where it is covered by the ventral endochondral outgrowths of the basisphenoid, as in the pholidophorids (Patterson 1975). Anteriorly this ridge gradually decreases in height and passes between the lateral ethmoids as the parasphenoid enters the nasal region. Just in front of the ascending processes, on either side of the median ridge, the dorsal surface of the parasphenoid is marked by a pair of antero-laterally directed grooves. Each groove carried a lateral branch of the palatine nerve which passed ventrally via a notch in the edge of the bone. The main branches of the palatine nerves ran forwards for some distance on either side of the median ridge, then, at a level slightly anterior to the lateral palatine notches, they entered a pair of canals in the side of the ridge, presumably to emerge on the ventral surface ofthe parasphenoid near its anterior end (see below).

Figure 5. Pachycormus sp. Composite reconstruction of parasphenoid in (a) ventral, (b) lateral and (c) dorsal view. Based on P10146, P24410 and P10145.

Figure 6. Pachycormus curtus. P10145 unrestored drawing of left vomer in (a) dorsal and (b) ventral view.

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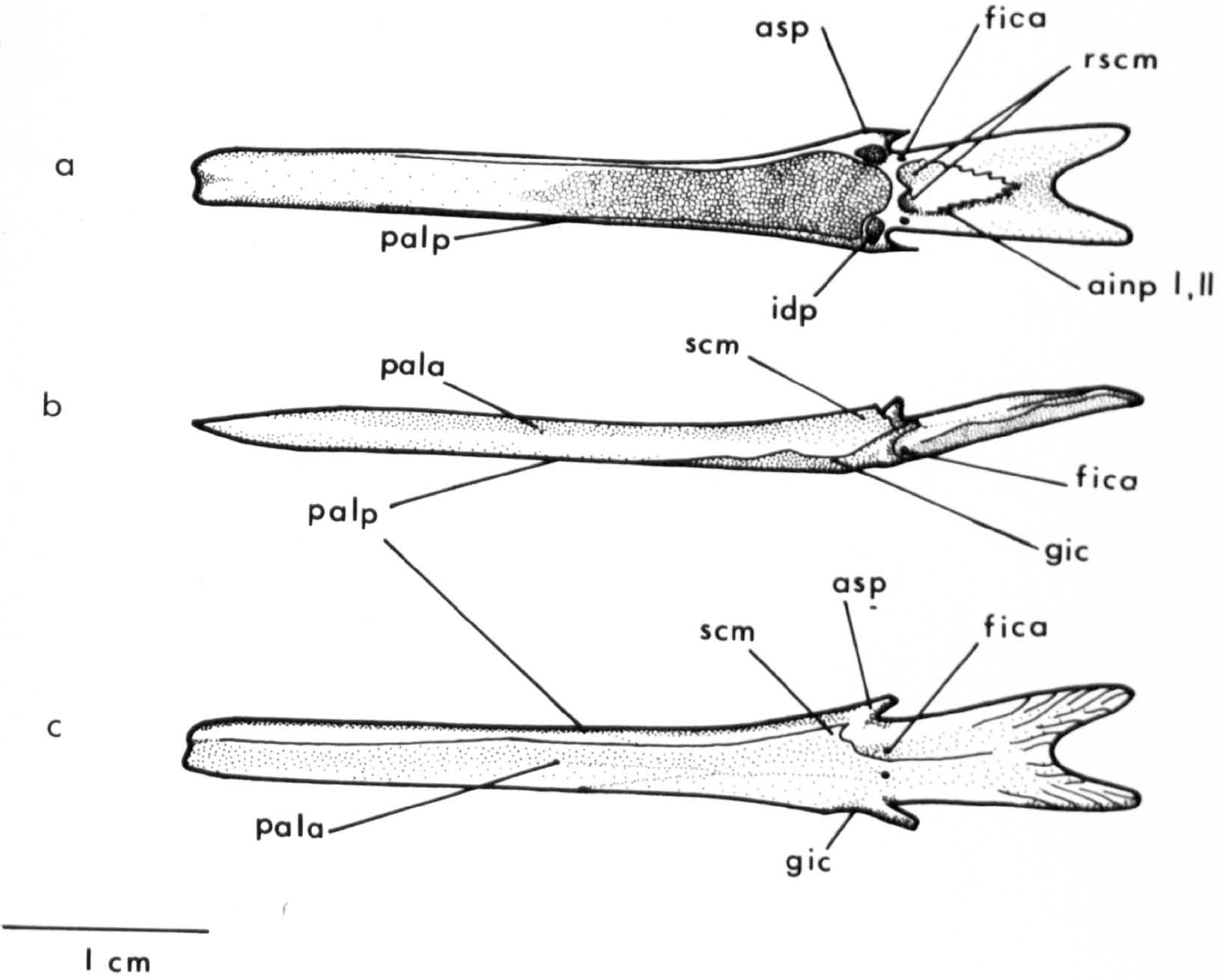
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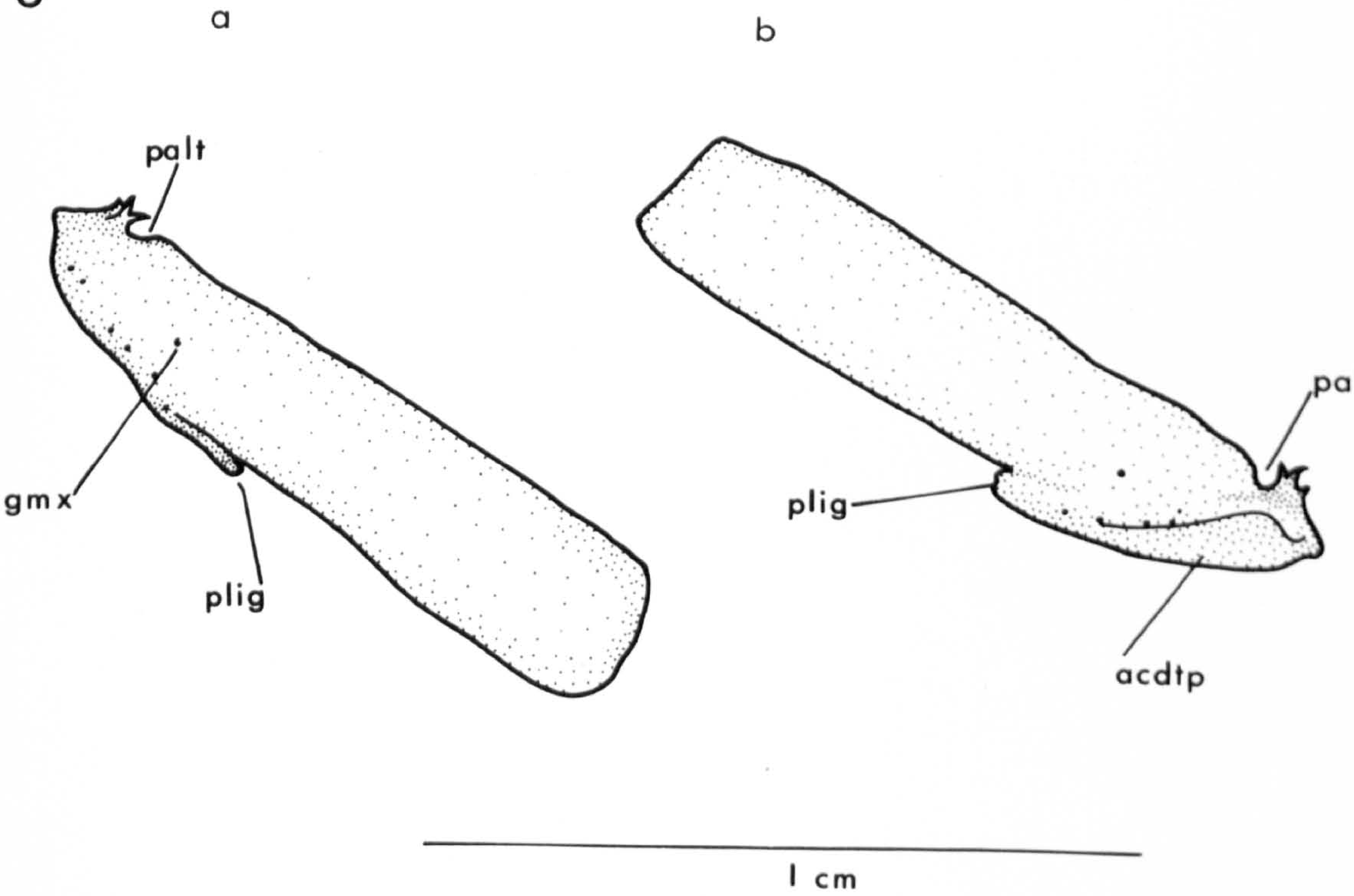
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Ventrally, the anterior portion of the parasphenoid is toothed from the level of the ascending processes anteriorly at least as far as the lateral palatine notches and sometimes beyond (though Lehman, 1949, reported that these teeth were restricted to the area between the ascending processes). Posterior to the lateral palatine notches the edges of the parasphenoid are smooth, and slightly postero-dorsally inclined. These lateral flanges increase in width posteriorly until they meet the anterior edges of the ascending processes; the relatively small size of which suggests that the adductor arcus palatinae muscles inserted mainly on these flanges. Anteriorly the parasphenoid lies dorsal to the vomers, and supports the ethmoid region.

The ascending processes themselves are short and only extend half-way to the jugular groove, though they do meet the lateral commissure dorsally to butress the posterior wall of the orbit. Ventrally, the base of each process is covered by a small independent tooth plate (P10145). Posteriorly each process is penetrated by an anteriorly, and somewhat medially directed canal that emerges on the dorsal surface of the bone on either side of the median ridge. These canals carried the internal carotid arteries, as do similar canals in the pholidophorids and leptolepids.

Behind the ascending processes, the cranial portion of the parasphenoid rises at an angle of approximately 15°, and supports the brain case. It extends back beyond the level of the fisura oticalis ventralis to underlie the basi-exoccipital. In *Pachycormus* the parasphenoid ends at the level of the vagus foramen, as in *Pholidophorus macrocephalus* and Leptolepis coryphaenoides, and immediately anterior to the housing of the aortic ligament as in the parasemionotids. In caturids, and teleosts the parasphenoid extends posteriorly well beyond the vagus, often ending at the level of the occipital condyle. On the ventral surface of the parasphenoid, immediately behind the ascending processes, there are a pair of posteriorly open depressions. These depressions probably housed the subcephalic muscles, as they do in caturids. Pholidophorids and leptolepids have similar depressions but in those fish they are situated well back on the bone. Posterior to the depressions, mid-way along the cranial portion of the bone, there is a low V-shaped projection with the apex of the "V" directed posteriorly. The anterior processes of the second and third infrapharyngobranchials articulated against the posterior edge of this projection.

The vomers are illustrated in Figure 6. They are a pair of plate-like ossifications that meet the rostro-dermethmoid anteriorly, the palatal ossifications laterally and the parasphenoid postero-dorsally (Plate 5). The vomers are in contact with one another in the mid-line. The antero-lateral portion of each vomer is thickened and projects below the general level of the ventral surface. This region lacks vomerine teeth such as are found on the median vomer of both pholidophorids and leptolepids, but Pachycormus curtus (P10145) indicates that a separate tooth plate was present here and continued the dentition forward from the dermopalatine. The thickened regions of the two vomers combine to form a transverse "vomerine head" that fits into the arc between the arms of the rostro-dermethmoid. About one-third of the way along its lateral border there is a deep recess which may have housed part of the ethmo-palatine ligament.

Antero-medially each vomer gives rise to a number of small bony projections that must have given anchorage to ligaments binding the two vomers together and to the rostro-dermethmoid. Posterior to these bony projections, the medial edge of each vomer shows a deep, semi-circular notch. When these notches are opposed, as they were in life, they form a single median foramen that must have transmitted the main branches of the palatine nerves. The foramen for the maxillary nerve passes through each vomer posterior and lateral to the palatine foramen. The thickened, anterior parts of the vomers are penetrated by numerous tiny canals that must have transmitted blood vessels to the area.

(f) Bones of the palate and suspensorium

The palate and suspensorium are illustrated in Figures 7 and 8 and Plates 5, 6, 7 and 8. They comprise two series of bones, one vertical, the other nearly horizontal. The vertical series, that of the suspensorium, consists of paired hyomandibulars, quadrates, quadratojugals and symplectics. The horizontal, palatal series comprises paired endopterygoids, ectopterygoids and two pairs of dermopalatines. The paired metapterygoids are common to both series.

The hyomandibulars are large, broad and inclined anteriorly at an angle of approximately 60°. Each hyomandibular is divided by a conspicuous waist into dorsal and ventral portions; the latter occupying two-thirds of the height. The dorsal portion gives rise to a short opercular process posteriorly, and a broader anterior process that meets the metapterygoid laterally. Between these two processes, near the centre of ossification of the bone, the medial surface is penetrated by the ventro-laterally directed canal that transmitted the hyomandibular branch of the facial nerve onto the lateral surface of the bone. As usual, the dorsal and ventral ends of the hyomandibular lack perichondral bone indicating that they were cartilage covered. The head of the bone fits into an elongated facet in the lateral wall of the neurocranium. Its lower end articulated with the sympletic and interhyal.

The quadrate is large and roughly triangular in shape. Its apex is strongly ossified and forms the antero-ventrally directed articulation for the lower jaw. Above the condyle, the quadrate fans out to form a slightly laterally concave, bony plate that meets the metapterygoid dorsally. Patterson (1973:274) noted that the posterior border of the quadrate was particularly thickened, and he suggested that this thickening represented a quadratojugal, which had become completely fused with, and indistinguishable from the quadrate. However, P10146 shows that a distinct quadratojugal is present in Pachycormus in the form of a postero-dorsal process similar to that described by Patterson in the pholidophorids (Fig. 9). Rayner illustrates, but apparently did not recognise, a similar process in P. curtus (1948, fig. 17).

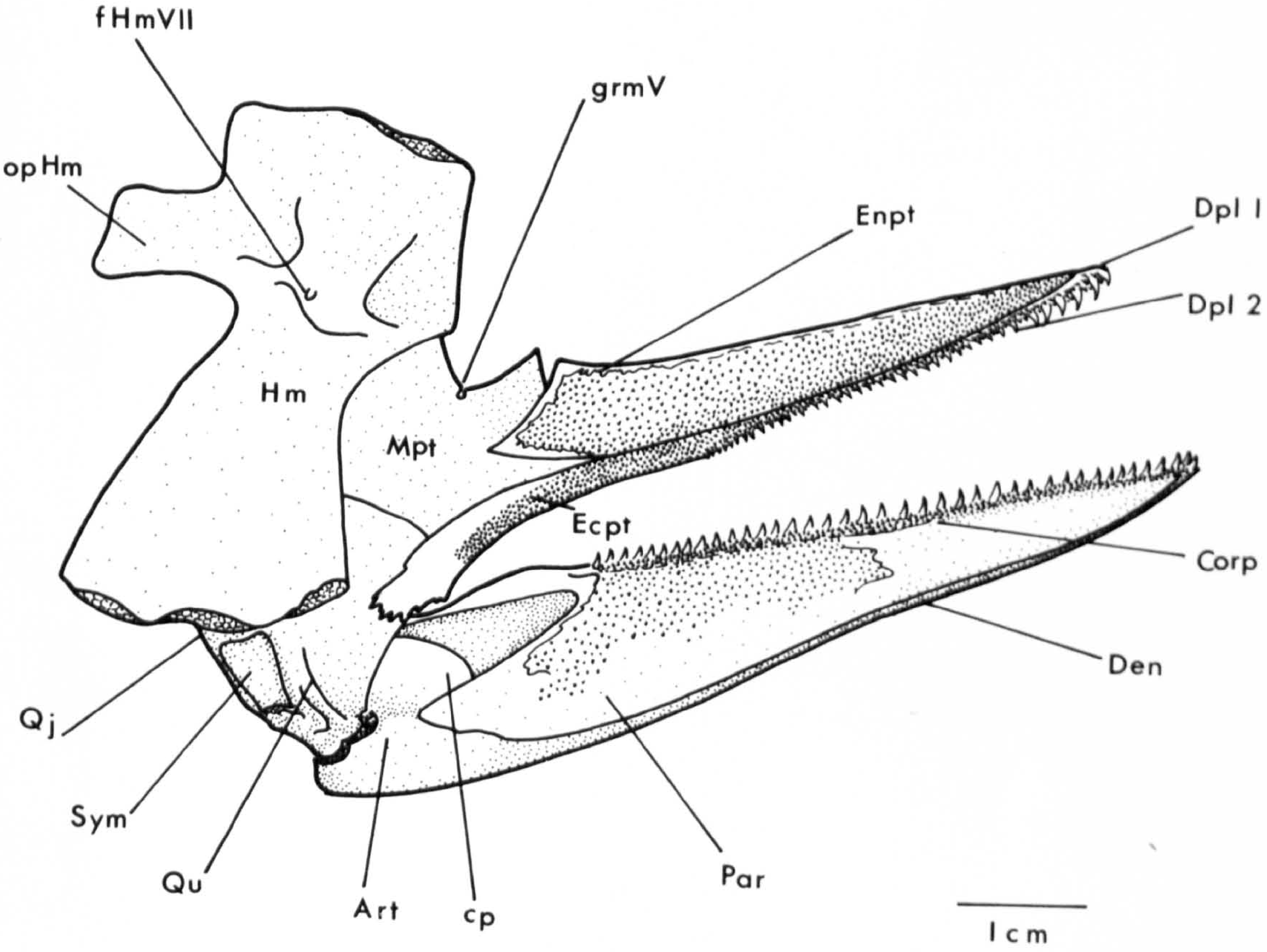
The symplectics complete the vertical series of the suspensorium. Each is a small tubular rod of bone that lies postero-dorsally inclined in a shallow groove on the medial surface of the quadrate. There, the symplectic may be completely free from the larger bone (as in P10146), or may be attached to it by its ventral surface. In either case the symplectics do not form a secondary articulation for the lower jaw, as do their halecormorph homologues.

The metapterygoids link the suspensorium to the palate, and this

Figure 7. *Pachycormus macropterus*. Reconstruction of left palate in medial view. Based on P24410.

Figure 8. *Pachycormus macropterus*. Reconstruction of left palate in lateral view. Based on P24410.

7


fHmVII
grmV
opHm
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Dpl 1
Dpl 2
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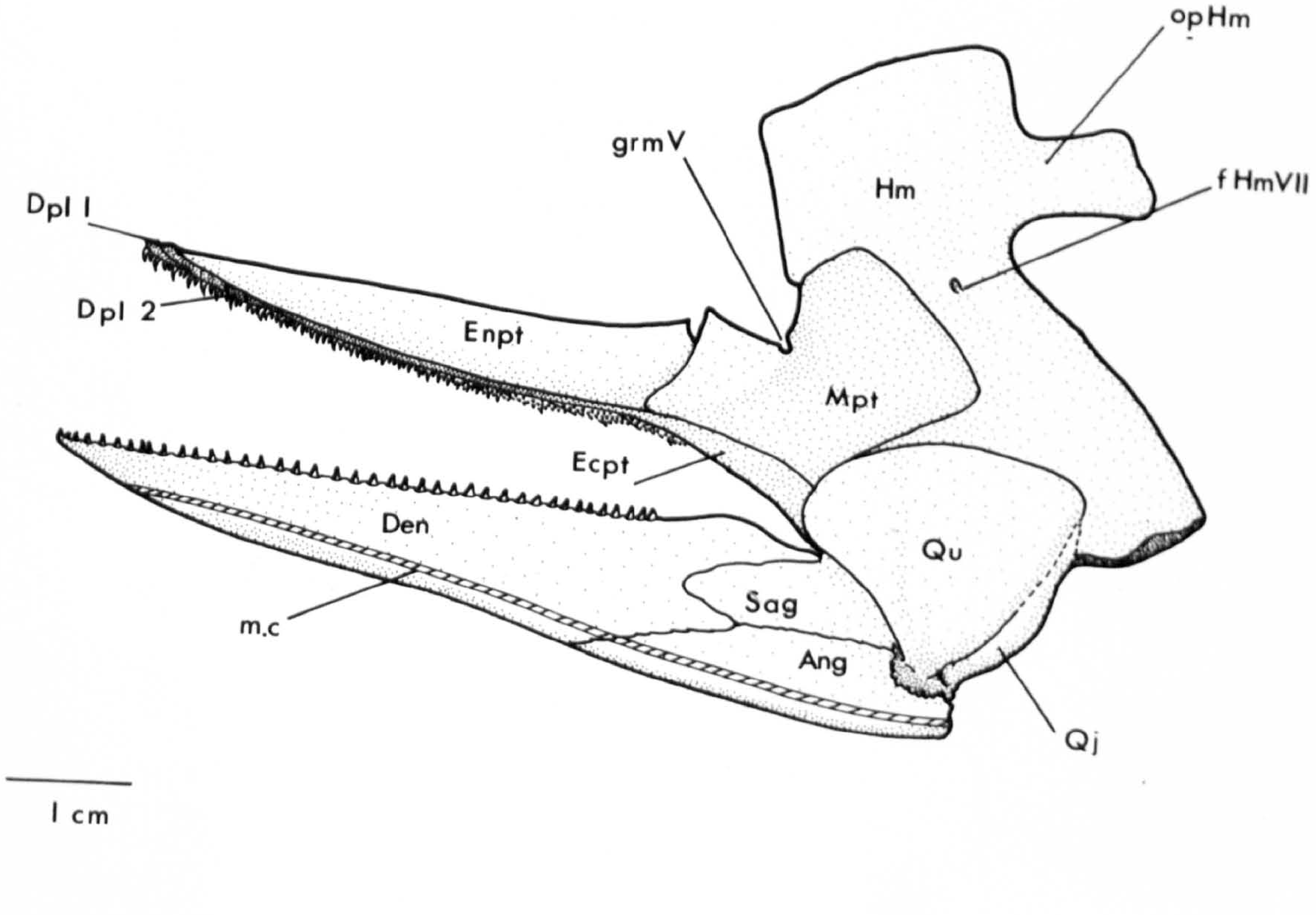
8


opHm
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Dpl 1
Dpl 2
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function is reflected in their structure. Each metapterygoid is divided into two portions, horizontal and vertical. The small horizontal, anterior portion meets the parasphenoid immediately in front of the ascending process, and meets the endopterygoid and ectopterygoid medially and laterally respectively. The larger, vertical portion of the bone overlies the lateral surface of the hyomandibular and meets the quadrate ventrally. Anteriorly the intersection of these two portions forms a deep notch which probably marks the passage of the mandibular branch of the trigeminal nerve.

The endopterygoids are a pair of horizontal, elongated, triangular bony plates that pass anteriorly on either side of the parasphenoid. Their smooth dorsal surfaces meet the metapterygoids posteriorly and anteriorly insert beneath the lateral ethmoids. The ventral surface of each endopterygoid is covered by numerous minute teeth, except for two narrow strips where the bone meets the parasphenoid medially and the ectopterygoid and dermopalatines. laterally.

The ectopterygoids are extremely long and narrow, and form most of the lateral margins of the pālate (Plate 6). Anteriorly each lies adjacent to the ectopterygoid, and extends forwards to meet the second dermopalatines , posteriorly it overlies the medial surface of the quadrate. Both parts of the ectopterygoid bear teeth. Those on the posterior portion of the bone are minute, resembling the teeth found on the endopterygoid, and insert directly onto the surface of the bone. The anterior portion of the ectopterygoid is covered by a number of tooth plates each of which supports several simple conical teeth, that increase in size anteriorly, the largest being approximately equal in size to those of the maxilla.

The palate is completed by two pairs of dermopalatines; no autopalatine has been found in any of the material examined. The posterior pair of dermopalatines are extremely small (Plate 6, DpII), each hardly more than an independent tooth plate. Anteriorly each meets dermopalatine 1 in a movable, hinge-like joint. This joint must have allowed the posterior part of the palatine to drop when the mouth was opened.

The anterior dermopalatines (Plates 5 and 6, Dpl), are two or three times longer than the posterior pair, and their anterior margins are rounded to fit into the arc of the snout. Medially each meets the lateral edge of the vomer and its ventral surface bears several large, conical teeth. These teeth are generally larger than those found on the maxilla. The dorsal surface of each dermopalatine is marked by a conspicuous longitudinal groove that cradles the articular process of the maxilla where it enters the snout.

(g) The visceral arch skeleton

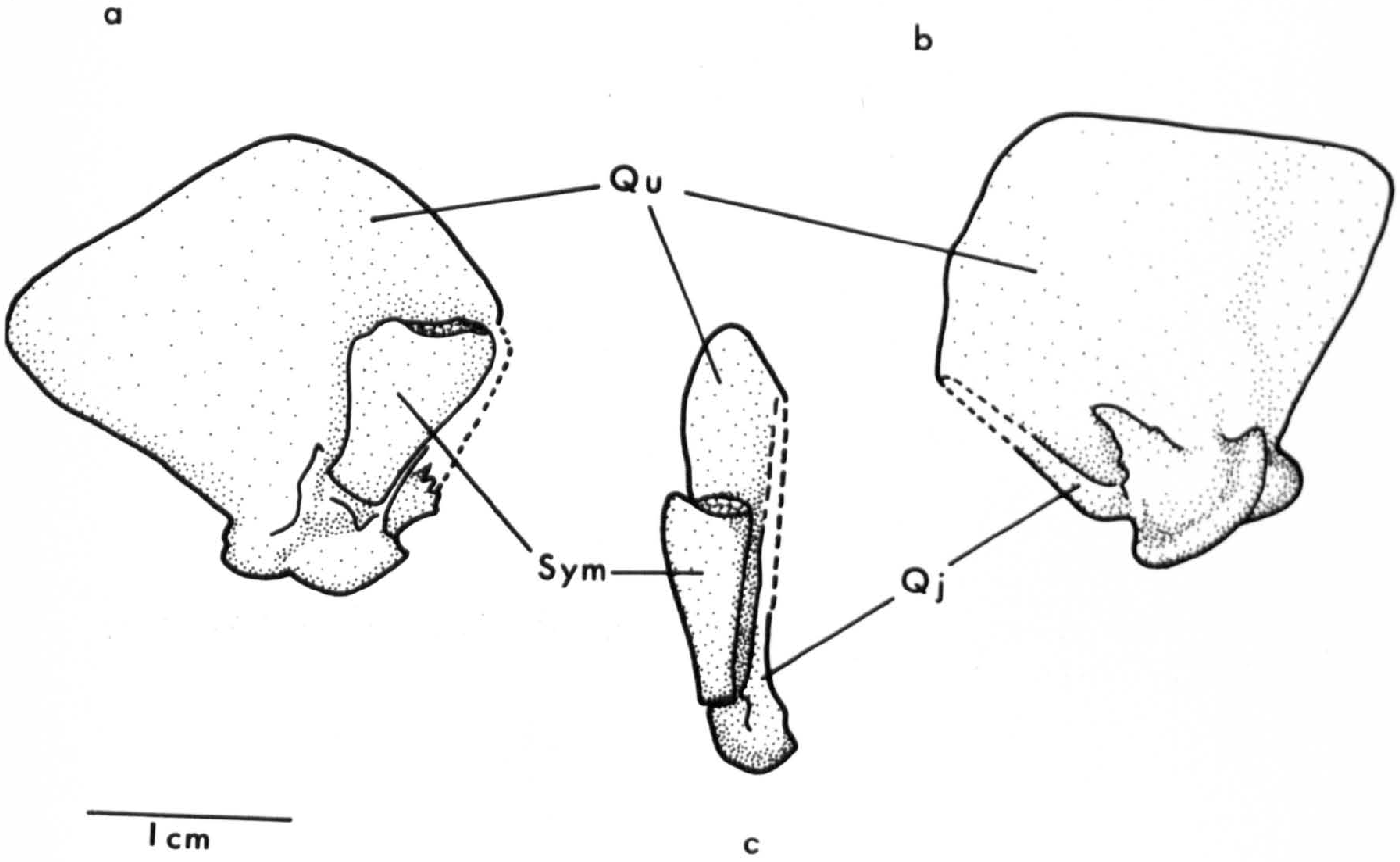
The visceral arch skeleton is particularly well preserved in Pachycormus, so that its characteristics may be studied in some detail. Before proceeding to a detailed description, it is useful to consider some of the points made by Nelson (1969) in his paper on the gill arches of fishes and in particular to refer to his notation as a convenient means of identifying the basi-branchials and hypo-branchials (see Fig. 10).

Nelson states that the basi-hyal and the basi-branchials may ossify as individual bones, they may form a series of copulae each of which comprises two or more elements which have fused, or there may be a mixture

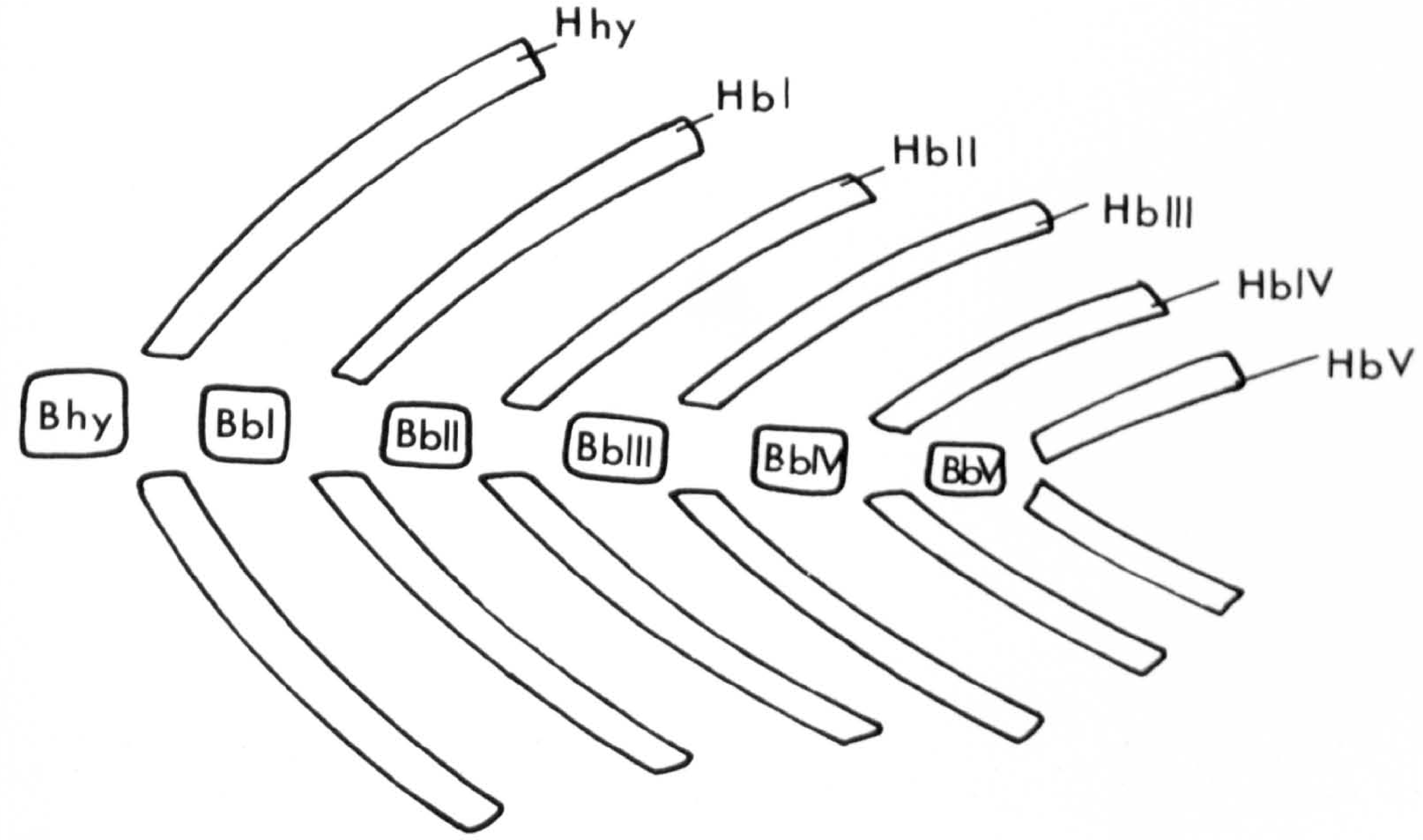
Figure 9. *Pachycormus macropterus*. Reconstruction of right quadrate, quadratojugal and symplectic in (a) lateral, (b) medial and (c) posterior view. Based on P10146 and 32432.

Figure 10. Basic plan of the arrangement of the ventral visceral arch elements of fishes based on Nelson (1969).

9


a
b
Qu
Sym
Qj
1 cm
c

10


Hhy
HbI
HbII
HbIII
HbIV
HbV
Bhy
BbI
BbII
BbIII
BbIV
BbV

of single bones and copulae. He argues that, even when copulae are present, the individual elements of the basi-hyal - basi-branchial series can be identified by reference to the hypo-branchials which will articulate at the same points along the series whether the individual bones have fused or remain separate. Where the bones are separate, the hypo-branchials articulate between successive bones, but where two bones have fused they articulate with the side of the copula thus formed and, according to Nelson, the point of articulation is then perfectly juxtaposed to the point of fusion.

In Nelson's model, the point of articulation of the hypo-hyal is between the basi-hyal and the anterior basi-branchial (basi-branchial 1 in Nelson's notation). Similarly the articulation of the anterior pair of hypo-branchials (hypo-branchial 1) lies posterior to basi-branchial 1, between it and basi-branchial II, and so on. So that each pair of hypo-branchials has the same number as the basi-branchial immediately anterior to it. Using this notation Nelson is able to identify each element in a copula.

The hyomandibular of P. macropterus has already been described. The remainder of the hyoid arch is illustrated in Figure 11. It is made up of the following paired elements, hypo-hyals, anterior and posterior cerato-hyals, and inter-hyals. There is no median basi-hyal.

The hypo-hyals are small, gently curved ossifications that meet each other in the mid-line. Each is penetrated by a dorso-laterally directed canal that carried the afferent pseudobranchial artery from the medial to the lateral surface of the bone.

Each anterior cerato-hyal is an oblong vertical plate of bone, thickened ventrally. The afferent pseudobranchial artery ran along its dorso -lateral surface. During preparation of some specimens fragments of tooth plate were found on the medial surface of the anterior ceratohyal but it is not clear if this was their position in life and, if so, how much of the surface they covered.

The posterior cerato-hyals are almost triangular. The lateral surface of each is deeply marked by the afferent pseudobranchial artery; posteriorly the dorsal edge bears a facet for the inter-hyal.

The inter-hyals are known from a single individual P24410 and even here only one of the pair has survived (Plates 10 and 11). This is a small, almost square ossification whose dorsal and ventral surfaces lack perichondral lining. No trace of an inter-hyal was found in three other specimens prepared to show this region - though other structures of similar size are preserved in them. In several aspects P24410 appears to be more heavily ossified, though no larger, than the other specimens studied and it is suggested that the inter-hyal either failed to ossify or ossified later in life than most of the other visceral arch structures.

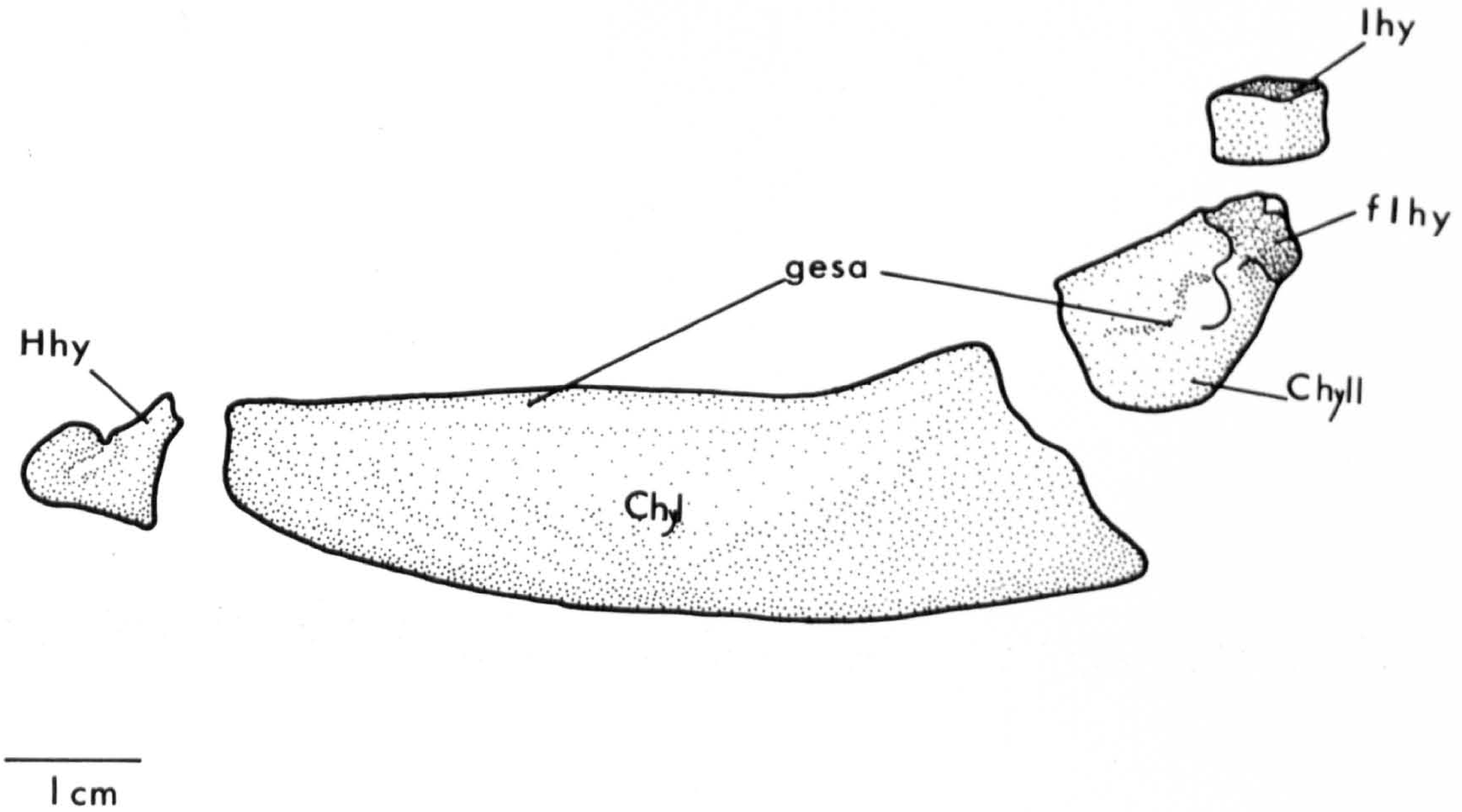
The branchial arches as usual are made up of median, ventral basibranchials, paired lateral hypo-branchials, cerato-branchials, epi-branchials and infra pharyngo-branchials. No suprapharyngobranchials have been found.

The basi-branchials and hypo-branchials are dealt with together as the distribution of the hypo-branchials along the basi-branchial series is the key to the identification of the individual basi-branchial

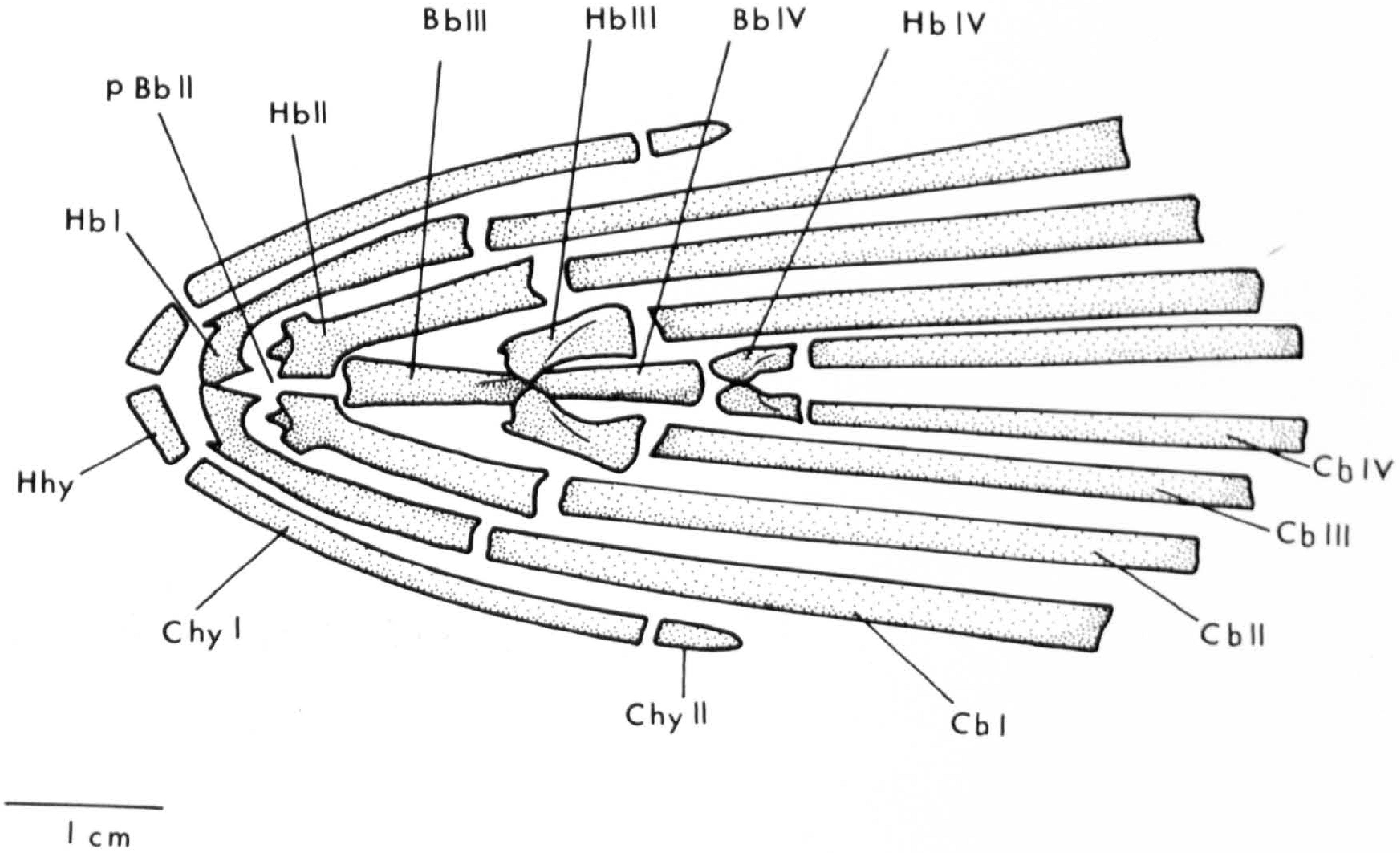
Figure 11. *Pachycormus macropterus*. Reconstruction of the left hyoid arch, excluding the hyomandibular, in lateral view. Based on P10146 and P24410.

