

THE HOLONEMATIDAE
(PLACODERM FISHES), A REVIEW BASED ON
NEW SPECIMENS OF *HOLONEMA*
FROM THE UPPER DEVONIAN
OF WESTERN AUSTRALIA

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A new species of the placoderm fish *Holonema* is described from the Frasnian of Western Australia as *H. westolli*. A detailed account of the head and trunk shields is given; the palatoquadrate, opercular cartilage and gnathals are also described and receive special attention in view of the interest that attaches to these structures. Restorations of the armour are given in connexion with a discussion of the possible mode of life, and its convergent resemblance to antiarchs is noted.

In a section on comparative morphology, some specimens of *Arctolepis decipiens* from Spitsbergen are partly redescribed; the variation in the dermal bones of the snout in *Holonema westolli* is analysed with respect to their possible ontogeny; and the structure of the nasal capsules and nasal openings in arthrodires is discussed, with the result that the usual elasmobranch model used in their interpretation is discarded; three possible interpretations of the snout in *Holonema* are proposed and one is tentatively accepted after a discussion of the available evidence, although it implies that some of the normal morphological relationships in the arthrodire snout have been seriously modified. The comparative morphology of the lateral-

lines of the cheek and flank is considered, as well as of the jaw apparatus and gill cover. This last discussion is summarized in a general account of jaw suspension in placoderms.

In a review of the family Holonematidae, the type and all referred genera (*Holonema*, *Deirosteus*, *Rhonenema*, *Gyroplacosteus*, *Megaloplax*, *Deveonema*) are tentatively defined, although the available information is not fully adequate for this purpose, and all named species and recent records are considered. The poorly known genera *Aspidichthys*, *Glyptaspis*, *Groenlandaspis*, *Grazosteus*, *Tropidosteus* and *Arctonema*, are excluded from the family. New material is described from Germany, Belgium and Scotland as *Holonema* spp. Throughout this review *Holonema westolli* is used as a standard of comparison rather than the poorly known type species *H. rugosum*.

Finally the relationships and classification of the holonematids are considered. It is concluded that they are arthrodires at the advanced coccosteomorph level of organization, phylogenetically equally distinct from all other brachythoracids, and it is recommended that the Brachythoraci should be divided into the collateral taxa Holonematei and Eubrachythoracei, the former with the single family Holonematidae.

I. INTRODUCTION

Holonema was first described from the Devonian of North America by Claypole (1883; *H. rugosum* as *Pterichthys rugosus*), more than eighty years ago. Since that time holonematids have been obtained from many localities in the Devonian of N. America and Europe. Yet the structure and affinities of these placoderms have remained poorly understood, mostly because of the fragmentary nature of the fossils. The present study has been prompted by the discovery at Gogo in Western Australia of a new species of *Holonema*, in a much better state of preservation than any hitherto known form. The Australian species permits the dermal skeleton to be described in detail for the first time.

The specimens were collected in a Frasnian inter-reef deposit, the Gogo Formation, on a joint expedition in 1967 by the British Museum (Natural History), the Western Australian Museum and the Hunterian Museum, Glasgow. A brief account of the expedition with a synopsis of the geology of the Gogo Station area has been published by Brunton, Miles & Rolfe (1969 with references). The fish fauna given in that paper now requires extensive revision (see also Miles 1970, 1971 a).

The fishes occur in calcareous concretions and have been prepared by the standard acetic acid techniques (Toombs & Rixon 1959). The dermal plates have usually been completely freed from the matrix, although two specimens with articulated flank plates have been prepared as resin transfers. The individual plates are typically uncrushed, but those of the trunk-shield and cheek have usually drifted slightly apart from each other, and occur with the more completely articulated skull-roofs in large, flattish nodules, which are frequently badly weathered. The large plates of the trunk-shield are relatively thin, and have a highly cancellous middle layer, with thin outer and inner layers. These bones are easily damaged during the course of preparation, and require much repair and strengthening once they have been removed from the rock. The relatively thicker plates of the head-shield have been more easily prepared. In some specimens, extensive deposits of quartz hold the plates together, obscuring their surfaces. It has proved to be a difficult task to disengage these plates without inflicting severe damage.

The Gogo fishes collected by the 1967 expedition have been allotted numbers in the registers of the Fish Section, Department of Palaeontology, British Museum (Natural History). This has enabled the numerous individual plates (commonly more than 50 for one specimen of a placoderm) to be handled easily during preparation and study, and it provides a permanent record of the material (the hypodigms) on which the descriptions will be based, obviating the need to publish extensive lists. The specimens will eventually be apportioned to the three museums concerned, with the types going to the Western Australian Museum.

This is the first of a projected series of papers on the Gogo placoderms. It falls into four distinct sections: first, an attempt to describe the anatomy of the new Gogo *Holonema* as fully as possible, and to establish a terminology for the features of the plates that can be applied to less well-known forms; secondly, a discussion of some aspects of placoderm comparative morphology arising from the preceding section; thirdly, a brief review of previously described holonematids in the light of new knowledge; fourthly, a discussion of the relationships of the holonematids.

Specimen numbers are prefixed as follows: I.R.Sc.N.B., Institut royal des Sciences naturelles de Belgique; P. (without additional prefix), British Museum (Natural History); P.M.O., Palaeontological Museum, Oslo; R.S.M., Royal Scottish Museum; S.M.N.H., Swedish Museum of Natural History.

2. *HOLONEMA* FROM WESTERN AUSTRALIA

Holonema westolli sp.nov.

'a form...with a holonematid-like ornamentation' (Brunton, Miles & Rolfe 1969, p. 82)

Holonema (Miles 1971a, p. 213)

Preliminary statements

Name. After Professor T. S. Westoll, F.R.S.

Definition. The armour reaches a length of at least 350 mm; breadth/length index of skull-roof about 92; skull-roof length/nuchal length index about 260; nuchal plate with bicuspid median posterior process; breadth/length index of trunk-shield about 94; median dorsal plate without median anterior or posterior process, and with breadth/length index of about 31; anterior lateral plate with suprascapular margin about $1\frac{1}{2}$ times as long as suprapectoral margin; spinal plate about 10 times as long as it is high; anterior ventrolateral plate with *Lsp/Lt* index of about 50, and with a distinct prepectoral angle.

Type specimen. P. 50984 (figure 73) is the holotype; it has a fairly complete set of trunk plates, part of the skull-roof, extra-scapular plates and part of the scapulocoracoid. Dr D. Merrilees has kindly provided the Western Australian Museum registration number 70.4.243 for this specimen, but the provisional British Museum number is used throughout this work. It is from locality 80 (see below).

Material. Approximately 40 specimens collected by the 1967 Gogo expedition.

Occurrence. Figure 1 is a map of the Gogo Formation localities prepared by Dr W. D. I. Rolfe, a member of the 1967 expedition. *Holonema* has been found at localities 30, 37, 42, 67, 73, 77, 79, 80, 85, 86, 89, 90, 91, 92, 93 and 97. Students of ammonoids and conodonts have correlated the Gogo Formation with the Frasnian 'Zonen' *Manticoceras* to *I α -* to *I γ* of the Rhenish Schiefergebirge (Glenister 1958; Glenister & Klapper 1966; Seddon 1970).

Size. *H. westolli* is one of the largest fishes in the Gogo fauna, and in life it was exceeded in length perhaps only by the arthrodire *Eastmanosteus* sp. Placoderms, like present-day fishes, probably continued to grow throughout life. It is not possible, therefore, to give a terminal size for any particular species, and the statistical study of variability (a notable feature of the dermal skeleton) is enormously complicated by changes in proportions during growth. Terms such as 'juvenile', 'immature' and 'adult' are used very loosely in placoderm studies, and although widely adopted they are undoubtedly best avoided. However, considerable wear of the gnathals may indicate that an individual has reached an advanced age.

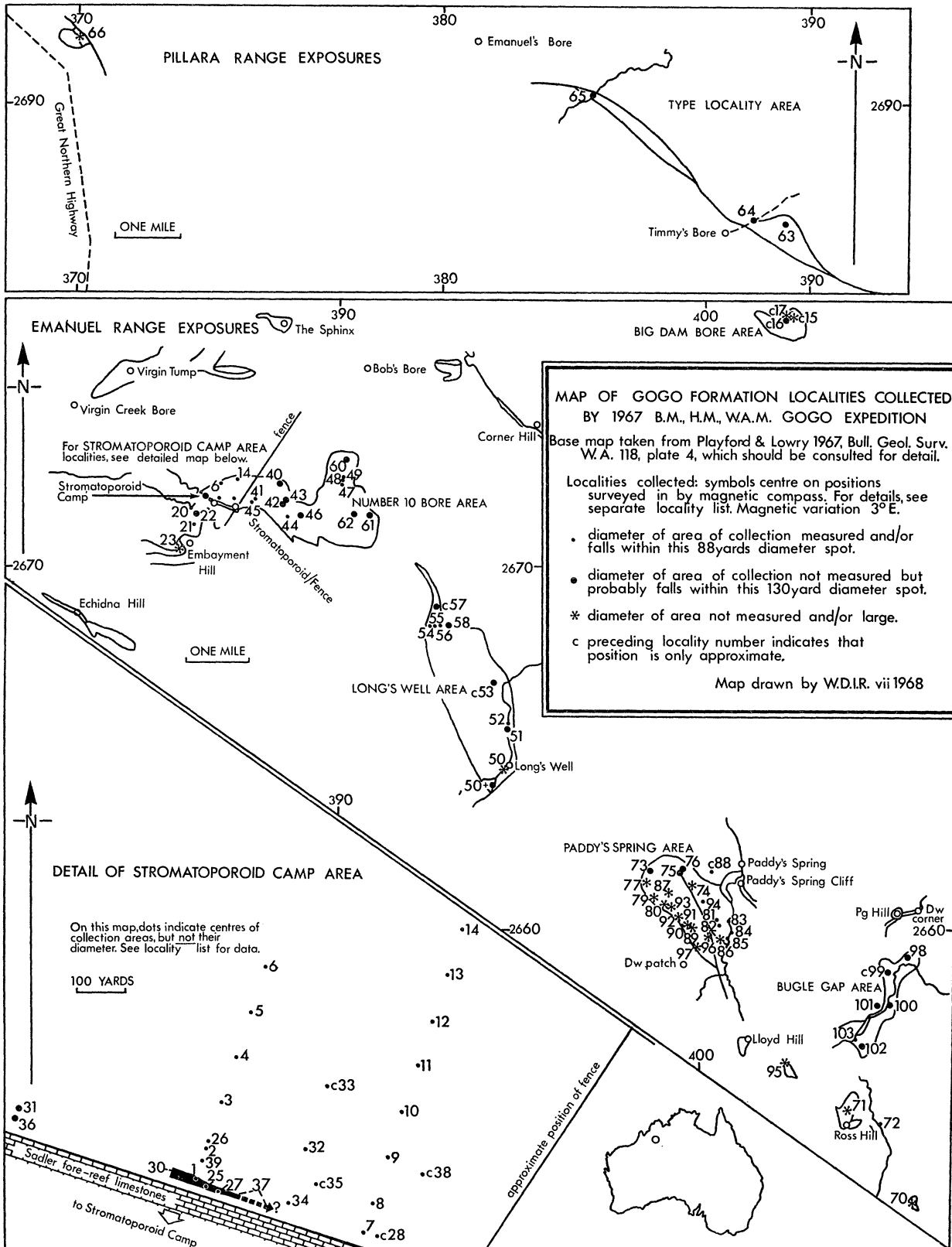


FIGURE 1. Sketch-map of Gogo Formation localities, prepared by Dr W. D. I. Rolfe. Details of all the localities have been deposited in the British Museum (Natural History), the Hunterian Museum, Glasgow, and the Western Australian Museum. Localities 100 and 101 are not in the Gogo Formation.

A series of standard linear dimensions has yet to be generally adopted for arthrodires (see Obrucheva 1962; Miles & Westoll 1968). Some uncontroversial measurements for *H. westolli* are given in table 1. Approximate dimensions for other specimens may be obtained from the illustrations. It will be noted that there is considerable size variation in the material. The largest specimens are of the same order of size as *H. radiatum* Obruchev, which may be regarded as a moderately large placoderm.

TABLE 1. SELECTED MEASUREMENTS (IN MILLIMETRES) OF *HOLONEMA WESTOLLI*, SP.NOV.

P. 50984 (holotype)	length of median dorsal plate	215
P. 50893	estimated length of median dorsal plate	125
P. 51157	estimated length of median dorsal plate	225
P. 50982	length of skull-roof	130
P. 50982	length of nuchal plate	50
P. 51152	length of nuchal plate	54
P. 50995	length of nuchal plate	35
P. 50986	estimated length of spinal plate	100
P. 50893	length of spinal plate	62
P. 50982	length of posterior superognathal	29
P. 50893	length of posterior superognathal	20

Skull-roof

General features

The exoskeletal skull-roof (figures 2 to 4) embraces the usual arthrodiran series of median and paired lateral plates, which interlock to form a unit separate from the cheek. The plates are somewhat specialized in their shape compared with other arthrodires, but a detailed examination of the shield shows that the prepineal region is fundamentally like that of a dolichothoracid and the posterior region fundamentally like that of a brachythoracid. Stensiö (1963 *b*, p. 118) has noted a similar mixture of dolichothoracid and brachythoracid characters in the skull-roof of the arthrodire *Buchanosteus*, which is, however, unrelated to *Holonema*. These characters are noted below in the descriptions of the individual plates, and in the discussion (p. 227). With respect to the type of interspecific variation normally found in families of arthrodires, it may be noted that in *Holonema* the postorbital plate sutures with the paranuchal to separate the central and marginal plates, and the pineal plate sutures with centrals posteriorly and with the rostral (see p. 110) anteriorly, to separate the left and right preorbitals.

The skull-roof is broad and depressed. No complete examples are available, but from the restorations (figures 2, 4) based on uncrushed specimens the roof is almost as broad as it is long, with a breadth/length index (Heintz 1934) of 92. In longitudinal profile the dorsal surface of the head is concave both between the posterior margin and the interorbital region, and between the interorbital region and the rostral margin. The degree of upward sweep of the nuchal varies, and is particularly well marked in P. 51152. The 'dorsolateral edge' ('Dorsolateralkante', Gross 1932, 1937) is not a distinct ridge, but its position is discernible as an axis of fold running approximately from the posteromesial angle of the roof (*pmaa*; figure 4) to the point at which the suture between the postnasalo-rostral (p. 110) and preorbital plates cuts the edge of the orbit. The angle between the dorsolateral and lateral surface about the dorsolateral axis varies with the degree of upward sweep of the nuchal (figure 3). In P. 51152 it is about 160°, and in P. 50982 about 150°. The angle between the axis of the lateral articular fossa and the dorsolateral surface