Figure 12. *Pachycormus sp*. 32438 unrestored drawing of the ventral visceral arch elements in ventral view

11


Ihy
fIhy
gesa
Hhy
ChyII
ChyI
1 cm

12


BbIII
HbIII
BbIV
HbIV
p BbII
HbII
HbI
Hhy
CbIV
CbIII
CbII
Chy I
Chy II
Cb I
1 cm

units.

In the basic plan described by Nelson (1969), (see Fig. 10) the first pair of hypo-branchials articulates between basi-branchials I and II. However, in Pachycormus macropterus (Fig. 12, Plate 9) there is no basi-branchial unit anterior to the first pair of hypo-branchials, so that these hypo-branchials meet in the mid-line, shortly behind the hypo-hyals. That is to say, the first median unit present in P. macropterus is that designated basi-branchial II by Nelson. It is noteworthy that basi-branchial II has only been found in P24410. However, in specimens where this ossification is absent (eg. 32438 Plate 14) the fact that the site of the ossification is vacant, together with the finely preserved and undisturbed state of the visceral skeleton, indicates that basi-branchial II was present, but had remained cartilaginous throughout life.

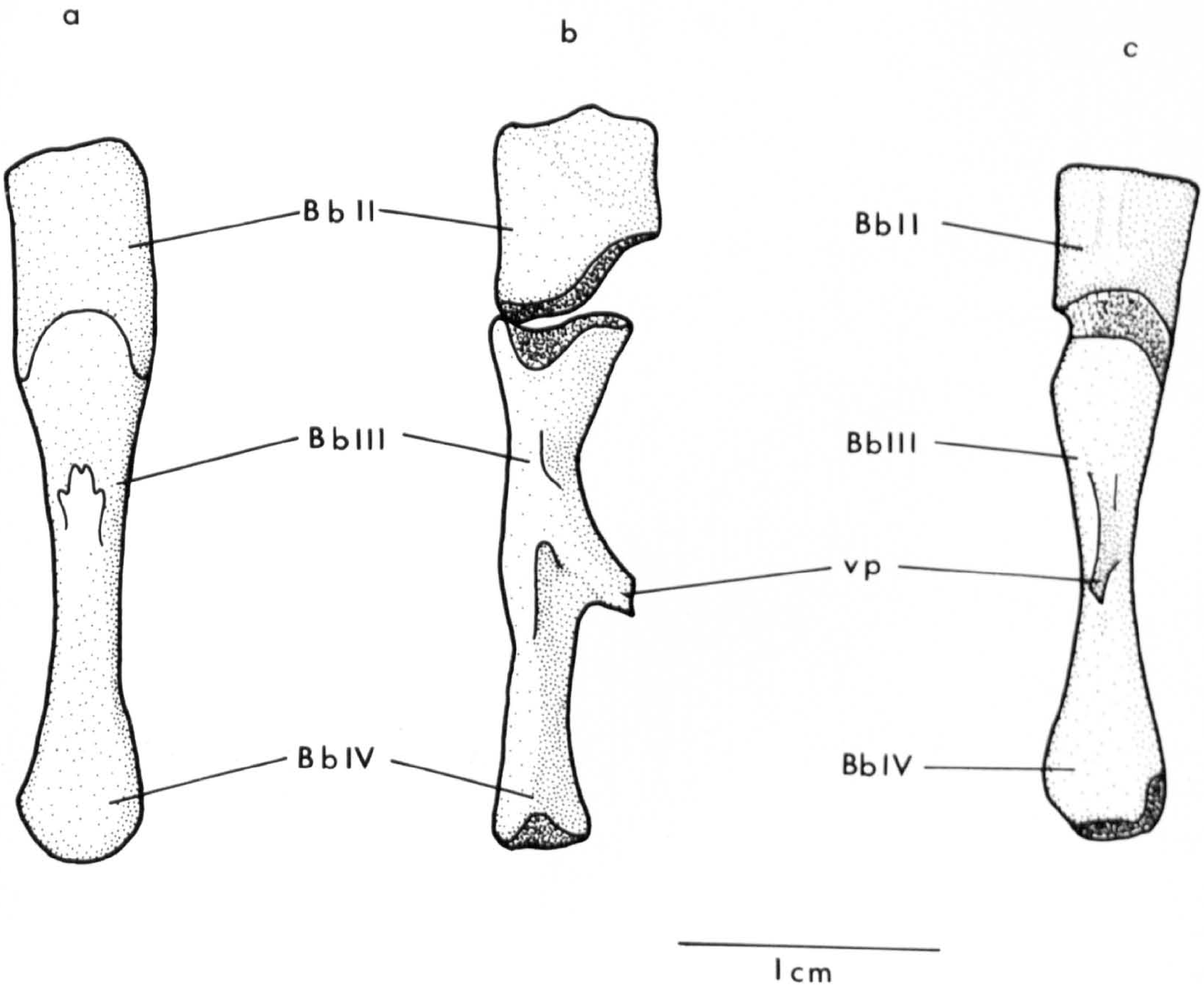
Posterior to basi-branchial II is the second median structure in the series, which in P24410 was separated from basi-branchial II by a ventral wedge of cartilage (Fig. 13), so that the two ossifications meet dorsally only in a horizontal suture. This second structure articulates with hypo-branchial II anteriorly, with hypo-branchial III midway along its length, at either side of a postero-ventrally directed process, and with hypo-branchial IV posteriorly. Bearing in mind that each pair of hypo-branchials lies posterior to its corresponding median unit, this second basi-branchial structure must consist of basi-branchial III, anterior to the articulation of hypo-branchial III, and basi-branchial IV posterior to that articulation.

A small bony tooth plate, lying posterior to the median basi-branchial

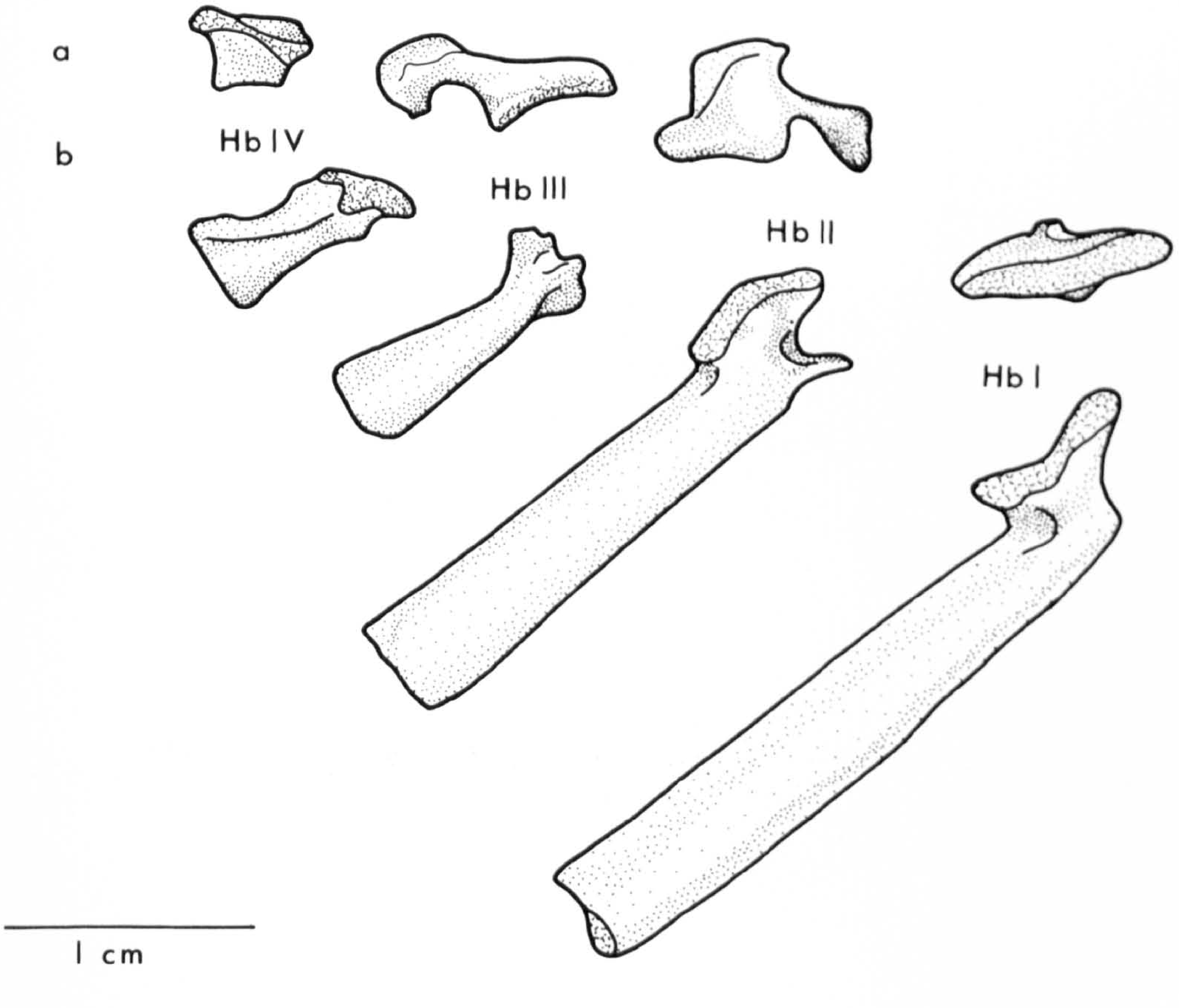
Figure 13. Pachycormus macropterus. P24410 unrestored drawing of the basibranchials in (a) dorsal, (b) lateral and (c) ventral view.

Figure 14. Pachycormus macropterus. 32432 unrestored drawing of the hypobranchials showing (a) their anterior articular surfaces and (b) these elements in dorsal view.

13


a
b
c
Bb II
Bb II
Bb III
Bb III
vp
Bb IV
Bb IV
1 cm

14


a
b
Hb IV
Hb III
Hb II
Hb I
1 cm

tooth plate (see below) suggests the presence of an additional cartilaginous median structure - basi-branchial V.

In summary, the basi-branchial series in Pachycormus macropterus consisted of a single anterior unit, basi-branchial II which may remain unossified, a copula that comprised branchials III and IV (Plate 9) and a final cartilaginous unit - basi-branchial V.

There are four pairs of hypo-branchials (Figs 12 and 14, Plate 9), each of which comprises an elaborate anterior articulating process and an elongated, ventrally concave, posterior process. The configuration of the anterior process of each pair of hypo-branchials differs from that of the other three pairs; they are illustrated in text Figure 14. The posterior processes of each successive pair of hypo-branchials becomes progressively shorter; those of the fourth pair are only rudimentary.

There are five pairs of cerato-branchials (Fig. 15, Plate 10) and again each successive pair is shorter (rostro-caudally) than its predecessor. The first three pairs; cerato-branchials I, II and III, are all simple, elongated ossifications, n-shaped in cross section, though anteriorly the ventral hollow of the "n" is infilled with bone to form the anterior articular surface with the hypo-branchials. The fourth pair, cerato-branchial IV, is basically similar in structure to the preceeding pairs, but differs from them in the formation of the anterior articulation. In cerato-branchial IV the anterior end of each element is laterally compressed, and forms a vertical, medially concave articulation rather than the plain horizontal one of the preceeding arches. The posterior portions of the fourth pair still retain the n-shape in cross section, but the concave ventral surfaces have become rather medially inclined. The fifth pair of cerato-branchials have the same vertical articulation as seen in cerato-branchial IV, and probably articulated directly with the cartilaginous basi-branchial V. However, posteriorly this final pair have solid posterior processes that are oval in cross-section and twist laterally along their lengths, so that the posterior portions of these bones are inclined at approximately 30° to their anterior, vertical articulations.

There are four pairs of epi-branchials (Fig. 16, Plate 11) forming an oblique, antero-dorsally directed series, that links the ventral, horizontal elements to the infra-pharyngo-branchials. The first three pairs; epi-branchial I, II and III, are all basically similar in structure, though each successive pair is shorter than its predecessor. Each of these epi-branchials is elongated, and "u"-shaped in cross section. Antero-dorsally the edges of epi-branchial II and III are produced to form a primitive uncinate process that articulated with the infra-pharyngo-branchials.

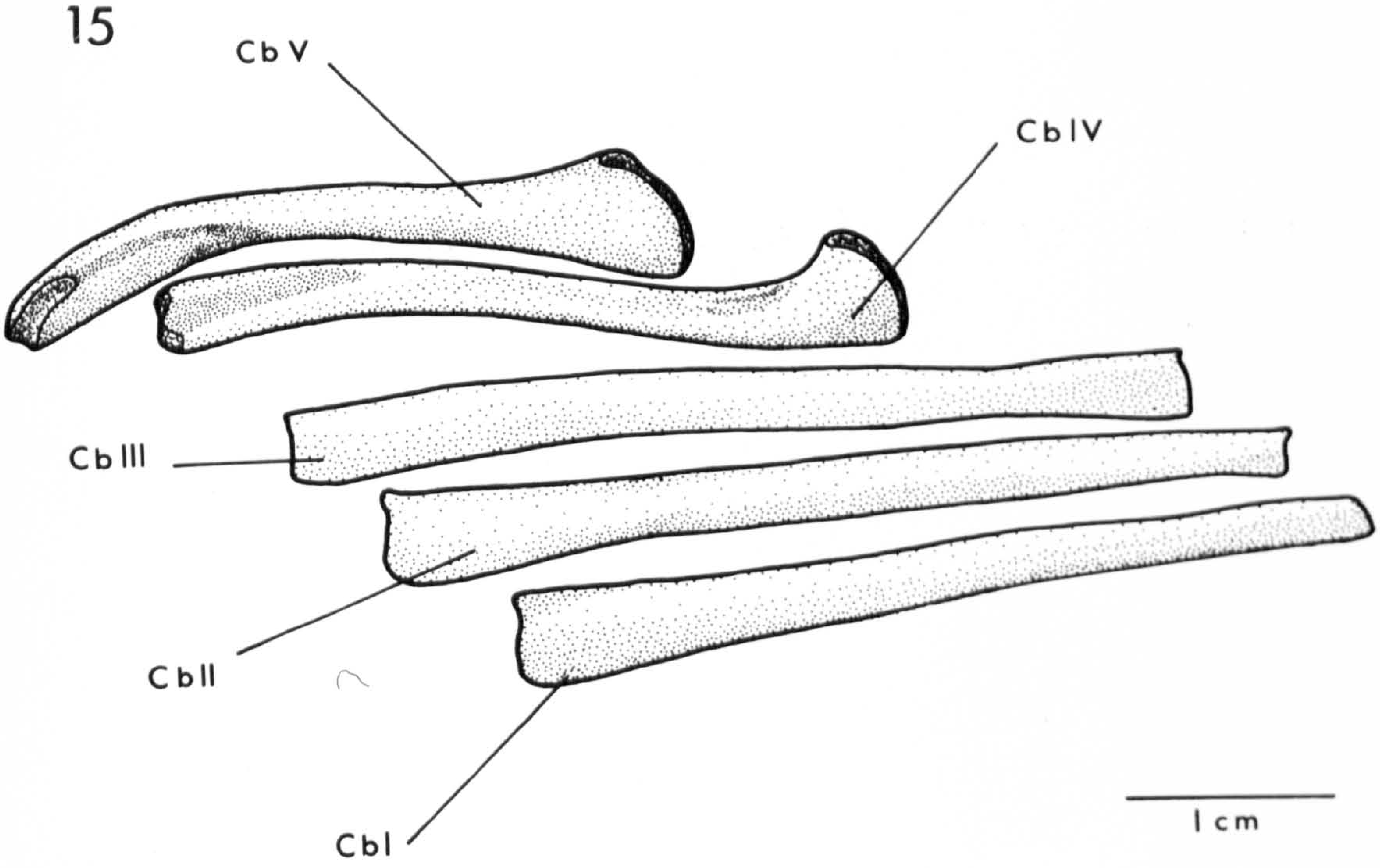
The fourth pair of epi-branchials is completely unlike the anterior three pairs. Each of these elements can be divided into two portions, a postero-ventral portion that lies obliquely in series with the anterior three pairs, and an antero-dorsal portion in the form of solid rod of bone that arches forwards and has its anterior end modified to articulate directly with the parasphenoid.

There are three pairs of infra-pharyngo-branchials (Fig. 17). The first pair consists of two simple, squat, cylindrical ossifications that lie almost at right angles to the braincase. Each articulated

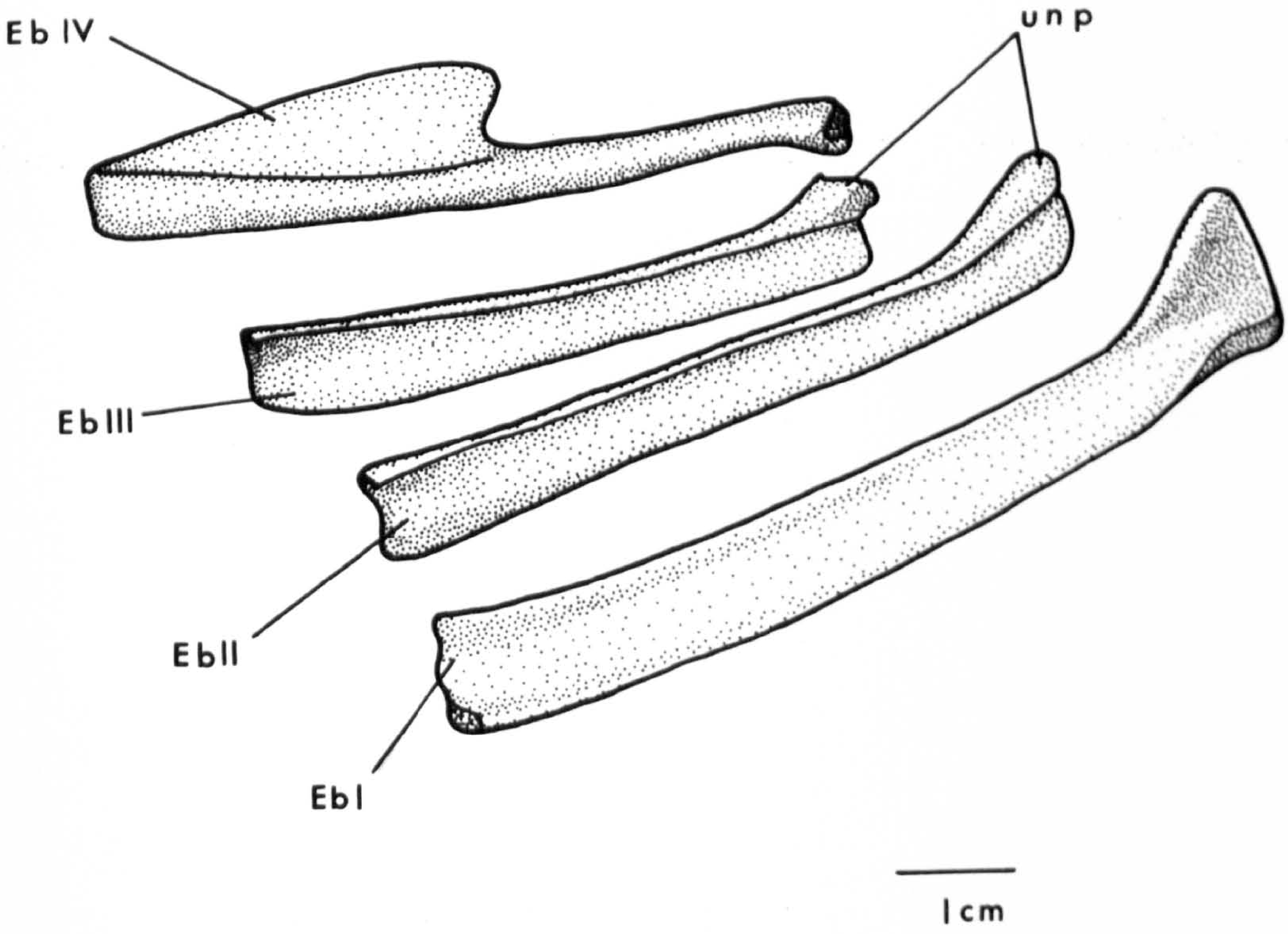
Figure 15. *Pachycormus macropterus*. P24410 unrestored drawing of the right ceratobranchials in dorso-lateral view.

Figure 16. *Pachycormus macropterus*. P24410 unrestored drawing of the right epibranchials in lateral view.

15



16



dorso-medially with a slightly raised, circular area on the prootic, immediately behind the ascending process of the parasphenoid. Posteriorly and laterally they articulate with the first pair of epi-branchials. The remaining two pairs; infra-pharyngo-branchials II and III are more complex in structure. Each is basically a horizontal, triangular ossification, whose apex is drawn out into an anterior process, particularly well developed in the posterior pair. These anterior processes articulate with the ventral surface of the parasphenoid where they contact the V-shaped horizontal ridge described above. On the anterior part of the lateral surface of each of these infra-pharyngo-branchials, there is a process again particularly well developed on the third pair. These lateral processes articulate with the uncinate process of the epi-branchials of the preceeding arch. Posteriorly each infra-pharyngo-branchial articulates with the epi-branchial of its own series.

I have not found any ossified supra-pharyngo-branchials in the specimens that I have examined. Patterson (1975:398) however, describes a circular area, lacking perichondral lining, on the lateral surface of the pro-otic, just anterior to the vestibular fontanelle, which, he suggests, was probably the site of articulation of the first supra-pharyngo-branchial. I have examined this region on the right side of P24410, and bearing in mind the clarity of this articulation in the caturids (Patterson, 1975, fig. 99), I am unable to support Patterson's interpretation in <u>Pachycormus</u>. The feature described by him may have resulted from post-mortem damage to that particular specimen. Examination of the left side of the same individual (P24410), and of P32432 and P10146, all of which lack such an endochondral area on the pro-otic, leads me to conclude that if there were suprapharygo-branchials in *Pachycormus*, their sites of articulation were inconspicuous, as is the case in leptolepids.

Large dermal tooth plates (Plate 8) were found associated with the buccal surfaces of most of the visceral arch elements, and a single cylindrical plate was identified ventral to the basi-branchial (Plates 13, 14, 19 and 20). In addition numerous, minute, independent tooth plates (Plates 15, 15a, 16, 16a, 17, 17a) were found scattered throughout the buccal cavity.

The most complete tooth plate prepared, was the median plate that covered the basi-branchial. In P24410, the anterior portion of this tooth plate was found, in place, on the dorsal surface of the basi-branchial and its displaced posterior part was found, cemented by its dorsal surface to the posterior, central surface of the endopterygoid (Plate 8). Posterior to this and also attached to the surface of the endopterygoid is a separate, smaller tooth plate. It is the presence of this small independent plate that leads me to infer the presence of a fifth, cartilaginous, basi-branchial in *Pachycormus* (see above).

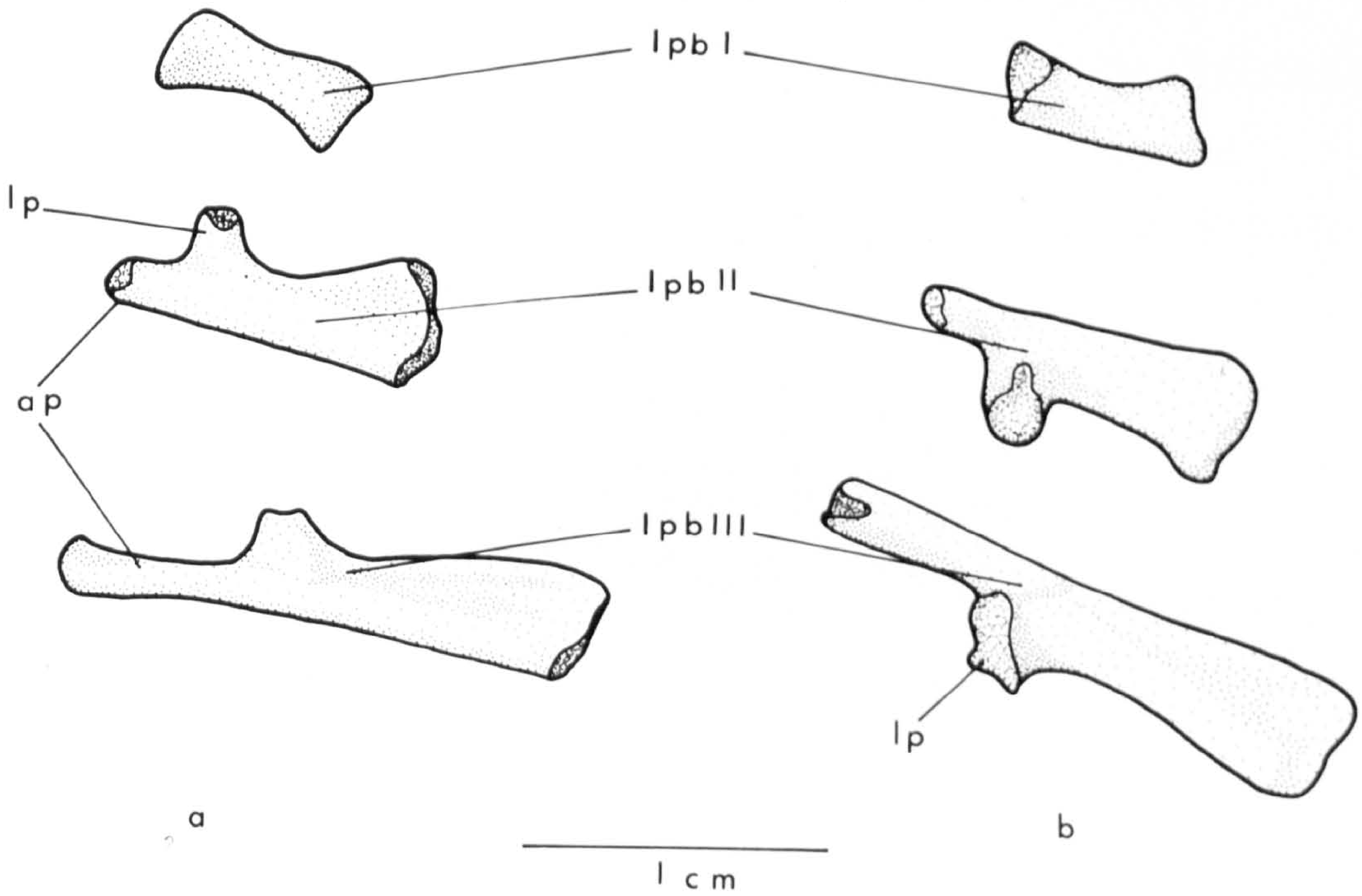
A considerable number of small, individual tooth plates were found disassociated inside the buccal cavity of several specimens. No particular pattern of arrangement could be distinguished. Several of these small tooth plates from P10146 were examined under a scanning electron microscope, and some of the S.E.M. photo micrographs are included in Plates 15, 15a, 16, 16a, 17, 17a, 18 and 19. From these it can clearly be seen that each tooth plate comprises: a basal plate, the exact shape of which varies according to the position inside the buccal cavity; a deep median groove which must have conveyed nerves and blood vessels and a series of sharply pointed, conical teeth, that increase in size distally. (High powered magnifications of individual teeth are included in the selection of photo-micrographs.)

A moderately large median tooth plate was found beneath the ventral visceral arch elements in both P24410 and P32438 (Plates 13, 14,19 and 20). This tooth plate forms a nearly complete, hollow, cylinder of bone, whose ventral edges meet but do not suture; its outer surface is covered by numerous tiny conical denticles. By comparing Plate 13, which was taken at an early stage in the preparation of P32438, with Plate 14, which shows the basi-, hypo-and cerato-branchials in ventral view at a later stage, it can be seen that this tooth plate lay between hypo-branchials II and III. The only element normally found in this position is the urohyal. In his paper "The exoskeleton versus the endoskeleton", Patterson (1977a) discusses bones of variable histogenesis, and cites as his second example the development of the urohyal. He states that in pholidophorids the urohyal comprises a median, vertical plate, and a horizontal ventral plate, so that it has the form of an inverted 'T' in section (Patterson, 1977, fig. 5). Patterson goes on to say that the vertical plate is pre-formed in cartilage, while the horizontal plate is dermal in origin and has its external surface ornamented with peculiar multicuspid denticles, which once projected through the skin at the isthmus. With this information in mind, my initial conclusion was that the median ventral tooth plate in *Pachycormus* was homologous with the dermal component of the urohyal in pholidophorids. However, two inconsistencies refute this conclusion. Firstly, in *Pachycormus* the median ventral tooth plate curves downwards, not upwards as in the dermal component of the urohyal in pholidophorids. Secondly, examination of this ventral tooth plate in *Pachycormus* under a scanning electron microscope (Plate 20) shows that its

Figure 17. *Pachycormus macropterus.* P24410 unrestored drawing of the right infra-pharyngo-branchials in (a) dorsal and (b) ventral view.

Figure 18. *Pachycormus macropterus.* P10146 unrestored drawing of the basi-exoccipital of P10146 in (a) posterior and (b) lateral view.

17


lpb I
lp
lpb II
ap
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a
b
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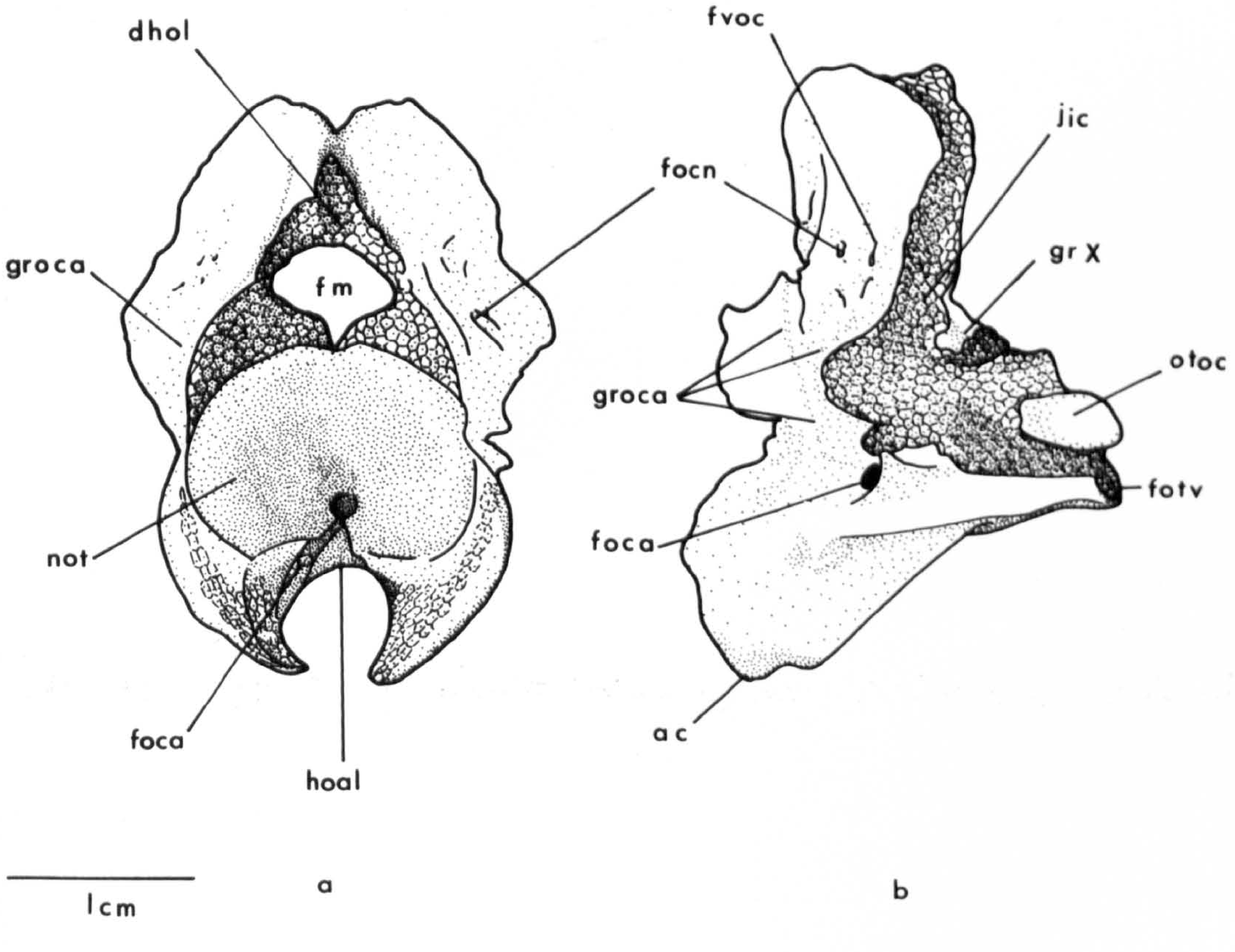
18


dhol
fvoc
jic
focn
groca
fm
gr X
otoc
groca
fotv
not
foca
foca
ac
hoal
1cm
a
b

surface is covered by simple conical teeth quite unlike the multicuspid denticles found on the urohyal of pholidophorids. Therefore, it seems unlikely that this ventral tooth plate in Pachycormus is a part of the urohyal, and for reasons discussed below it is equally unlikely to be an anterior extension of part of the pectoral girdle. Its identity remains a mystery.

(h) The neurocranium

The neurocranium is large and well ossified. Most of its bony components are distinct, and were separated by wide bands of cartilage in the juvenile fish. In nearly all individuals the cranial fissures completely separate the occipital from the otic region; there are no membrane bone outgrowths extending across them. Laterally the most conspicuous feature is the elongated hyomandibular facet which passes above the poorly developed sub-temporal fossa. The orbits are large; the eyes were supported by well ossified sclerotic rings, and the rectus muscles extended into a deep posterior myodome. Dorsally, the bones of the neurocranium are separate from the dermal bones of the skull roof. The parasphenoid strengthens the braincase ventrally.

(1) The occipital region of the neurocranium

This consists of a co-ossified basi-exoccipital and separate paired intercalars. There is no trace of either a median supra-occipital or of lateral paired epi-occipitals (Patterson, 1975:425).

The basi-exoccipital is illustrated in Figures 18 and 19. It is the major component of the posterior wall of the neurocranium. It surrounds the foramen magnum, forms the occipital condyles and houses the posterior part of the otolith chamber. It also forms the postero-medial wall of the vagus canal and borders the vertical fissura otica occipitalis (Nielson, 1949). The vagus canal is perichondrally lined as also is the sub-vagal portion of the fissure; the supra-vagal portion of the fissure is unlined and in life was closed in cartilage.

Although the basioccipital and exoccipitals are ossified as a single unit, there are residual sutures on the internal surface of the bone. The suture between opposing exoccipitals runs medially dorsal and ventral to the foramen magnum. In some specimens the highest point of the dorsal suture is obliterated, as it is in the Callovian *Pholidophorus sp.* described by Patterson (1975). The ventral suture ends posterior to the otolith chamber (in the specimen illustrated, Fig. 19, this ventral suture has been lost in preparation, but it can be seen in P32436). No distinct suture can be traced between the basioccipital and the exoccipitals. However, there is a pronounced constriction in each lateral wall of the basi-exoccipital at about the same horizontal level as the ventro-medial suture, which perhaps suggests that the bone ossified from at least three centres.

In the posterior wall of the neurocranium, surrounded by the exoccipitals, is the large, transversely oval foramen magnum. Its median ventral edge is notched as it is in the Callovian *Pholidophorus sp.* (Patterson, 1975). The occipital condyles are located on either side of the foramen magnum, posterior and slightly ventral to it. They are small, and lack perichondral lining. Dorso-medial to the foramen magnum is a small triangular depression, lacking perichondral lining where the dorsal ligaments to the vertebrae were inserted.

In P24410 (Fig. 20, Plates 21 and 23) the external opening of the foramen magnum is surmounted by an occipital arch (oca) the piers of which rest just above the occipital condyles. The base of each pier is concave and endochondral and, with the corresponding occipital condyle forms one of the articular surfaces for the first vertebra.

On each side of the neurocranium, immediately anterior to the condyle and lateral to the foramen magnum, runs a groove which skirts the notochordal pit. This groove is opposed by a notch in the antero-ventral wall of the pier of the occipital arch, so forming a foramen through which passed the posterior branch of the occipital artery. The occipital arch is pierced at its apex to allow the passage of the dorsal ligament to the vertebra.

Beneath the foramen magnum lies the notochordal pit (Plate 23), which is cone-shaped and tapers antero-ventrally. It penetrates about two-thirds of the depth of the basioccipital - far deeper than it does in pholidophorids, parasemionotids or caturids.

Below the notochordal pit run a pair of ventral longitudinal crests, deepest posteriorly, whose posterior surfaces lack perichondral lining. These crests form the walls of the aortic groove. The presence of perichondral lining along the ventral edges of the aortic crests indicates that the groove was open ventrally in life, unlike that of the pholidophorids, where a transverse band of cartilage between the crests formed an aortic canal (Patterson, 1975).

Within the aortic groove, close to its anterior end, is a flat horizontal septum of perichondral bone connecting the joining two sides of the

Figure 19. Pachycormus macropterus. P10146 unrestored drawing of the basi-exoccipital in (a) ventral and (b) anterior view.

Figure 20. Pachycormus macropterus. Reconstruction of the posterior wall of the neurocranium based on P24410.