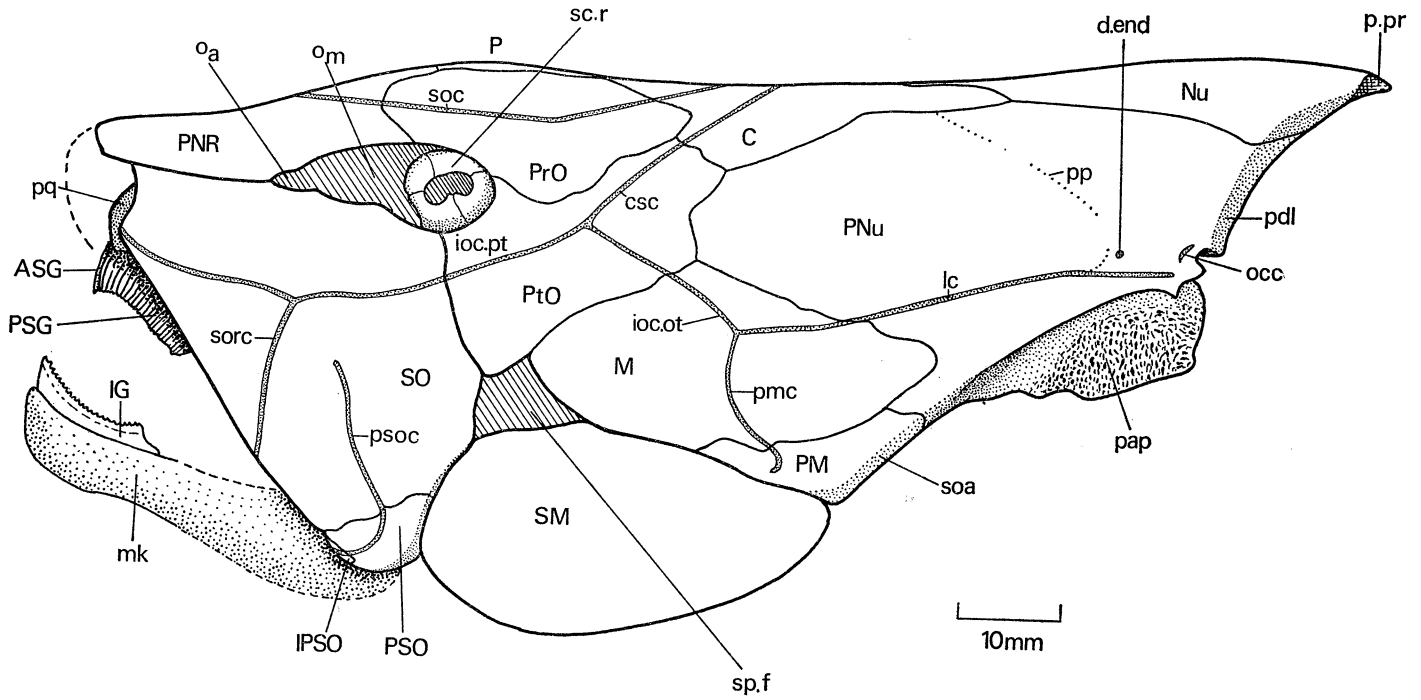


FIGURE 2. *H. westolli* sp.nov. Restoration of head-shield in lateral view.

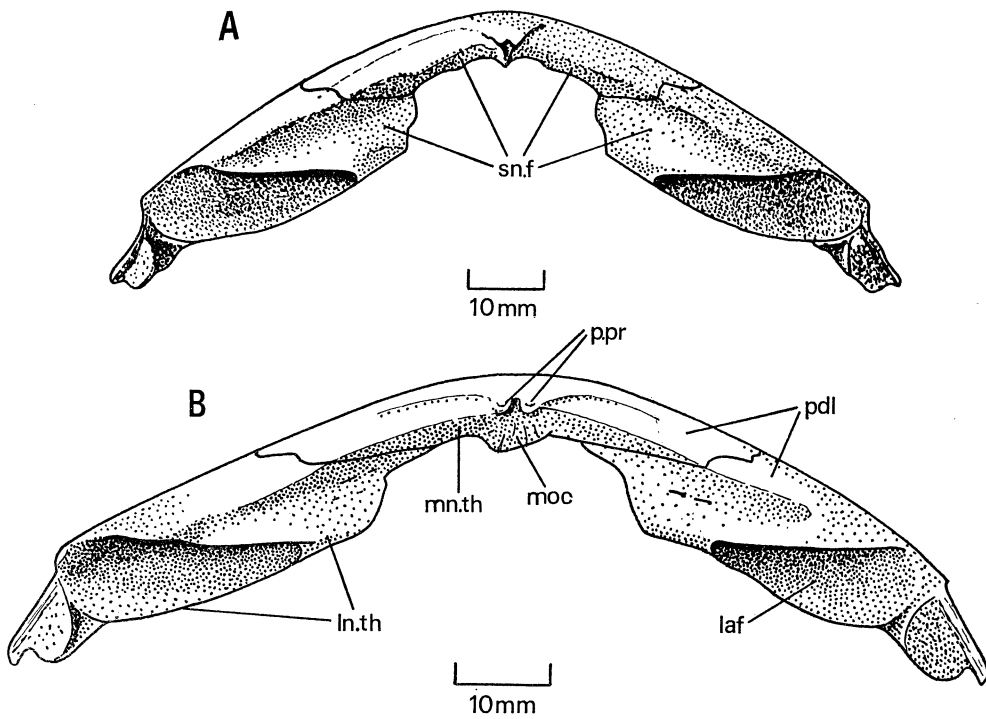


FIGURE 3. *H. westolli* sp.nov. Nuchal and paranuchal plates in posterior view. A, after P. 51152; B, after P. 50982.

(Heintz 1934) also varies. It is about 37° in P.51152 and about 25° in P.50982. The lateral articular fossae are broad, each one occupying between one-third and one-quarter of the breadth of the roof between the posteromesial angles (*pmaa*). The nuchal is relatively short (cf. Stensiö 1963*b* on taxonomic significance), and in the only specimen that can be measured accurately (P.50982), the skull-roof length/nuchal length index (Miles & Westoll 1963, 1968) is 260; the

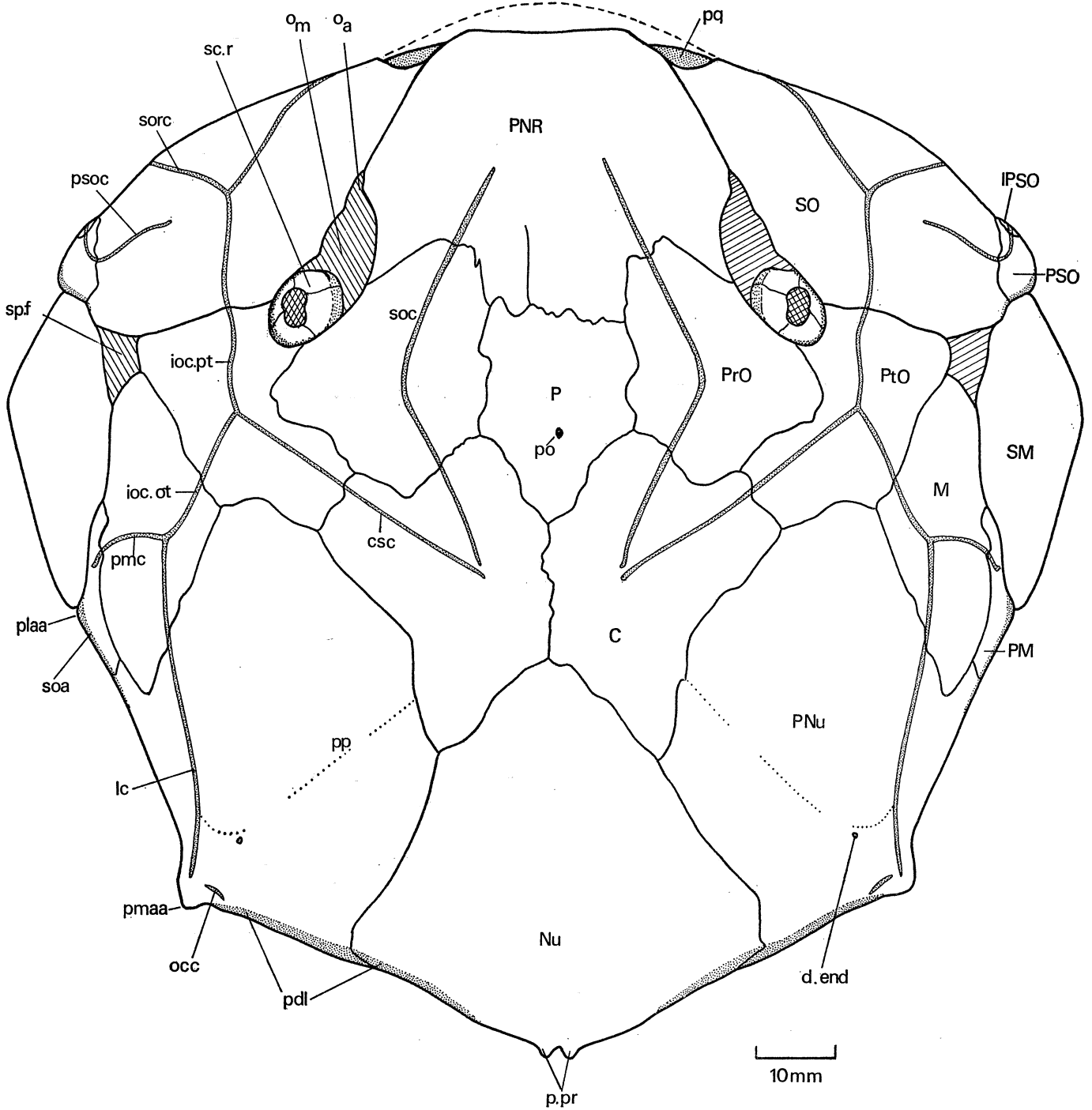


FIGURE 4. *H. westolli* sp. nov. Restoration of head-shield in dorsal view, with cheek bones spread out slightly.

nuchal covering about 38% of the total length of the skull-roof. The orbitoethmoid region is elongated, with the area in front of the pineal opening (the prepineal length) occupying about 38% of the total length of the skull-roof.

In dorsal view the roof can be regarded as an irregular hexagon (figure 4). It has a markedly convex posterior margin delimited by the posteromesial angles (*pmaa* = posterolateral angles of paranuchal plates), with a median, bicuspid posterior process (*p.pr*). Lateral to this process the posterior margin is bevelled to form the posterior descending lamina (*pdl*). The posterolateral margin carries the large occipital para-articular process (*pap*, figure 2), which reaches far along the margin of the paranuchal plate (*PNu*) before merging with the subobstantic area (*soa*). The

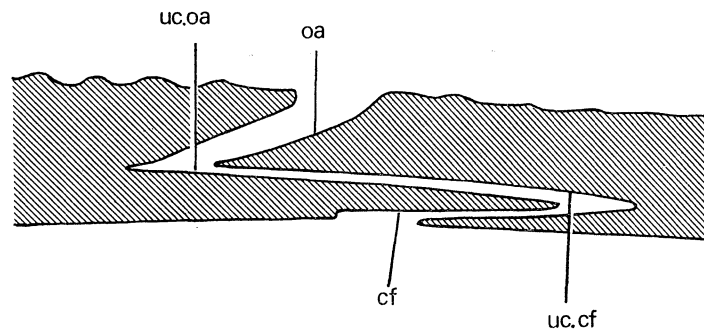


FIGURE 5. *H. westolli* sp. nov. Terminology used for overlap relations between plates in skull-roof.

posterolateral margin ends at the posterolateral angle (*plaa*). The anterolateral margin is unusually irregular in form. This is because of the long, narrow shape of the fenestra orbitalis (p. 141), which deeply embays the anterior edge of the postorbital plate (*PtO*) posteriorly, and the margins of the preorbital (*PrO*) and postnasalo-rostral (*PNR*) plates mesially; and because of the extensive development of the postorbital and marginal (*M*) plates lateral to the main lateral-line canal. There is no distinct dermal postorbital process, as for example in *Coccosteus* (Miles & Westoll 1968); but both anterior and posterior postorbital notches (*apon*, *ppon*, figure 53), lying between the postorbital and marginal and postmarginal plates respectively, are present, as in '*Kujdanowiaspis*' (Stensiö 1945, p. 33, Figure 8A). The anterolateral margin joins the suborbital (*SO*) and submarginal (*SM*) cheek plates in a series of butt joints.

The component plates of the skull-roof interlock in a more complicated system of tongue-and-groove overlaps (figure 5) than is usual in arthrodirans (e.g. Heintz 1932*a*, 1934; Miles & Westoll 1963, 1968; Miles 1966*b*). The system is described as fully as possible in the following account of the individual plates, although it is more variable than can be demonstrated here. The term 'dorsal surface' is used for the ornamented surface of a plate exposed on the outside of the skull-roof, i.e. the outer surface excluding the fringing overlap area. The term 'overlap area' is used for a dorsally overlapped surface (*oa*), and the term 'contact face' for an underlapped surface (*cf*). Arthrodiran overlap areas are usually more deeply impressed in the bone than contact faces, but this is not always the case in *Holonema*. An overlap area or contact face is said to be 'undercut' if a cavity exists between it and the surface of the plate, for the reception of a tongue of bone from an adjacent plate (*uc.oa*, *uc.cf*, figure 5).

The radiation centres of the plates are indicated by the orientation of the neurovascular canals in the basal bone layer. These canals are, however, difficult to see on the bone surface. In some of the stylized drawings in this paper, the shading of the overlap areas and contact faces

has been used to indicate the position of the radiation centres (e.g. figure 6). In such cases the shading lines do not necessarily correspond accurately in orientation to the neurovascular canals on these surfaces, which are often directed towards the radiation centres of adjacent plates, rather than to the radiation centre of their own plate. This phenomenon may be observed in other arthrodires (e.g. *Dickosteus threiplandi* Miles & Westoll), although it has not yet been described in detail. The subject requires further study, and is outside the scope of this paper.

The visceral surface of the skull-roof is not well preserved because of the tendency of the basal, lamellar bone layer to exfoliate during preparation. As far as possible the details of the visceral surface are described below for the individual plates, and the descriptions are summarized in a

TABLE 2. BONE COMBINATIONS IN THE ROSTRALO-PINEAL REGION OF
HOLONEMA WESTOLLI SP.NOV.

P. 50979	PN+R	—	P
P. 50980	PN+R	—	P
P. 50982	PN+R	—	P
P. 51004	PN+R	—	P
P. 51153	PN	R	P
P. 51155	PN	—	R+P
P. 51172	PN+R	—	P†

† Bone not preserved but its existence as a separate element is inferred with a high level of confidence.

composite restoration (figure 53). At this point it may be noted that there is no well-marked median depression for the dorsal surface of the brain-case, except most posteriorly where the paranuchal and transverse occipital cristae (*cr. PN_u, toc*) are well developed. There is no lateral consolidated region, such as usually occurs on the postorbital and marginal plates of brachythoracids (Heintz 1932*a*; Miles & Westoll 1968). There is, however, a well-developed nuchal thickening (*mn.th, ln.th*), consonant with the presence of large lateral articular fossae (*laf*). The lateral part of the paranuchal is not developed as a distinct cucullaris fossa, in contrast to '*Kujdanowiaspis*' (Stensiö 1945, 1963*b*), and is in this respect similar to brachythoracids (e.g. Miles & Westoll 1968, Figure 2*a*; Stensiö 1963*b*, Figure 113), and there are no distinct grooves for the postorbital processes of the brain-case (see p. 143).

Rostral and pineal regions

The exoskeleton of the rostral and pineal regions comprises combinations of the rostral (*R*), pineal (*P*) and postnasal (*PN*) plates (figures 6 to 9). Where the rostral and pineal plates occur separately, each is clearly homologous with the plate of the same name in 'normal' arthrodires. The paired postnasals of brachythoracids are, however, represented by a large median bone. Whether or not the equivalent of the internasal bone was present is not clear. This problem is discussed on p. 189.

Table 2 summarizes the combinations of bones found in the rostral and pineal regions in the seven specimens. Five specimens exhibit the usual condition, there is a large, compound postnasalo-rostral plate and a separate pineal plate (*PNR, P*, figures 6, 7D). The sixth specimen (figure 7A) has independent median postnasal (*PN*), rostral (*R*) and pineal (*P*) plates. The seventh specimen (figure 8) has a median postnasal plate (*PN*) and a separate, compound rostral-pineal plate.