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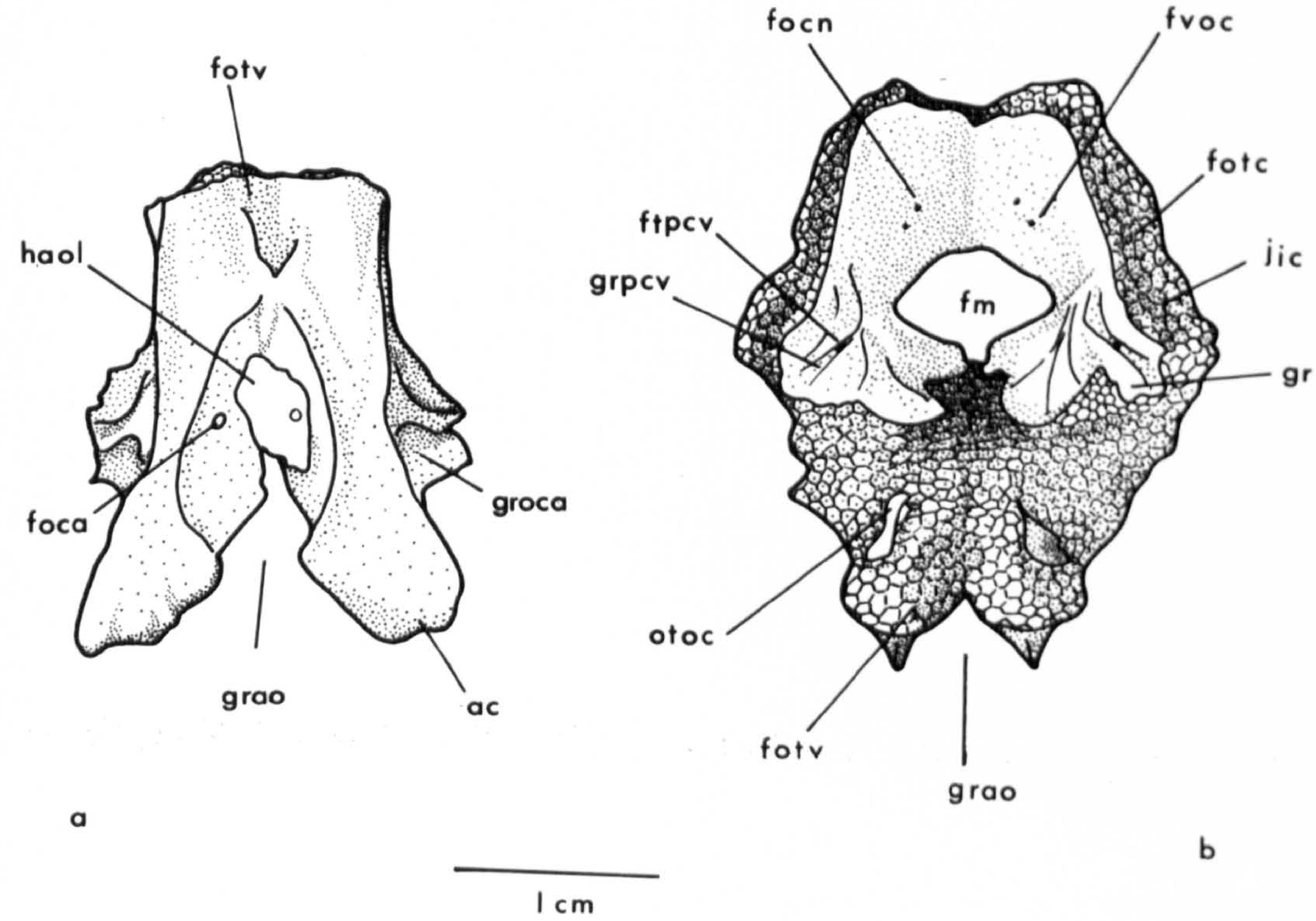
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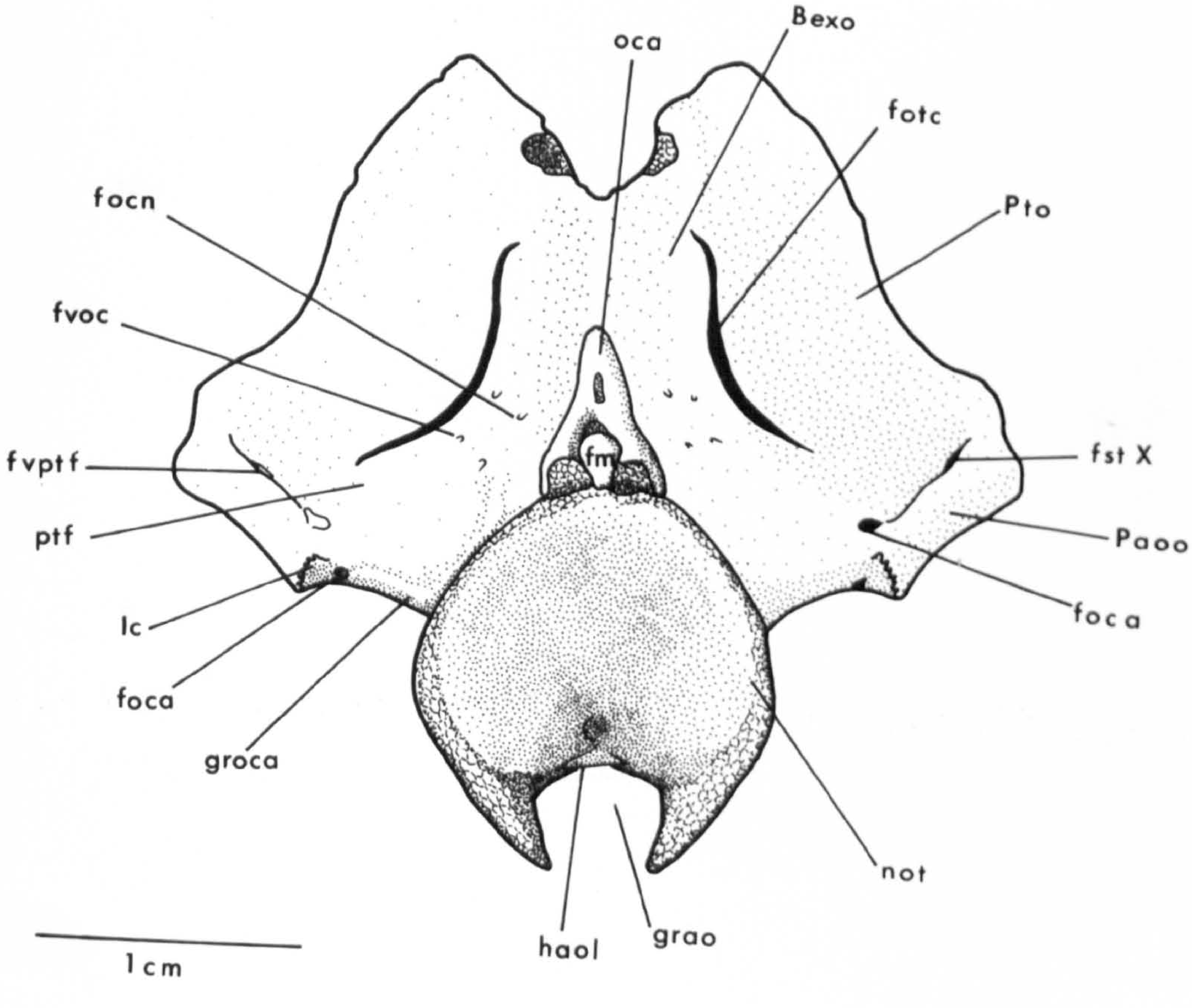
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groove and forming a posteriorly open pocket similar to those in the pholidophorids and leptolepids described by Patterson (1975), which, he suggests, housed the aortic ligament. Immediately posterior to this pocket, the walls of the aortic groove are pierced by a pair of dorso-laterally directed canals, which carried the occipital arteries. (In P10146 (Fig. 19) there is also a foramin in the in the intact left portion of the horizontal septum itself; presumably in this individual at least one of the occipital arteries pierced the septum before passing into the canals.) This arrangement, in which the housing of the aortic ligament lies anterior to the foramen of the occipital arteries, resembles that found in the pholidophorids; whereas in the parasemionotids, caturids and amiidae, the housing of the aortic ligaments lies posterior to these foramina.

Each occipital artery emerged onto the lateral wall of the basioccipital, where its course can be traced as a dorsally-directed groove that divides almost immediately into an anterior and a posterior branch. The anterior branch passes onto the intercalar (see below). The posterior branch passes upwards above the notochordal pit and itself divides: one subdivision passes onto the surface of the exoccipital, while the other enters the foramen magnum by way of the foramen between the occipital arch and the exoccipital (Fig. 22; described above).

On the internal surface of the exoccipital are two pairs of foramina, one pair posterior and slightly above the other. The posterior pair carried branches of the occipital nerve running postero-dorsally to the roof of the neurocranium, and each nerve foramina bifurcates in the thickness of the bone, emerging through two separate foramina, one ventrally-directed, the other dorsally-directed. The anterior pair of internal foramina appear to imitate the posterior and they too connect with two pairs of external openings, though their precise function is not certain. The same arrangement of foramina is found in Pholidophorus germanicus. Patterson (1975) suggests that while the posterior pair carried the occipital nerve, the anterior pair anastomoses with a canal which carried the posterior branch of the posterior cerebral vein.

A perichondrally lined groove runs ventro-laterally from the cranial cavity onto the anterior face of the exoccipital. This groove forms the postero-medial wall of the vagus canal. It is divided by a ridge of bone into a broad ventral channel and a narrower dorsal one. The ventral channel carried the vagus nerve, the dorsal channel the post^r cerebral vein. A small tributary of the post^r cerebral vein joined the main vessel via a tiny canal which emerges into this groove.

On the ventral surface of the basi-exoccipital there is a distinct V-shaped cleft, starting immediately anterior to the origin of the aortic crests, and becoming more marked towards the anterior end of the bone. The fact that the configuration of Pachycormus is similar to that of Pholidophorus germanicus in this respect at first suggested that their internal structure was also similar and specifically, that the posterior myodome of Pachycormus macropterus may penetrate the basi-exoccipital as in Pholidophorus germanicus. However, radiographs of P24410 have shown that this is not the case, and that the posterior myodome is confined to the otic region.

Antero-ventrally, the endochondral surface of the basi-exoccipital forms the posterior wall of the fissura oticalis ventralis. The basi-exoccipital also forms part of the posterior wall of the fissura otica-occipitalis. This vertical fissure is perichondrally lined in the vagus canal and below this to the point where the fissure meets the vestibular fontanelle; dorsal to the intercalar the fissure lacks perichondral lining and here it passes along the endochondral anterior face of the exoccipital. In life, the greater length of this dorsal portion of the fissura otica-occipitalis was closed in cartilage. The fissure is obliterated at its dorsal extremity in P24410 where the exoccipital has fused to the posterior otic bones.

The intercalars (the post-opisthotics of Lehman, 1949), are illustrated in Figure 21. Each is a small, compact, endochondral bone, with all but its medial surface perichondrally lined and this unlined surface meets the basi-exoccipital in synchondrosis immediately behind the vagus canal, part of whose postero-lateral wall the intercalar forms. In Pachycormus the intercalar lacks membrane bone outgrowths of the kind commonly found in pholidophorids and caturids, in both of which they extend across the cranial fissure onto the otic region. However, there is one membrane bone out-growth, in the form of the flange, which extends downwards into the mouth of the vagus canal. The post-cerebral vein emerged anterior and the vagus nerve posterior to this flange.

In intact neurocrania, above the vagus canal, the antero-dorsal surface of each intercalar is completely covered by the opposing otic bone. An isolated intercalar from the dissociated neurocranium of P10146 shows that this surface is perichondrally lined. The supra-vagal portion of the fissura otica occipitalis passes across this antero-dorsal surface before rejoining the basi-exoccipital dorsally. A narrow groove (gr ptv) runs laterally along the ventral edge of this concealed surface until it meets a wider channel (grStX) passing upwards from the vagus. Both then pass dorsally into the post-temporal fossa. The wider of these two grooves probably carried the supra-temporal branch of the vagus nerve, and the narrower one blood vessels. In intact neurocrania neither of these grooves is visible; the only indications of their presence are a foramen in the roof of the vagus canal, hidden behind the flange of membrane bone (described above), and dorsally either a single large foramen, or, in some individuals, a pair of foramina opening into the post-temporal fossa. Where a pair of foramina occur, as in P24410 and P10146, the supra-temporal branch of the vagus nerve emerged lateral to the blood vessels.

A channel for the anterior branch of the occipital artery (Figs 18 and 21) runs from the basi-exoccipital onto the postero-ventral surface of the intercalar. From here it appears to have followed one of three courses into the post-temporal fossa: (1) It continued in an open channel (P10146, 32432); (2) It runs through a simple unbranched canal (P24410, and right side of 32438); (3) It enters a canal which bifurcates within the intercalar and opens into the post-temporal fossa by two separate foramina (left side of 32438).

(2) The otic and orbitotemporal region of the neurocranium

The otic and orbitotemporal region is made up of separate, paired, opisthotics, pterotics, prootics, sphenotics and pterosphenoids and the median basisphenoid and orbitosphenoid. In addition two extra pairs of ossifications have been identified: (1) a pair of endochondral ossifications which form part of the postero-lateral skull wall above the vagus canal and foramen; these separate the opisthotics from the intercalars, and meet the pterotics dorsally, so forming part of the floor of the post-temporal fossa. (2) a pair of bones line part of the anterior cranial cavity above the prootic bridge, and extend onto the medial surface of the sphenotic. For convenience these additional bones will be referred to as the posterior and anterior additional otic-ossifications respectively; the homologies of both are discussed below.

The otic region is separated from the occipital by the cranial fissures (Rayner, 1951). The anterior wall of the vertical fissura otica-occipitalis passes down the posterior faces of the pterotic, of the opisthotic and of the posterior additional otic-ossification. Horizontally the fissura oticalis-ventralis separates the posterior part of the prootic from the basi-exoccipital.

The lateral wall of the otic region of the neurocranium (Plates 21 and 24) is divided by the hyomandibular facet: the dorsal otic bones (the sphenotics and pterotics) are inclined ventro-laterally, their endochondral ventral surfaces forming the dorsal edge of the facet; the ventral ossifications (the prootics, opisthotics and the posterior pair of additional otic-ossifications) are ventro-medially inclined, their endochondral, dorsal surfaces forming the ventral edge of the facet. In Pachycormus macropterus the hyomandibular facet acts as a barrier between the dorsal and ventral ossifications of the otic region, preventing encroachment of one bone upon the other. This is different from the arrangement found in the pholidophorids, where dorsal extensions of the prootic enter the fossa bridgei, and the pterotic extends ventrally, to form part of the ventral edge of the facet and enter the sub-temporal fossa.

The opisthotics are illustrated in Figure 21. They are a pair of moderately large, endochondral bones, each lying immediately in front of the vagus canal and forming approximately one-third of the ventrolateral wall of the neurocranium. Each opisthotic touches the prootic anteriorly, and meets the posterior additional otic-ossification dorsally. It is in contact with the intercalar dorsal and ventral to the vagus foramen and the two bones together form its rim, but their contact is only superficial, dorsally they are separated by the posterior additional otic-ossification, ventrally the suture between them extends for a very short distance into the vagus canal but the intercalar is soon replaced by the basi-exoccipital. Thus the opisthotics do not meet the pterotics dorsally in the post-temporal fossa, as previously reported. Ventrally each opisthotic lies adjacent to the basi-exoccipital though it is separated from it antero-ventrally by the vestibular fontanelle.

The posterior surface of the opisthotic is perichondrally lined. It can be divided into two portions, a thinly-lined ventral portion which represents the *fissura otica-occipitalis*, and a thickly-lined dorsal portion recessed into the body of the bone and forming the anterior and ventral walls of the vagus canal. A bony ridge runs along the anterior wall of the canal and extends as far as the mouth of the foramen dividing it, and the canal, into a narrow, dorsal, vascular channel, and a broader, ventral channel which carried the vagus nerve. The degree of development of this ridge varies between and within individuals. In P24410 the ridge is rudimentary, hardly protruding into the foramen. While in P10146 and 32432 it extends upwards almost meeting the descending flange (df.Ic) from the intercalar and so dividing the foramen into antero-dorsal and postero-ventral portions.

A subsidiary branch of the vagus nerve left the canal via a foramen in the floor of the ventral channel, and emerged onto the lateral surface of the neurocranium via a foramen slightly anterior and ventral to that transmitting the main branch. Of the specimens examined, only the left opisthotic of P10146 (Fig 21) lacks this subsidiary foramen; and in this instance its function is apparently fulfilled by a notch in the antero-ventral rim of the main vagus foramen.

The posterior extension of the jugular groove runs onto the lateral surface of the opisthotic, above the vestibular fontanelle. As it passes across the opisthotic it becomes less and less distinct, finally disappearing just in front of the vagus foramen. The glossopharyngeal nerve emerged through a small foramen into the anterior end of this groove. Immediately dorsal to the jugular groove is the posterior part of the poorly developed, shallow, sub-temporal fossa. In Pachycormus the external semi-circular canal does not form a conspicuous arch separating the sub-temporal fossa from the post-temporal fossa, as it does in the pholidophorids, but is embedded unobtrusively in the wall of the neurocranium at the junction of the opisthotic and the pterotic.

In the left side of P24410 the antero-ventral edge of the opisthotic is produced forwards to form a narrow bridge (Fig. 22), which spans the vestibular fontanelle and meets the prootic anteriorly. The right side of this specimen is too worn to indicate whether or not this feature was also present on this side. This structure has not been observed in any other individual and though its function is unknown, it is clear that it is a genuine feature of this individual neurocranium, and not merely the result of post-mortem distortion.

Internally the medial surface of the opisthotic lacks perichondral lining, except for a small recess immediately in front of the vagus canal. This recess housed the ampullar chamber of the posterior semi-circular canal. The endochondral surface of the bone above this recess is opposed by the pterotic and between them they housed the external semi-circular canal.

Contrary to previous descriptions (Rayner, 1941, 1948; Lehman, 1949; and Patterson, 1975), the opisthotic does not oppose the intercalar dorsally. Consequently it does not form part of the floor of the post-temporal fossa. In fact, the opisthotic is confined to the ventro-lateral wall of the neurocranium extending only as far as and not beyond the ventral edge of the hyomandibular facet. The area of bone, dorsal to the vagus foramen, which meets the intercalar and forms part of the floor of the post-temporal fossa and which has previously been regarded as part of the opisthotic, is really an independent ossification, the posterior additional otic-ossification previously referred to. It is significant that the opisthotic is smaller than was previously thought because the supposed large size of this bone has been mentioned as a point of similarity between the pachycormids and caturids (Patterson, 1975). In the pholidophorids, this bone is either rudimentary or absent.

The additional ossifications in the postero-lateral wall of the otic region (the posterior additional otic-ossification, Fig. 21) are endochondral and slightly larger than the intercalars. They lie dorsal to the vagus canal and foramen, and separate the opisthotics from the intercalars. Their posterior and lateral surfaces are perichondrally lined and their remaining surfaces are endochondral.

Figure 21. *Pachycormus macropterus*. P10146 unrestored drawing of the left opisthotic, intercalar and posterior additional otic-ossification in (a) lateral, (b) medial and (c) posterior view, and (d) anterior face of the intercalar.

Figure 22. *Pachycormus macropterus*. Reconstruction of the lateral surface of the neurocranium based on P24410.

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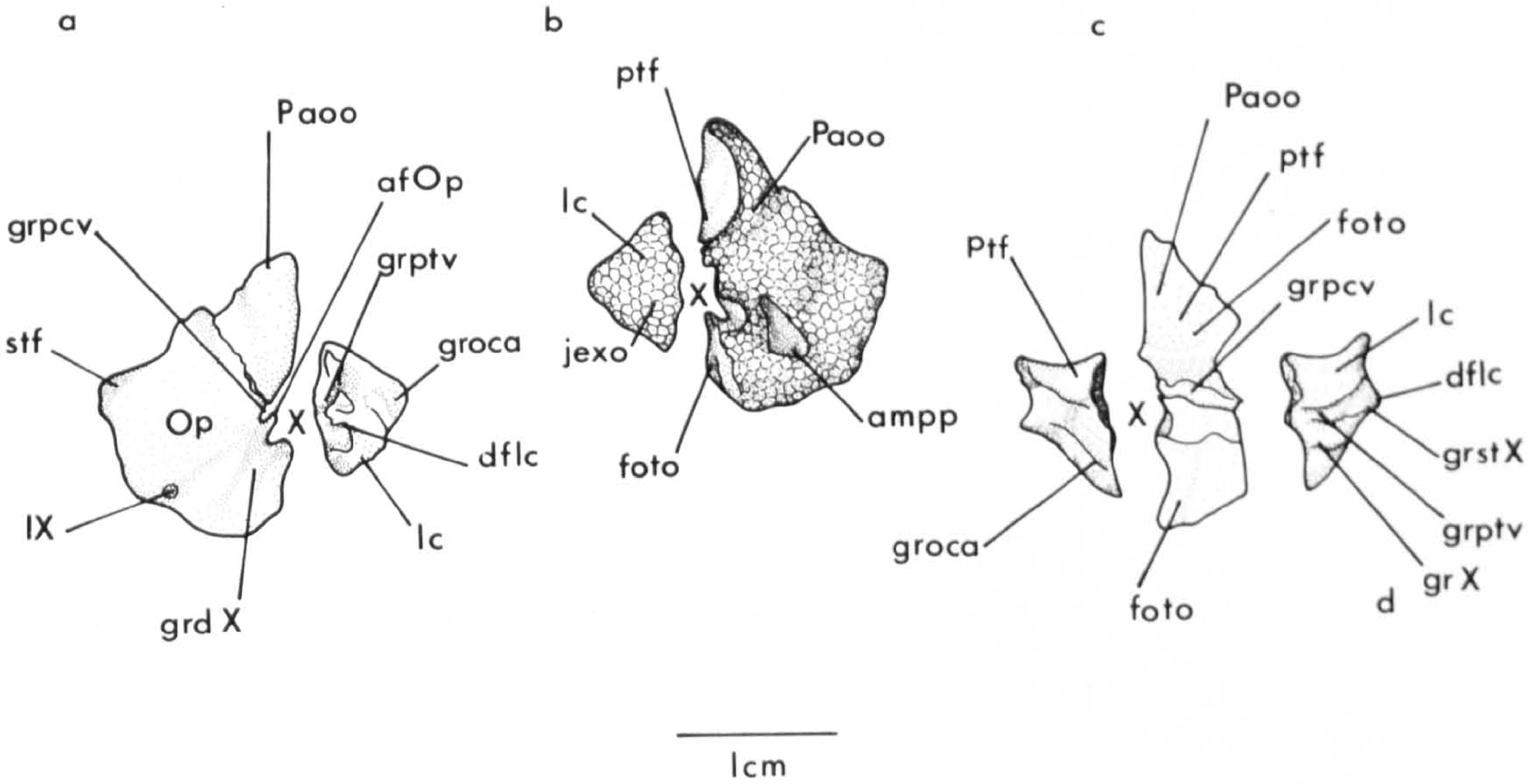
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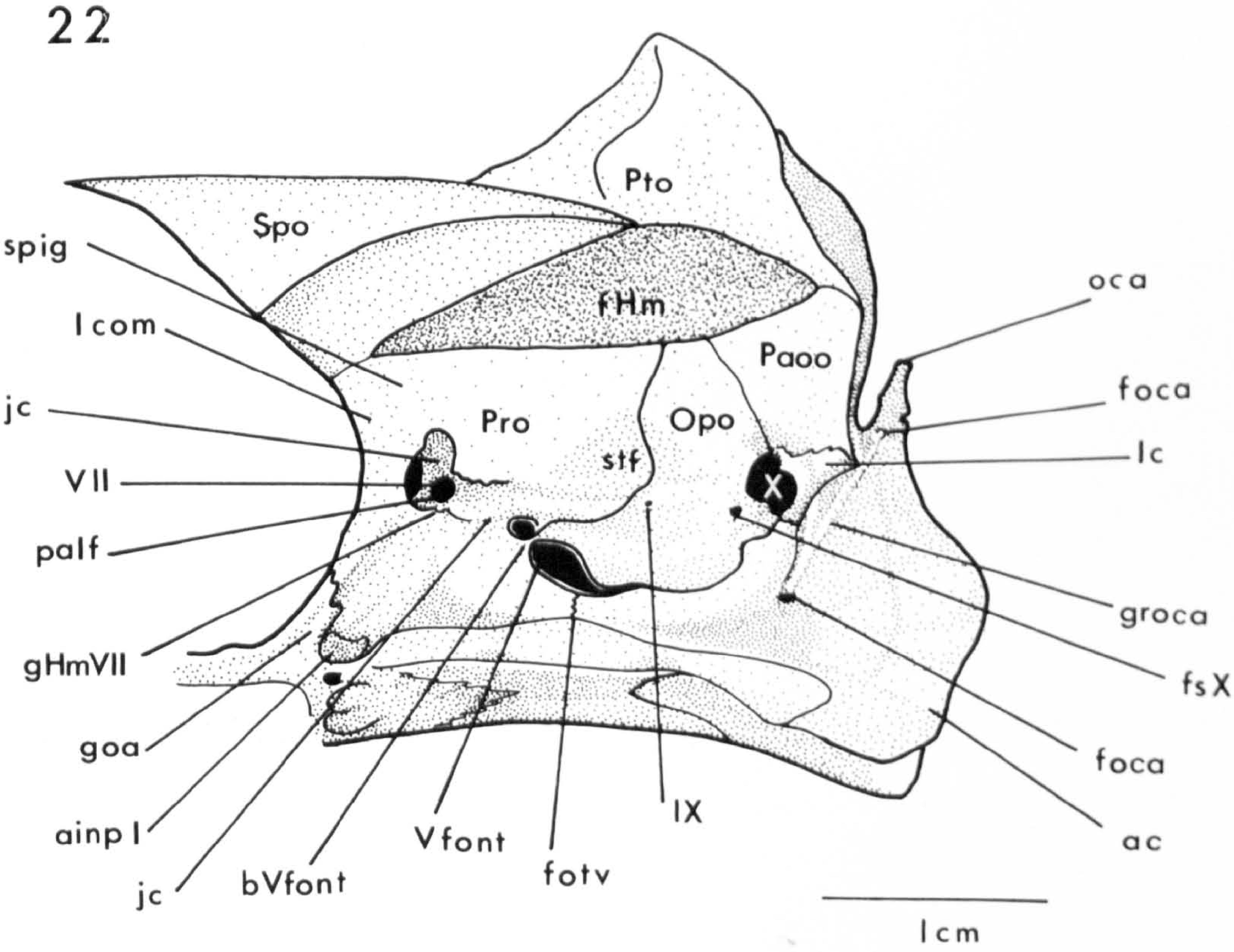
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The suture between the dorsal wall of the opisthotic and the ventral wall of this additional ossification can be seen in P10146 (left: Fig 21) The suture passes along the posterior wall of both bones, just above the vagus canal. It emerges from the mouth of the vagus foramen and runs antero-dorsally towards the hyomandibular facet. The posterior additional otic-ossification forms the postero-ventral edge of the facet. The suture between this ossification and the intercalar has been partially described above. The posterior face of the additional ossification clearly sutures with, and underlies, the antero-dorsal surface of the intercalar. A single, large foramen (or in some individuals a pair of smaller foramina) emerges at this suture; this carried the supra-temporal branch of the vagus and blood vessels into the post-temporal fossa. The supra-vagal portion of the fissura otica-occipitalis also passed between these perichondrally lined surfaces before returning to the endochondral basi-exoccipital. The remainder of the posterior wall of this additional ossification forms the floor of the post-temporal fossa.

Additional ossifications, similar to the posterior additional otic-ossification in Pachycormus macropterus, have been identified by Patterson (1975) in the neurocranium of Pholidophorus germanicus and Pholidophorus macrocephalus . In the former, it is rudimentary, ossifies over the middle part of the posterior semi-circular canal; and is attached to the basi-exoccipital above the vagus canal (Patterson, 1975: fig.45). In the latter, the ossification is a small independent element which ossifies over the posterior part of the external semi-circular canal in approximately the position of the leptolepid pterotic bone and is visible on the external surface of the neurocranium (Patterson, 1975:fig 84). In Pachycormus macropterus and P. curtus (Plate 29) the posterior additional otic-ossification lies behind the external semi-circular canal and above the posterior semi-circular canal that is, in about the same position as in Pholidophorus macrocephalus. However, in Pachycormus macropterus the ossification is conspicuously larger and more robust.

Patterson (1975:422) points out that the significance of these ossifications depends on their homologies; specifically, whether they, and not the pholidophorid pterotic, are the homologue of the leptolepid and teleostean pterotic; "whichever interpretation is adopted, a shift in the ossification centre of each bone must have taken place". In Pholidophorus macrocephalus and Pachycormus macropterus the ossification centre would have to have moved anteriorly to occupy the position it does in the leptolepids, over the centre of the external semi-circular canal. This is a relatively minor change compared with the major shift in the position of the ossification centre required if the pholidophorid pterotic is the homologue. Referring to the additional ossifications in Pholidophurus macrocephalus Patterson states that "if this small ossification could be shown to be a normal component of the braincase of early pholidophorids, or other primitive actinopterygians, the interpretation that it was the phylogenetic homologue of the leptolepid pterotic would be attractive" - "provided the candidate concerned also exhibits a pterotic of the pholidophorid type".

In Pholidophorus macrecephalus, the additional ossification is closely associated with the posterior extension of the descending lamina of the dermopterotic. Having examined the neurocrania of several pholidophorids and of other primitive actinopterygians, Patterson found that only Pholidophoroides limbata possessed a posterior extension to the descending lamina of the dermopterotic, and that that species, in common with all the others he examined, lacked the additional ossification. He concludes that the additional ossification in *Pholidophorus macrocephalus* must be regarded as a specialization of that species, and not as a general feature of the pholidophorids. Furthermore, he regards the pholidophorid pterotic as the homologue of the leptolepid pterotic bone, owing "its different form to a radical shift in the position of the ossification centre". He attributes this shift to the extension of the epioccipital across the cranial fissure, so that it occupies part of the territory formerly held by the pholidophorid bone.

It is impossible to draw any firm conclusion about the significance of the posterior additional otic-ossification in *Pachycormus macropterus* and *P. curtus* but their similarity to the additional ossification in *Pholidophorus macrocephalus* is striking and seems to invite further enquiry into the relationships between the pholidophorid pterotic and the leptolepid pterotic.

The pterotics (Fig. 23) are a pair of large endochondral ossifications lying anterior to the basi-exoccipital, and dorsal to the opisthotics, the posterior additional otic-ossifications, and the intercalars. They are the major components in the dorso-lateral wall of the neurocranium. They border the anterior dorsal fontanelle, house the posterior part of the fossa bridgei and complete the post-temporal fossa. They form a small part of the dorsal edge of the hyomandibular facet but do not contribute to its ventral edge or to the formation of the sub-temporal fossa. The dorsal unlined portion of the *fissura otica-occipitalis* passes across the posterior surface of each pterotic. The internal surface of each bone houses the lateral cranial canal, as Patterson suggests (1975), and also the posterior semi-circular canal and part of the external semi-circular canal.

Only the lateral and medial surface of the pterotic is perichondrally lined, its unlined, endochondral, posterior surface forms the antero-dorsal wall of the fissura otica-occipitalis. In P10146 this part of the cranial fissure was closed in cartilage, while in P24410 the fissure has been obliterated dorsally by the fusion of the pterotic with the exoccipital part of the basi-exoccipital.

The ventral surface of the pterotic is particularly wide and undulating; a pronounced convexity on this ventral surface fits into a concavity in the dorsal wall of the opisthotic, in such a way that the perichondrally-lined ampullar chamber of the posterior semi-circular canal, (housed in the opisthotic), lies adjacent to the perichondrally-lined medial surface of the pterotic, which supported the posterior semi-circular canal itself. The external semi-circular lies at the horizontal junction of these two bones which together enclose it (Plate 28).

From P24410 it can be seen that only that portion of the ventral surface of the pterotic immediately in front of the posterior additional otic-ossification forms part of the edge of the hyomandibular facet. The remainder of the pterotic passes medially behind the sphenotic and forms the medial edge of the dorsal opening of the spiracular canal.

In P24410 and P10146 the two pterotics are separated from each other by the anterior dorsal fontanelle which extends from the orbitosphenoid back to the basi-exoccipital. In 32432, however, the two pterotics are fused dorsally so that they cover the cranial cavity posteriorly and contain and restrict the posterior extension of the anterior dorsal fontanelle.

Externally, the anterior portion of the surface of each pterotic, which lies adjacent to the fontanelle, houses the posterior part of the fossa bridgei, while the posterior portion of the bone completes the post-temporal fossa. These two features are confluent in *Pachycormus macropterus*, and it is possible that the trunk musculature extended forwards into the fossa bridgei. This confluence of fossa bridgei and post-temporal fossa, though lacking in early pholidophorids, parasemionotids and caturids (where they are separated by a stout bony ridge) was developed in later pholidophorids and is always found in the leptolepids. In the latter, however, the epioccipital, and not the pterotic, houses them, and there is no dorsal opening for the spiracular canal as seen in *Pachycormus macropterus* and *P. curtus*.

The pterotics enclose the lateral cranial canals, whose surfaces are perichondrally lined.

The prootics are illustrated in Figure 24. They are a pair of large, complex, endochondral ossifications that form part of the lateral and the orbital surfaces of the neurocranium. However, they do not extend onto the roof of the neurocranium and so do not contribute to the fossa bridgei, as do their pholidophorid homologues.

The orbital surface of the prootic begins as an arc of thick endochondral bone at the postero-ventral corner of its medial surface. This arc

Figure 23. *Pachycormus macropterus.* P10146 unrestored drawing of the right sphenotic in (a) lateral, (b) dorsal, (c) anterior view and of the left pterotic in (d) lateral and (e) medial view.

Figure 24. *Pachycormus macropterus.* P10146 unrestored drawing of the left prootic in (a) lateral, (b) medial, (c) anterior, (d) posterior, (e) dorsal and (f) ventral view.

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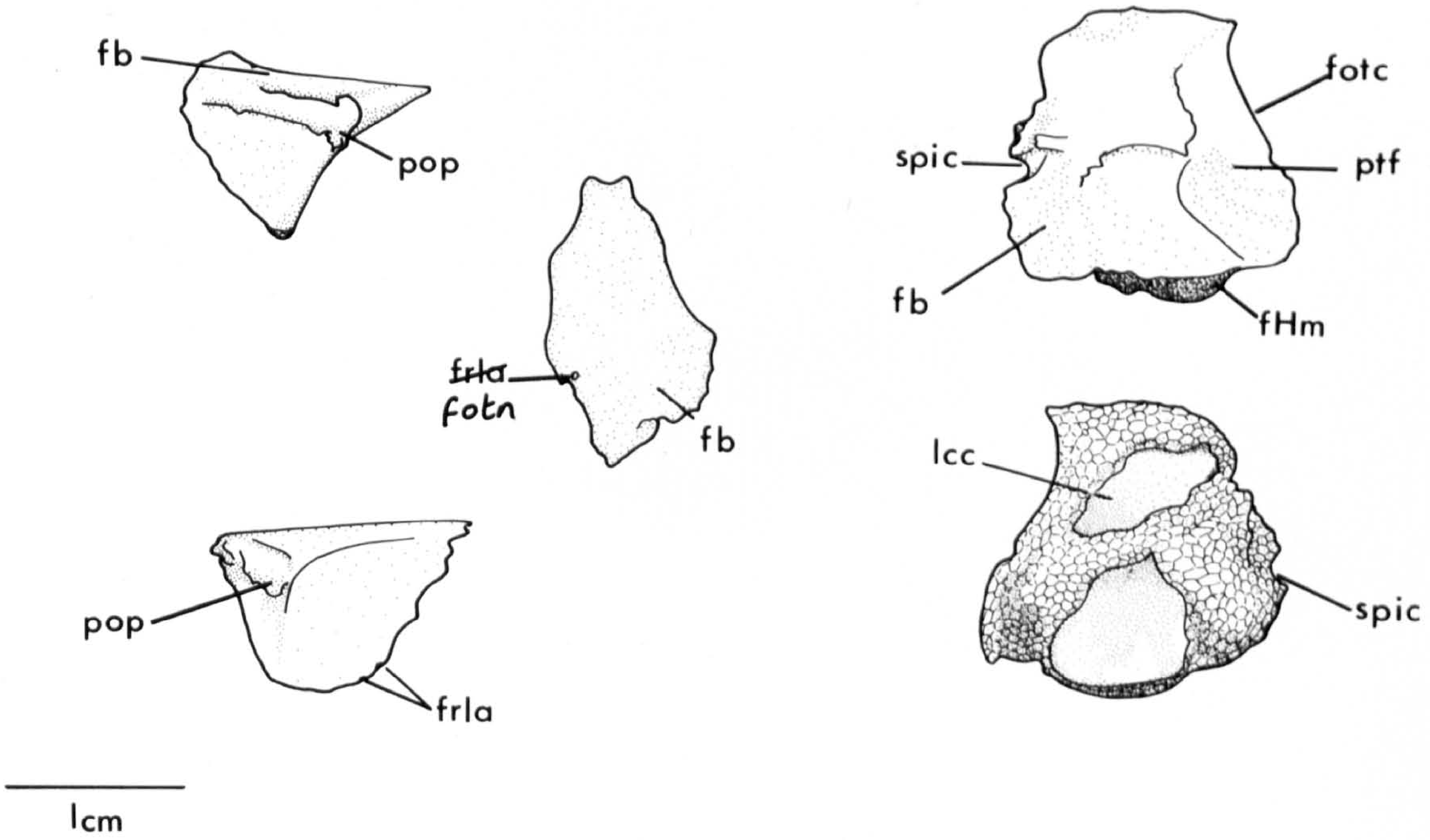
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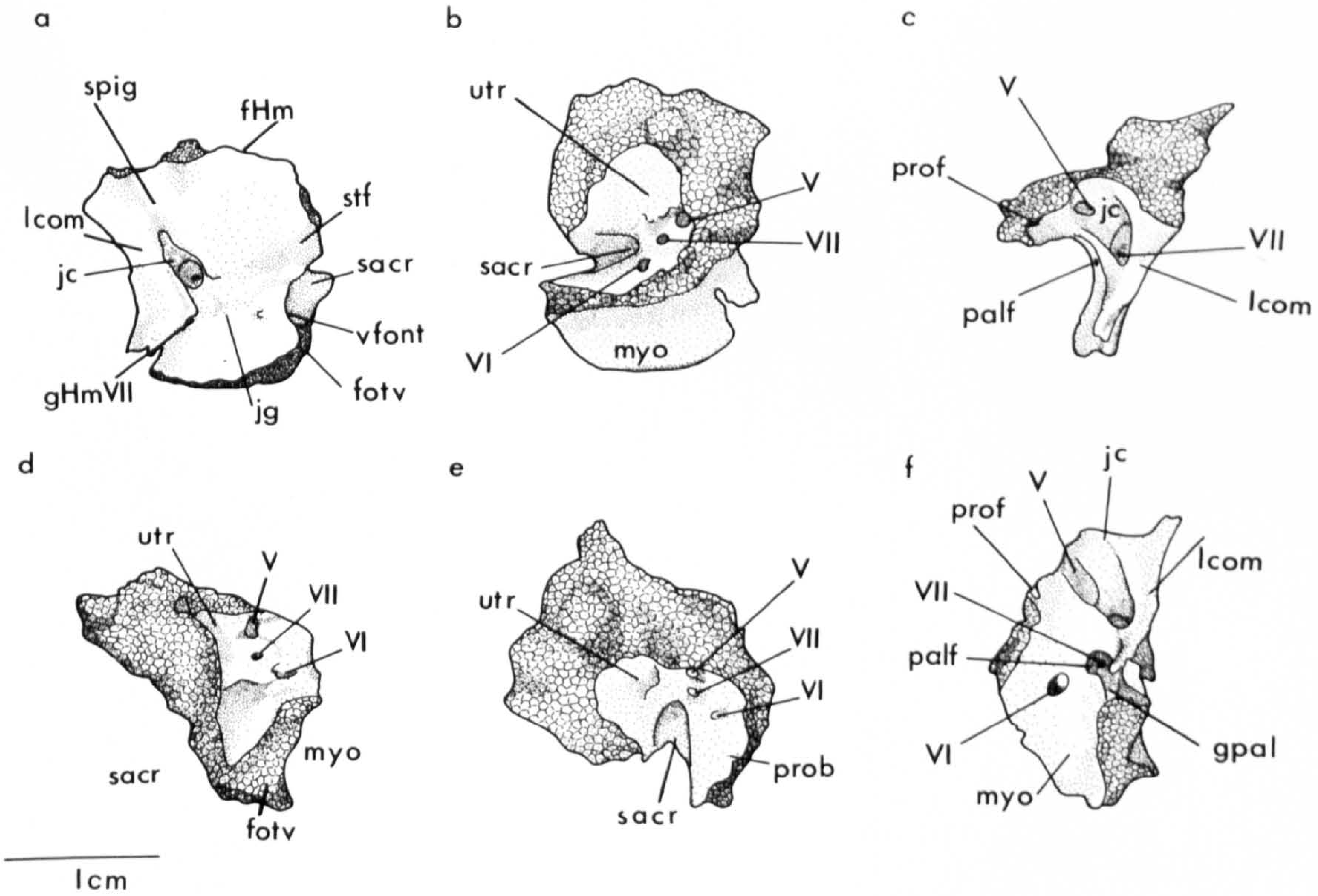
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passes diagonally, from the postero-ventral to the antero-dorsal corner of the bone. The arcs of opposing prootics meet mid dorsally to form the prootic bridge. Both the dorsal and ventral surfaces of the bridge are perichondrally lined; dorsally they complete the floor of the cranial cavity, housing the saccular and utricular recesses; while ventrally they roof the posterior myodome. The unlined posterior surface of the prootic forms the anterior wall of the fissura oticalis-ventralis. In some individuals this ventral fissure was closed in cartilage (P10146, 32432), while in others (P24410) its two surfaces meet with only a suture remaining to indicate its position.

Above the level of the ventral fissure the lateral surface of the prootic is deeply notched forming the anterior border of the vestibular fontanelle. A horizontal groove just dorsal to this marks the course of the large jugular vein, which passed posteriorly from the prootic onto the opisthotic where its course is less distinct. Anteriorly, the edges of this jugular groove form sharp ridges which cradled the blood vessel as it passed out of the jugular canal. Antero-ventrally there is a notch in the edge of the groove marking the passage of the hyomandibular branch of the VII nerve. This notch may also have served the orbital artery, as no separate channel has been identified for it. Patterson (1975) reported an endochondral depression on the lateral surface of the right prootic in P24410, immediately in front of the vestibular fontanelle. He suggested that this was the site of articulation of the first supra-pharyngo-branchial. The depression is poorly defined, is clearly not present on the other side of this specimen, (exposed subsequent to Patterson's description) or on either of the sides of at least three other, better preserved individuals.

In view of the interpretation of the visceral arch skeleton given above (section g) it seems likely that the supra-pharyngo-branchials if present were only poorly developed and are unlikely to have left distinct articulation scars on the neurocranium. The most probable explanation of the depression described by Patterson is that it is an artifact resulting from injury or post mortem damage.

Above the jugular groove the prootic carries the anterior part of the sub-temporal fossa, the remainder lies on the opisthotic as described above. This fossa contains the origin of the opercular adductor muscles. The site of attachment of the hyomandibular adductor muscles could not be identified. Immediately dorsal to the posterior opening of the jugular canal lies the vertical spiracular groove. This can be traced on the prootic as far as the ventral edge of the hyomandibular facet; it then continues into the sphenotic as the spiracular canal (Plate 28).

At the junction between the lateral and orbital faces of the prootic the bone is thickened to form a prominent vertical ridge that links the ascending process of the parasphenoid and the post-orbital process of the sphenotic to form a buttress strengthening this region of the neurocranium. The jugular canal has a single common posterior opening for the jugular vein, the hyomandibular and opercular branches of the facial nerve, and for the orbital artery, so that the canal and the lateral commissure are short. Within this posterior opening can be seen the palatine fenestra leading through to the posterior myodome. In P24410 a tiny foramen opens into the wall of the jugular canal, just above the palatine fenestra, its function was presumably vascular. The small facial foramen opens inconspicuously into the upper part of the palatine fenestra, into a space partly in the medio-ventral wall of the jugular canal, and partly in the dorso-lateral corner of the myodome. Anteriorly, the orbital face of the prootic is dominated by the anterior opening of the jugular canal, anterior and medial to which lies the trigeminal foramen. This latter foramen is much larger than that transmitting the facial nerve into the jugular canal, and its size reflects its dual function as transmitting not only the trigeminal nerve, but also the superficial ophthalmic and lateralis branches of the facial nerve. Both the trigeminal and facial canals are narrow throughout their lengths, and internally the wall of the prootic is not excavated in relation to either of these canals. This indicates that the trigeminal and facial ganglia must have lain well within the cranial cavity. Behind these internal foramina (Fig. 24) the last in a series of three, lies the foramen of the abducens (VI) nerve which opens into the back of the posterior myodome. Antero-medially, just within the roof of the myodome, either at the extreme anterior edge of the prootic or, in some individuals, between the prootic and the pterosphenoid, lies the profundus foramen, in the same relative position as in the pholidophorids. Dorsally the suture between the prootic and the sphenotic is penetrated by a pair of ventrally directed foramina. These foramina lie in line with the trigeminal foramen, and are connected to it by a shallow groove. By comparison with Pholidophorus bechei, and the Callovian Leptolepis (Patterson, 1975), and bearing in mind the slightly different proportions of the prootics and sphenotics in those species, the foramina in P. macropterus probably transmitted the first branches of the superficial opthalmic nerves, innervating the neuromasts of the posterior part of the supra-orbital sensory canal, and the recurrent branch of the facial nerve.

In *Pachycormus macropterus* there is a single posterior myodome contained within the otic region.

The cavity is roughly triangular in sagittal section, and approximately as wide as it is long; it is endochondrally lined throughout. Its anterior opening is bisected by the basisphenoid, and its lateral walls are braced by the ascending processes of the parasphenoid. The roof of the myodome is penetrated by a pair of foramina that convey the abducens (VI) nerves to the posterior rectus muscles of the eye. Dorso-laterally the palatine fenestrae open into the myodome, from each of these the palatine nerve passed antero-ventrally in a groove and entered a canal at the side of the base of the basisphenoid. The walls of the myodome give no evidence of the sites of muscle attachment, nor is there any evidence of a myodomenic membrane.

The sphenotics (Fig. 23) are a pair of large, trapezoid, endochondral ossifications, with all but their medial surfaces perichondrally lined. Each contributes to the post-orbital wall and completes the dorsal and lateral surfaces of the neurocranium.

The exact proportions of the sphenotic vary between specimens, and reflect the stage of growth of the individual. In the well ossified, intact neurocranium of P24410 there were no large cartilage filled gaps between ossifications; each bone meets its neighbour in a clear suture. In this individual (Fig 22) the sphenotic is elongated, its dorsal and lateral surfaces extending posteriorly beyond the suture of the prootics and opisthotics. In contrast the sphenotics from the dissociated neurocranium of P10146 (Fig 23) have truncated dorsal and lateral surfaces, which only extend half-way along the prootic bone and indeed the separation of the component bones of this skull indicates that each ossification was separated from its neighbour by a band of cartilage. In this respect P24410 can be regarded as exhibiting the neurocranium of a mature individual, and this view is supported by evidence from the visceral arch skeleton (see above), while P10146 although larger than P24410, appears to be a relatively immature individual whose braincase was still in the process of growth and ossification.

The elongation of the lateral surface of the sphenotic resembles the condition found in leptolepids where the greater development of the sphenotic coincides with a reduction of the prootic which consequently lacks its dorsal extensions; as it has in *Pachycormus macropterus*. This development also changes the proportion in which these two bones contribute to the formation of the hyomandibular facet. In pholidophorids, the anterior margin of the facet stops short behind the ventral opening of the spiracular canal; the facet rarely intruding more than half-way along the surface of the sphenotic. With the greater development of the sphenotic at the expense of the prootic and pterotic the facet migrates somewhat anteriorly, its foremost part lying entirely within the sphenotic; the prootic forming only a minor contribution to its ventral edge. During the course of these changes the spiracular canal is reduced and finally lost altogether. In *Pachycormus macropterus* the hyomandibular facet occupies the whole of the ventral part of the lateral surface of the sphenotic, running to the very edge of the orbit. However the prootic still forms a substantial portion of its ventral margin, but has no dorsal extensions into the fossa bridgei. The spiracular canal is still present, its ventral opening possibly concealed in the wall of the hyomandibular facet. The course of the canal is shown in relief in

Pachycormus curtus (32434) where it is infilled with calcite (Plate 28).

Above the hyomandibular facet, along the dorsal edge of the lateral surface of the sphenotic there is a prominent post-orbital process. This process overhangs a deep recess which housed the origins of the levator arcus palatini and dilatator operculi muscles; there is no distinct dilatator fossa.

Above the post-orbital process, the dorsal surface of the sphenotic contributes to the roof of the neurocranium, and can be divided into two portions; an anterior or supra-orbital portion and a post-orbital portion. The supra-orbital portion is more or less horizontal, its surface is uneven where it contacts the dermal skull roofing bones. The post-orbital portion of the bone varies in length, as described above; its development depending on the stage of ossification of the skull. In P10146 (Fig. 23) this post-orbital portion is rudimentary, and bears only the dorsal foramen of the otic nerve on its medial margin. In Pachycormus curtus (32434) however, the wall is more fully developed and forms the lateral margin of the dorsal opening of the spiracular canal, and houses the anterior part of the fossa bridgei; which is confluent with the post-temporal fossa.

The orbital surface of the sphenotic meets the prootic ventrally, their suture penetrated by a pair of foramina for the recurrent branch of the facial nerve and the first branches of the superficial opthalmic nerve as described above. Patterson (1975) identified a small foramen in Pachycormus curtus on the sphenotic-pterosphenotic boundary as that of the otic nerve, this occupies the same relative position as it does in pholidophorids. Anteriorly the sphenotic meets the orbitosphenoid.

From the dissociated neurocrania (P10146, 32432) examined it first appeared that the medial surface of the sphenotic was entirely endochondrally lined and, as Patterson had suggested (1975:399), was not involved in the support of the anterior semi-circular canal. However, evidence from two intact neurocrania disputes these initial conclusions. In Pachycormus curtus (32434) the right side of the brain-case clearly shows part of the anterior semi-circular canal embedded in the sphenotic which also suggests that this region of the bone, at least, was perichondrally lined (Plate 28).

In Pachycormus macropterus (P24410, Plate 27) a pair of anterior additional otic-ossifications were identified lying above the prootic bridge, with their convex lateral surfaces in close contact with the medial surfaces of the sphenotics. The position of these additional ossifications and the fact that the anterior semi-circular canal does lie partly within the sphenotic, suggest that these additional bones are homologous with the bridge of bone on the inner surface of the teleostean sphenotic which encloses part of the anterior semi-circular canal and named the pons moultoni by Haedrich (1971).

The pterosphenoids (Fig. 25) are small, paired, endochondral ossifications, wedged-shaped in cross-section, and with their lateral and medial surfaces perichondrally lined. They occupy considerably less of the orbital wall than do the pholidophorid or caturid pterosphenotics, and play no part in either the lining of the main cranial cavity, or in the housing of anterior semi-circular canal and its ampullar chamber.

Each pterosphenoid meets the sphenotic postero-dorsally. The sphenotic excludes it from the dorsal margin of the orbit, so that, as in leptolepids, the pterosphenoid make no contribution to either the anterior part of the fossa bridgei, or to the posterior part of the supra-temporal fossa. The otic nerve foramen sometimes penetrates the pterosphenoid -sphenotic suture, as in pholidophorids. However in the latter, due to the increased size of the pterosphenoid, the otic foramen lies more lateral than in its pachycormid homologue.

Postero-laterally, each pterosphenoid meets the medial edge of the prootic, but does not contribute to the formation of the dorsal margin of the trigeminal foramen, as it does in caturids. This again is a result of the relatively small size of the pachycormid bone. However, *Pachycormus macropterus* does resemble caturids in having the oculomotor foramen at the posterior end of the pterosphenoid - basisphenoid suture, though in some individuals this foramen lies completely within the pterosphenoid.

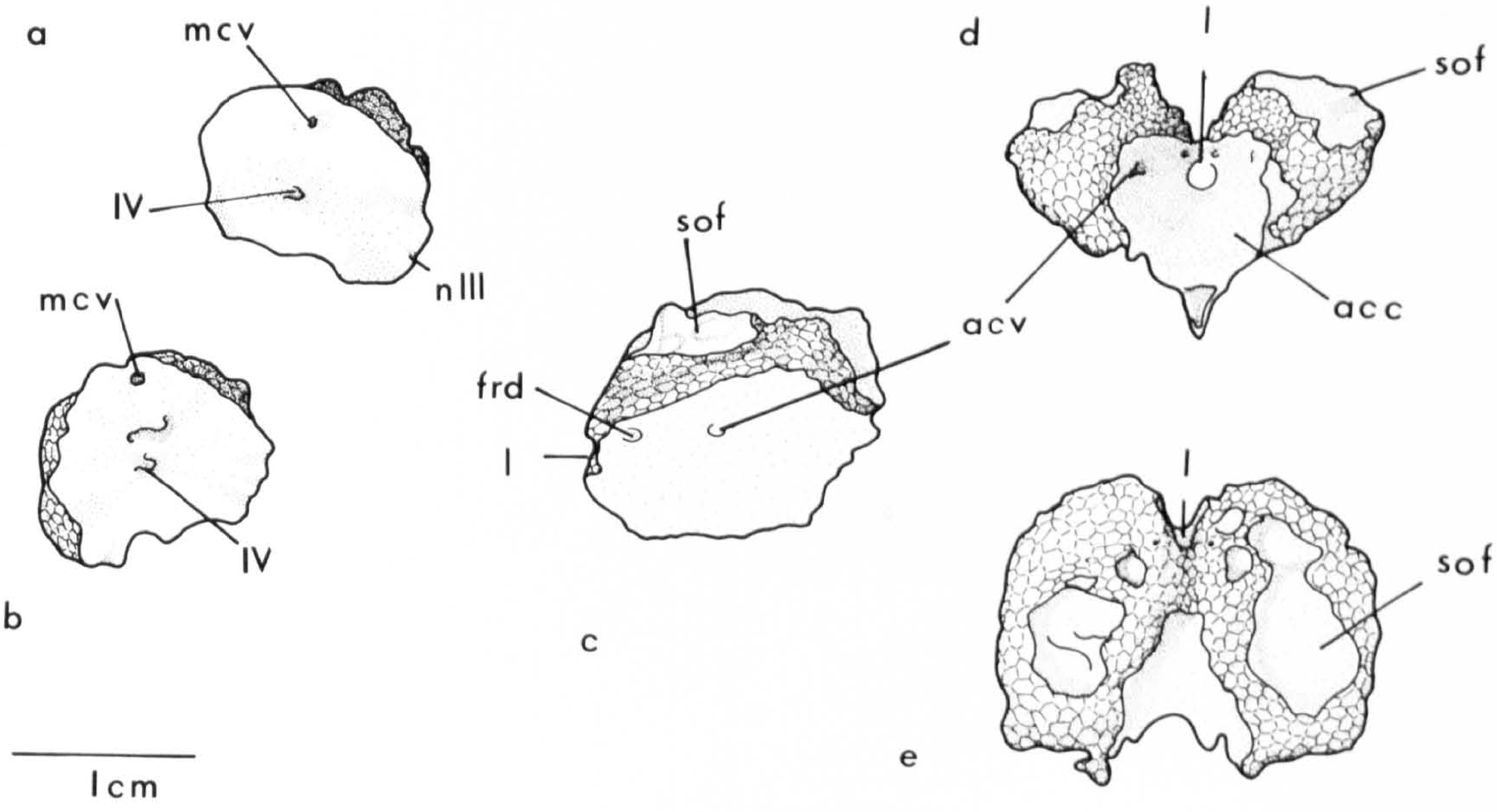
Medially the pterosphenoid forms the curved lateral margin of the optic fenestra. The foramen of the trochlear nerve (IV) penetrates or notches this edge of the bone. Lateral and dorsal to this small foramen, at about the same horizontal level as the trigeminal foramen, lies the foramen of the middle-cerebral vein. Both the trochlear and middle -cerebral vein foramina can be traced on to the internal surface of the bone, where a pronounced groove marks the entrance to the trochlear canal.

Anteriorly the pterosphenoid meets the orbito-sphenoid. The basisphenoid (Fig. 26) is a stout, median, endochondral ossification in the form of a vertical pillar that divides the mouth of the posterior myodome into left and right openings. As in the palaeoniscids and the early pholidophorids, the pachycormid basisphenoid has

Figure 25. Pachycormus macropterus. P10146 unrestored drawing of the pterosphenotic in (a) lateral and (b) medial view; and of the orbitosphenoid in (c) lateral, (d) posterior and (e) dorsal view.

Figure 26. Pachycormus macropterus. P24410 unrestored drawing of the posterior wall of the orbit.

25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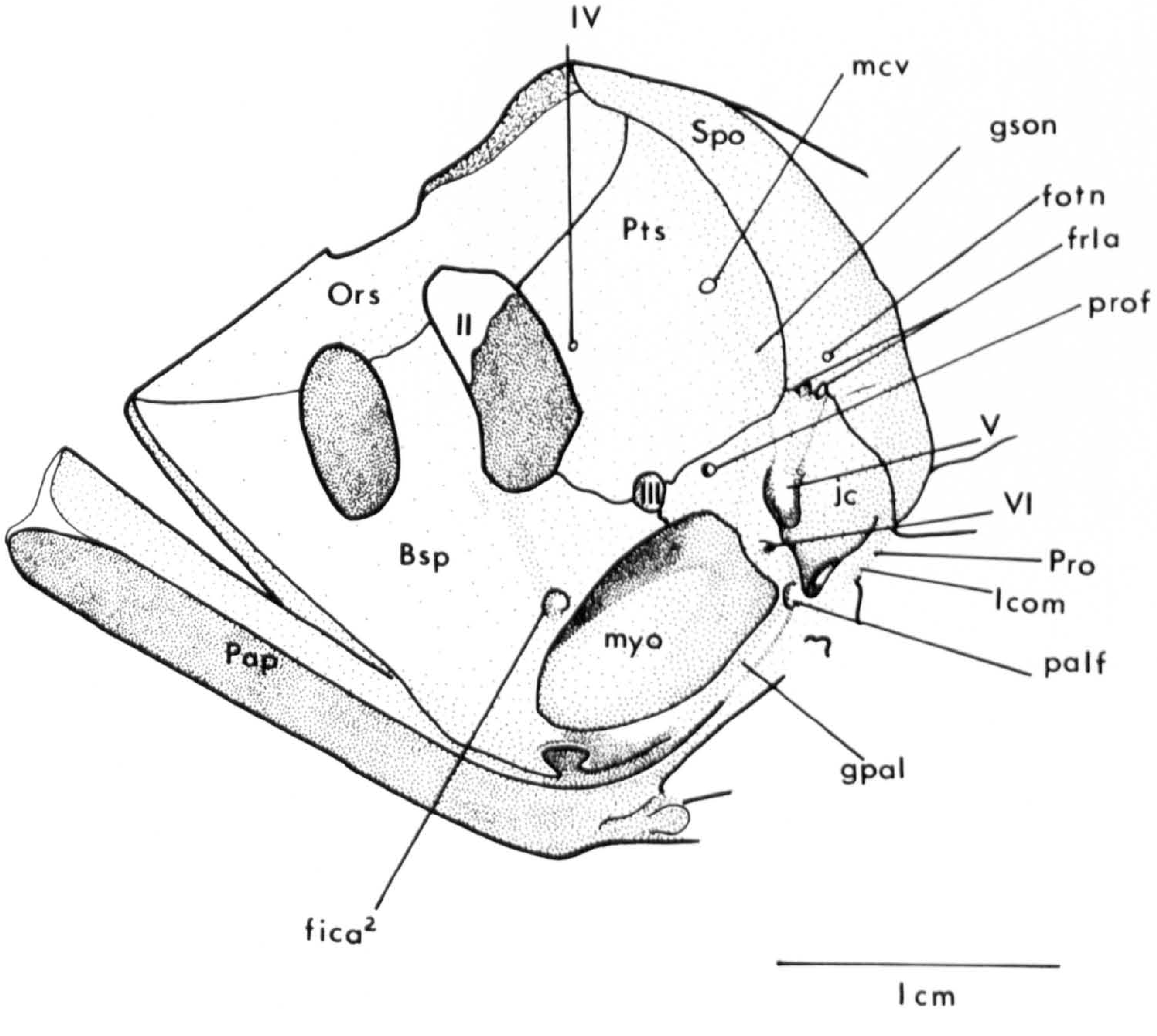
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ventral endochondral extensions. Anteriorly the basisphenoid forms a thin median slender portion, which contributes to the bony interorbital septum, and meets the orbitosphenoid below the optic fenestra in a discontinuous suture interrupted by the interorbital fenestra.

The posterior surface of the basisphenoid is divided both dorsally and ventrally. Dorsally, the division gives rise to two stunted, dorso-laterally directed arms, which contact the prootic posteriorly and the pterosphenoid dorso-laterally. The pterosphenoid -basisphenotic suture may be penetrated by the oculomotor nerve, as described above. Between these two arms the posterior surface of the basisphenoid forms a deep, posteriorly open, median recess in the floor of the cranial cavity that housed the pituitary fossa; each dorsal arm of the basisphenoid separating the pituitary fossa from the optic fenestra. The ventral end of the basisphenoid gives rise to a transverse bolster of endochondral bone that flares out on either side of the median crest on the dorsal surface of the parasphenoid; projecting forwards in the floor of the orbit, and posteriorly becoming continuous with the endochondral lining of the posterior myodome. A pair of horizontal canals emerge through this myodomal lining and end in a foramen on either side of the basisphenoid. The canals carried the palatine nerves and the foramen also transmitted the ascending internal carotid arteries, which passed through the parasphenoid in a pair of antero-dorsally directed canals, to emerge on either side of the median crest on its dorsal surface. The internal carotid arteries then passed through the palatine foramen onto the lateral surface of the basisphenoid pedicel where they entered a pair of vertical canals and so gained entry to the cranial cavity. In <u>Pachycormus macropterus</u> there are no canals for the efferent pseudobranchial arteries, which passed superficially onto the lateral surface of the neurocranium.

Anteriorly the basisphenoid forms a thin vertical septum of bone, whose ventral edge curves gradually upwards as it passes towards the orbitosphenoid, though it does remain in contact with the parasphenoid for about three-quarters of its length. Anteriorly the basisphenoid meets the orbitosphenoid in an oblique, discontinuous suture that frames the interorbital fenestra.

The orbitosphenoid (Fig. 25) is a median endochondral ossification, 'Y'-shaped in cross-section, with its lateral and medial surfaces perichondrally lined. The ventral part of the bone is a thin vertical sheet that forms a large part of the interorbital septum. Dorsally the bone encloses the anterior extension of the cranial cavity that contained the olfactory tracts. This cavity is widest and deepest, and its walls thickest posteriorly where the orbitosphenoid meets the pterosphenoid and the sphenotic. Anteriorly it gradually narrows and its walls become thinner and meet the postero-dorsal ends of the lateral ethmoids. The olfactory tracts leave the front end of the orbitosphenoid through either a single foramen (P10146) or through a pair of closely spaced foramina, separated by a thin median septum of bone (32432). The lateral walls of the cavity are penetrated by a number of small foramina. The largest of these, lying at about the middle of the wall, served for the anterior cerebral vein; smaller, more dorsally situated foramina transmitted subdivisions of the supra-orbital opthalmic nerves. The bony roof of the cavityis formed posteriorly by the dermal bones but anteriorly ingrowths of the dorsal edges of the orbitosphenoid extend towards the mid-line and join to roof the cavity anteriorly. The dorsal surface of this part of the orbitosphenoid is roughly excavated on each side of the mid-line to form the posterior part of the supra-orbital fossa. In 32432 a pair of narrow canals run dorso-laterally from the anterior end of the cranial cavity to open into the supra-orbital fossae: these probably carried an anterior branch of the superficial opthalmic nerves.

(3) The cranial fissures

These have already been described in some detail in conjunction with the ossifications that border them.

In summary, the horizontal *fissura oticalis ventralis* is endochondrally lined. It passes between the antero-ventral surface of the basi-exoccipital and the postero-ventral surfaces of the prootics. In some individuals (32432) this fissure was filled with cartilage, a wide gap separating its adjacent walls; in others (P24410) the two walls meet, but a distinct suture always remains to indicate its position.

The dorsal part of the *fissura otico-occipitalis*, walled by the 'exoccipital' part of the basi-exoccipital and the pterotics, was cartilage filled though fusion between the walls did take place in some individuals (P24410). The remaining, ventral part of this fissure is perichondrally lined. In neither *Pachycormus macropterus* nor *P. curtus* are there any membrane bone out-growths bridging the fissure from the occipital to the otic region of the neurocranium. The *fissura otico-occipitalis* is therefore more completely perichondrally lined than has been previously recognized (Patterson, 1975). It exhibits a condition between stages one and two of Patterson's six stages (Patterson, 1975:419) of the closure of this vertical fissure. This indicates that Pachycormus lies nearer to the beginning of this evolutionary series.

(4) The ethmoid region of the neurocranium

The ethmoid region contains two pairs of endochondral ossifications: the large lateral ethmoids and the rudimentary pre-ethmoids. No ossified, median mesethmoid has been found in any of the specimens that I have examined.

The lateral ethmoids (Fig. 27) have all but their ventral surfaces perichondrally lined. They complete the anterior wall of the orbit; house the anterior part of the supra-orbital fossa; support the rostro-dermethmoid and the frontals; and form the posterior wall of the nasal pits.

Each is a vertical pillar of bone, triangular in cross-section, with the apex of the triangle directed medially. The short, anterior face of the lateral ethmoid is strongly concave where it houses the posterior part of the olfactory pit, the taller posterior, orbital wall is slightly concave posteriorly, so that the lateral ethmoid is "hour-glass"-shaped in lateral view. The difference in height between the nasal and orbital faces results in the dorsal surface of the bone sloping steeply antero-ventrally; its ventral surface rises gently antero-dorsally.

Postero-dorsally each lateral ethmoid meets and sutures with the anterior end of the dorsal part of the orbitosphenoid and in this region the two lateral ethmoids are separated by some little distances. Shortly beneath this the posterior surfaces of the bones increase in width, so that the two lateral ethmoids are in close contact in the mid-line for about half their height ventrally; posteriorly they are joined by the anterior end of the ventral part of the fenestrated interorbital septum. Thus the posterior walls of the lateral ethmoids almost completely separate the orbital region of the neurocranium from the nasal region. The only communication between these is through a median dorsal fenestra, the foramen olfactorium evehens, and a number of small canals. A single foramen on each lateral ethmoid, just lateral to the median suture which leads through into the nasal pit, and must have carried the orbito-nasal vessel. Two additional pairs of foramina have been found on the preorbital wall of both P11929 and 32437; these lead into antero-dorsally directed canals that open into the dorsal surface of the bone and carried branches of the superficial opthalmic nerves. Ventro-medially the posterior wall of the lateral ethmoid is slightly hollowed. This marks the site of insertion of the inferior oblique muscle. There is no anterior myodome.

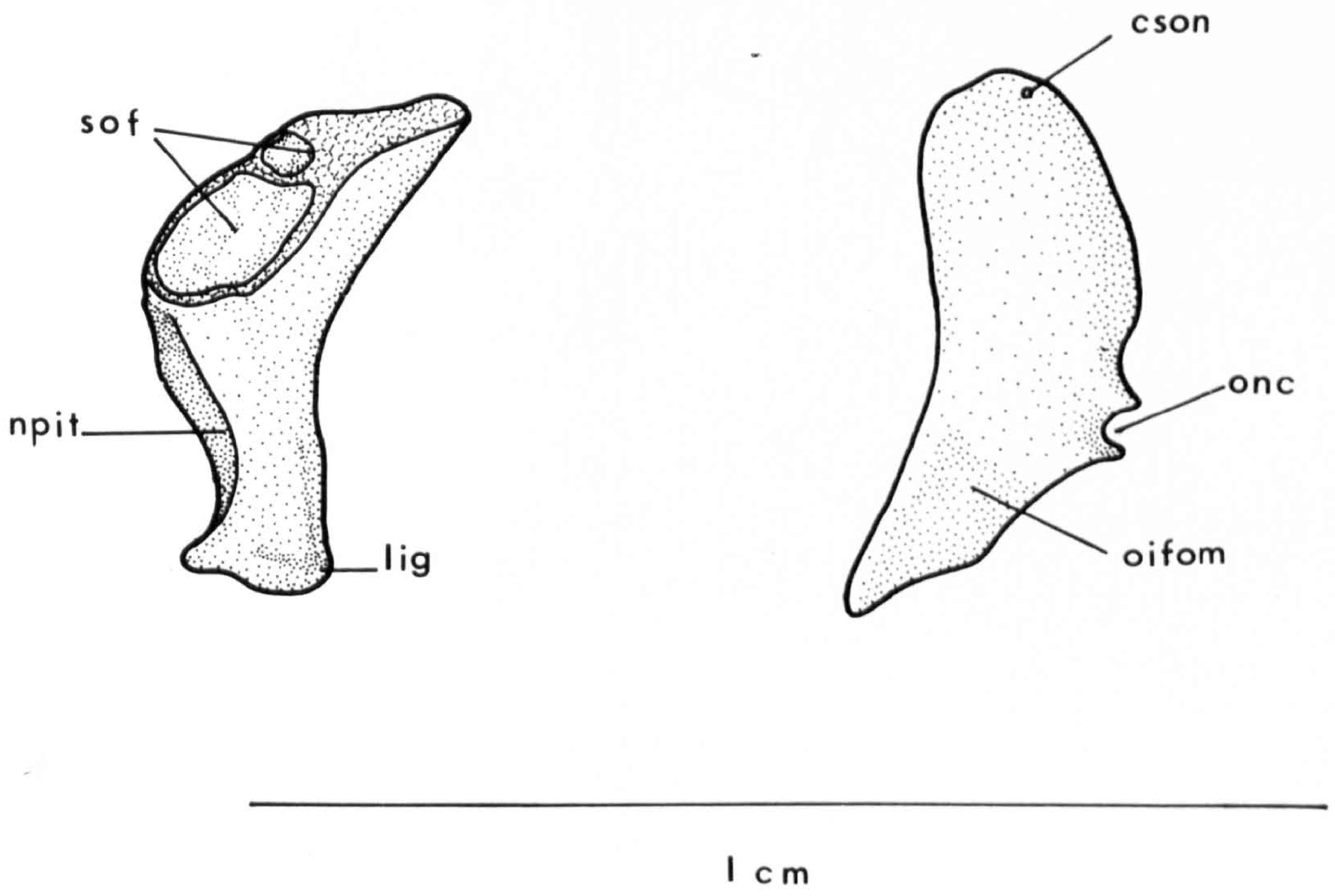
The dorsal surface of the lateral ethmoid underlies the dermal roofing bones, and meets the orbitosphenoid posteriorly. From the isolated lateral ethmoid of 32437 it can be seen that this dorsal surface houses a deep depression, separated from the nasal pit by a thin septum of bone. I interpret this dorsal depression as the anterior part of the supraorbital fossa that entends forwards from the orbitosphenoid.

The lateral surface of the lateral ethmoid shows a slight vertical ridge close and roughly parallel to the lower part of its posterior margin. This ridge probably marks the insertion of a ligament running to the palate or maxilla.

Figure 27. <u>Pachycormus curtus</u>. 32437 unrestored drawing of the right lateral ethmoid in (a) antero-lateral and (b) posterior view.

Figure 28. <u>Pachycormus sp.</u> Reconstruction of the caudal fin. Based on 32425 and P59545.

27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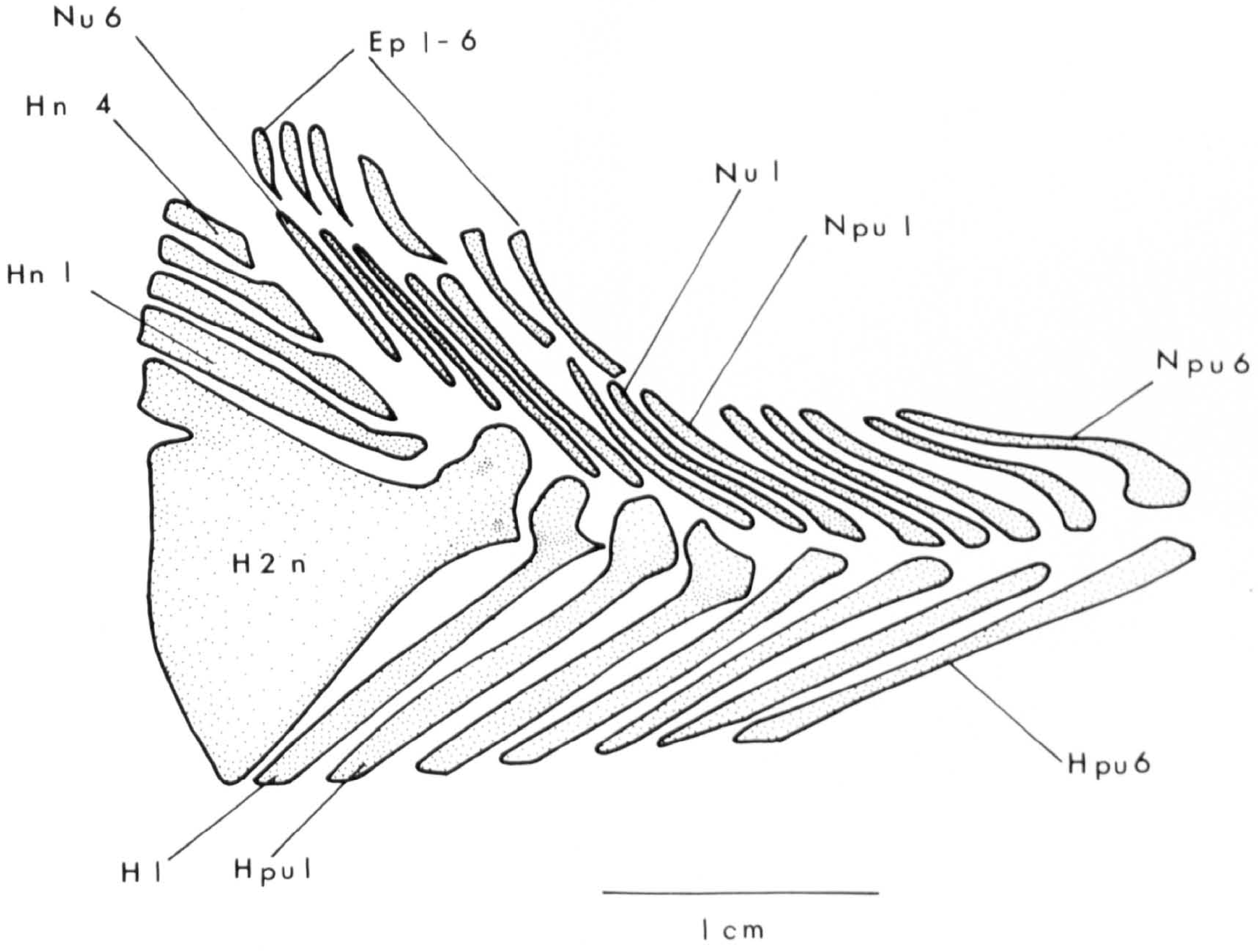
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The ventral surface of the lateral ethmoid has no perichondral lining and was covered in cartilage during life. This ventral cartilage met and articulated with the anterior end of the palate. The buccal and maxillary branches of the facial and trigeminal nerves must have passed through this cartilage after they left the orbit, as there are no foramina or grooves on the bony components to indicate their passage.

The occurrence of pre-ethmoid ossifications in the Pachycormidae was first reported in Hypsocormus by Stensio (1935); this was later confirmed by Rayner (1951) and Patterson (1975). Lehman (1949) mentioned the presence of pre-ethmoids in Pachycormus but was unable to give their precise position and Patterson (1975) failed to find these ossifications in the specimens of Pachycormus that he examined. I am able to confirm Lehman's identification of pre-ethmoid bones in the snout of Pachycormus macropterus and P. curtus where they lie anterior to the lateral ethmoids, sandwiched between the lateral dermethmoids and the vomers; in exactly the same relative position as the pre-ethmoid bones in Amia (Plates 3 and 4). Each pre-ethmoid is trapezoid in shape, with the ventral and antero-lateral surfaces perichondrally lined. Their lateral surfaces probably formed the anterior articulations for the heads of the maxillae but, unlike their counterparts in Amia, they do not encroach onto the articular surface ofthe palatines.

(i) The axial skeleton and the endoskeleton of the caudal fin

In Pachycormus the notochord apparently persisted through out life. Small hemichordacentra were present in some individuals (32430), but even here are restricted to the middle portion of the trunk.

In contrast the neural arches, transverse processes, haemal arches and associated spines are all robust endochondral structures. The neural spines are clearly paired in the anterior trunk but seem to be single structures in the tail region (Patterson, 1973:275). Immediately in front of, and beneath the dorsal fin the neural spines articulate with a series of supraneurals, which are restricted to that area. Ventrally, the haemal spines articulate with the endoskeleton of the anal fin.

Posteriorly, in the caudal region, haemal and neural arches are modified to form the endoskeleton of the tail. Patterson (1973:275) describes its structure in some detail, and for the main I agree with his interpretation. However, I have found that besides hypural I, and the large fan-shaped hypural, designated phypural h2+n by Patterson, that there are in some individuals (Pachycormus sp, Fig. 28, Plate 30) up to four reduced free hypurals lying along the dorsal edge of this large fan-shape. Patterson's final epural (32430, fig. 19 ep7) is in fact one of these additional reduced hypurals. Therefore there are only six epurals, and not seven as previously thought, an important point where the relationships of the Pachycormidae are concerned. Patterson distinguished seven ural neural arches which have grown forwards from their point of origin and which he regards as uroneurals of a peculiar type. These differ from those of other teleosts as they grade into unmodified pre-ural neural arches anteriorly.

As for dermal fin-ray supports of the caudal, anal and dorsal fins, these are described in detail by Wenz (1968) and I refer readers to that paper.

(j) The appendicular skeleton

In the genus Pachycormus only the pectoral girdle develops; the pelvic girdle is completely absent. Externally the pectoral girdle comprises six pairs of dermal bones (Fig. 2) that almost encircle the head, framing the dermal bones of the cheek and skull roof.

The suprascapulars are large, roughly triangular ossifications that lie behind the dorsal limbs of the dermopterotics and the parietals, their anterior margins almost meeting in the mid-line. Posteriorly the suprascapulars meet the supracleithrum and the pre-supracleithra. Internally, on the medial surface of each suprascapular there is a well developed ventro-laterally directed process. The lateral line sensory canal entered the suprascapular via a posteriorly open pore at the proximal end of this process and passed ventro-laterally within it to emerge through a foramen at its distal end. From there the canal entered the dermopterotic.

The supra-cleithra are robust, elongated, blade-like ossifications that underly the suprascapulars anteriorly, and meet the operculars and the cleithra ventrally. The anterior margin of each supracleithrum is drawn out into a single anterior process which lies immediately posterior to the origin of the ventro-lateral process of the suprascapular. Posteriorly, mid-way along the border, the supracleithrum is crossed diagonally by the lateral line sensory canal. This canal passes antero-dorsally into the anterior process and so entered the ventro-lateral process of the suprascapular, as described above.

A pair of superficial pre-supracleithra (Nybelin, 1976),

Figure 29. Pachycormus macropterus. 32432 unrestored drawings of the pectoral girdle in (a) lateral and (b) medial view.

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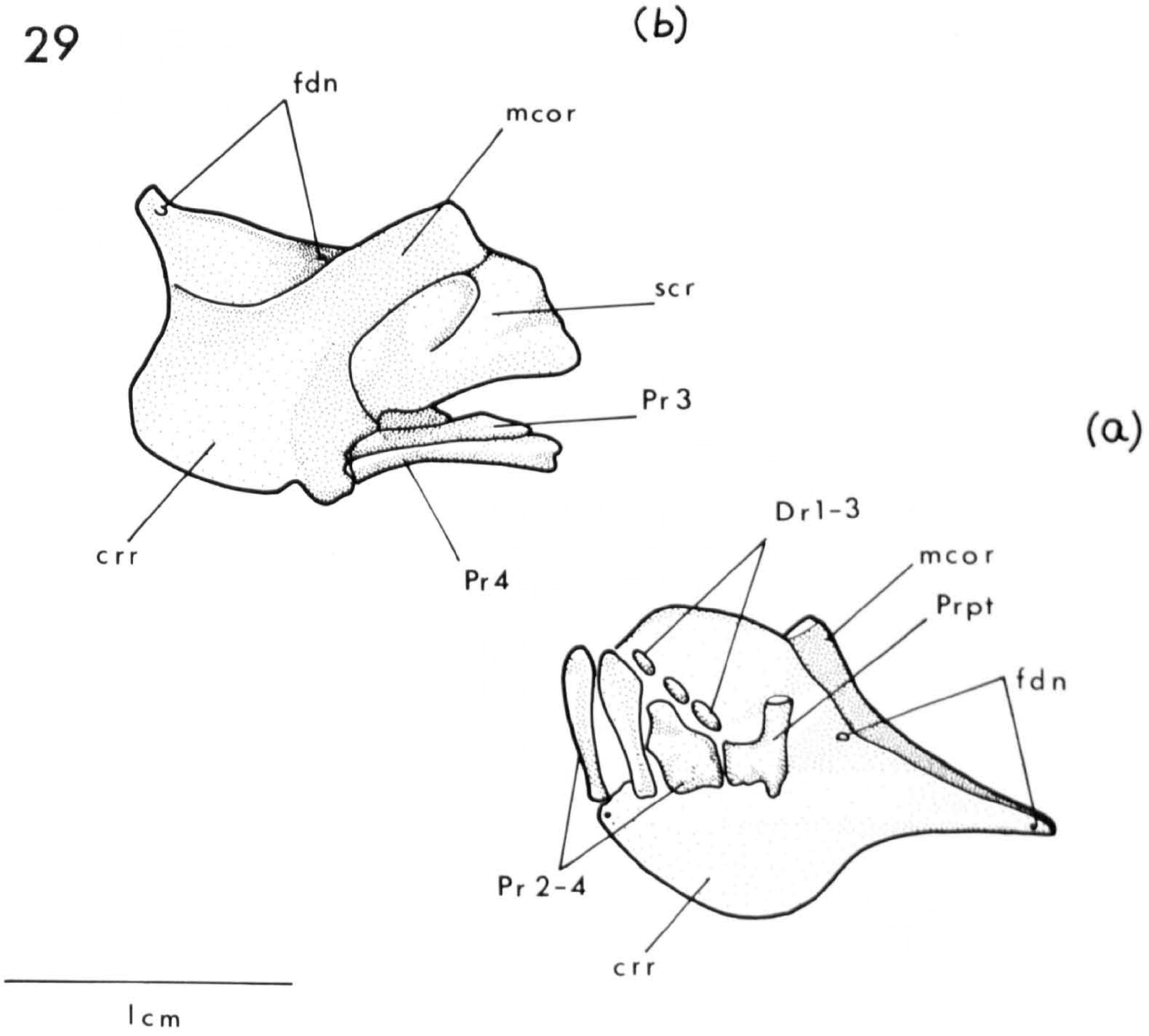

(Lehman's bone X, 1949) overlay the junction of the suprascapular and supracleithrum and conceals the passage of the sensory canal between those two bones. Previously, both Lehman (1949) and Wenz (1968) illustrated the lateral line canal as running dorsal to the pre-supracleithrum and entering the antero-dorsal margin of the supracleithrum whereas in fact the canal runs directly from the anterior process of the supracleithrum to the origin of the ventro-lateral process of the suprascapular as described above.