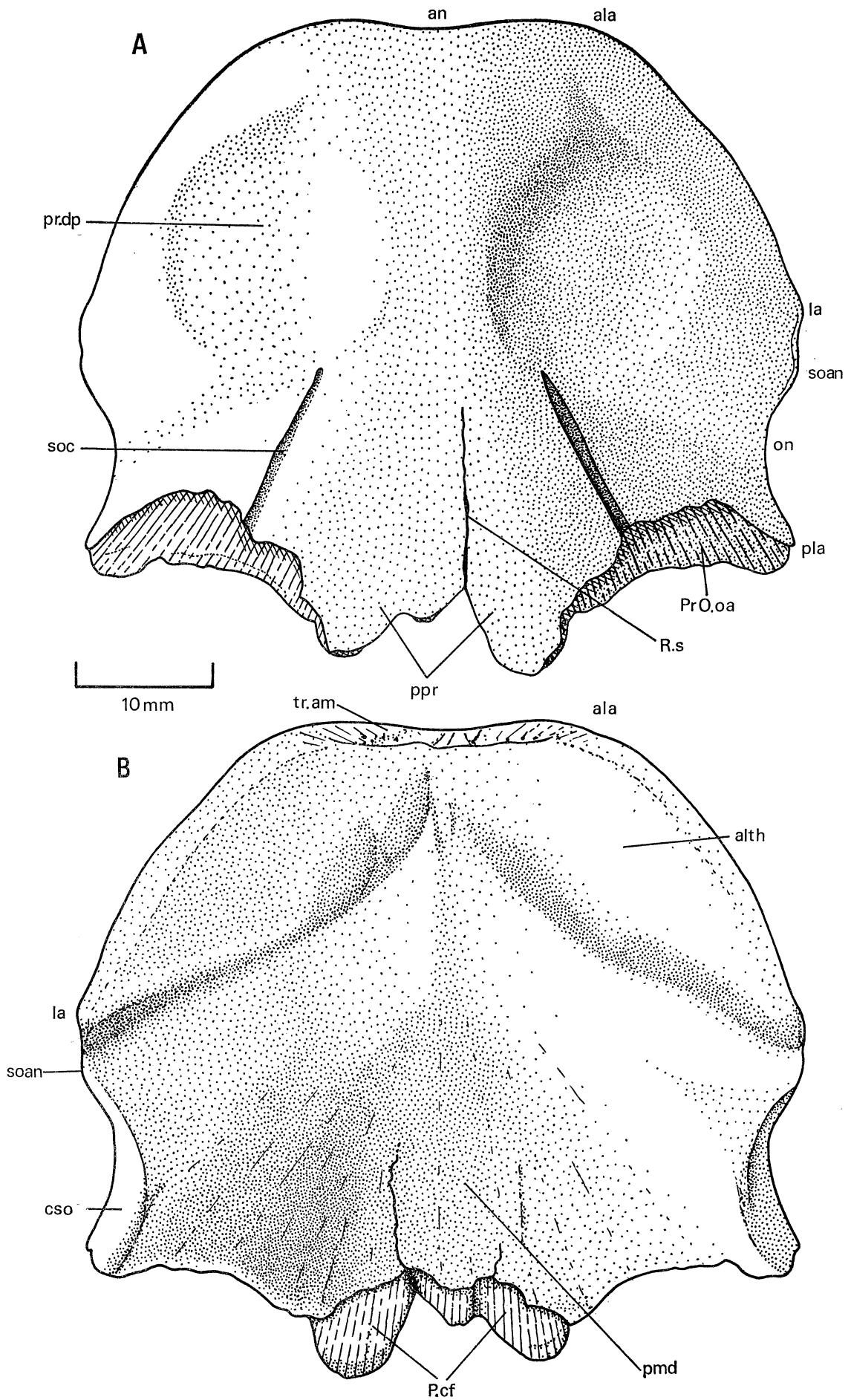


FIGURE 6. *H. westolli* sp.nov. Postnasalo-rostral plate in A, dorsal and B, visceral view. After P. 50979.

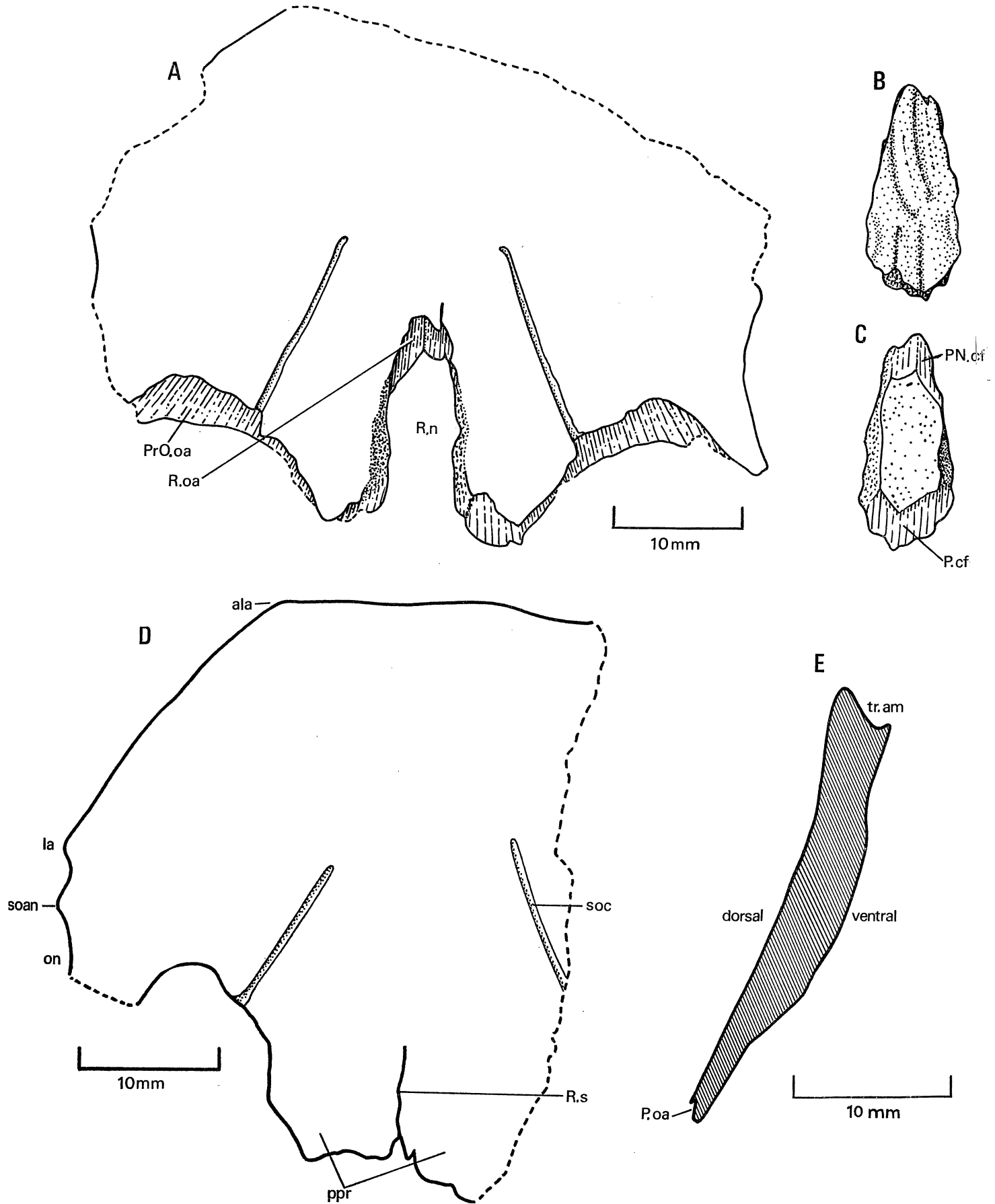


FIGURE 7. *H. westolli* sp. nov. A, postnasal plate in dorsal view, and B, C, rostral plate in dorsal and visceral view, P. 51153. D, postnasalo-rostral plate in dorsal view, P. 50980. E, longitudinal section in middle line of postnasalo-rostral plate, P. 51172.

Postnasal and rostral plates (figures 3, 4, 6 to 8, 16, 40, 53)

The inclusion of the postnasals in the anterior median plate of the skull-roof is indicated by the supraorbital sensory lines (*soc*), which run forward from the preorbital plates. This large plate forms part of the margin of the orbit, like the paired postnasals of some dolichothoracids (but see below, p. 182; Denison 1958, Figure 105; Stensiö 1963 *b*, 1969 *a*). Heintz (1962, Figures 4 to 7) has shown, however, that a comparable postnasalo-rostral plate, carrying the supraorbital lines, is present in the dolichothoracid *Arctolepis*, and possibly in *Bryantolepis*, although he interprets it as a rostral plate, and unconvincingly seeks the postnasal plate in a more lateral