The cleithra are the usual sigmoid-shaped bones. The anterior end of each is thickened and produced forwards to meet its fellow in the mid-line ventrally, between the last pair of ceratobranchials. Dorsally each cleithrum tapers to a point which lies medial to the ventral border of the supracleithrum.

The dermal part of the pectoral girdle is completed by two pairs of plate-like ossifications, the dorsal and ventral post-cleithra.

In Pachycormus macropterus the endoskeletal part of the pectoral girdle is well developed and supported the enormous pectoral fins. The girdle ossified in two distinct halves (Fig. 29, Plates 31 and 32) each half comprising a single bone with only one suture and this lies between the dorsal part of the mesocoracoid arch and the scapular region. There is no large scapular foramen beneath the mesocoracoid arch, though a narrow canal does open onto the medial surface of the scapular region. Ventro-medially the deep, plate-like coracoid region lacks an anterior process, its posterior border forms the glenoid fossa which articulates with the last proximal radial. The coracoid is penetrated by three small foramina that probably transmitted the diazonal nerves.

The pectoral fin is connected to the girdle by a series of proximal and distal radials which articulate with the dermal fin rays. There are only four proximal radials (Jessen, 1972: plate 25.1.). The first, the propterygium, is fused to the first dermal fin ray; its base is penetrated by the propterygian canal. The second proximal radial (identified by Jessen as radials 1 and 2, plate 24.1.) is by far the largest in the series, and occupies approximately half the length of the fin-base. Anteriorly this second radial is short but the bone increases in width posteriorly so that here it is almost twice as long as anteriorly. Two rudimentary distal radials articulate with it distally. The third proximal radial is slightly flattened and spindle-shaped, and equal in length to the posterior edge of proximal radial two. A single distal radial articulates with it. The fourth proximal radial is long and slender ; distally this radial may remain single (32432) or may be bifid (P900).

The arrangement of the dermal fin-rays is described in considerable detail by Wenz (1968), and I have nothing to add to her description. As she points out the fin-rays are curved convexly to give the characteristic scythe-like fin of the Pachycormidae. The leading edge of the fin is formed by the second or third ray, successive rays exhibiting a peculiar dichotomous branching where the posterior half only of each bifurcation itself divides. This results in the posterior edge of the fin having a particularly thick fringe.

SYSTEMATICS

(a) Historical Background

Most of the species in the family Pachycormidae were described during the nineteenth century, although one specimen, later identified as *Pachycormus macropterus* was illustrated by Dezalier d'Argenville as early as 1755.

Woodward, in his *Catalogue of fossil fishes*, part III (1895), gives a comprehensive revision of the genera and species known at that date. He recognised seven genera, *Sauropsis*, *Prosauropsis*, *Euthynotus*, *Asthenocormus*, *Pachycormus*, *Hypsocormus* and *Protosphyraena* as definitely belonging in the family and suggested that an eighth genus, *Leedsichthys*, should be provisionally included. The following year Woodward (1896) reinstated the genus *Saurostomus* Agassiz, which he had previously considered to be a junior synonym of *Pachycormus*. Other notable additions to the family subsequent to Woodward (1895) include: the three monospecific genera, *Eugnathides* (Gregory, 1923), *Orthocormus* (Weitzel, 1930) and *Ohmdenia* (Hauff, 1940); several species of *Protosphyraena* from North America described by Cope (1872, 1874, 1875, 1877, 1878), Stewart (1898, 1899) and Loomis (1900), and reviewed by Hay (1903); *Protosphyraena stebbingi* (Woodward, 1908); *Hypsocormus combesi* (Sauvage, 1902) and *H. beaugrandi* (Sauvage, 1905); *Asthenocormus retrodorsalis* (Eastman, 1914); *Sauropsis depressus* and *S. curtus* (Eastman, 1914); *S. veruinalis* (White, 1925) and *S. ?woodwardi* (Gregory, 1923).

A list of the genera and species attributed to the family Pachycormidae by various workers, but excluding those judged to be junior synonyms or *nomina nuda* by Woodward (1895) and Hay (1903) and not subsequently reinstated, is given in Table 1. For reasons given below not all of these are retained in the present work.

Table 1. Classification of the family Pachycormidae as given by Woodward 1895 with additions to date but preceding present review.

Genus *Sauropsis* Agassiz, 1832

- *S. latus* Agassiz, 1832
- *S. longimanus* Agassiz, 1833
- *S. depressus* Eastman, 1914
- *S. curtus* Eastman, 1914
- *S. veruinalis* White, 1925
- *S. ?woodwardi* Gregory, 1923

Genus *Prosauropsis* Sauvage, 1894

- *P. elongatus* Sauvage, 1894

Genus *Euthynotus* Wagner, 1860

- *E. incognitus* Wagner, 1860
- *E. intermedius* (Agassiz) 1844
- *E. speciosus* Wagner, 1860
- *E. milloti* (Sauvage) 1891

Genus *Asthenocormus* Woodward, 1895

- *A. titanius* (Wagner) 1863
- *A. retrodorsalis* Eastman, 1914

Genus *Pachycormus* Agassiz, 1833

- *P. macropterus* (Blainville) 1818
- *P. acutirostris* Agassiz, 1844
- *P. curtus* Agassiz, 1832

Genus *Saurostomus* Agassiz, 1833

- *S. esocinus* Agassiz, 1833

Genus *Hypsocormus* Wagner, 1860

- *H. insignis* Wagner, 1860
- *H. macrodon* (Wagner) 1858
- *H. leedsi* Woodward, 1889
- *H. tenuirostris* Woodward, 1889

H. combesi Sauvage, 1902

H. beaugrandi Sauvage, 1904

Genus Protosphyraena Leidy, 1857

P. ferox Leidy, 1857

P. compressirostris Woodward, 1895

P. minor (Agassiz) 1844

P. tenuirostris Woodward, 1895

P. keepingi Woodward, 1895

P. stebbingi Woodward, 1909

P. ornata Woodward, 1895

P. brevirostris Woodward, 1895

P. depressa Woodward, 1895

P. nitida (Cope) 1872

P. gladius (Cope) 1873

P. perniciosa (Cope) 1874

P. ziphioides (Cope) 1877

P. dimidiata (Cope) 1878

P. recurvirostris Stewart, 1898

P. bentonia Stewart, 1898

P. gigas Stewart, 1899

P. occidentalis Stewart, 1898

P. tenuis Loomis, 1900

P. sequax Hay, 1903

Genus Eugnathides Gregory, 1923

E. browni Gregory 1923

Genus Orthocormus Weitzel, 1930

O. cornutus Weitzel, 1930

Genus Ohmdenia Hauff, 1953

O. multidentata Hauff, 1953

Genus Leedsichthys (Woodward) 1898

L. problematicus (Woodward) 1898

(b) Revision of the family Pachycormidae

In 1895, Woodward gave a diagnosis of the family Pachycormidae, and drew up a key to delimit each genus on the basis of certain anatomical features which he believed to be significant. Although some of these characters are still considered valid others such as the degree of development of vertebral centra are suspect. Moreover in the genus Euthynotus characters cited in the generic diagnosis conflict with the description of the type species.

During the course of this study other anatomical features which are thought to provide a sounder basis for the definition of the genera and species have been noted, and these are used in the revised classification that follows this section.

Woodward distinguished the type genus Pachycormus by the shape of the body (trunk robust and fusiform) by the absence of pelvic fins, by the position of the median fins (dorsal fin completely in advance of the anal) and by the non-extension of the anal fin base. All these features are considered valid here. To them may be added:- the presence of a pronounced fronto-parietal boss, the presence of a single row of teeth on the mandible, and the presence of a post-supracleithrum (Lehman's bone X (1949)).

In the 1895 Catalogue Woodward listed four species in the genus Pachycormus, of which P. esocinus, was originally the type species of Agassiz's genus Saurostomus. The following year, Woodward (1896a) transferred this species back to the genus Saurostomus which he reinstated. In distinguishing the genus Saurostomus, (which may be done by the shape of the opercular and the position of the median fins) both Woodward, and later Wenz (1968) stated that S. esocinus lacks a cranial boss. However, a poorly developed cranial boss is clearly present in conjunction with longitudinal cranial grooves on the dermopterotics in a particularly fine example of the species (M1307a) in the Moore collection, at Bath.

Woodward (1897) also suggested that P. acutirostris was synonymous with P. macropterus. This seems to be so, since all examples of P. acutirostris examined have been crushed dorso-ventrally in such a way as to distort the actual length of the snout. Moreover there seems to be no single identifiable features by which the two "species" may be separated.

The distinguishing features of the genus Sauropsis - the somewhat elongated body, the presence of the small pelvic fins, the relative positions of the median fins (which are usually opposed, though in some individuals the dorsal fin is slightly in advance of the anal) - remain valid. However its constituent species need revision.

In Woodward's Catalogue the genus Sauropsis contains two species, S. longimanus and S. latus. S. longimanus is distinguished by the criteria that the length of its head is greater than the maximum depth of its body, and that its pelvic fins are nearer to the pectoral fins than to the anal. In S. latus the length of the head is less than the maximum depth of the body, and its pelvic fins are nearer to the anal fin than to the pectorals.

Of the two species of Sauropsis described by Eastman (1914) S. depressus has the same proportions and fin dispositions as S. longimanus, and comes from the same locality and horizon. As they cannot be distinguished in any way, notwithstanding Eastman's claim to the contrary, S. depressus is here considered to be a junior synonym of S. longimanus. S.curtus according to Eastman, has a particularly short and deep body, with pectoral fins not particularly well developed, and the pectoral fin-rays articulating throughout their lengths. From Eastman's figure (plate lxvi) it appears that the axial skeleton of this fish continutes for some distance into the epaxial lobe of the tail. All these features are inconsistent with its being a pachycormid, and therefore this species must be removed from both the genus and from the family.

In 1923 Gregory added S. ?woodwardi to this genus. The specimen Gregory described comprises a crushed, incomplete head and anterior trunk, with part of a pectoral fin posterodorsal to which lie some fin fragments identified by Gregory as pelvic fins. The mode of branching of the pectoral fins suggests that they may well be a pachycormid, but, if so, to which genus it should be attributed is impossible to say. Therefore this species is retained within the family for the present but is placed incertae sedis as to genus.

In 1925 White established the latest species to be attributed to this genus to date, S. veruinalis.

The genus Euthynotus was reported by Woodward (1895) as differing from Sauropsis only in the presence of well developed hypocentra and pleurocentra and in exhibiting minute fulcra on the median fins. The condition of the vertebral centra is of little value as a distinctive feature for in no pachycormid are they well developed; the presence or absence of fulcral scales cannot satisfactorily be established in several of the species attributed to this genus. The type species, E. incognitus, can most easily be distinguished from other, broadly similar genera (Pachycormus, Saurostomus, Sauropsis) by its relatively small head and slender body and by the posterior position of the dorsal fin which arises opposite the middle of the extended anal fin. This combination of characters, though perhaps not entirely satisfactory, can at least be tested in all, or nearly all, of the relevant species.

Woodward included four species within the genus Euthynotus, but three of these, E. intermedius, E. milloti and E. speciocus must now be removed.

Woodward's diagnosis for E. intermedius states that the dorsal and anal fins are opposed. The type specimen has been lost, and no other material is available for examination. Agassiz's figure of this species shows the anal fin, but no sign that there was a dorsal fin opposing it; the anterior dorsal region of the trunk is incomplete; but the portion directly opposite the anal fin appears intact and undamaged. Therefore it seems that the dorsal fin must have been located anterior to the anal fin, which suggests that this species should be attributed to the genus Pachycormus where this arrangement of median fins exists. As the figured specimen is incomplete it is not possible to say whether it would have constituted a new species of Pachycormus, or belongs to one of the described species. It is therefore assigned to the genus Pachycormus, incertae sedis as to species.

The species E. milloti is diagnosed by Woodward (1895) as having the dorsal fin slightly in advance of the anal. The proportions of the head and body, the relationship of the head length to body depth, and the position of the pelvic fins in this species are all as seen in Sauropsis longimanus, but in view of the difference in geological age it is considered prudent to retain them as separate species, at least for the present.

Finally, of E. speciosus Woodward (1895) stated that the dorsal fin arose immediately in advance of the anal fin. As it has been established that in the type species of Euthynotus the anal fin commences in advance of the dorsal it cannot belong to that genus as here defined. In fact in the disposition of the fins, and proportion of the body, as described by Woodward, it conforms exactly with the genus Sauropsis and differs from all other pachycormid genera. As the type material was lost during the Second World War, and as there is no other material available for study, it is impossible to determine whether or not this species is conspecific with either of the species already in the genus.

Woodward (1895) distinguished the genus Hypsocormus from the genus Protosphyraena by the nature of the principal teeth, stating that only in the latter are these teeth laterally compressed. Moreover, though Woodward never cited it as a distinguishing character, it is clear from his description of these genera that he considered that Protosphyraena possessed only paramedial ("vomerine" and "premaxillary") teeth on their rostra, while Hypsocormus bore the usual marginal teeth in front of a pair of paramedials. These have not proved entirely satisfactory means of separating these genera and here the form of the dermal skull roof and the development of the rostro-dermethmoid is considered more fundamental and hence of greater significance. In Hypsocormus the rostro-dermethmoid does not project beyond the mandibular symphysis; the skull roof, anterior to the frontoparietal boss, is relatively short and rises at a steep angle to the horizontal. In Protosphyraena the rostro-dermethmoid is produced anteriorly into a distinct rostrum that projects beyond the mandibular symphysis, the skull roof is relatively long and rises at a comparatively low angle.

In his Catalogue Woodward reports four species within the genus Hypsocormus. Of these, there are fairly complete examples of the type species, H. insignis, and H. macrodon, which are both deep bodied, their median fins are approximately opposed to each other, pelvic fins are present, they have a double row of teeth on the mandible, and a pair of paramedial teeth on the rostro-dermethmoid in addition to the usual marginal teeth. H. macrodon is obviously similar to the type species and must remain within the genus, but the other two species included by Woodward must be removed for the following reasons:- these two species, H. leedsi and H. tenuirostris, are represented only by incomplete skulls. In H. leedsi only the rostro-dermethmoid is known, while in H. tenuirostris although the type specimen consists of a rostro-dermethmoid, an almost complete head is available for study. Both these species have rostro-dermethmoids with flattened dorsal surfaces, suggesting that the anterior dermal skull roof sloped upwards at only a low angle. This is certainly the case with H. tenuirostris. In both these species the rostro-dermethmoids are produced forwards beyond the lower jaw, though this projection is only slight in H. leedsi, and the paramedial teeth are large, anteriorly directed, and must have extended out of the mouth. All these features are entirely in keeping with those now associated with the genus Protosphyraena, and therefore they should be transferred to that genus.

Finally, a specimen described by Holmgren and Stensiö (1936) and later by Rayner (1948) as Hypsocormus sp. is now identified as a new species of Protosphyraena, P. obtusirostris sp. nov. This individual is represented by an almost complete head and clearly illustrates the projecting rostro-dermethmoid, the paramedial teeth and the elongated, almost horizontal skull roof with its poorly developed cranial boss, characteristic of the genus.

H. combesi based on a "prémaxillaire" and a portion of "maxillaire" from the Upper Kimmeridgian of Fumel, France, was described and referred with some doubt to this genus by Sauvage in 1902. The "prémaxillaire" has a canine-like anterior tooth and, in front of this, another much smaller tooth. The "maxillaire" carries only small teeth on its posterior part.

H. beaugrandi Sauvage 1905 is based on a "parasphénoide" and the anterior part of a "maxillaire supérieure" from the Upper Kimmeridgian of Boulogne-sur-mer. The latter bone carries a row of closely spaced large teeth and an external series of smaller teeth.

From the published descriptions it seems most unlikely that either of these two species belongs to the family Pachycormidae and they are therefore removed.

As far as the genus Protosphyraena is concerned, Woodward distinguished the various species by the shape of the rostrum, as in most cases only the rostra are known. He paid little attention to the nature of the paramedial ("vomerine") teeth, except to say that they were laterally compressed. However by examination of these teeth it is possible to divide Woodward's protosphyraenas into three groups, as follows:-

1. A group containing the type species P. ferox, P. compressirostris and Woodward's P. tenuirostris. (This last specific name was also used for Hypsocormus tenuirostris, which, as has already been demonstrated, is in fact a protosphyraena and must be transferred to that genus. P. tenuirostris (Woodward) 1889 [= H. tenuirostris Woodward] pre-dates P. tenuirostris Woodward 1895 and therefore has precedence. P. tenuirostris Woodward, 1895 is re-named P. woodwardi, nomen novum.) These species all have small, posteriorly directed paramedial teeth and extremely elongated rostro-dermethmoids.

2. A group containing P. nitida, P. penetrans [=P. nitida] (Hay 1905), P. depressa and P. brevirostris. These all have large, anteriorly directed, paramedial teeth. Their rostro-dermethmoids vary greatly in length; in P. nitida it is extremely elongate, while in P. brevirostris it hardly extends beyond the lower jaw.

3. A group containing P. ornata, P. minor and P. stebbingi. All these species are founded, as were the others, on isolated rostra, but in none of these are the characteristic paramedial teeth present,

and it seems unlikely that any of these species are in fact protosphyraenas.

P. ornata has by far the best preserved and most complete rostrum. This is laterally compressed, and is elaborately ornamented at its proximal end. This ornamentation indicates that some subsidiary plates met the rostrum posteriorly. Ventrally, there is a pair of longitudinal ridges, which narrow anteriorly but do not converge. Each ridge bore a series of tiny teeth implanted along its edge. Thus it can be seen that the rostrum in P. ornata is unlike that of any Pachycormidae. The presence of the longitudinal grooves and the posterior ornamentation suggest that the rostrum in this individual is not formed by the rostro-dermethmoid, as in pachycormids, but more probably by the premaxillae, as in the aspidorhynchids.

P. minor and the larger P. stebbingi each has an elongated hollow, compressed rostrum, the surface of which is entirely covered with longitudinal ridges. In both, one groove is particularly wide and shallow, and seems to contain a longitudinal suture. In individuals where the hollow end of the rostrum can be prepared, a second suture can be detected on the internal surface of the wall directly opposite to the other suture; the second suture cannot be traced onto the external surface of the bone. This suggests that in both species the rostrum comprises two bones which together form a hollow cylinder. It seems evident from the structure of these rostra, that neither P. minor nor P. stebbingi belong to the genus Protosphyraena nor to the family Pachycormidae.

Finally, the validity of P. keepingi must be considered. All that is known of this species is an isolated solid cone of bone, without paramedial teeth, and with no distinctive ornamentation. Comparison with other protosphyraenas suggests that it does belong to a member of that genus but it is quite impossible to determine, from the limited evidence available, whether or not it is distinct at the species level. The evidence for the establishment of this species seems insufficient for it to be continued.

At least thirteen species based on fragmentary North American specimens have been attributed to the genus *Protophyraena*. Woodward (1893) described only two of these, *P. nitida* and *P. penetrans* [= *P. nitida*] (Hay, 1903), and very briefly mentioned several others, but Hay (1903) reviewed all of this North American material and reduced the number of species to the following: *P. nitida* (Cope) 1872; *P. gladius* (Cope) 1873; *P. perniciosa* (Cope) 1874; *P. ziphioides* (Cope) 1877; *P. dimidiata* (Cope) 1878; *P. recurvirostris* Stewart, 1898; *P. bentonia* Stewart, 1898; *P. gigas* Stewart, 1899; *P. occidentalis* Stewart, 1898; *P. tenuis* Loomis, 1900; and added a new species *P. sequax.* Of these species *P. nitida* has already been discussed; *P. dimidiata* and *P. tenuis* appear to be valid species; *P. recurvirostris* is indistinguishable from the type species and is to be regarded as a junior synonym of *P. ferox*. The remaining seven species, *P. gladius*, *P. perniciosa*, *P. ziphioides*, *P. bentonia*, *P. gigas*, *P. occidentalis* and *P. sequax*, are based on such fragmentary material that their specific distinctness is highly questionable and these specimens are therefore included within the genus *Protosphyraena incertae sedis* as to species.

In 1895 Woodward included two other genera, Prosauropsis and Asthenocormus, within this family. Prosauropsis, with its single species P. elongatus, was established by Sauvage in 1894. According to Sauvage it differs from the genus Sauropsis only in the non-extension of its anal fin. Recently, when reviewing this genus, Wenz (1968) noted that the type material had been lost, and that all the other specimens attributed to this species were really distorted members of the genus Pachycormus. All that remains, therefore, of Prosauropsis elongatus is the original description and figure by Sauvage. Wenz concluded that that material provides sufficient evidence for the genus to be maintained. However examination of Sauvage's figure (Plate I) shows that the most posterior anal fin-ray illustrated is much longer than would be expected if the fin did, in fact, end at this level, and that the ventral body wall is incomplete behind that fin-ray. Since the non-extension of the anal fin(the sole character separating this genus from the genus Sauropsis) cannot be established beyond doubt, and because there is no longer any material available to settle the point, the genus Prosauropsis must be considered of doubtful authenticity, and it is proposed to include its single species in the genus Sauropsis. As the specimen illustrated by Sauvage is incomplete - the pre-orbital region is missing - it is not possible to decide whether the species formerly known as *Prosauropsis elongatus* should be retained as a distinct species of *Sauropsis* or should be attributed within the genus *Sauropsis*, *incertae sedis* as to species.

At the time of Woodward's Catalogue the genus *Asthenocormus* contained only one species, *A. titanius*, but Eastman (1914) added a second species, *A. retrodorsalis*. The type species is known only from descriptions and rather poor illustrations (Quenstedt, 1852; Wagner, 1863; Vetter, 1881) the holotypes having been lost during the Second World war. According to Woodward the genus *Asthenocormus* differs from the genus *Sauropsis* in two main features:- the absence of pelvic fins, and in the position of the median fins. However, Eastman (1914) remarked that although there was no trace of pelvic fins on the type specimen yet "there is reason to believe that the latter organs were present" - as they are in *A. retrodorsalis* (Eastman, 1914, fig . 6). Woodward states that in *Asthenocormus* the dorsal fin is in advance of the anal but it is not clear if that fin is wholly in advance as in *Pachycormus*, or only partly as in *Sauropsis* and *Hypsocormus*. As there is no recorded material of *A. titanius* in existence it is no longer possible to investigate these differences.

A. retrodorsalis Eastman (1914) has the dorsal fin posterior to the origin of the anal fin and possesses pelvic fins. It therefore differs in two important points from the diagnosis of the genus given by Woodward (1895), and in fact appears to be almost identical with *Euthynotus incognitus* the only other pachycormid where the origin of the dorsal fin lies posterior to that of the anal, and therefore it is transferred to the genus *Euthynotus*.

Asthenocormus therefore no longer exists as a separate genus

Woodward (1895) suggested that the genus *Leedsichthys* be included in this family in the hope that the discovery of more complete examples of the species would vindicate this judgement. However, no such discoveries have been made, and all that is known of this fish are a number of huge hyomandibulars, incomplete quadrates, and a series of bones which may be either disassociated gill arches or fin-ray supports. As these isolated fragments give no clue as to the affinities of the genus, and show none of the characteristic features of pachycormids, the genus *Leedsichthys*, with its single species *L. problematicus*, should be removed from the family.

In 1923 Gregory established the genus *Eugnathides* with a single species *E. browni* from the Jurassic of Western Cuba. The unique type specimen consists of a badly crushed, incomplete skull. Gregory fails to put forward any convincing reason for attributing this species to the Pachycormidae, and his brief description and figure fail to provide one. This genus must therefore be listed as *incertae sedis* as to family.

In 1930 Weitzel established a new genus, *Orthocormus* with the single species *O. cornutus*. This is undoubtedly a *Protosphyraena*. Unfortunately it has not been possible to examine the specimen and from his descriptions and figures (Weitzel, 1930) one cannot tell if it is a distinct species or conspecific with one of the other short-snouted protosphyraenas. Weitzel's species is of Kimmeridgian age and the only other Jurassic protosphyraenas known, *P. tenuirostris* and *P. leedsi*, both incidentally short-snouted, are of Oxfordian age. In view of this slight difference in horizon *P. cornutus* (Weitzel) is retained as a separate, but undefined species pending further investigations.

Finally, in 1953, Hauff founded the genus *Ohmdenia* with the single species

O. multidentata, and referred it to the Pachycormidae. Hauff's illustration of the type specimen shows it to be poorly preserved. In the head region, only the lower jaw can be distinguished with any clarity, the other dermal bones are indistinguishable, and there is no sign of the rostro-dermethmoid or of the neurocranium. A portion of the pectoral fin can be seen and also part of the caudal fin; Hauff's reconstruction of the former shows the typical pachycormid mode of branching but his reconstruction of the tail fin is completely unlike that of any pachycormid. There seems to be no real evidence in favour of retaining this species within the Pachycormidae.

Table 2 illustrates the changes in the composition of the family Pachycormidae resulting from this review.

Table 2 Revised classification of the family Pachycormidae

Genus *Pachycormus* Agassiz, 1833

P. macropterus (Blainville) 1818

P. curtus Agassiz, 1832

"Species" *incertae sedis*

P. intermedius (Agassiz) 1844

Genus *Saurostomus* Agassiz, 1833

S. esocinus Agassiz, 1833

Genus *Sauropsis* Agassiz, 1832

S. latus Agassiz, 1832

S. longimanus Agassiz, 1833

S. milloti (Sauvage) 1891

S. veruinalis White, 1925

"Species" *incertae sedis*

S. specious (Wagner) 1860

S. elongatus (Sauvage) 1894

Genus *Euthynotus* Wagner, 1860

E. incognitus (Blainville) 1818

E. retrodorsalis (Eastman) 1914

Genus *Hypsocormus* Wagner, 1860

H. insignis Wagner, 1860

H. macrodon (Wagner) 1858

Genus *Protosphyraena* Leidy, 1857

P. ferox Leidy, 1857

P. compressirostris Woodward, 1895

P. woodwardi *Nomen novum*

P. nitida (Cope) 1872

P. depressa Woodward, 1895

P. brevirostris Woodward, 1895

P. tenuirostris (Woodward) 1889

P. obtusirostris sp. nov.
P. leedsi (Woodward) 1889
P. dimidiata (Cope) 1878
P. tenuis Loomis, 1900
P. cornutus (Weitzel) 1930

"Species" incertae sedis

- P. gladius (Cope) 1873
- P. perniciosa (Cope) 1874
- P. gigas Stewart, 1899
- P. bentonia Stewart, 1898
- P. occidentalis Stewart, 1898
- P. ziphioides (Cope) 1877
- P. keepingi Woodward, 1895
- P. sequax Hay, 1903

Genus incertae sedis

- Asthenocormus titanius (Wagner) 1863
- Sauropsis ?woodwardi Gregory, 1923
- Hypsocormus combesi Sauvage, 1902
- Hypsocormus beaugrandi Sauvage, 1905

Family incertae sedis

- Eugnathides browni Gregory, 1923
- Ohmdenia multidentata Hauff, 1953
- Leedsichthys problematicus (Woodward) 1889

(c) Revised classification of the family Pachycormidae

Division Halecostomi

Subdivision Teleostei

Family Pachycormidae Woodward 1895

Diagnosis of family

Shape deeply fusiform to moderately elongate. Premaxillae small, mobile and separated in the mid-line by tooth-bearing lateral-dermethmoids which are fused to the rostral. Rostro-dermethmoid may or may not be produced anterior to the symphysis of the lower jaw. Nasals separated. Supraorbitals absent; dorsal margin of orbit formed by the dermosphenotic; posterior margin of orbit formed by at least nine rectangular infraorbitals, which meet the two large suborbitals posteriorly. Extrascapular absent; dermopterotic enlarged and containing the supra-temporal commissural sensory canal. Ossification of the notochordal sheath either absent or in the form of hemichordacentra. Pectoral fins scythe-like; pectoral propterygium fused with the first dermal fin-ray; dermal fin-rays branching only near their extreme ends. Pelvic fins reduced or absent. Caudal fin deeply forked; ural neural arches modified as uroneurals. Squamation of numerous, small, thin, rhombic scales. Type genus Pachycormus Agassiz.

Genus Pachycormus Agassiz, 1833

Diagnosis

Trunk deeply fusiform. Rostro-dermethmoid not produced anterior to symphysis of lower jaw; dermal skull roof raised posteriorly into a pronounced fronto-parietal boss. Mandible with a single row of marginal teeth. Post-supracleithrum present. Pelvic fins absent; dorsal fin base completely in advance of the anal fin; and anal fin base not extended.

Type species *Elops macropterus* Blainville

Pachycormus macropterus (Blainville), 1818

Synonymy
1818 *Elops macropterus* Blainville : 324
1895 Pachycormus macropterus (Blainville), Woodward:383
1895 Pachycormus acutirostris Agassiz, Woodward:384
1896-7 Pachycormus acutirostris Agassiz, Woodward:165

Type material

Near complete fish in counterpart, Paris 10529-10530.

Other material examined. Several specimens in the BM(NH) and the Moore Collection, Bath.

Horizon and locality. Upper Lias: Britain; North and south France and Würtemberg.

Diagnosis

Pre-orbital region of skull moderately long, forming approximately one-third the length of the head. Opercular bone about twice as long as it is deep; its ventral angle lying in the posterior half of the bone.

Pachycormus curtus Agassiz, 1833

Synonymy
1844 Pachycormus curtus Agassiz : 112
1895 Pachycormus curtus Agassiz, Woodward:385

Type material

Nearly complete fish in a split nodule, BM(NH) P464, P3698.

Other material examined. Several specimens in the BM(NH); and the Moore Collection, Bath.

Horizon and locality. Upper Lias. Britain; North France and Würtemberg

Diagnosis

Pre-orbital region of skull short, forming approximately one-quarter of the length of the head. Opercular bone about twice as long as it is deep; its ventral angle at midlength or in the anterior half of the bone.

Species *incertae sedis*, *P. intermedius* (Agassiz), 1844, for reasons see Section (b) above.

Genus *Saurostomus* Agassiz, 1833.*

Diagnosis

Trunk fusiform. Rostro-dermethmoid much wider than long, and not produced anterior to the symphysis of the lower jaw; dermal skull roof wide, raised posteriorly in a poorly developed fronto-parietal boss. Mandible with small lateral and larger medial teeth. Opercular large, trapezoid in form. Post-supracleithrum present. Pelvic fins absent; dorsal fin base completely in advance of the anal fin; anal fin base not extended.

Type species *S. esocinus* Agassiz

Saurostomus esocinus Agassiz, 1833.

Synonymy

1833	*Saurostomus esocinus* Agassiz: 14
1895	*Pachycormus (Saurostomus) esocinus* (Agassiz), Woodward: 388
1896-7	*Saurostomus esocinus* Agassiz, Woodward: 158
1968	*Saurostomus esocinus* Agassiz, Wenz: 137

Type material

Dentary, whereabouts unknown.

Other material examined. Several specimens in the BM(NH); the Moore Collection, Bath and Paris.

Horizon and locality. Upper Lias. Britain; France; Baden and Würtemberg

Diagnosis

As for genus, only species.

Genus Sauropsis Agassiz, 1832

Diagnosis

Trunk elongate. Rostro-dermethmoid not produced anterior to symphysis of lower jaw; dermal skull roof without fronto-parietal boss. Mandible with small lateral and larger medial teeth. Small pelvic fins present; dorsal and anal fins usually opposed, or dorsal fin slightly in advance; anal fin base extended.

Type species S. latus Agassiz

Sauropsis longimanus Agassiz, 1833

Synonymy
1833 Sauropsis Longimanus Agassiz: 121
1895 Sauropsis longimanus Agassiz, Woodward: 375

1914 Sauropsis depressus Eastman: 412

Type material

Nearly complete fish, Munich 822.

Other material examined. Several specimens in the BM(NH); Munich.

Horizon and locality. Lower Kimmeridgian: Bavaria

Diagnosis

Head length equal to one-quarter of the total body length, and greater than the maximum depth of the body. Pelvic fins arising nearer to pectorals than to anal.

Sauropsis milloti (Sauvage) 1891

Synonymy

1891 Parathrissops milloti Sauvage : 37

1895 Euthynotus milloti (Sauvage): Woodward: 379

Type material

Imperfect fish, whereabouts unknown

Other material

None known

Horizon and Locality

Upper Lias: Yonne, France

Diagnosis

Head length slightly less than a quarter of the total body length and equal to the maximum depth of the body. Distance between pelvic and anal fins twice as great as that between pelvics and pectorals.

Sauropsis veruinalis White, 1925

Synonymy

1925 Sauropsis veruinalis White: 606

Type material

Nearly complete fish, BM(NH) P13007

Other material

None known

Horizon and locality

Upper Lias: Holzmaden, Würtemberg

Diagnosis

Head length one quarter of the total body length and greatly exceeding the maximum depth of the body. Pelvic fins rather nearer to the pectoral fins than to the anal fin.

Sauropsis latus Agassiz, 1832

Synonymy
1832 Sauropsis latus Agassiz : 142
1895 Sauropsis latus Agassiz, Woodward:376

Type material

Nearly complete fish, whereabouts unknown.

Other material examined.

Specimens in the BM(NH).

Horizon and locality. Upper Lias : Würtemberg and Baden

Diagnosis

Head length equal to one-quarter of the total body length, but less than the maximum depth of the body. Pelvic fins arising nearer to anal fin than to pectorals.

Species incertae sedis

S. speciocus (Wagner), 1860

S. elongatus (Sauvage), 1894, for reasons see section (b) above.

Genus Euthynotus Wagner, 1860

Diagnosis

Trunk slender, elongate; head length equal to one-fifth of the total body length, and greater than the maximum depth of the body. Rostro-dermethmoid not produced anterior to the symphysis of the lower jaw; dermal skull roof without fronto-parietal boss. Mandible with small lateral and larger medial teeth. Pelvic fins small, nearer to pectorals than to anal; dorsal fin arises opposite the middle part of anal fin; anal fin base extended.

Type species Esox incognitus Blainville

Euthynotus incognitus (Blainville) 1818

Synonymy

1818 Esox incognitus Blainville : 325

1895 Euthynotus incognitus (Blainville); Woodward: 377

Type material

Nearly complete fish, Paris 10537

Other material examined. A specimen in

BM(NH)

Horizon and locality

Upper Lias: Würtemberg

Diagnosis

As for genus

Euthynotus retrodorsalis (Eastman) 1914

Synonymy

1914 Asthenocormus retrodorsalis Eastman : 417

Type and only material

Imperfect fish, Carnegie Museum 4863

Horizon and locality

Lithographic limestone: Kelheim, Bavaria

Diagnosis

It is impossible to give a diagnosis of this species. It appears to be identical to E. incognitus, but in view of the difference in horizon it is provisionally retained pending further investigations.

Genus Hypsocormus Wagner, 1860

Diagnosis

Trunk fusiform to moderately elongate. Rostro-dermethmoid, with a row of marginal teeth and a pair of paramedial teeth, not produced anterior to symphysis of lower jaw. Dermal skull roof inclined at steep angle to the horizontal, and developed posteriorly into a pronounced fronto-parietal boss. Mandible with small lateral and larger medial teeth. Small pelvic fins present; dorsal and anal fins opposed, or dorsal slightly in advance of anal; anal fin base extended. Type species H. insignis Wagner

Hypsocormus insignis Wagner, 1860

Synonymy

1860 Hypsocormus insignis Wagner:221
1895 Hypsocormus insignis Wagner, Woodward:391

Type material

An imperfect fish, Munich, labelled but unregistered.

Other material examined. Specimens in the

BM(NH).

Horizon and locality. Middle Kimmeridgian. Bavaria

Diagnosis

Trunk deeply fusiform. Head length equal to one-quarter of the total length of the body, but less than its maximum depth. Paramedial teeth not protruding out of the mouth. Pelvic fins nearer pectorals than to anal.

Hypsocormus macrodon (Wagner), 1858

Synonymy

1858 *Eugnathus macrodon* Wagner: 471
1895 *Hypsocormus macrodon* (Wagner), Woodward: 394

Type material

Nearly complete fish, Munich. Lost during World War II.

Other material examined. Specimens in the

BM(NH).

Horizon and locality. Middle Kimmeridgian. Bavaria and Würtemberg

Diagnosis

Trunk moderately elongate. Head length equal to one-fifth total body length, and less than its maximum depth. Paramedial teeth well developed, but not protruding out of the mouth.

Genus *Protosphyraena* Leidy, 1857

Diagnosis

Trunk unknown. Rostro-dermethmoid with either a row of marginal teeth and a pair of paramedial teeth, or with paramedial teeth only; rostro-dermethmoid always produced anterior to symphysis of lower jaw. Dermal skull roof inclined at a low angle to the horizontal, fronto-parietal boss poorly developed. Mandible with small lateral and larger medial teeth; anterior teeth on dentary procumbent, and anterior coronoid plate inflated. Distal ends of pectoral fin-rays fused to form characteristic 'zig-zag' structure at posterior margin of fin.

Type species P. ferox Leidy

Protosphyraena ferox Leidy, 1857

Synonymy
1857 Protosphyraena ferox Leidy: 95
1895 Protosphyraena ferox Leidy, Woodward: 400
1898 Protosphyraena recurvirostris Stewart:

Type material

Isolated rostrum, BM(NH), P5630.

Other material examined. Specimens in the B.M.(N.H) and the Sedgwick Museum, Cambridge.

Horizon and locality. Senonian, Turonian, and Cenomanian: S.E. England

Diagnosis

Extremely long rostro-dermethmoid, circular in cross-section throughout its length, except within a short distance of paramedial teeth where it develops flattened surfaces dorsally and dorso-laterally. Paramedial teeth small, laterally compressed, and posteriorly-directed; marginal teeth absent from rostro-dermethmoid.

Protosphyraena compressirostris Woodward, 1895

Synonymy

1895 Protosphyraena compressirostris Woodward, Woodward: 405

Type material

Isolated rostrum, BM(NH), P5631.

Other material examined. Specimens in the B.M.(N.H.) and the Sedgwick Museum, Cambridge.

Horizon and locality. Senonian : Kent, England.

Diagnosis

Extremely long rostro-dermethmoid, laterally compressed in its proximal half so that it is oval in section. Paramedial teeth small, laterally compressed, and posteriorly-directed; marginal teeth absent from rostro-dermethmoid.

Protosphyraena woodwardi nomen novum

Synonymy

1895(a)	*Protosphyraena tenuirostris* Woodward:211
1895	*Protosphyraena tenuirostris* Woodward, Woodward:407
1889	[non] *Protosphyraena tenuirostris* (Woodward):451

Type material

Isolated rostrum, Sedgwick Museum, Cambridge

Other material examined. Specimens in the BM(NH).

Horizon and locality. Cenomanian. Cambridgeshire, England; Kursk, Russia

Diagnosis

Extremely long rostro-dermethmoid, cylindrical throughout its length, but somewhat flexed upwards shortly in front of paramedial teeth. Paramedial teeth very small, laterally compressed, and posteriorly-directed; marginal teeth absent from rostro-dermethmoid.

Protosphyraena nitida (Cope) 1872

Synonymy

1872 Erisichthe nitida Cope : 280

1875 Pelecopterus chirurgus Cope : 244E, 273

1877 Erisichthe penetrans Cope : 822

1878 Protosphyraena penetrans (Cope); Newton: 795

1895 Protosphyraena nitida (Cope); Woodward : 409

1900 Protosphyraena obliquidens Loomis : 225

1902 Protosphyraena chirurgus (Cope); Hay : 379

1903 Protosphyraena nitida (Cope); Hay : 3

Type material

AMNH No. 2105

Other material examined. Specimens in the BM(NH) and Munich

Horizon and locality

Upper Cretaceous (Niobrara group): Kansas, USA

Diagnosis

Extremely long rostro-dermethmoid, slightly recurved; anterior cross section semi-circular, with a strong angle limiting the dorsal surface; posterior cross section at the base of the rostrum, oval. Paramedial teeth large, laterally compressed, and projecting anteriorly from the mouth; marginal teeth absent from the rostro-dermethmoid.

Protosphyraena depressa Woodward, 1895

Synonymy

1895 Protosphyraena depressa Woodward, Woodward: 408

Type material

Isolated, imperfect rostrum, Sedgwick Museum, Cambridge. B8988.

Other material

None Known

Horizon and locality. Cenomanian: Cambridgeshire, England

Diagnosis

Short rostro-dermethmoid; circular in cross section anteriorly, becoming almost triangular in section at level of paramedial teeth. Paramedial teeth large, laterally compressed and project anteriorly from the mouth; marginal teeth absent from the rostro-dermethmoid.

Protosphyraena brevirostris Woodward, 1895

Synonymy

1895 Protosphyraena brevirostris Woodward, Woodward: 408

Type material

Isolated, imperfect rostrum, BM(NH) P7253.

Other material

None Known

Horizon and locality. Cenomanian: Cambridgeshire, England.

Diagnosis

Extremely short, acutely pointed rostro-dermethmoid, triangular in cross section throughout its length. Paramedial teeth moderately large, laterally compressed and projecting anteriorly from the mouth; marginal teeth absent on rostro-dermethmoid.

Protosphyraena obtusirostris sp. nov.

Synonymy

1936 *Hypsocormus* sp. Holmgren and Stensio:482

1948 *Hypsocormus* sp. Rayner:310

Type material

Incomplete fish, Stockholm P425

Other material

None Known

Horizon and locality. Lithographic stone (Kimmeridgian). Solenhofen.

Diagnosis

Extremely short, acutely pointed rostro-dermethmoid, widening rapidly to meet the lateral ethmoids; a depressed oval in cross section. Paramedial teeth small, laterally compressed, close together, projecting almost vertically downwards from the mouth; a single row of marginal teeth present on rostro-dermethmoid.

Protosphyraena tenuirostris (Woodward), 1889

Synonymy

1895 *Hypsocormus tenuirostris* Woodward, Woodward:396

Type material

Remains of skull, BM(NH), P6916.

Other material examined. Specimens in the BM(NH).

Horizon and locality. Oxfordian: Huntingdonshire, England.

Diagnosis

Extremely short, pointed rostro-dermethmoid, circular in cross section, widening very gradually from its rounded apex towards the lateral ethmoids. Paramedial teeth large, widely separated, rounded in section and projecting antero-ventrally from the mouth; with a single row of marginal teeth present on rostro-dermethmoid.

Protosphyraena leedsi (Woodward), 1889

Synonymy

1889	Hypsocormus Leedsi Woodward: 450
1895	Hypsocormus leedsi Woodward, Woodward: 395

Type material

Remains of a skull, BM(NH) P6913.

Other material examined. Specimens in the BM(NH).

Horizon and locality. Oxfordian. Huntingdonshire, England.

Diagnosis

Rostro-dermethmoid obtusely pointed, the lateral edges of the bone meeting anteriorly almost in a right angle; and extending only fractionally beyond to symphysis of lower jaw. Paramedial teeth widely separated rounded in section and projecting antero-ventrally from the mouth; a single row of marginal teeth present on the rostro-dermethmoid.

Species incertae sedis

P. keepingi Woodward, 1895, (b) above.

Protosphyraena dimidiata (Cope) 1878

Synonymy

1877 Erisichthe nitida Cope: 822

1878 Erisichthe dimidiata Cope : 300

1903 Protosphyraena dimidiata (Cope); Hay : 16

Type material

Rostro-dermethmoid, AMNH 1635

Other material

None known

Horizon and locality

Cretaceous. Kansas, USA

Diagnosis

Extremely long rostro-dermethmoid, greatly recurved, anterior cross section semi-circular, with a strong angle limiting the dorsal surface; posterior section at the base of the rostrum, round. Paramedial teeth laterally compressed, and projecting anteriorly from the mouth; marginal teeth absent from rostro-dermethmoid.

Protosphyraena tenuis Loomis, 1900

Synonymy

1900 Protosphyraena tenuis Loomis : 226

1900 Protosphyraena penetrans Stewart : 370

1903 Protosphyraena tenuis Loomis; Hay : 14

Type material

According to Hay (1903) the type material, consisting of the fragmentary remains of three individuals, was in the museum at Munich but I failed to find it there in 1975.

Other material

Several specimens are reported to be in the collection of AMNH (Hay, 1903).

Horizon and locality

Upper Cretaceous (Niobrara group): Kansas, USA

Diagnosis

Extremely long, slender, rostro-dermethmoid; a depressed oval in section throughout its length.

Protosphyraena cornutus (Weitzel) 1930

Synonymy

1930 *Orthocormus cornutus* Weitzel : 101

Type material

Other material

None known

Horizon and locality

Kimmeridgian: Solenhofen

Diagnosis

It is not possible to give a meaningful diagnosis of this species at this stage (see section (b)).

"Species" *incertae sedis*

- *P. gladius* (Cope) 1873
- *P. perniciosa* (Cope) 1874
- *P. ziphioides* (Cope) 1877
- *P. keepingi* Woodward, 1895
- *P. bentonia* Stewart, 1898
- *P. occidentalis* Stewart, 1898
- *P. gigas* Stewart, 1899
- *P. sequax* Hay, 1903

Genus *incertae sedis*

- *Asthenocormus titanius* (Wagner) 1863
- *Sauropsis ?woodwardi* Gregory, 1923

Hypsocormus combesi Sauvage, 1902

Hypsocormus beaugrandi Sauvage, 1905

Family *incertae sedis*

Eugnathides browni Gregory, 1923

Ohmdenia multidentata Hauff, 1953

Leedsichthys problematicus (Woodward) 1889

THE RELATIONSHIPS AND EVOLUTION OF THE PACHYCORMIDAE

The family Pachycormidae, as defined in the Systematics section above, has six genera: Pachycormus, Saurostomus, Sauropsis, Euthynotus, Hypsocormus and Protosphyraena.

(a) Character states.

The characters of the various genera are listed below. (The following abbreviations are used: Pachycormus - Pa.; Saurostomus - St.; Sauropsis - Sp.; Euthynotus - Eu.; Hypsocormus - Hy.; Protosphyraena - Pr.)

1. Large compound rostro-dermethmoid meeting the frontals posteriorly, and separating the paired premaxillae and nasals. (all)
2. No supraorbitals; dorsal margin of the orbit, formed by the dermosphenotic. (all)
3. At least nine rectangular infraorbitals forming the posterior margin of the orbit, and meeting the two large suborbitals posteriorly. (all)
4. Extrascapulars absent; dermopterotic enlarged and containing the supratemporal commissural sensory canal. (all)
5. Pectoral fins scythe-like; the dermal fin rays branching only at their extreme ends. (all)
6. Ural neural arches modified as uroneurals of a peculiar type. (Pa., St., Sp., Eu., Hy.) Unknown (Pr.).
7. Head length equalling one-fifth of the total body length, and exceeding the maximum depth of the body (Eu.). Unknown (Pr.).
8. Pelvic fins absent (Pa., St.). Unknown (Pr.).
9. Anal fin base not extended (Pa., St.). Unknown (Pr.).

10. Dorsal fin base completely in advance of the anal fin (Pa., St.). Unknown (Pr.).
11. Anal fin base in advance of the dorsal fin which starts opposite the middle part of the anal fin (Eu.). Unknown (Pr.).
12. Mandible with a single row of teeth (Pa.).
13. Fronto-parietal boss present (Pa., St., Hy., Pr.).
14. Opercular bone trapezoidal in shape (St.).
15. Post-supracleithrum present (Pa., St.).
16. Rostro-dermethmoid with marginal teeth and a pair of paramedial teeth (Hy., Pr.).
17. Anterior coronoid plate inflated (Pr.).
18. Rostro-dermethmoid produced forwards beyond the symphysis of the lower jaw (Pr.).
19. Anterior teeth on dentary procumbent (Pr.).
20. Distal ends of pectoral fin rays fused to form a peculiar rigid zig-zag structure (Pr.).

The first five characters are common to all the genera. The sixth character (ural neural arches modified as uroneurals) is shared by five genera, but has not been observed in Protosphyraena, where no complete caudal fin is known. However, the presence in that genus of the enlarged, fan-shaped hypural (2H+n) which occurs in all the other genera, suggests that it also had the accompanying specialisation of the ural neural arches. The sixth character listed above will therefore be considered as occurring in all the genera.

The remaining characters (7 - 20) are found in one or more, but not all, of the genera. (Character 11, the non-extension of the anal fin-base, is possibly a specialization within this family where the fin-base is usually extended.)

(b) Evidence for monophyly

Those derived character states which are particularly relevant to the question of monophyly are listed above as items 1 - 6. These characters are considered to be of equal importance, and the combination is unique to the Pachycormidae.

Characters 1, 5 and 6 were amongst those mentioned by Patterson (1973:273) as demonstrating monophyly in this group.

The rostro-dermethmoid (character 1) is unusual in combining features found separately in the pholidophorids and in the leptolepids. The pachycormids resemble the pholidophorids in having a large rostral component, which is completely traversed by the ethmoid commissure, and by retaining teeth on their lateral-dermethmoids. However, they are similar to the leptolepids in that the lateral-dermethmoids are fused to the rostral component, and do not extend back to meet the lateral ethmoids, and thus do not form the floor of the nasal pit.

The scythe-like shape of the pectoral fins (character 5) has been recognized as a pachycormid specialization almost since the creation of the family.

The uroneurals (character 6) are unusual, as Patterson pointed out in his examination of the structure of the caudal fin. They differ from those of other teleosts in that anteriorly they grade into unmodified pre-ural neural arches, with no clear division between the two types of structures.

An examination of the dermal bones around and dorsal to the orbit make it possible to include the three other characters 2, 3 and 4.

Character 2; only in the pachycormids is the dorsal margin of the orbit formed entirely by the lateral edge of the dermosphenotic. Moreover, the dermosphenotic is both an integral part of the skull roof, and in series with the infraorbitals posteriorly; also, it is independent of the endochondral sphenotic bone.

Character 3; the posterior margin of the orbit is formed by a series of infraorbitals which are more numerous, and more uniform in shape than those of most other groups of actinopterygians.

Character 4; above the orbit, and meeting the dermosphenotic anteriorly, are the large bones which for reasons given in the description of the anatomy of the type species are referred to as dermopterotics and whose dorsal limbs have replaced the extrascapulars.

The sharing of these six characters by all the genera shows without doubt, that the pachycormids are a monophyletic group.

(c) Relationships within the Pachycormidae

The results of a simple form of numerical analysis (Griffith, 1977:84) of the derived characters listed above are given in Tables 3 and 4.

Table 3 merely gives, for each genus, the total number of derived characters known to be present, the number of these unique to that genus and the number of characters of which the condition is unknown. From this Sauropsis appears to be the least specialized member of the family, closely followed by Euthynotus and Hypsocormus. Pachycormus,

Table 3 Distribution of derived characters in the Pachycormidae

Genus	Total number of derived characters	Total number of unique characters	Unknown characters
Pachycormus	12	1	0
Saurostomus	12	1	0
Sauropsis	6	0	0
Euthynotus	8	2	0
Hypsocormus	8	0	0
Protosphyraena	12	4	5

Saurostomus and Protosphyraena all have the same number of derived characters, but whilst the first two have no characters whose conditions are unknown, Protosphyraena has five. Thus the genus Protosphyraena could prove to be the most specialized of the pachycormids.

Table 4 is based on a formula devised to give a numerical indication of the degree of the similarity, and presumably also of relationship, of the genera; the higher the score, the closer the implied relationship. The formula used is $2C/(A+B)X100$, where C = the number of derived characters in common, and $A+B$ = the number of derived characters shown respectively by each member of the pair (Griffith, 1977). Of course, such a simple numerical approach, where all characters are given equal weight, has obvious limitations. Moreover, Griffith has pointed out that in these calculations an unknown character may be one of three things: either primitive, or specialized and like the other member of the pair, or specialized and unlike the other member of the pair. Within the Pachycormidae, character states are unknown only in Protosphyraena. In Table 4 the figures in brackets give the highest possible and lowest possible hypothetical scores for each pair of genera assuming respectively the most and least favourable states of the unknown characters. Thus, by this method Pachycormus and Saurostomus (score = 92) appear to be more closely related to each other than either is to any other genus. (The next highest score involving Pachycormus or Saurostomus is that where each was paired with Sauropsis.) Both Hypsocormus and Euthynotus appear equally related to Sauropsis (scores = 86 each), but those two genera appear less closely related to each other (score = 75) perhaps suggesting that both evolved separately from Sauropsis. Finally, Protosphyraena seems more closely related to Hypsocormus

Table 4 Similarity between pairs of genera in the Pachycormidae

Pairs of genera	Real Score	Hypothetical highest + lowest possible score where different from real score	Number unknown involved
Pachycormus/Saurostomus	92	-	0
Sauropsis/Euthynotus	86	-	0
Sauropsis/Hypsocormus	86	-	0
Hypsocormus/Protosphyraena	80	(80-64)	5
Euthynotus/Hypsocormus	75	-	0
Sauropsis/Protosphyraena	67	(67-52)	5
Pachycormus/Sauropsis	67	-	0
Saurostomus/Sauropsis	67	-	0
Saurostomus/Hypsocormus	60	-	0
Pachycormus/Hypsocormus	60	-	0
Saurostomus/Euthynotus	60	-	0
Pachycormus/Euthynotus	60	-	0
Euthynotus/Protosphyraena	60	(64-48)	5
Pachycormus/Protosphyraena	58	(68-48)	5
Saurostomus/Protosphyraena	58	(68-48)	5

Figure 30. Cladogram showing relationships of the genera within the Pachycormidae.

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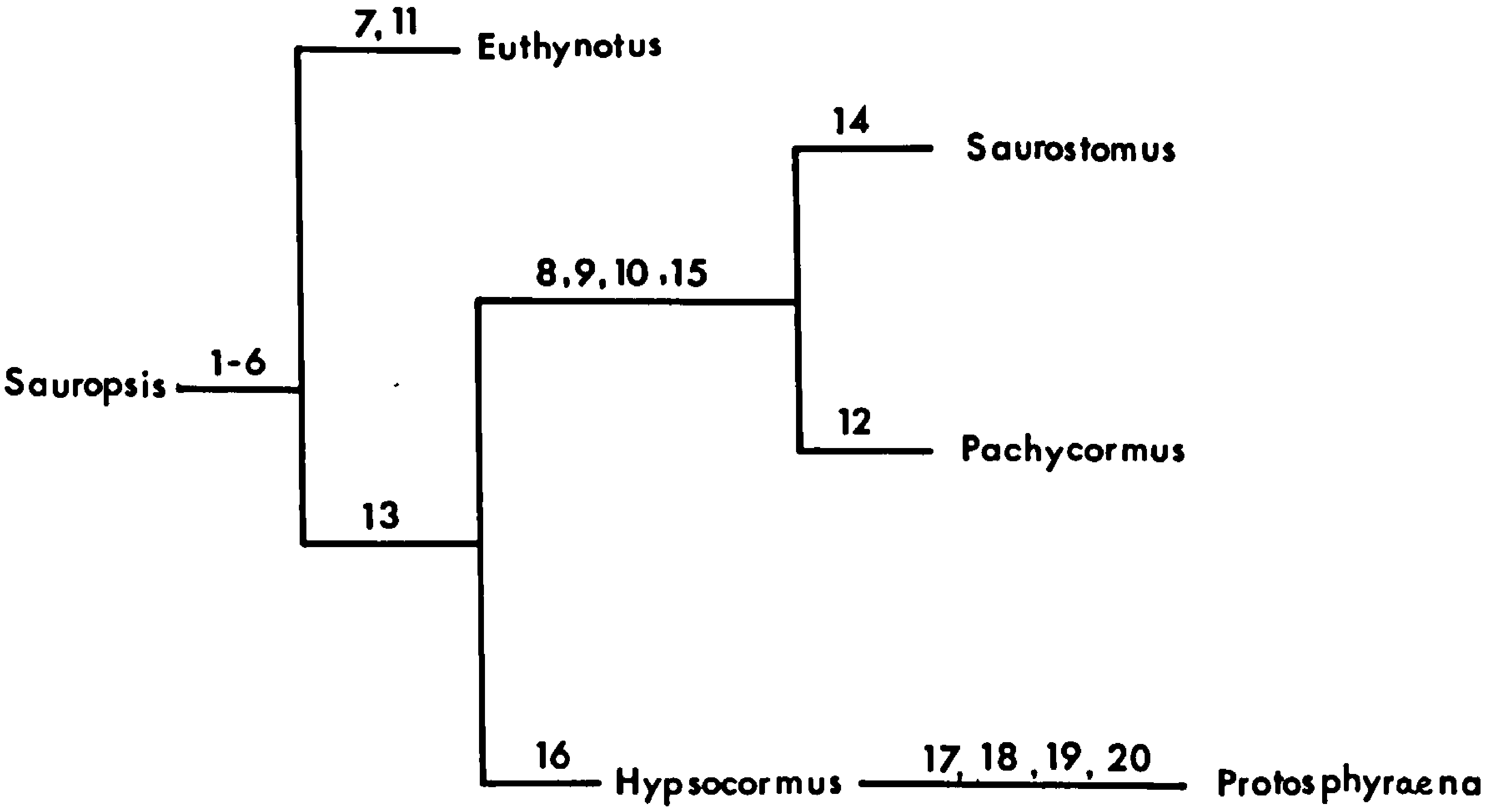

7, 11
Euthynotus
14
Saurostomus
8, 9, 10, 15
Sauropsis
1-6
12
Pachycormus
13
16
Hypsocormus
17, 18, 19, 20
Protosphyraena

than to any other genus. The genus Sauropsis possesses no derived characters above the basal pachycormid level and appears to be a paraphyletic group which gave rise independently to Euthynotus on the one hand, and the rest of the pachycormids on the other. Amongst this larger group Hypsocormus is the least specialized, sharing character 13 with the other three genera, and character 16 with Protosphyraena. Hypsocormus has no unique specializations of its own, and must be regarded as a second paraphyletic genus from which the protosphyraenas developed. Pachycormus and Saurostomus share four specializations separating them from Hypsocormus and Protosphyraena, and as such appear to be the most closely related genera in the family. Each of these genera is separated from the other by a single unique character. This view of the relationships is in agreement with numerical assessment outlined above.

(d) The relationships of the Pachycormidae to other groups

When Patterson reviewed the interrelationships of the Holosteans in 1973 he re-organized and characterised the major divisions within the Actinopterygii. On the basis of this new classification Patterson showed that the pachycormids possess the following neopterygian characters:

1. Body lobe of tail reduced so that outer principal rays of upper lobe of caudal fin are approximately equal in length to those of lower lobe.
2. Premaxilla with an internal (nasal) process lining the anterior part of the nasal pit.
3. Fin-rays equal in number to their endoskeletal supports in dorsal and anal fins.

4. Vomers differentiated and moulded to the underside of ethmoid region.
5. Articular with a coronoid process.
6. Suspensorium vertical or nearly so, preopercular with a narrow dorsal limb.
7. Symplectic developed as an outgrowth of the hyomandibular cartilage.
8. Clavicles lost or reduced to one or more plates overlying the post-branchial lamina of the cleithrum.

At that time it was not known if the upper pharyngeal dentition was consolidated or not (Patterson's last neopterygian character). Evidence from this study suggests that it was not.

Patterson then stated that the pachycormids showed the following halecostome characteristics:

1. Median neural spines present, at least in the caudal region.
2. Maxilla mobile, free from the cheek, with a peg-like internal head.
3. A single supramaxilla.
4. Interopercular present.
5. A large post-temporal fossa, without an endoskeletal roof, occupied by trunk musculature.
6. Quadratojugal lost as an independent element.
7. Epibranchials with uncinate processes at their upper ends.

In addition to these characters it is now known that the posterior myodome does occupy at least half the distance between the pituitary fossa and the vagus foramen (ie. positive for Patterson's fifth character) and also that the intercalars do lack membrane bone outgrowths onto the surface of the otic region (ie. negative for Patterson's seventh character). Both these conditions were predicted by Patterson. Patterson showed that the Pachycormidae possessed none of the derived characters of the Subdivision Haleeomorphi, thus removing the family from the "Holostei", where so many researchers (Rayner, 1941, 1948; Gardiner, 1967; Wenz, 1968) had placed it.

Patterson identified the following teleostean derived characters in the Pachycormidae:

1. Ural neural arches modified as uroneurals.
2. Premaxilla divided into a lateral mobile, toothed portion and a lateral dermethmoid (medial) which is incorporated into the ethmoid.
3. Quadratojugal fused with the quadrate as a postero-dorsal process, symplectic a spike-like bone ending blindly in a groove on the inner face of the quadrate. Patterson qualified this character in <u>Pachycormus</u>, saying that there was no distinct postero-dorsal process as seen in the pholidophorids, but that the posterior edge of the quadrate was thickened in such a way as to suggest that the quadratojugal had fused with the quadrate. However, P10146 and 32432 both show a quadratojugal of the pholidophorid kind, and both have the symplectic ending on the inner surface of the quadrate, and therefore taking no part in the articulation of the lower jaw.
4. Vertebral centra in the form of hemichordacentra.

On this evidence Patterson concluded that the Pachycormidae were teleosts and that they appeared to be the sister-group of all the other teleosts.

Patterson re-affirmed that statement of relationships in 1977 in his paper 'The contribution of palaeontology to teleostean phylogeny'. There, he constructed a momumental series of 52 derived character states, upon the progressive accumulation of which his system of teleostean evolution depends. A cladogram illustrates his scheme (Patterson, 1977:fig. 19). Only the first eleven of his derived character states (listed below) and the corresponding first six divisions on his cladogram (Fig. 31) need be referred to. Note that in Patterson's list the derived condition of each character is given first.

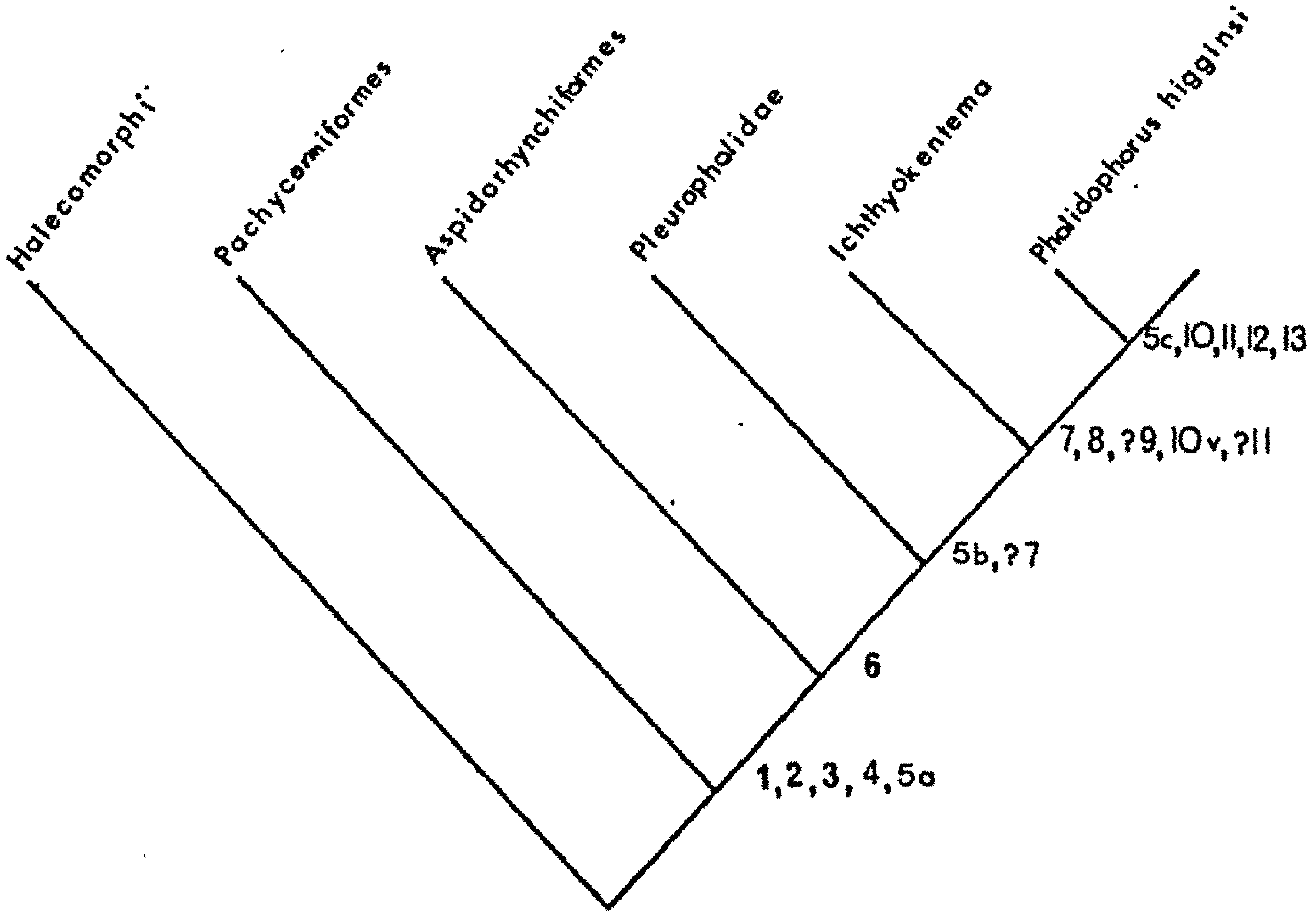
1. Ural neural arches modified as uroneurals, vs. unmodified.
2. Small, mobile premaxilla, lying lateral to rostral, vs. fixed premaxilla, lying beneath rostral.
3. Internal carotid foramen enclosed in parasphenoid, vs. a notch in margin of parasphenoid.
4. Pectoral propterygium fused with first pectoral fin-ray, vs. propterygium free.

5a. Epurals seven, vs. eight or more; 5b. epurals six, vs. seven; 5c. epurals five, vs. six; 5d. euprals four, vs. five; 5e. epurals three, vs. four.

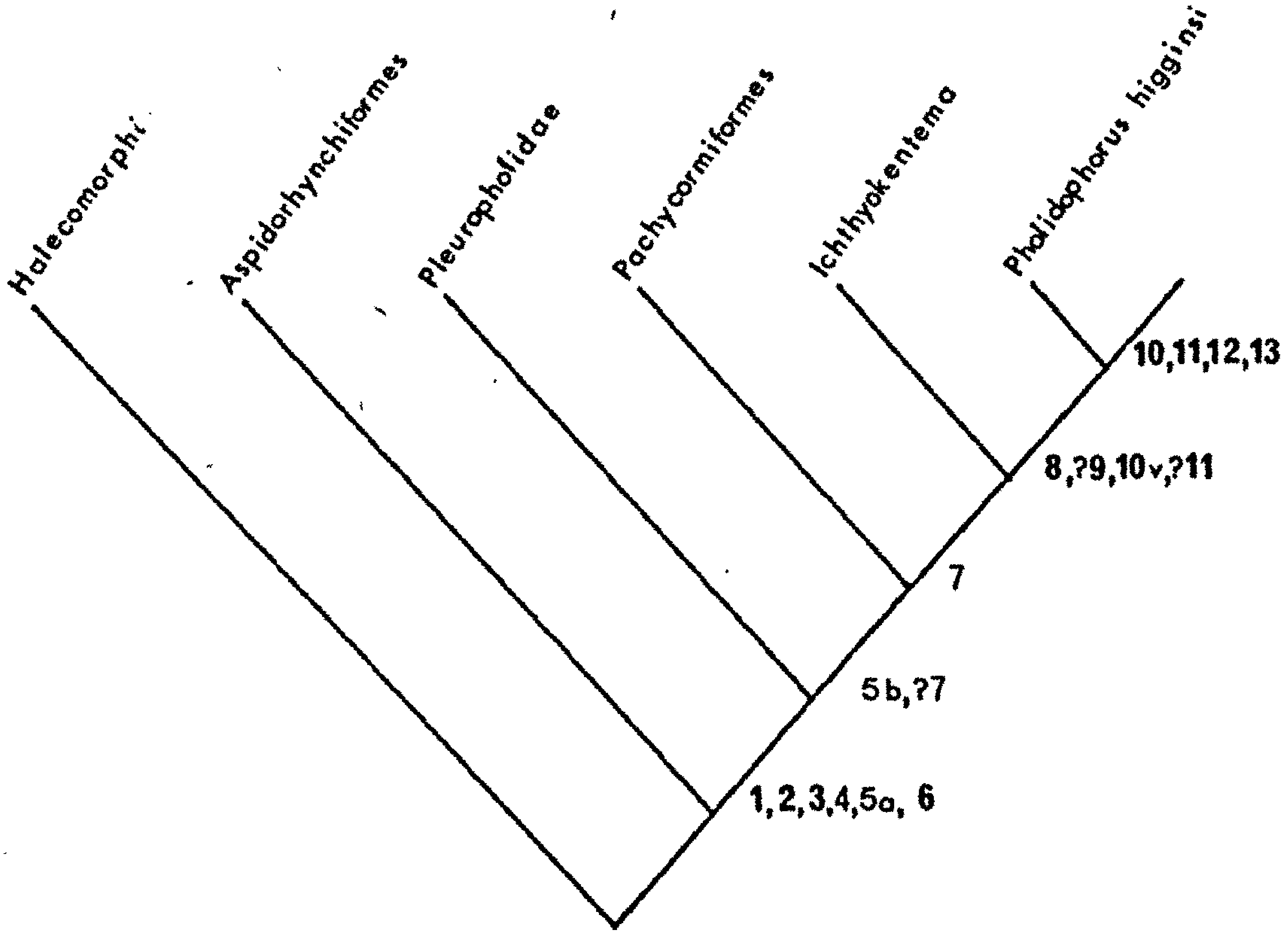
6. A median tooth-plate covers basibranchials 1-3 vs. smaller asymmetrical or paired toothplates
7. Quadratojugal fused with quadrate as a postero-dorsal process, enclosing a groove for the symplectic, vs. quadratojugal free or not recognisable.
8. A median, unpaired vomer, vs. paired vomers.
9. A median, basihyal tooth-plate, vs. tooth-plate paired or not recognisable.

Figure 31. Cladogram of the first six divisions of Patterson's (1977:262, fig. 19) cladogram showing a theory of relationships of certain fossil teleosts.

Figure 32. Cladogram showing the proposed relationships of the Pachycormidae to certain fossil teleosts.


Halecomorphi
Pachycormiformes
Aspidorhynchiformes
Pleurophalidae
Ichthyokentema
Pholidophorus higginsi
5c,10,11,12,13
7,8,?9,10v,?11
5b,?7
6
1,2,3,4,5a

32


Halecomorphi
Aspidorhynchiformes
Pleurophalidae
Pachycormiformes
Ichthyokentema
Pholidophorus higginsi
10,11,12,13
8,?9,10v,?11
7
5b,?7
1,2,3,4,5a, 6

10. Foramen of efferent pseudobranchial artery enclosed in parasphenoid vs. a notch in margin of parasphenoid.
11. A median (endoskeletal) supraethmoid ossification present, vs. ethmoid cartilage ossified in one piece, or from paired centres.

Patterson states that "numbers in heavy type in the figure indicate that the derived character-state is known in the taxon to the left at that dichotomy, and that the corresponding primitive character-state has been observed in at least one member (specimen) of the fossil taxon to the left at the next lower dichotomy. It does not follow that the primitive character-state has been observed in all the other fossil taxa at lower dichotomies, or that the derived character-state is known in all fossil taxa at higher dichotomies, but it is predicted that these conditions will be met when the character is investigated in those taxa."

"Numbers entered in light type in the figure indicate that the derived character-state is known in the taxon to the left at that dichotomy, but that the corresponding primitive character state has not been observed in the fossil taxon at the next lowest dichotomy, because the part in question is not yet accessible in the available specimens. Numbers in light type predict that the derived character state will be found in all fossil taxa above that dichotomy, but make no precise prediction about conditions in taxa at lower dichotomies. The numbers in the light type are therefore potentially mobile downwards."

Thus, Patterson established that Pachycormus possessed the following features, which he numbered as follows:

1. Ural neural arches are modified as uroneurals (Patterson, 1973).
2. Small, mobile premaxilla lying lateral to the rostral (Patterson, 1973).
3. Internal carotid foramen enclosed in the parasphenoid (Patterson, 1977).
4. Pectoral propterygium fused with the first pectoral fin-ray (Jessen, 1972).

It has now been established that Pachycormus does not exhibit Patterson's feature 5a and from this study the following three features on Patterson's list can be added:

5b. Six epurals.

6. A median tooth plate covering the basibranchials.

7. A quadratojugal fused with the quadrate as a postero-dorsal process.

From this additional information it will be seen that the Pachycormidae exhibit certain features thought to be associated with slightly more advanced groups. This necessitates the modification of Patterson's cladogram (see Fig. 32).

In the revised cladogram (Fig. 32) the Aspidorhynchiformes have become the sister-group to all other teleosts. The Pleuropholidae, exhibit character 5b and may show character 7; (in Patterson's cladogram a question mark preceeding the number indicates that that derived character-state has been observed in a fossil taxon at that dichotomy, but that the observation is open to question because of inadequacies or contradictions in the material). The Pachycormidae definitely exhibit characters 5b and 7 and are definitely known to show the primitive condition of the derived character-states listed for the taxon above, ie. characters 8, 9, 10 and 11.

On the whole this investigation has supported the conclusions reached previously by Patterson (Patterson, 1973, 1977) but it has been shown that the Pachycormidae can no longer be regarded as the sister-group of all other teleosts. The fact that they possess the derived condition of Patterson's characters 1, 2, 3, 4, 5b, 6 and 7 changes their position in his cladogram so that they lie between the Pleurophoïidae and Ichthyokentema, and as such become the sister-group of Ichthyokentema and all succeeding teleosts.

Plate 1. *Pachycormus macropterus*. Skull roof of 32433.

Plate 2. *Pachycormus macropterus*. Head in lateral view of 32433.

1

2

Plate 3. *Pachycormus macropterus*. Rostro-dermethmoid of 32432 in ventral view showing pre-ethmoid bones.

Plate 4. *Pachycormus curtus*. region of 32430 showing pre-ethmoid bone with vomer.

3

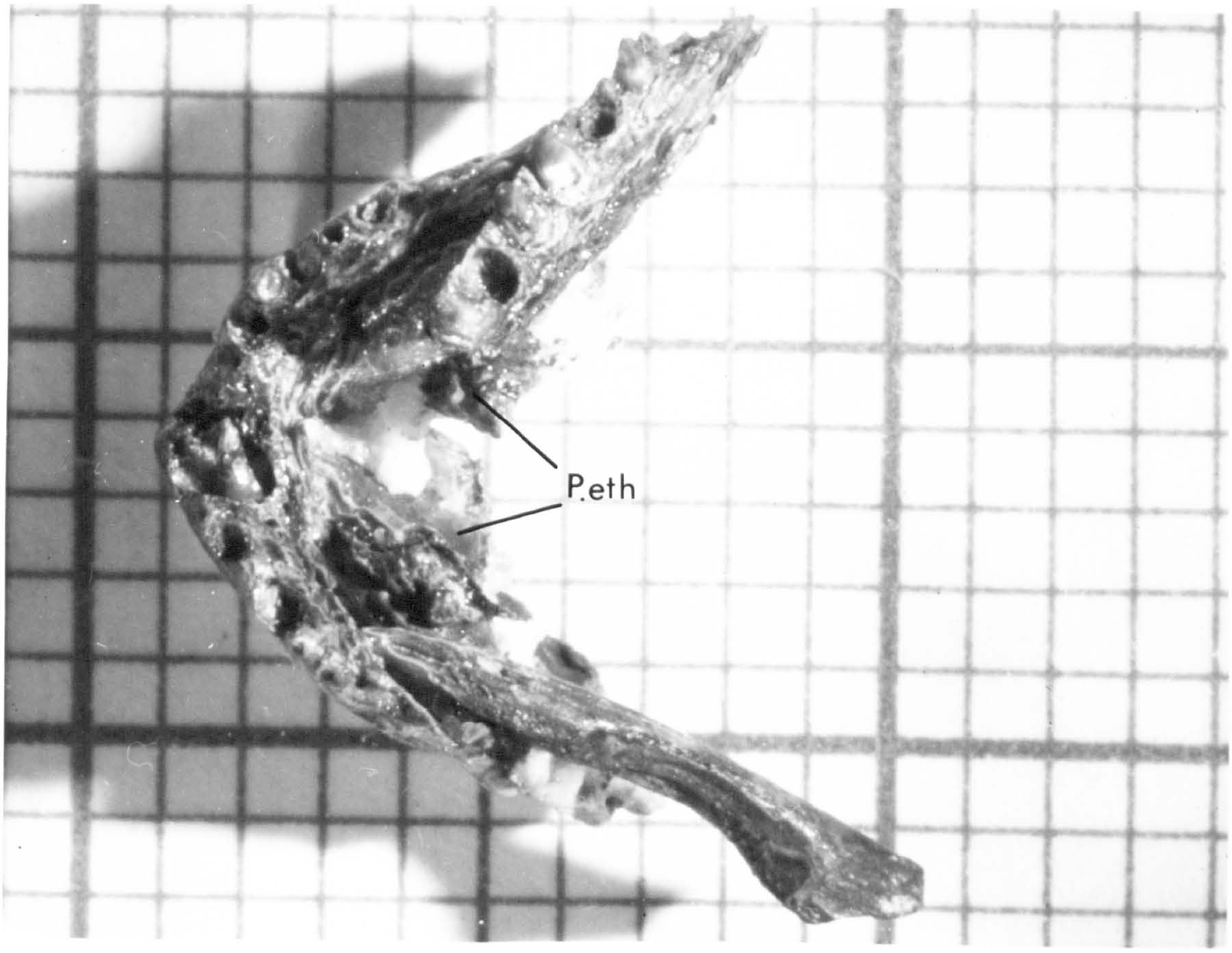


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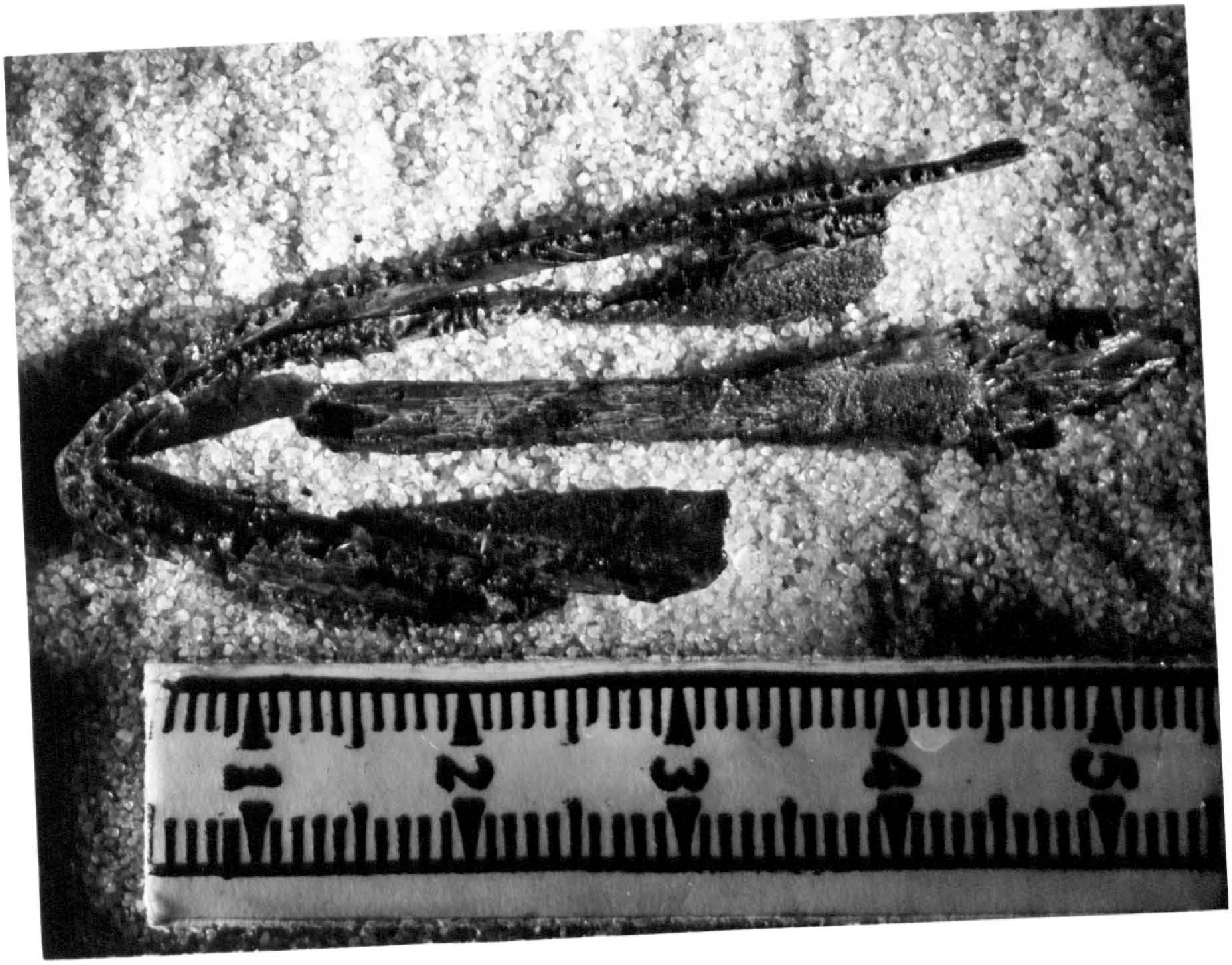
Plate 5. *Pachycormus curtus*. Isolated palatal bones of P10145 arranged in their probable original relationships.