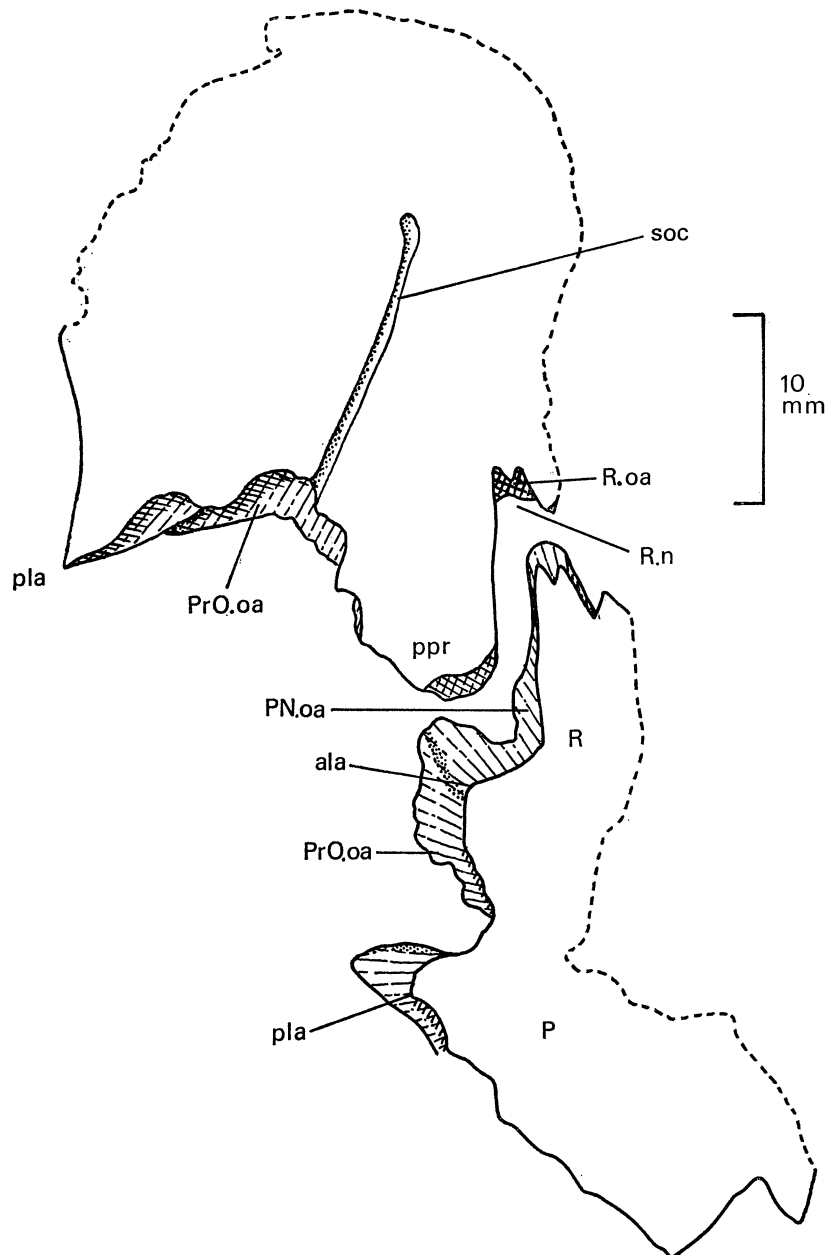


FIGURE 8. *H. westolli* sp.nov. Postnasal and rostral-pineal plates, P. 51155.

position (see p. 178). A similar large plate has been described in 'Radotina', where, however, it is situated in front of the dorsally placed nasal openings. Probably this plate is the fused postnasals, although it is termed the rostral by Gross (1959) and 'possible fused anterior supragnathals' by Westoll (1967).

There is evidence to suggest that an independent rostral plate was present in juvenile stages of *Holonema*. Usually the postnasalo-rostral exhibits a vestigial longitudinal suture in the rostral plate region (*R.s.*), which indicates that the rostral plate fused with the hind end of the postnasal at a late stage of growth. Sometimes this vestigial suture is to the left (P. 50982; figures 4, 16) and sometimes to the right (P. 50979; figures 6, 40) of the middle line. In P. 50980, however, it is in the middle line, presumably due to the lateral displacement of the rostral plate (figure 7D). In P. 50979 (figure 6B) there is also a trace of the left lateral suture on the visceral surface. Only in P. 51004 and P. 51172 has the suture between the postnasal and rostral bones been completely obliterated. It is noteworthy that in no case is the compound nature of the postnasalo-rostral plate revealed by the disposition of the surface ornament or the neurovascular canals that open on the visceral surface. The radiation centre of the postnasalo-rostral is situated in the middle line in the anterior region of the plate.

The postnasalo-rostral is gently arched transversely and has a concave longitudinal profile (figures 6A, 7E). The following features can be recognized. The anterior margin may bear an anterior notch (*an*), although this margin is convex near the middle line in P. 50980 and P. 51172 (figure 7D); there is an anterolateral angle (*ala*), well defined only in P. 50980; a lateral angle (*la*); a supraorbital angle (*soan*); an orbital notch (*on*); a posterolateral angle (*pla*); and a posterior process (*ppr*). The posterior margin of the posterior process sutures with the pineal plate, and is irregularly formed. Lateral to this process, there is an undercut overlap area for the pre-orbital plate (*PrO.aa*). On the upper surface the supraorbital sensory lines (*soc*) are directed towards the radiation centre, although they end well short of this point. Anterolaterally there are extensive, prerostal depressions (*pr.dp*), but they are shallow and to some extent obscured by the ornamentation.

The visceral surface (figure 6B) is thickened anterolaterally (*alth*), with the rounded posteromesial edge of each thickening (the posteromesial ridge) curving across the surface from the lateral angle (*la*) to fade out near the radiation centre. The lateral margins are slightly bevelled between the lateral (*la*) and anterolateral (*ala*) angles, where the plate makes a butt joint with the suborbital plate (figure 2). The edge of the orbital notch is more distinctly bevelled, to give a narrow supraorbital crista (*cso*). This thick anterior margin of the plate is truncated (*tr.am*), and appears either to have joined with another plate in a butt joint or to have continued forwards in soft tissues to give the animal a more elongated snout (p. 189). The posteromedian region of the visceral surface is in the form of a broad, triangular depression (the posteromedian depression, *pmd*). A clearly defined contact face (*P.cf*) for the rostral overlap surface of the pineal plate lies on its posterior margin.

In P. 51153 (figure 7A) the median postnasal plate has a deep posteromedian rostral notch (*R.n*) for the separately formed rostral plate. This rostral plate (figure 7B, C) has an anterior contact face (*PN.cf*) on its visceral surface for the rostral overlap area of the postnasal plate (*R.aa*), and a posterior, pineal contact face (*P.cf*). A deep rostral notch is also found in P. 51155 (*R.n*; figure 8), although here the rostral plate is fused with the pineal. The spongiosa of the middle bone layer is exposed on the lateral sides of the rostral notch and rostral plate in P. 51153, which suggests some incipient fusion between the postnasal and rostral plates.

Pineal plate (*P*, figures 4, 9, 16, 52, 53)

This is a large plate which usually has the pentagonal form found in other arthrodires. It is completely surrounded by deeply undercut overlap surfaces, anteriorly for the rostral plate (*R.oa*), laterally for the preorbital plates (*PrO.oa*) and posterolaterally for the central plates (*C.oa*). Contact faces for the preorbital and central plates are also found on the visceral surface (*Pro.cf*, *C.cf*, figure 9B), because of the tongue-and-groove overlap relationship with these plates. On the margin of the dorsally exposed surface of the pineal there are anterolateral (*ala*), posterolateral (*pla*) and posteromedian (*pma*) angles, which demarcate the fringing overlap