Plate 6. *Pachycormus macropterus*. Disassociated ectopterygoid and dermopalatines of 32432 in dorsal and ventral views.

5



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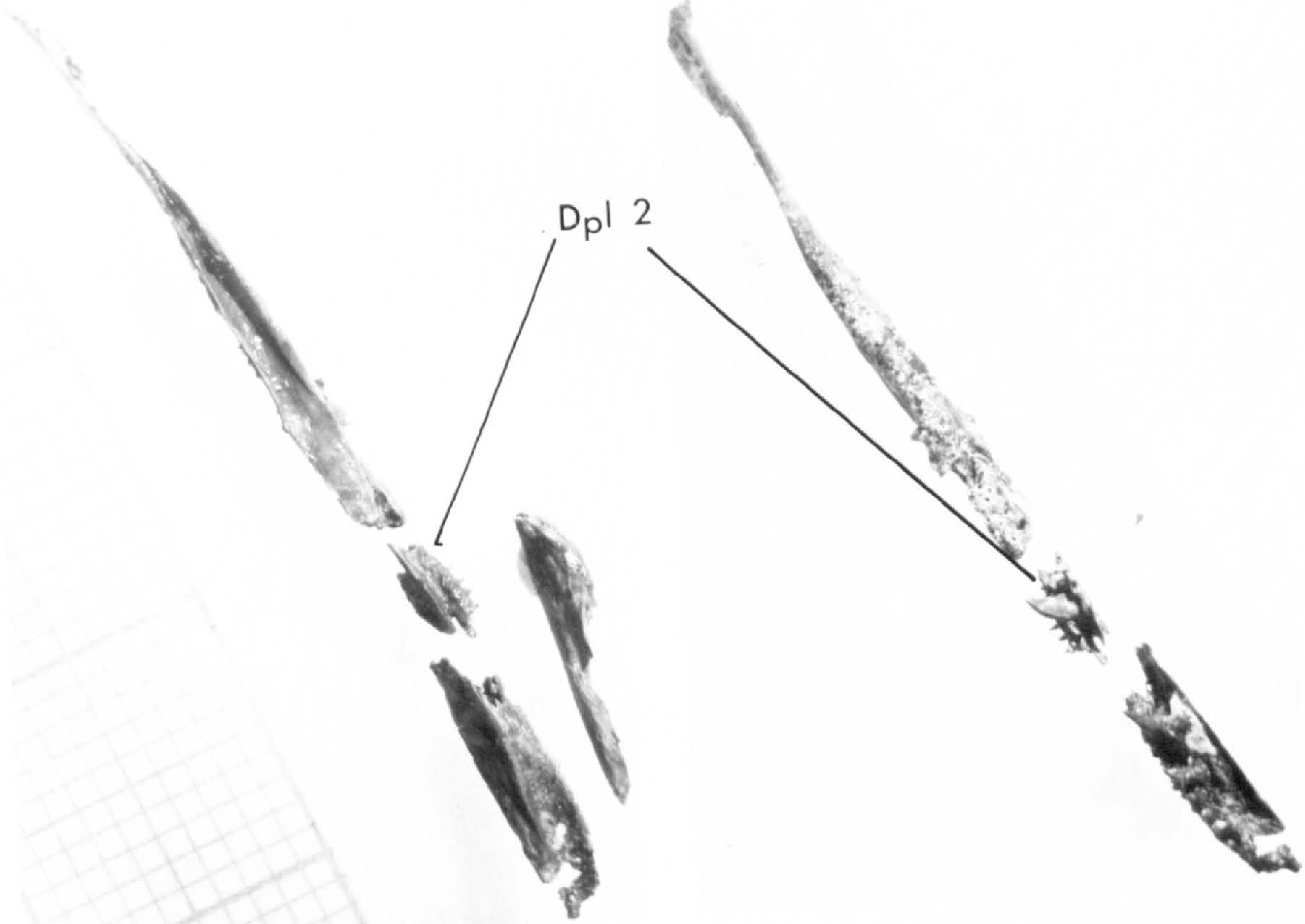
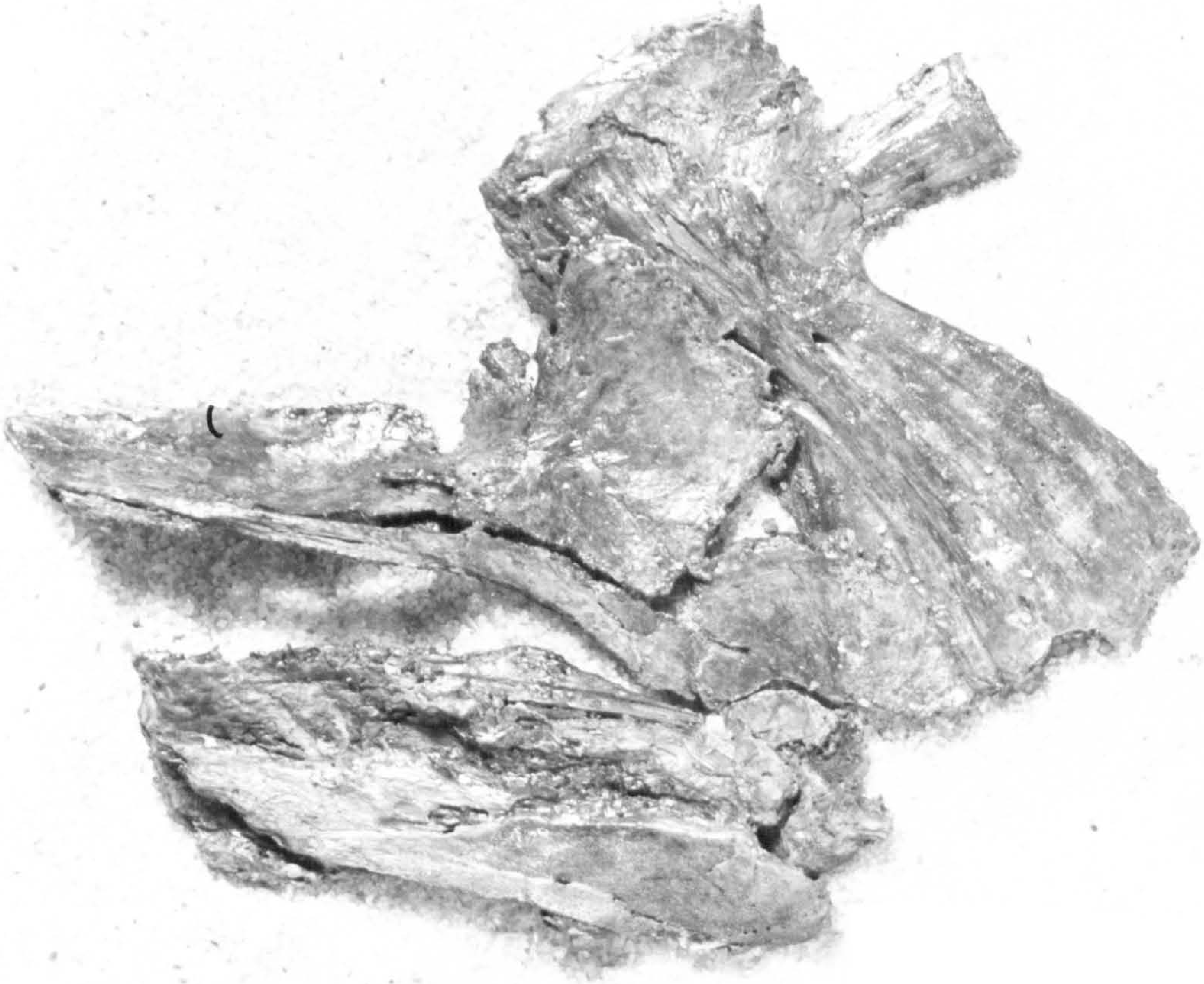


Plate 7. Pachycormus macropterus. Palate of P24410 in lateral view.

Plate 8. Pachycormus macropterus. Palate of P24410 in medial view.

7



8

Plates 9, 10 and 11. Pachycormus macropterus. Visceral arch elements of P24410 exposed at successive stages of preparation.

Plate 12. Pachycormus sp. Infra-pharyngobranchials of 32438 (those of right hand side still in articulation with the epibranchials.)

9

10

11

12

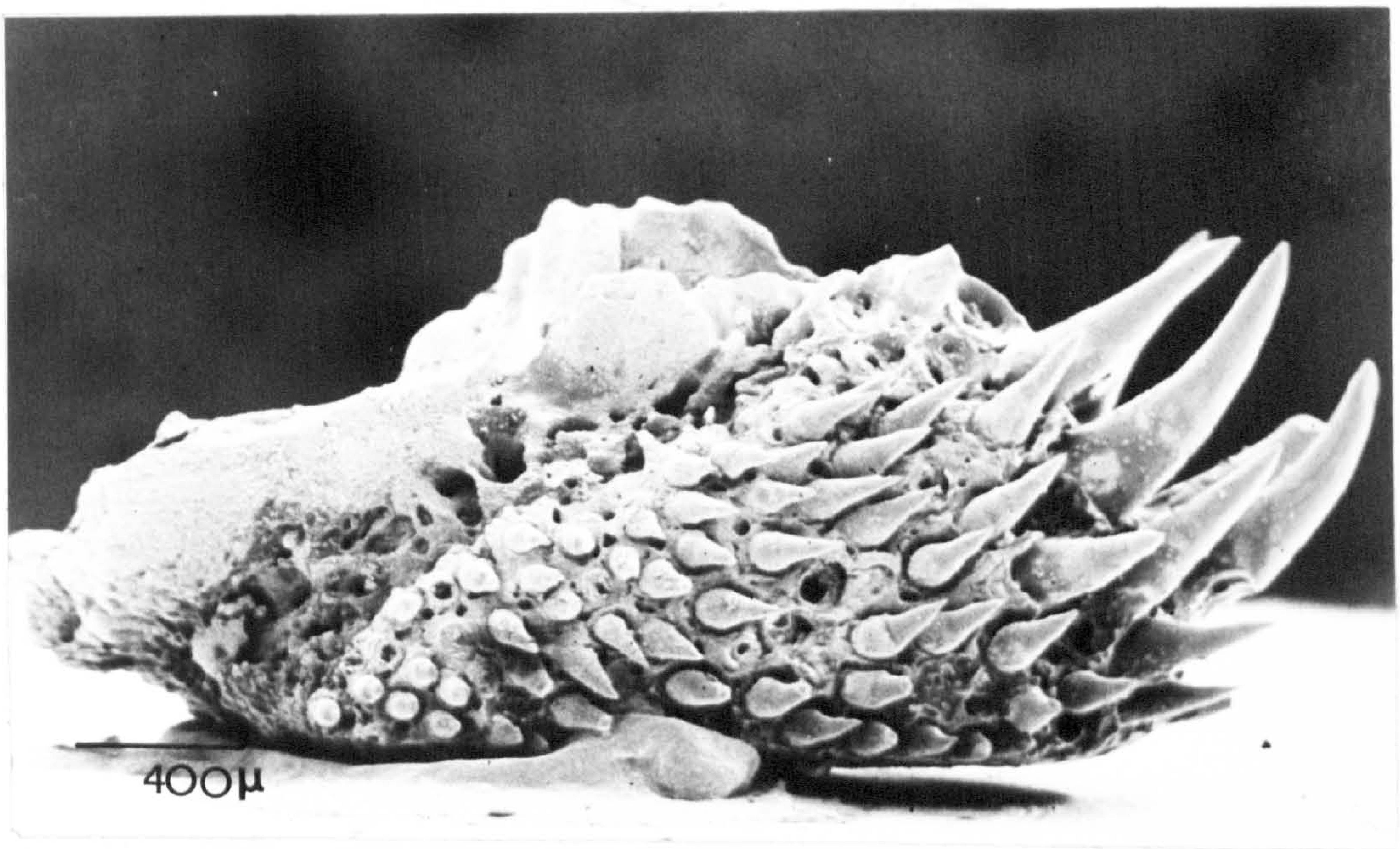
Plates 13 and 14. Pachycormus sp. Ventral visceral arch elements of 32438 in ventral view at successive stages of preparation. Note the relationship between the ventral tooth plate (Plate 13) with the underlying structures exposed by its removal (Plate 14).

13

14

Plates 15, 16 and 17. Pachycormus macropterus. S.E.M. of individual tooth plates associated with the visceral arch elements of P10146 in lateral view.

15



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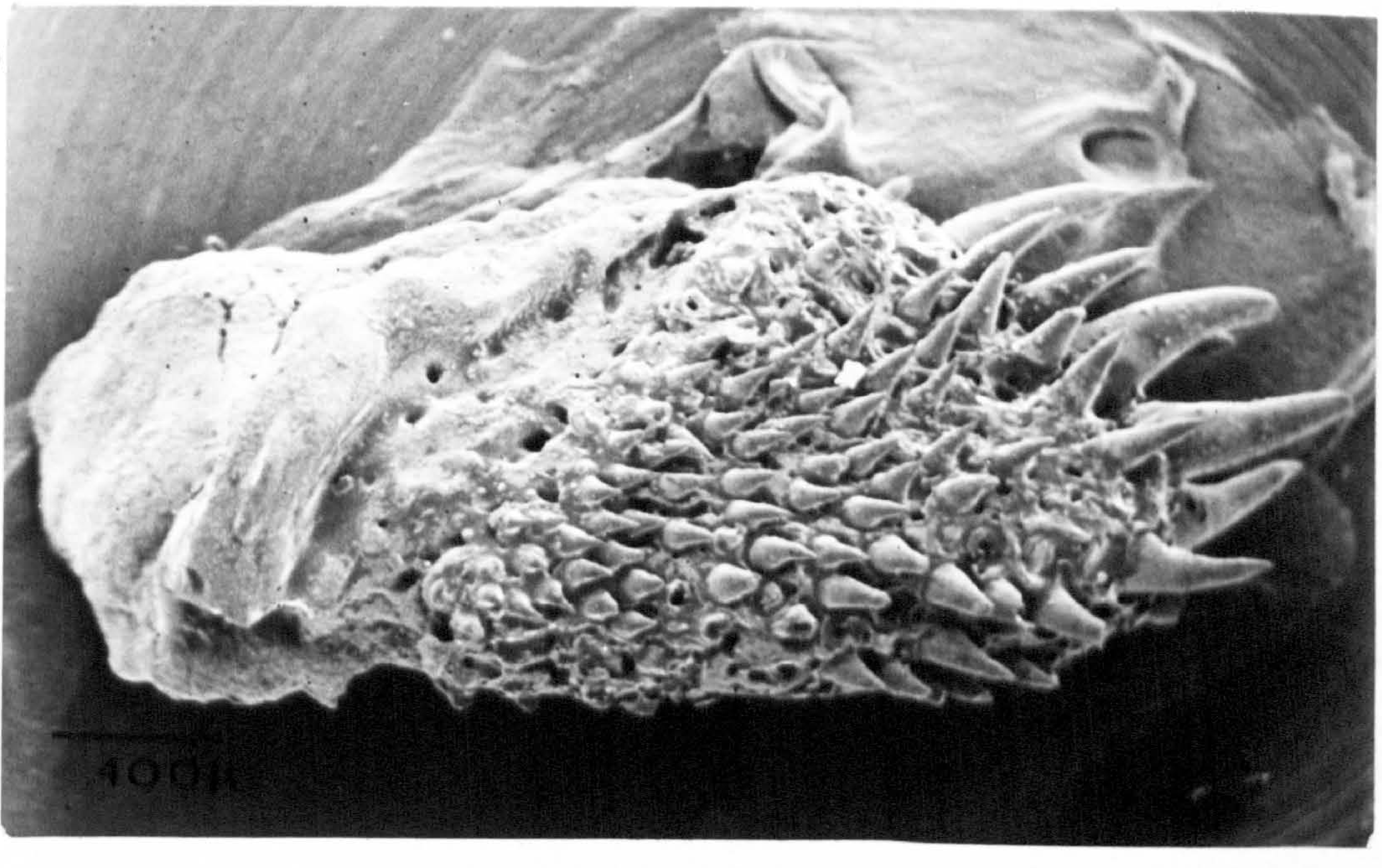

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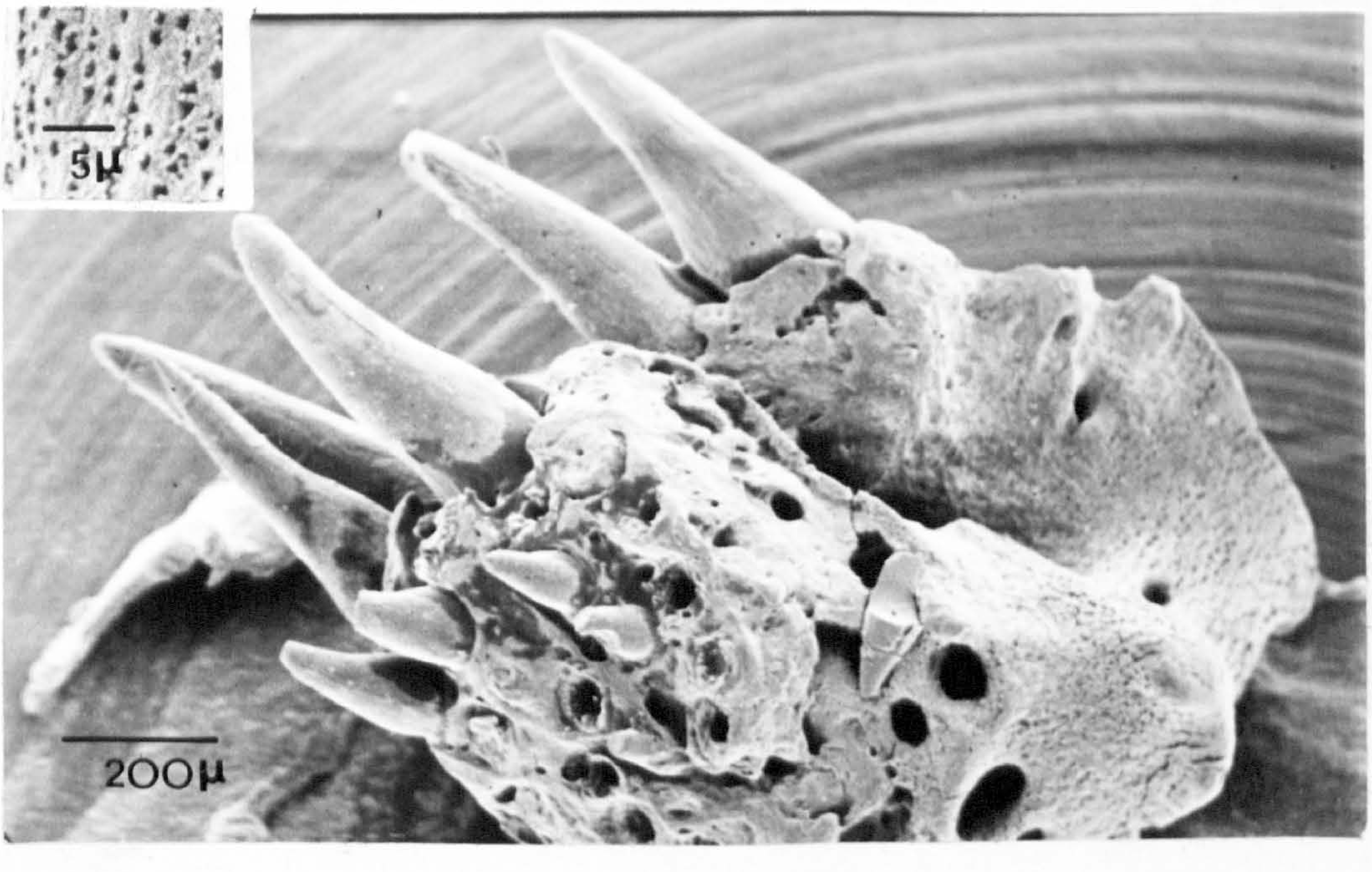
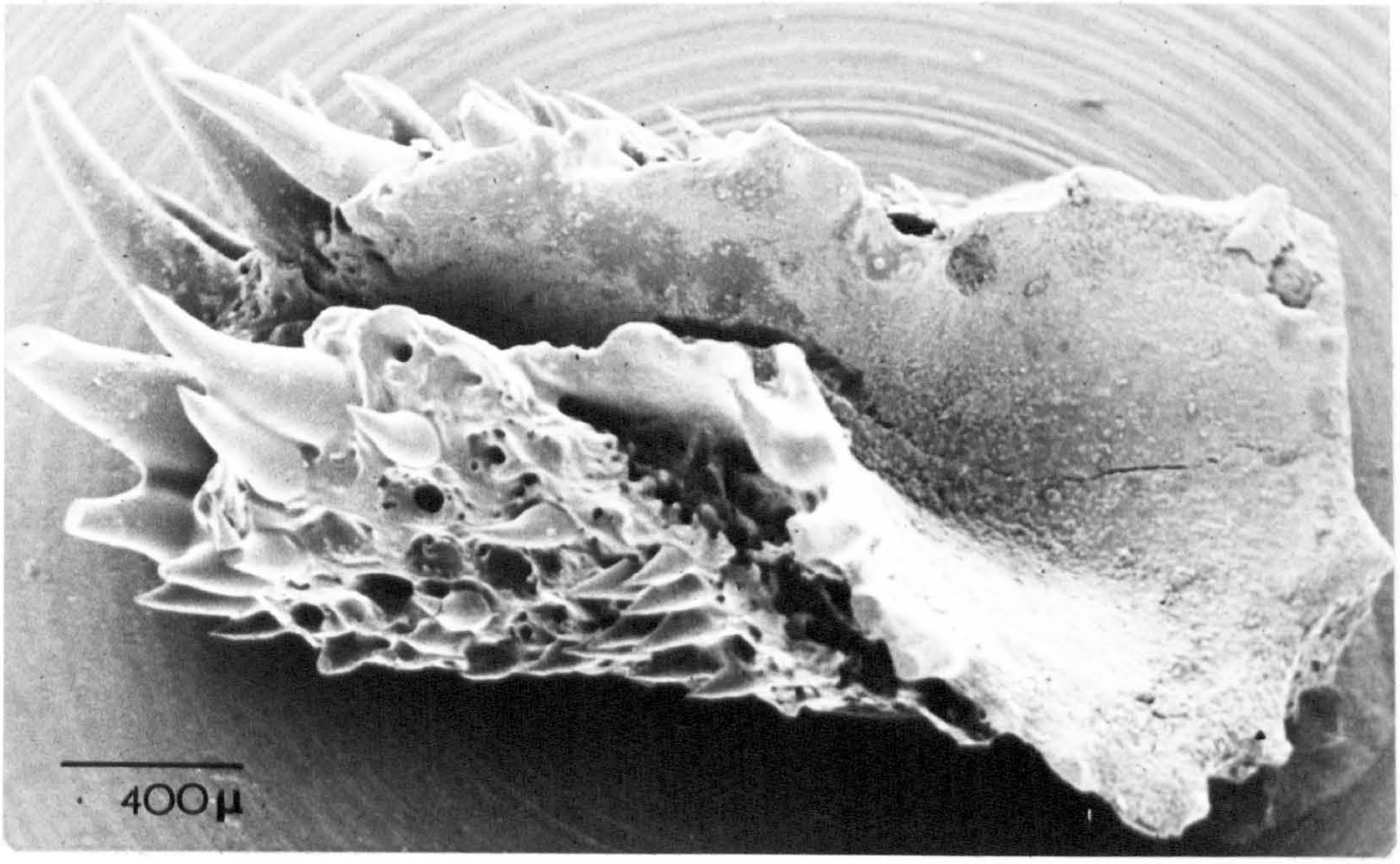
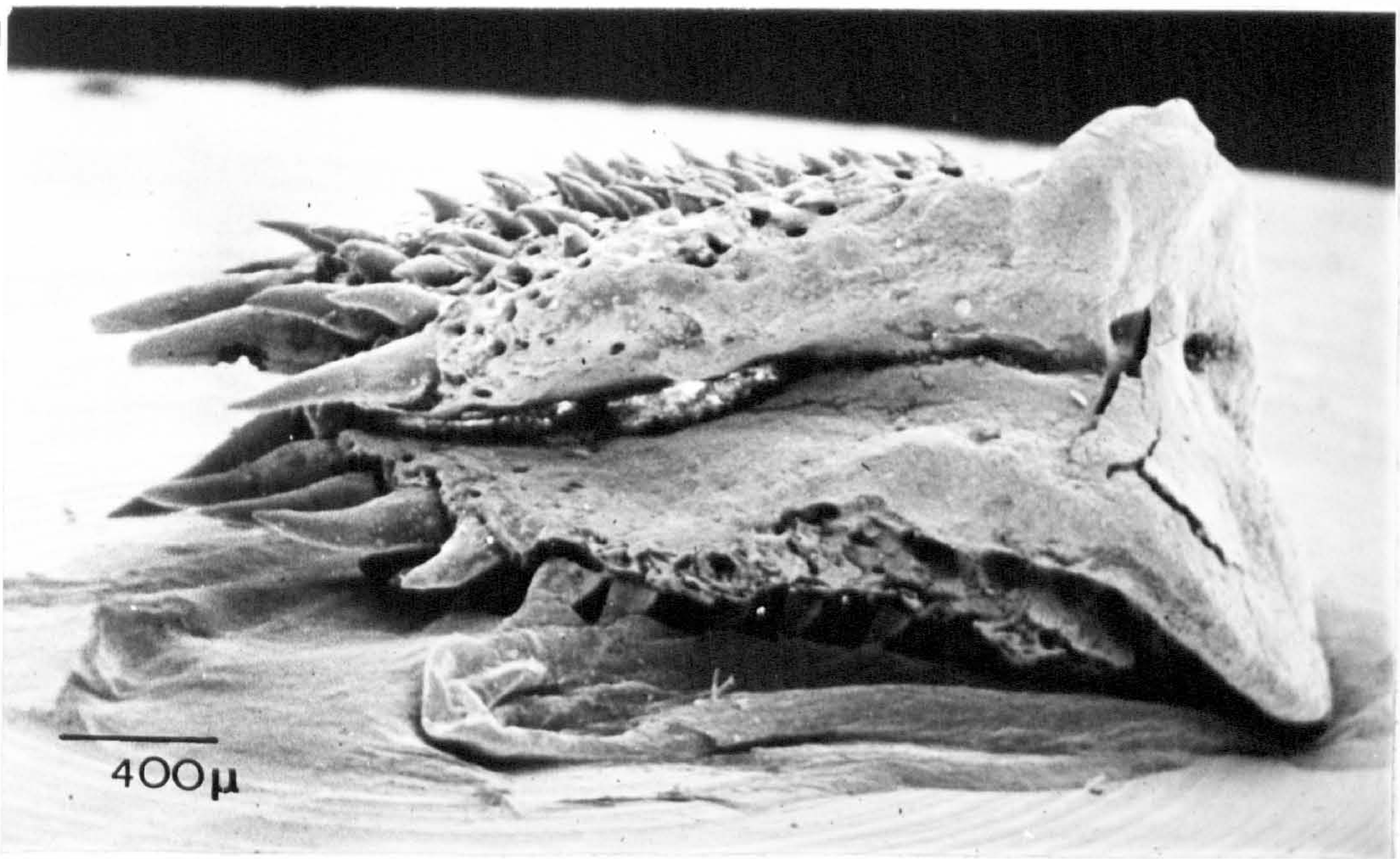


Plates 15a, 16a and 17a. Pachycormus macropterus. S.E.M. of individual tooth plates associated with the visceral arch elements of P10146 in posterior view.

15a



16a



17a

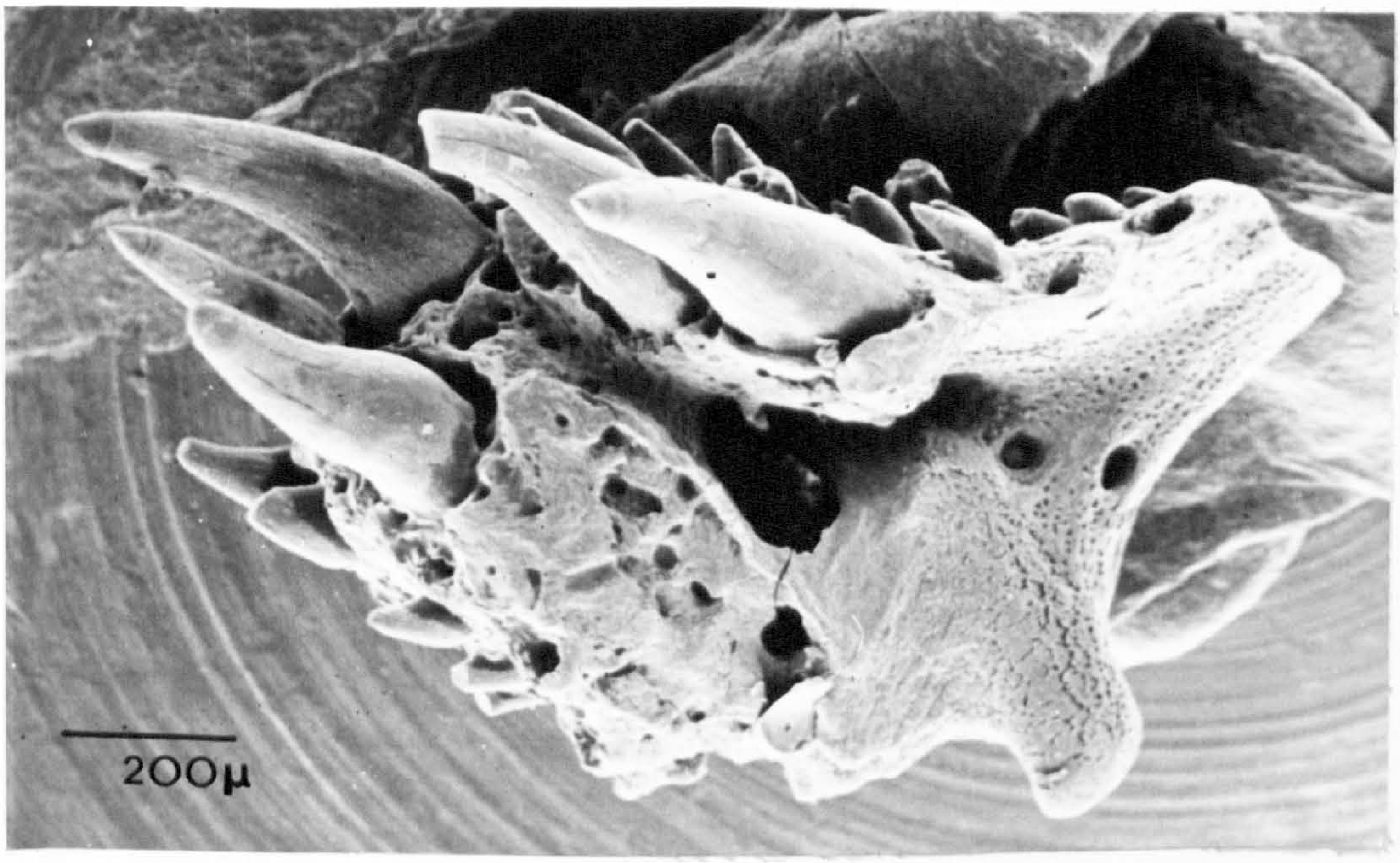
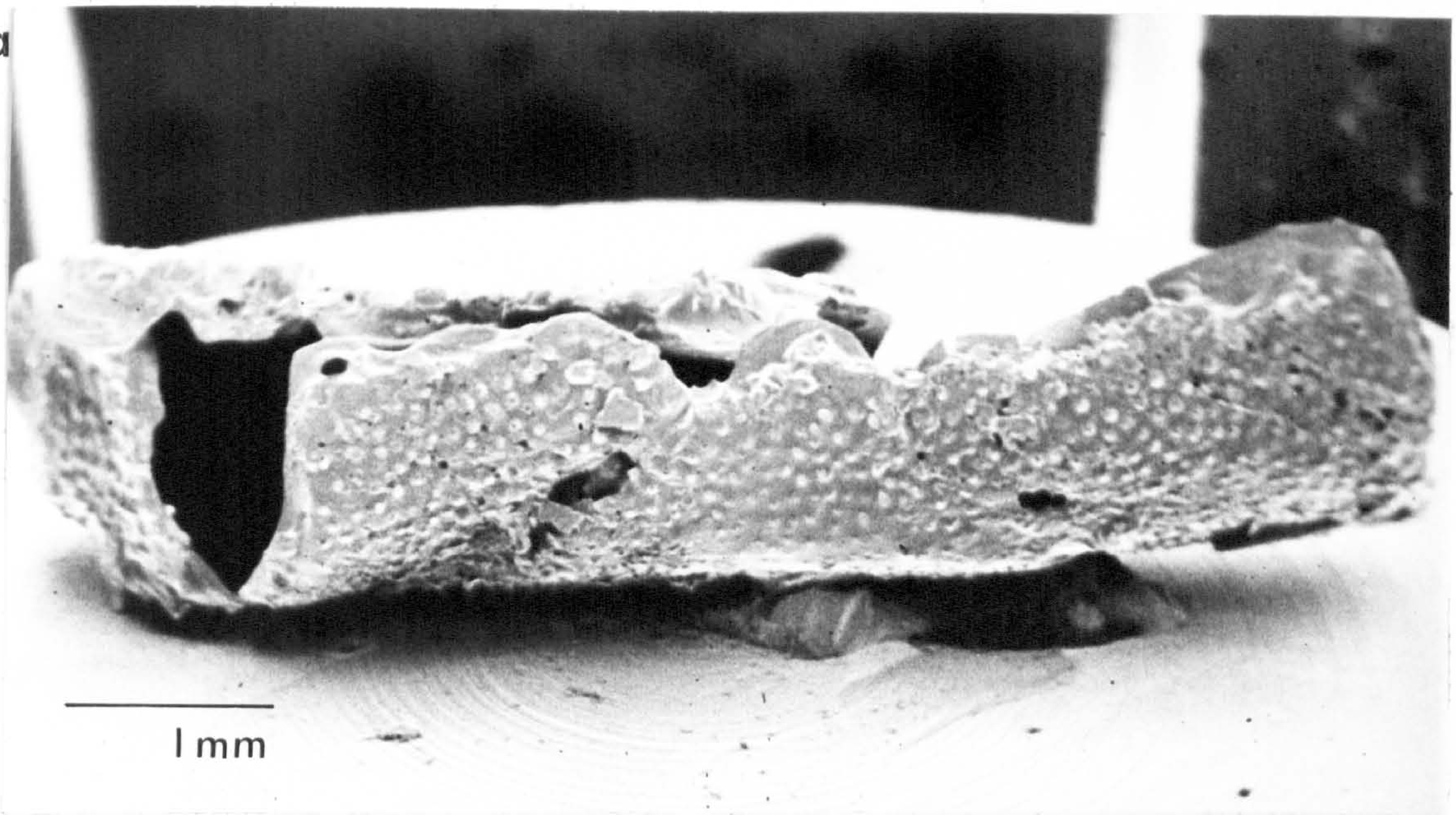


Plate 18. *Pachycormus macropterus*. S.E.M. high magnification of individual tooth plates of P10146 shown in Plates 15, 16 and 17, 15a, 16a and 17a.

18

Plate 19. Pachycormus sp. S.E.M. of ventral tooth plate of 32438 in (a) right lateral, (b) ventral and (c) left lateral view.

19a



b

c

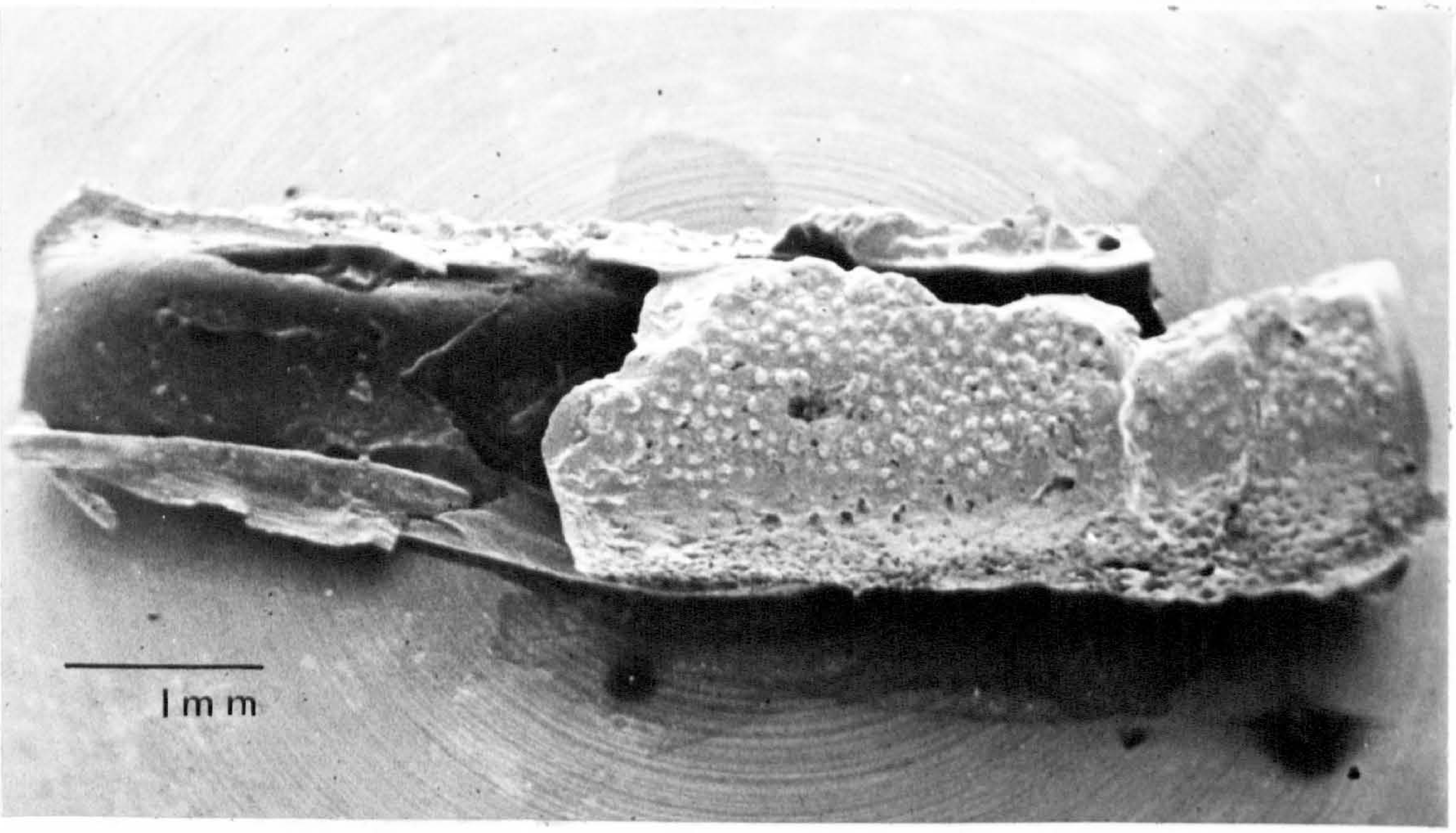


Plate 20. *Pachycormus sp.* S.E.M. high magnification of the surface of the ventral tooth plate of 32438.