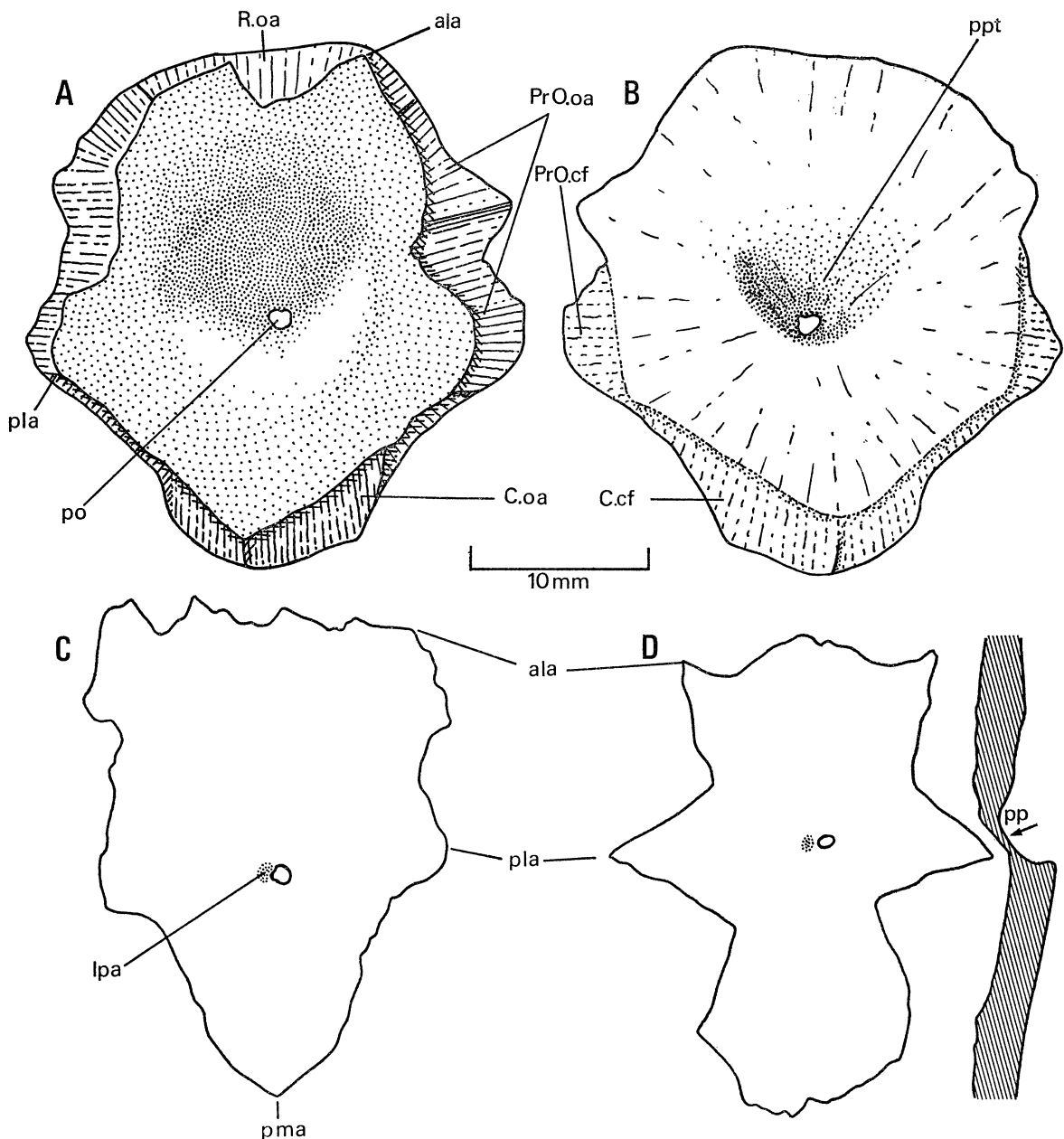


FIGURE 9. *H. westolli* sp. nov. Pineal plates. A, B, after P. 51153 in dorsal and visceral view; C, P. 50982; D, P. 51004 with longitudinal section in middle line; arrow points to level of pineal opening on the visceral surface. For *pp* read *ppt*.

surfaces. The lateral angles are particularly well marked in P. 51004 (figure 9D). There is a single pineal opening (*po*) which is sunk in an extensive, shallow depression on the dorsal surface. This depression is surrounded by a ridge of the ornament in P. 51004 (figure 52). On the visceral surface there is a deep, undivided pineal pit (*ppt*) which faces anteroventrally (figure 9D). In brachythoracid arthropods the pineal pit is normally divided into left and right chambers for paired pineal organs, which are roofed over by a thin sheet of bone, so that in well-preserved specimens there are no pineal openings (Edinger 1956; Stensiö 1963*b*; Miles & Westoll 1968). *Holonema* thus appears to be unusual in having an undivided pineal pit and a single pineal opening. However, in the three specimens examined, the pineal opening is situated to the right of the middle line, whilst an area of thin bone to the left, of similar extent to the opening (*lpa*), is translucent when viewed against a light. I believe that this area marks the position of the left pineal organ, and that the pineal opening marks the position of the right pineal organ. The thin bar of bone between these structures is equivalent to the longitudinal partition between the pits in other arthropods. The pineal opening may be a natural structure, or it may be a post-mortem feature caused by destruction of the thin bone during preparation.

The fusion of the rostral and pineal plates in P. 51155 (figure 8) has already been noted. The left anterolateral angle (*ala*) enables an approximate boundary between the rostral and pineal components to be recognized.

Preorbital plate (PrO, figures 2, 4, 10, 16, 52, 53)

The preorbital approaches a quadrilateral (although it has more than four angles), and is slightly arched in transverse and longitudinal planes. It lacks an anterior descending lamina, the structure which forms the dermal preorbital process of the skull-roof in typical brachythoracids (e.g. *Cocosteus*, Miles & Westoll 1968), and in this respect it shows an important similarity to dolichothoracids (see, for example, Denison 1958). The supraorbital canal (*soc*) crosses the upper surface in a gentle arc. The features of the upper exposed face (figure 10) include the anterior (*aa*), anterolateral (*ala*), postorbital (*poa*), posterolateral (*pla*), posterior (*pa*), posteromesial (*pma*) and anteromesial (*ama*) angles. The relationship of these angles to the adjacent plates can be seen in figures 2, 4. Posterolateral overlap surfaces are present for the postorbital and central plates (*PtO.oa*, *C.oa*). Anteriorly there is a narrow overlap surface for the postnasal plate (*PN.oa*) and mesially there are overlap areas for the postnasal (*PN.oa*) and pineal (*P.oa*) plates. These overlap surfaces are well seen in P. 51155 (figure 10C). Corresponding contact faces are present on the visceral surface of the plate, where they are more deeply undercut (figure 10B), showing that the margins of the preorbital inserted into the adjacent plates in a series of complicated tongue-and-groove joints. The postnasal area, however, becomes a simple contact face most laterally (*PN.cf*). Associated with the complex tongue-and-groove joints, the postorbital contact face is deeply excavated behind the postorbital angle in P. 51153 (*x*, figure 10B), for a process of the postorbital plate. A similar excavation is found in front of the posteromesial angle in P. 51155 (*y*, figure 10C) for a process of the pineal plate. In the same position in P. 51153, the overlap surface is channelled on the visceral surface for a corresponding thickening of the pineal plate (*ch₁*, figure 10B), and a similar channel is found on the postorbital overlap surface (*ch₂*).

On the visceral surface the plate is thickened posterolaterally, where it forms part of the supraorbital crista (*cso*, figure 10B). The crista is constricted at the anterolateral angle, but it widens posteriorly. There is a broad, transverse groove (*tg*), and anterior to this a shallow, oval