20

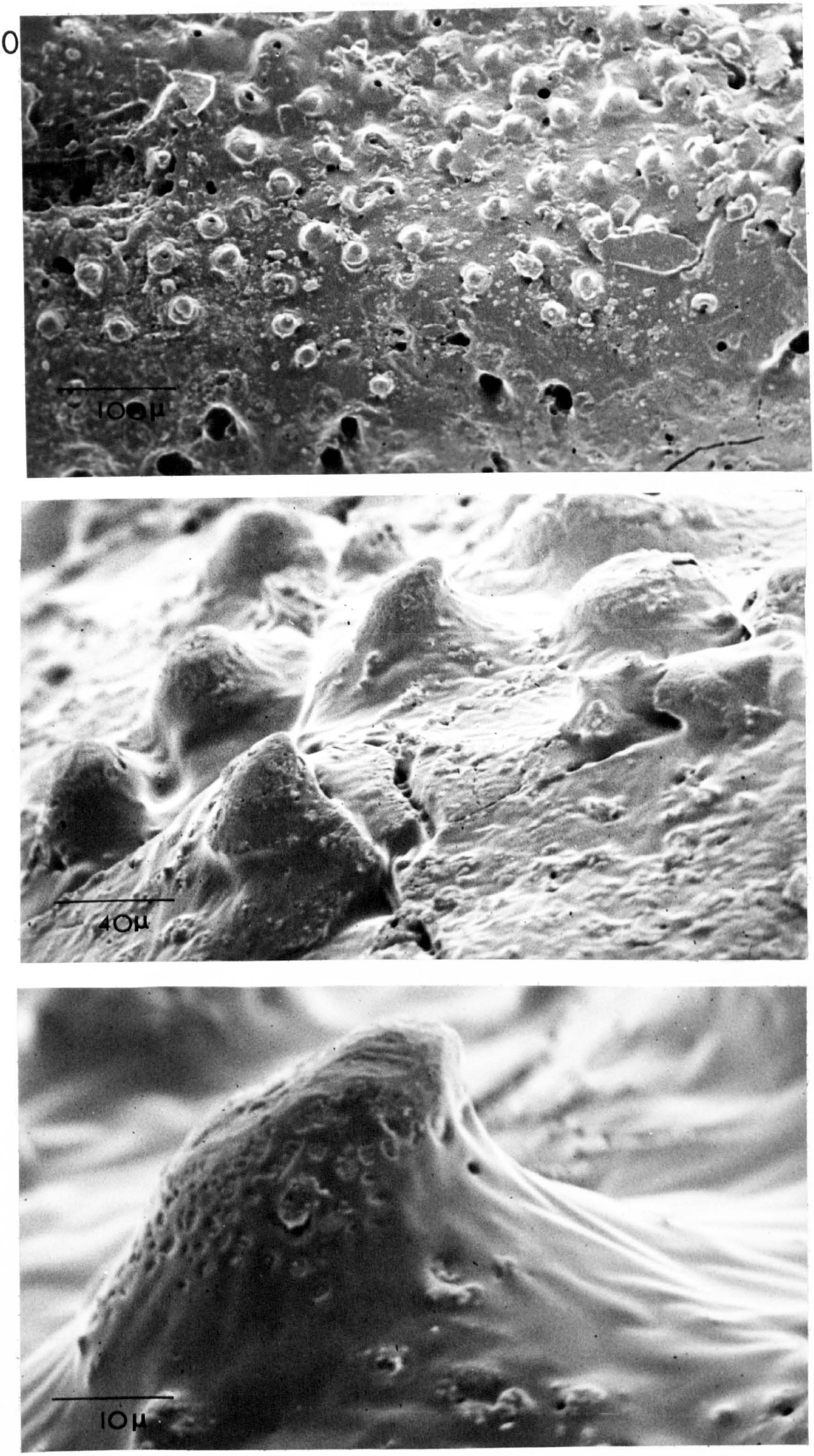


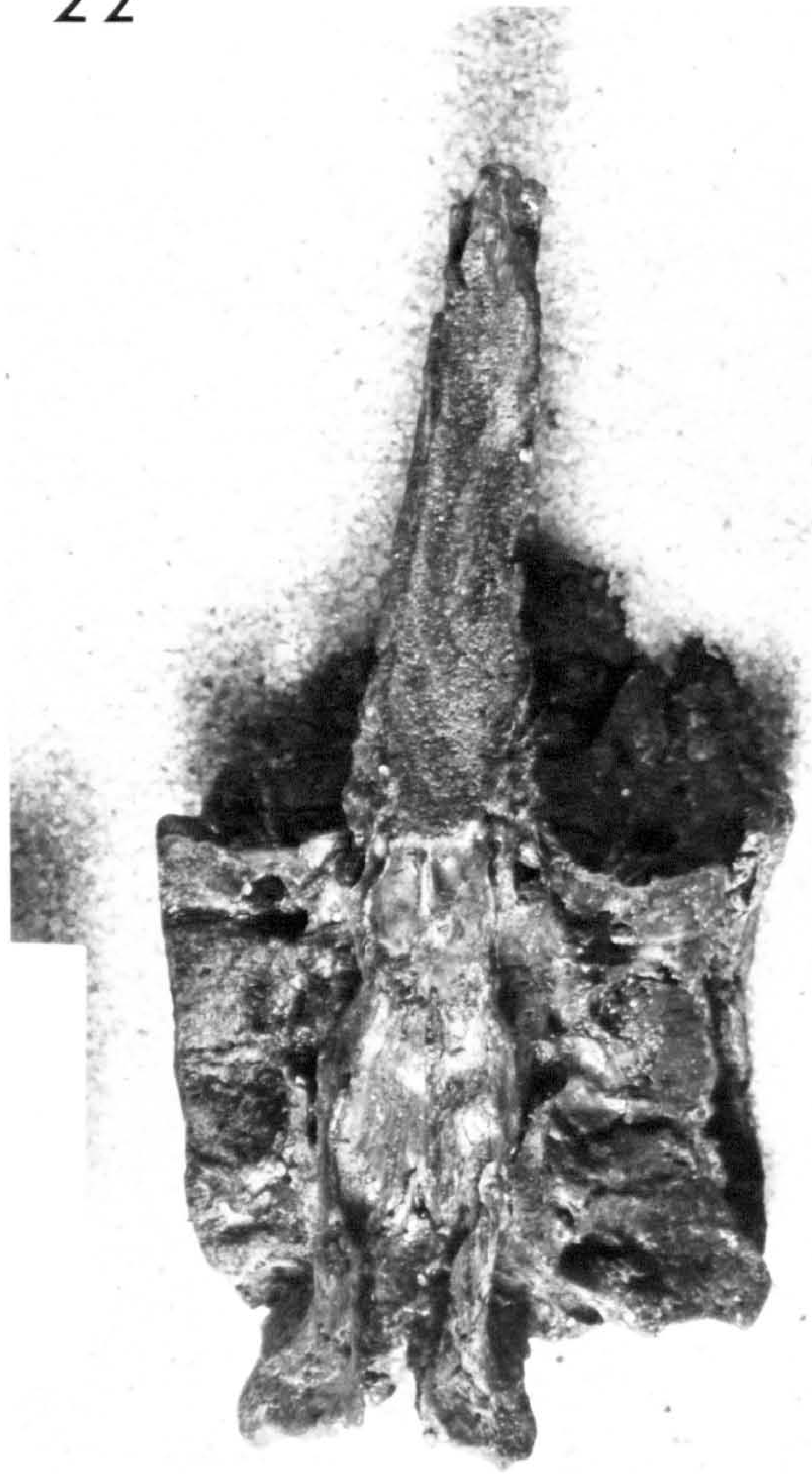
Plate 21. *Pachycormus macropterus*. Neurocranium of P24410 in right lateral view.

Plate 22. *Pachycormus macropterus*. Neurocranium of P24410 in ventral view.

Plate 23. *Pachycormus macropterus*. Neurocranium of P24410 in posterior view.

21

22



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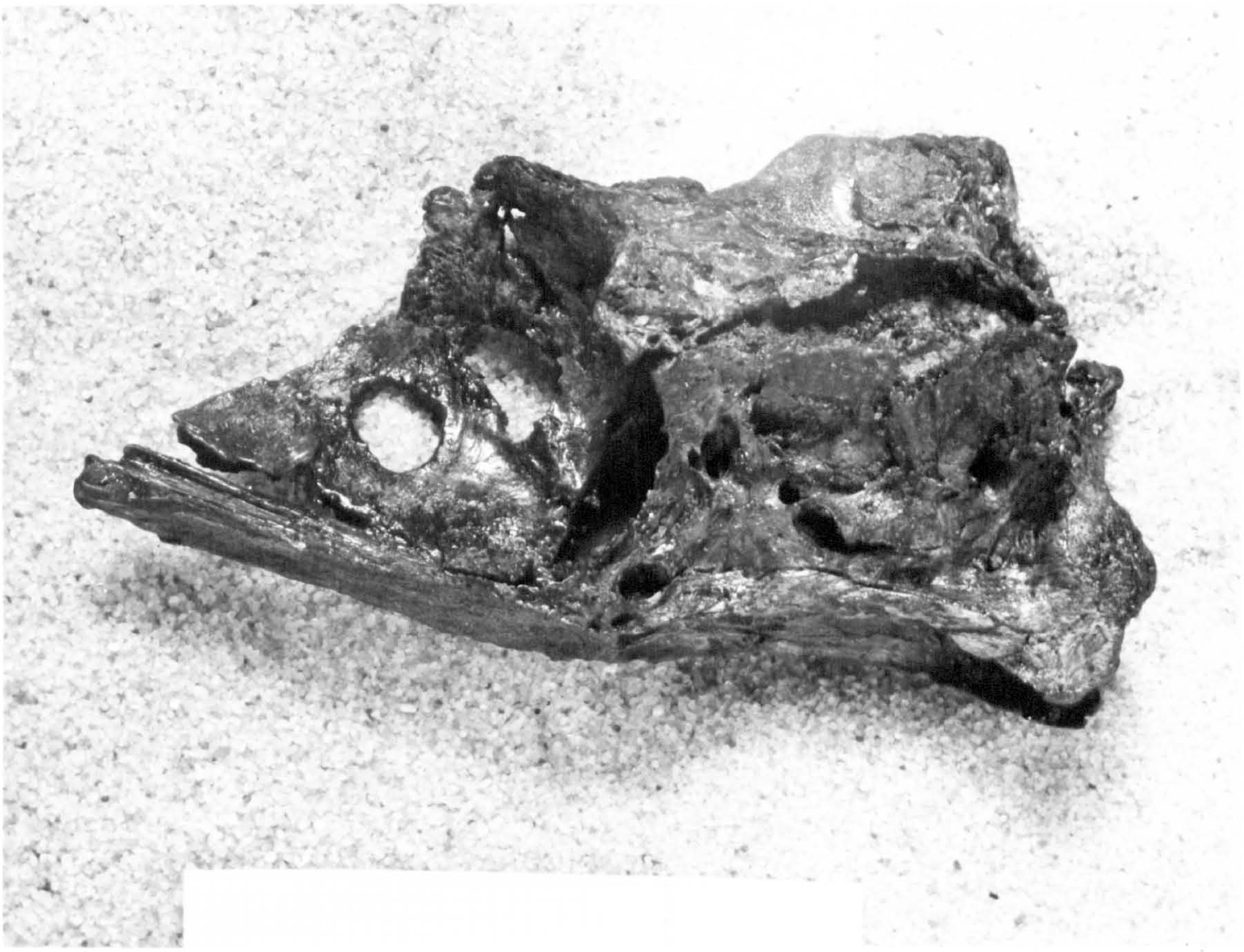
Plates 24 and 25. Pachycormus macropterus. Photograph (Plate 24) and corresponding radiograph (Plate 25) of the neurocranium in left lateral view of P24410.

24

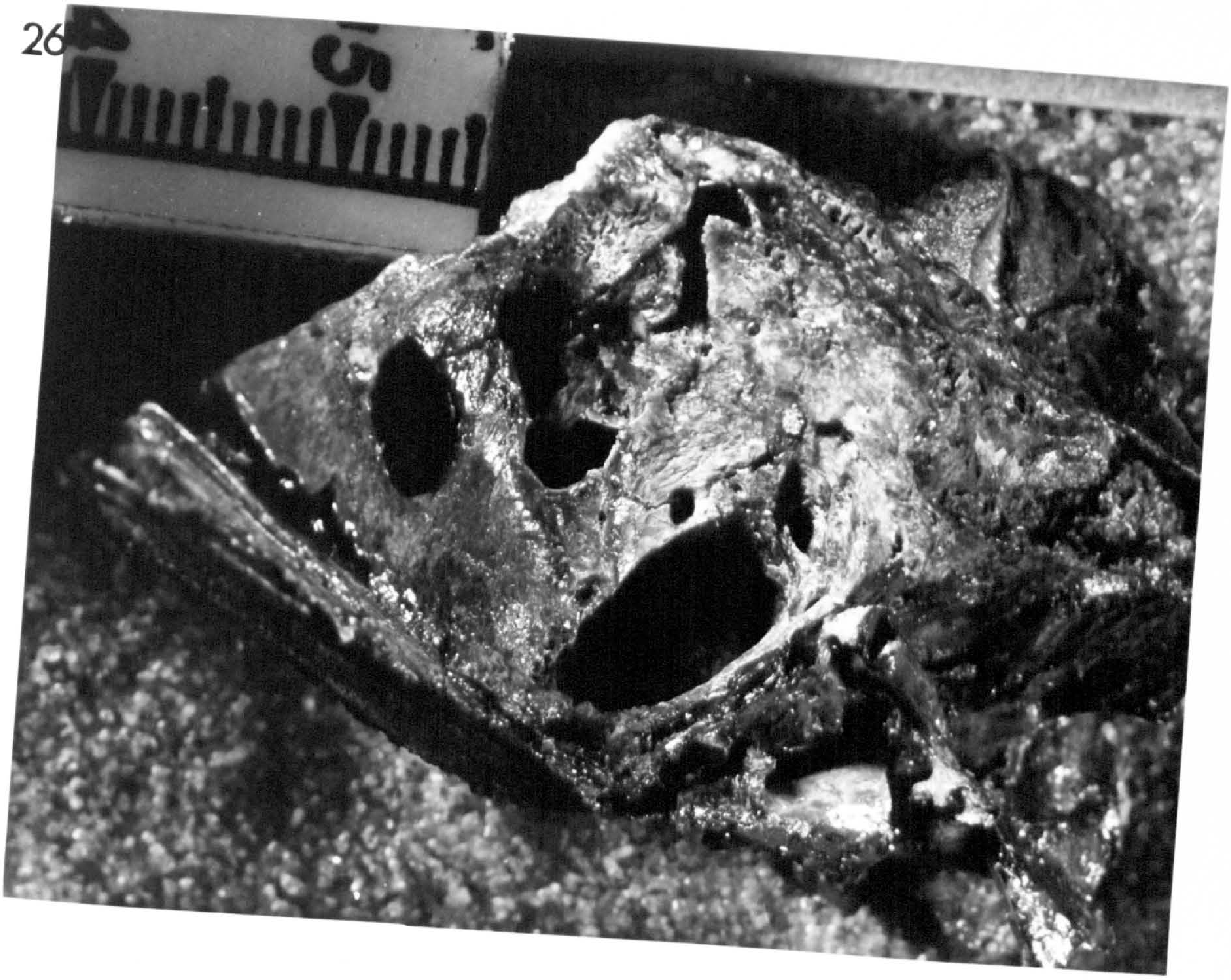


25

Plate 26. *Pachycormus macropterus*. The neurocranium of P24410 in orbitotemporal view.

Plate 27. *Pachycormus macropterus*. The neurocranium of P24410 in dorsal view.

26

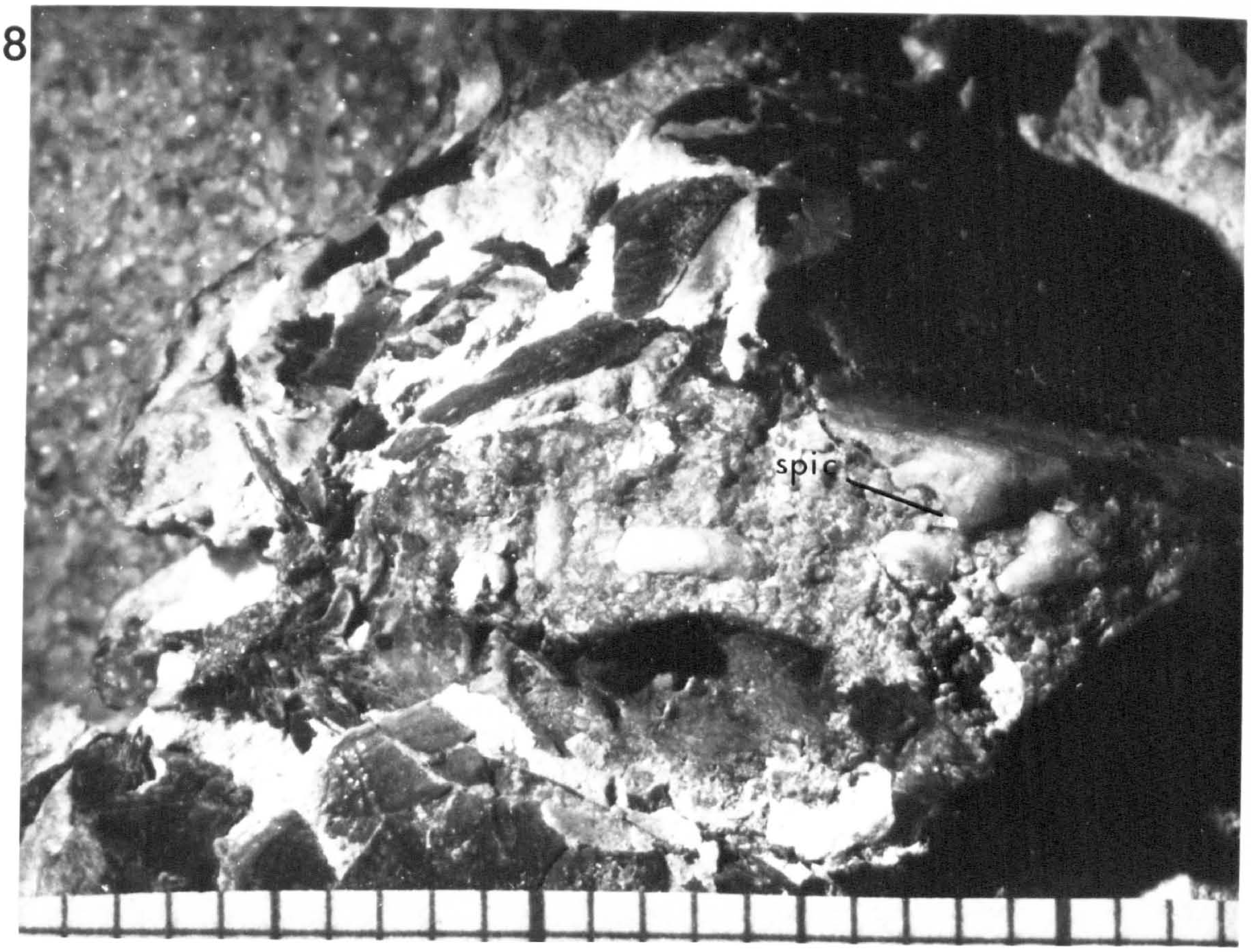


27

Plate 28. <u>Pachycormus curtus</u>. Semicircular canals and the spiracular canal of 32434 infilled with calcite.

Plate 29. <u>Pachycormus macropterus</u>. P10146, the posterior additional otic-ossification with the opisthotic and intercalar.

28



29

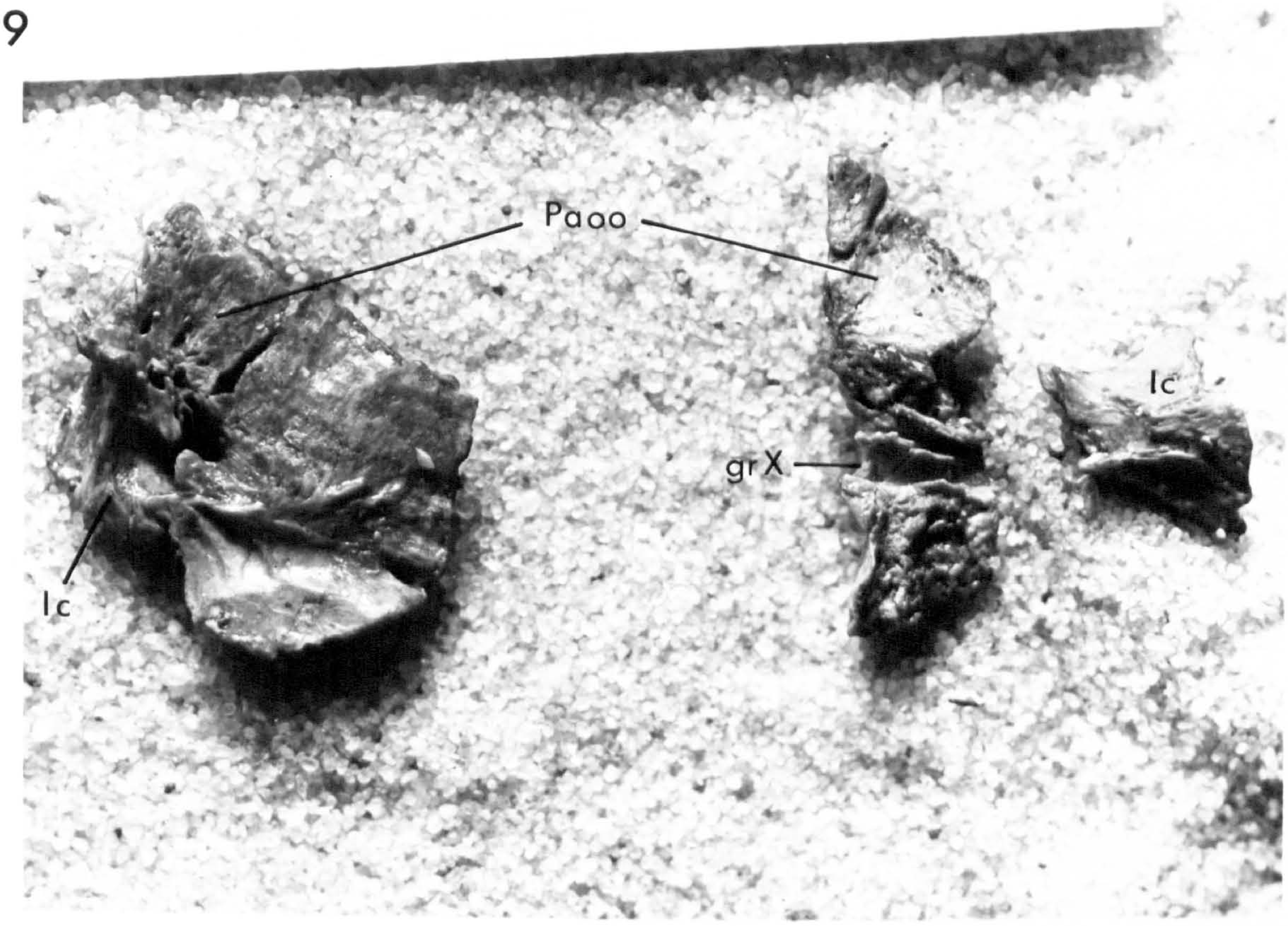


Plate 30. Pachycormus sp. Caudal fin of P59545.

30

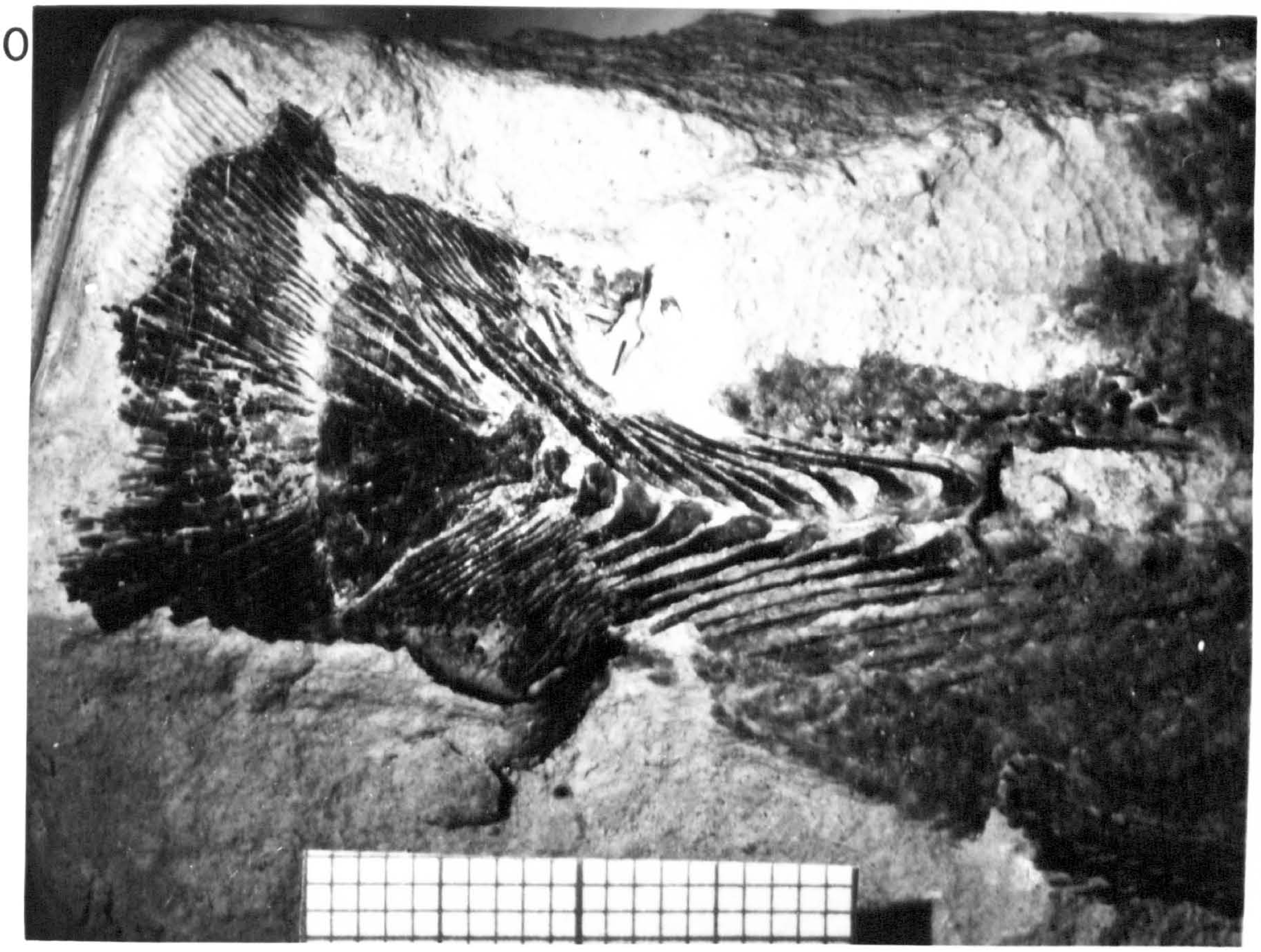


Plate 31. Pachycormus macropterus. Isolated pectoral girdle of 32432 in (a) lateral and (b) medial view.

Plate 32. Pachycormus curtus. Both halves of the exposed pectoral girdle of P900.

31 a

b

32

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ABBREVIATIONS

Aaoo	Anterior additional otic-ossification
Ang	Angular
Ant	Antorbital
Art	Articular
ac	aortic crest
acdtp	area of ventral surface of the vomer covered by a dermal tooth plate
acv	foramen of anterior cerebral vein
adf	anterior dorsal fontanelle
afOp	ascending flange of the opisthotic
ainp I, II, III	articular facets of infra-pharyngo-branchial I, II or III
ainpl II, III	articulation of the lateral process of infra-pharyngo-branchial II and III
al	anterior process of infra-pharyngo-branchials II and III
ampa, ampe, ampp	anterior, external and posterior ampulary chambers
ano	anterior nostril
apmx	articular surface on Rostro-dermethmoid for premaxilla
asp	ascending process of parasphenoid
Bb I-V	basibranchials I-V
Bexo	basi-exoccipital
Bhy	Basi-hyal
Br	branchiostegal rays
Bsp	basisphenoid
bvfont	bridge over vestibular fontanelle observed only in P24410

Cb I-IV	ceratobranchials
Chy, I, II	anterior and posterior ceratohyals
Cl	cleithrum
Copr	coranoid plate
cb	cranial boss formed by parietals and part of the frontals
cg	cranial grooves on dermal skull roofing bones
cp	coranoid process
crr	coracoid region
cson	canal for superficial ophthalmic nerves
Den	dentary
Dfy	dermal fin rays
Dpcl	dorsal post cleithrum
Dpl 1, 2	dermopalatines 1 and 2
Dpto	dermopterotic
Dr	distal radials of pectoral fin
Dspo	dermosphenotic
dfIc	descending flange of intercalar
dhol	triangular depression above the foramen magnum housing the dorsal ligaments to the vertebrae
Eb i-IV	epibranchials
Ecpt	ectopterygoid
Enpt	endopterygoid
Ep 1-6	epural bones
eth.com.	ethmoid commissural sensory canal
Fr	frontal
fb	fossa bridgei
f dn	foramen of diazonal nerve
fHm	hyomandibular facet

fHmVII	foramen of hyomandibular trunk of facial nerve
fica	foramen for internal carotid artery in parasphenoid
$fica^2$	foramen of internal carotid artery in basisphenoid pedicel
fIhy	facet for the interhyal
fm	foramen magnum
foca	foramen of occipital artery
focn	foramen for occipital nerve
fotc	fissura-otica-occipitalis
fotn	foramen of otic nerve
fotv	fissura oticalis ventralis
fpb	fronto parietal boss
frd	foramen for ascending branch of superficial ophthalmic nerves
frla	notch or foramen for recurrent branch of facial nerve
f.sc	foramen in scapular
fstX	foramen of supratemporal branch of the vagus nerve
fsX	foramen of subsidiary branch of vagus nerve
ftpcv	foramen of posterior tributary of posterior cerebral vein in hind wall of vagus groove
fvoc	foramen of tributary of posterior cerebral vein in 'exoccipital'
fvptf	foramen in intercalar transmitting vessels into the post-temporal fossa
Gp	gular plate
gesa	groove of efferent pseudobranchial artery
gHm.VII	groove of hyomandibular branch of VII
glf	glenoid fossa
goa	groove of orbital artery

gpal	groove for palatine nerve
gmx	groove for maxillary nerve
grao	groove of dorsal aorta
grdX	groove of descending branch of X
grmV	groove for the mandibular branch of the Trigeminal nerve
groca	groove of occipital artery
grpcv	groove of posterior cerebral vein
grptv	groove taking blood vessel into post-temporal fossa
gson	groove for superficial ophthalmic nerves
grstX	groove of post-temporal branch of vagus nerve
grX	groove for vagus nerve
H1	hypural I
H2+n	hypural plate compressing the second and an unknown number of succeeding hypurals
HbI-V	Hypobranchials I-V
Hhy	hypohyal
Hm	hyomandibular
Hn+I-4	free hypural bones
HI	first hypural bone
Hpu 1-6	haemal arches and spenes of first six pre ural vertebrae
haol	housing of aortic ligament
Ic	intercalar
Ihy	interhyal
Io	infraorbital bone
Iop	interopercular bone
Ipb I-III	infra-pharyngo-branchial
idp	small independent tooth plate covering ventral surface of ascending process of parasphenoid

io.c	infraorbital sensory canal
jc	jugular canal
jexo	area of intercalar joining exoccipital
jg	jugular groove
jic	area of basi-exoccipital joining intercalar
Ldec	lateral-dermethmoid component of rostrodermethmoid
Le	lateral ethmoid
lcc	lateral cranial canal
lcom	lateral commissure
lig	area of insertion of ligaments to the palate or maxilla
ll.c	lateral line sensory canal
lp	lateral process of infra-pharyngo-branchial II and III
Mpt	metapterygoid
Mx	maxilla
m.c.	mandibular sensory canal
mcor	mesocoracoid arch
mcv	foramen of middle cerebral vein
myo	posterior myodome
Na	nasal
Npu 1-6	neural arches and spines of first six pre-ural vertebrae
Nul	ural neural arches
nIII	notch on ptresphenotic contributing to occulomotor foramen
not	notochordal pit
npit	nasal pit
npro	nasal process of lateral-dermethmoid
Op	opercular
Opo	opisthotic
Ors	orbitosphenoid

oca	occipital arch
occ	occipital condyle
oifom	origin of inferior oblique muscles
onc	canal for orbitonasal vessels
op Hm	opercular process of Hyomandibular
otoc	occipital portion of otolith chamber
Pa	parietal
Paoo	posterior additional otic-ossification
Par	pre-articular
P.eth	pre-ethmoid bone
Pmx	premaxilla
Pop	preopercular
Pr$^{2-4}$	proximal radials of pectoral fins
Pro	prootic
Prpt	propterygian
Psp	parasphenoid
Pssc	pre-suprascapular
Pto	pterotic
Pts	pterosphenotic bone
pala	canal for anterior branch of palatine nerve
palf	palatine fenestra in roof of myodome
palp	notch for posterior branch of palatine nerve
palt	notch for terminal branch of palatine nerve
p.BbII	position of basibranchial II
pdtp	position of dermal tooth plate on basibranchial II-IV
plig	pit housing origin of ethmo-palatine ligaments
pno	posterior nostril
po.c	pre-opercular sensory canal
pop	post orbital process of sphenotic

prob	prootic bridge
prof	notch or foramen for profundus nerve
ptf	post-temporal fossa
Qyj	quadratojugal
Qu	quadrate
Roc	rostral component of rostro-dermethmoid
Rode	rostro-dermethmoid
rscm	recess on parasphenoid housing origin of subcephalic muscles
Sag	supra angular
Scl	supracleithrum
Scr	sclerotic ring
Smx	supramaxilla
Sop	subopercular
Spo	sphenotic bone
Ssc	suprascapular
Sym	symplectic
sacr	sacular recess
scr	scapular region
smc	crest on upper surface of parasphenoid forming floor of myodome
so.c	supraorbital sensory canal
sof	supraorbital fossa
spic	dorsal opening of spiracular canal
spig	spiracular groove
stf	subtemporal fossa
unp	uncinate process of epibranchial
utr	utricular recess
Vo	vomer

Vpcl	ventral postcleithrum
vfont	vestibular fontanelle
vp	ventral process of basibranchial III-IV
I	foramen of olfactory tract
II	optic fenestra
III	notch of occulomotor nerve
IV	foramen or notch of trochlear nerve
V	foramen of trigeminal nerve
VI	foramen of abducans nerve
VII	foramen of facial nerve
IX	foramen of glossopharyngeal nerve
X	foramen of vagus nerve

FIGURE LEGENDS

Figure 1. *Pachycormus macropterus*. Reconstruction of head in dorsal view. Based on 32433 and P10146.

Figure 2. *Pachycormus macropterus*. Reconstruction of head in lateral view. Based on 32433 and P10146.

Figure 3. *Pachycormus curtus*. P10145 unrestored drawing of rostrodermethmoid in posterior view.

Figure 4. *Pachycormus macropterus*. Reconstruction of the left lower jaw in (a) lateral and (b) medial views. Based on P10146 and 32432.

Figure 5. *Pachycormus sp*. Composite reconstruction of parasphenoid in (a) ventral, (b) lateral and (c) dorsal view. Based on P10146, P24410 and P10145.

Figure 6. *Pachycormus curtus*. P10145 unrestored drawing of left vomer in (a) dorsal and (b) ventral view.

Figure 7. *Pachycormus macropterus*. Reconstruction of the left palate in medial view. Based on P24410.

Figure 8. *Pachycormus macropterus*. Reconstruction of the left palate in lateral view. Based on P24410.

Figure 9. *Pachycormus macropterus*. Reconstruction of the right quadrate, quadratojugal and symplectic in (a) lateral, (b) medial and (c) posterior view. Based on P10146 and 32432.

Figure 10. Basic plan of the arrangement of the ventral visceral arch elements of fishes based on Nelson (1969).

Figure 11. *Pachycormus macropterus*. Reconstruction of the hyoid arch, excluding the hyomandibular, in lateral view. Based on P10146 and P24410.

Figure 12. *Pachycormus sp.* 32438 unrestored drawing of the ventral visceral arch elements.

Figure 13. *Pachycormus macropterus*. P24410 unrestored drawing of the basibranchials in (a) dorsal, (b) lateral and (c) ventral view.

Figure 14. *Pachycormus macropterus*. 32432 unrestored drawing of the hypobranchials showing (a) their anterior articular surfaces and (b) these elements in dorsal view.

Figure 15. *Pachycormus macropterus*. P24410 unrestored drawing of the right ceratobranchials in dorso-lateral view.

Figure 16. *Pachycormus macropterus*. P24410 unrestored drawing of the right epibranchials in lateral view.

Figure 17. *Pachycormus macropterus*. P24410 unrestored drawing of the right infra-pharyngo-branchials in (a) dorsal and (b) ventral view.

Figure 18. *Pachycormus macropterus*. P10146 unrestored drawing of the basi-exoccipital of P10146 in (a) posterior and (b) lateral view.

Figure 19. *Pachycormus macropterus*. P10146 unrestored drawing of the basi-exoccipital in (a) ventral and (b) anterior view.

Figure 20. *Pachycormus macropterus*. Reconstruction of the posterior wall of the neurocranium based on P24410.

Figure 21. *Pachycormus macropterus*. P10146 unrestored drawing of the left opisthotic, intercalar and posterior additional otic-ossification in (a) lateral, (b) medial and (c) posterior view, and (d) anterior face of the intercalar.

Figure 22. *Pachycormus macropterus*. Reconstruction of the lateral surface of the neurocranium based on P24410.

Figure 23. *Pachycormus macropterus*. P10146 unrestored drawing of the right sphenotic in (a) lateral, (b) dorsal, (c) anterior view and of the left pterotic in (d) lateral and (e) medial view.

Figure 24. *Pachycormus macropterus*. P10146 unrestored drawing of the left prootic in (a) lateral, (b) medial, (c) anterior, (d) posterior, (e) dorsal and (f) ventral view.

Figure 25. *Pachycormus macropterus*. P10146 unrestored drawing of the pterosphenotic in (a) lateral and (b) medial view; and of the orbitosphenoid in (c) lateral, (d) posterior and (e) dorsal view.

Figure 26. *Pachycormus macropterus*. P24410 unrestored drawing of the posterior wall of the orbit.

Figure 27. *Pachycormus curtus*. 32437 unrestored drawing of the right lateral ethmoid in (a) antero-lateral and (b) posterior view.

Figure 28. *Pachycormus sp*. Reconstruction of the caudal fin. Based on 32425 and P59545.

Figure 29. *Pachycormus macropterus*. 32432 unrestored drawings of the pectoral girdle in (a) lateral and (b) medial view.

Figure 30. Cladogram showing relationships of the genera within the Pachycormidae.

Figure 31. Cladogram of the first six divisions of Patterson's (1977:262, fig. 19) cladogram showing a theory of relationships of certain fossil teleosts.

Figure 32. Cladogram showing the proposed relationships of the Pachycormidae to certain fossil teleosts.

PLATES

Plate 1. Pachycormus macropterus. Skull roof of 32433.

Plate 2. Pachycormus macropterus. Head in lateral view of 32433.

Plate 3. Pachycormus macropterus. Rostro-dermethmoid of 32432 in ventral view showing pre-ethmoid bones.

Plate 4. Pachycormus curtus. Ethmoid region of 32430 showing pre-ethmoid bone with vomer.

Plate 5. Pachycormus curtus. Isolated palatal bones of P10145 arranged in their probable original relationships.

Plate 6. Pachycormus macropterus. Disassociated ectopterygoid and dermopalatines of 32432 in dorsal and ventral views.

Plate 7. Pachycormus macropterus. Palate of P24410 in lateral view.

Plate 8. Pachycormus macropterus. Palate of P24410 in medial view.

Plates 9, 10 and 11. Pachycormus macropterus. Visceral arch elements of P24410 exposed at successive stages of preparation.

Plate 12. Pachycormus sp. Infra-pharyngobranchials of 32438 (those of right hand side still in articulation with the epibranchials.)

Plates 13 and 14. Pachycormus sp. Ventral visceral arch elements of 32438 in ventral view at successive stages of preparation. Note the relationship between the ventral tooth plate (Plate 13) with the underlying structures exposed by its removal (Plate 14).

Plates 15, 16 and 17. Pachycormus macropterus. S.E.M. of individual tooth plates associated with the visceral arch elements of P10146 in lateral view.

Plates 15a, 16a and 17a. Pachycormus macropterus. S.E.M. of individual tooth plates associated with the visceral arch elements of P10146 in posterior view.

Plate 18. Pachycormus macropterus. S.E.M. high magnification of individual tooth plates of P10146 shown in Plates 15, 16 and 17, 15a, 16a and 17a.

Plate 19. Pachycormus sp. S.E.M. of ventral tooth plate of 32438 in (a) right lateral, (b) ventral and (c) left lateral views.

Plate 20. Pachycormus sp. S.E.M. high magnification of the surface of the ventral tooth plate of 32438.

Plate 21. Pachycormus macropterus. Neurocranium of P24410 in right lateral view.

Plate 22. Pachycormus macropterus. Neurocranium of P24410 in ventral view.

Plate 23. Pachycormus macropterus. Neurocranium of P24410 in posterior view.

Plates 24 and 25. Pachycormus macropterus. Photograph (Plate 24) and corresponding radiograph (Plate 25) of the neurocranium in left lateral view of P24410.

Plate 26. Pachycormus macropterus. The neurocranium of P24410 in orbitotemporal view.

Plate 27. Pachycormus macropterus. The neurocranium of P24410 in dorsal view.

Plate 28. Pachycormus curtus. Semicircular canals and the spiracular canal of 32434 infilled with calcite.

Plate 29. Pachycormus macropterus. P10146, the posterior additional otic-ossification with the opisthotic and intercalar.

Plate 30. Pachycormus sp. Caudal fin of

Plate 31. Pachycormus macropterus. Isolated pectoral girdle of 32432 in (a) lateral and (b) medial views.

Plate 32. Pachycormus curtus. Both halves of the exposed pectoral girdle of P900.