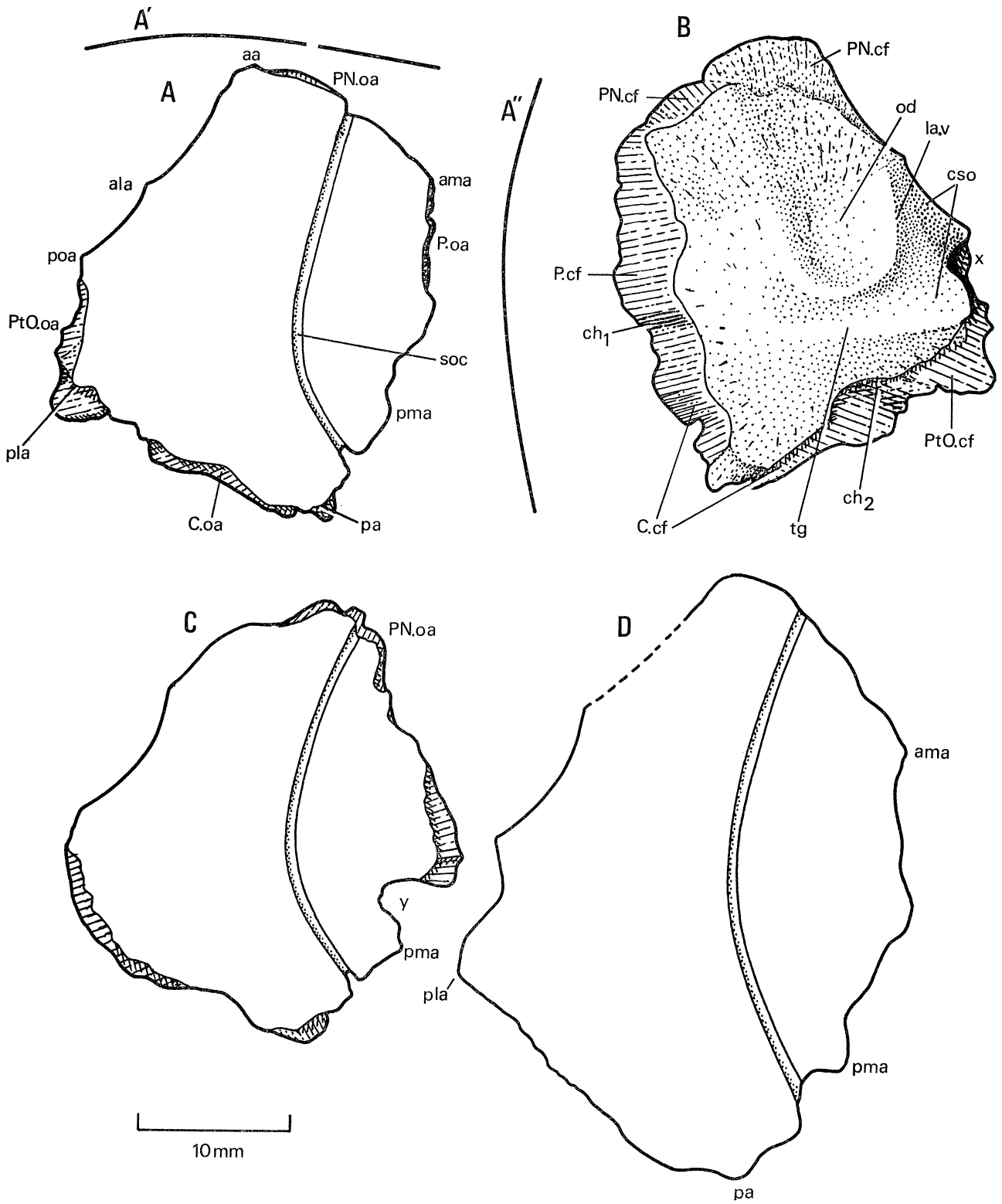


FIGURE 10. *H. westolli* sp. nov. Preorbital plates, left. A, B, after P. 51153 is dorsal and visceral view with A', transverse and A'', longitudinal profiles; C, P. 51155 in dorsal view; D, P. 50980, dorsal view.

depression which is well-defined posteriorly (*od*). I cannot explain the depression, but the groove may have received the dorsal surface of the antorbital and supraorbital processes of the brain-case. If this is so, the ridge (*la.v*, figures 10B, 53) which defines the groove anterolaterally is equal to the 'ventral lamina of preorbital plate' in '*Kujdanowiaspis*' (Stensiö 1945, Figure 8B, 1963*b*; see also *Cocosteus*, Miles & Westoll 1968, Figure 2A). Another explanation, which I feel is less

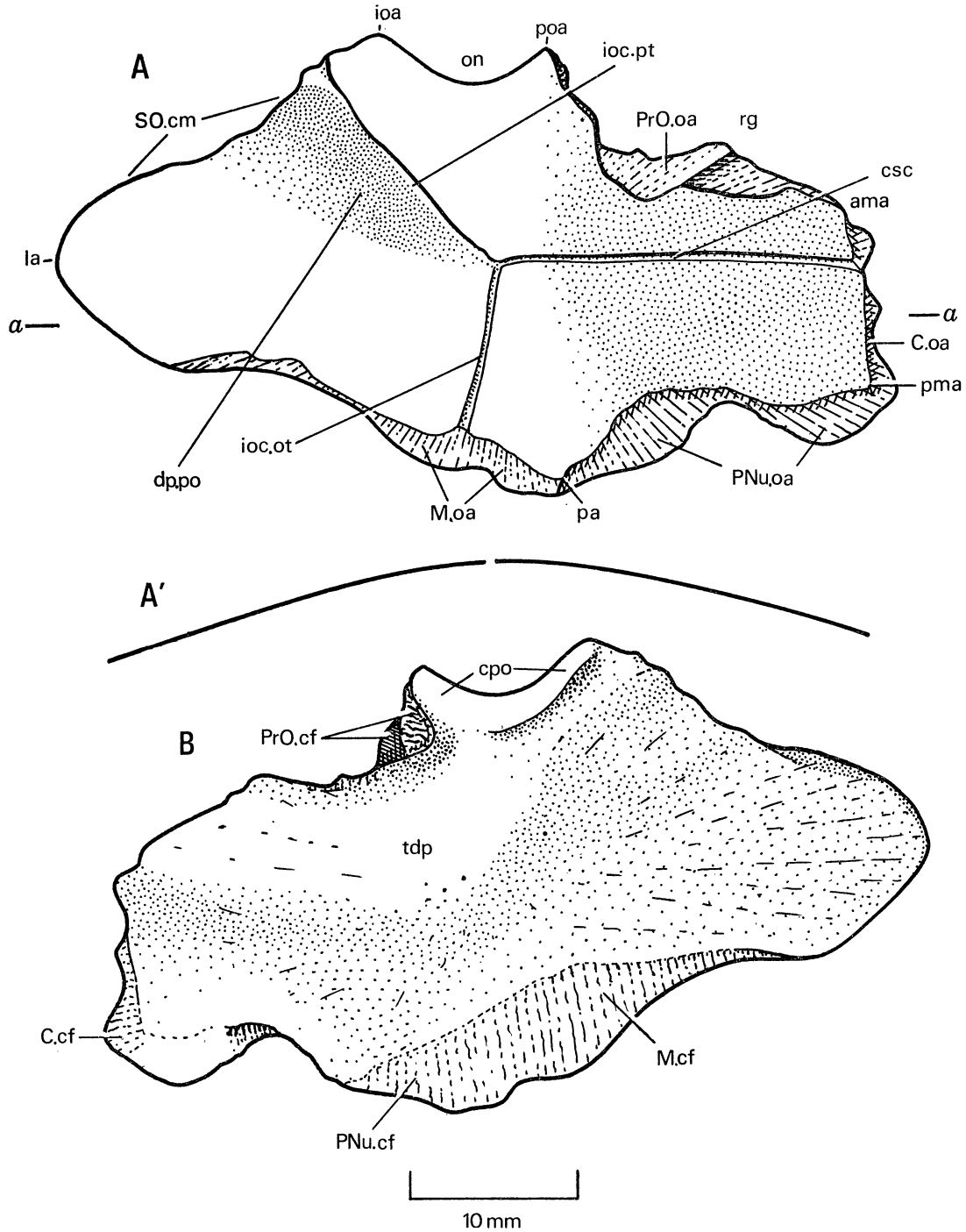


FIGURE 11. *H. westolli* sp.nov. Postorbital plate, left, in A, dorsal and B, visceral view with A', profile at *a-a*. After P.51153 and P.51171.

likely, is that the groove corresponds to the canal in pholidosteid brachythoracids which Stensiö (1963*b*, 1969*a*) interprets as a myodome for the superior oblique eye muscles and possibly also for a large vein from the dorsal surface of the endocranium.

Postorbital plate (PtO, figures 2, 4, 11, 16, 52, 53)

Although steeply inclined in the skull-roof and crossed by the dorsolateral axis of the head (p. 106), the postorbital plate is only gently bowed from side to side (figure 11A). However, it is thickened just behind the orbit, and in some specimens this results in a distinct postorbital depression in the upper surface (*dp.po*, figure 11A). This surface is indistinctly divided into anterior, mesial and lateral laminae. A complete plate has not been found, but by combining specimens it can be restored with some confidence. The postorbital (*ioc.pt*) and otic (*ioc.ot*) branches of the infraorbital sensory line meet the central line (*csc*) at the radiation centre. The anterior lamina bears a distinct orbital notch (*on*), which is bounded by well-developed infra-orbital (*ioa*) and postorbital (*poa*) angles. Lateral to the postorbital angle the edge of the plate is thick and rounded, where it makes a simple contact with the suborbital plate (*SO.cm*), but this margin thins more laterally where it lay free in the dermis. Mesial to the supraorbital angle is the deeply undercut overlap area for the preorbital plate (*PrO.oa*). In P.51153 (figure 11A) this overlap surface carries a short oblique ridge (*rg*) for a corresponding depression on the pre-orbital plate (*ch₂*, figure 10B). The mesial margin bears a narrow overlap area for the central plate (*C.oa*), and the posterior margin bears deeply undercut overlap areas for the paranuchal (*PNu.oa*) and the marginal (*M.oa*) plates. These areas are defined on the external surface of the plate by the anteromesial (*ama*), posteromesial (*pma*) and posterior (*pa*) angles. The lateral lamina of the plate ends in a distinct lateral angle (*la*). The tip of this lamina is not in contact with other plates in the skull-roof (figure 2).

The visceral surface is marked by central (*C.cf*), paranuchal (*PNu.cf*) and marginal (*M.cf*) contact faces, the last two merging into one continuous area. There is also a small contact area for the preorbital plate (*PrO.cf*), lateral to the postorbital cresta (*cpo*). This cresta is particularly deep and well defined laterally, where it projects away from the general surface of the plate. A shallow depression (*tdp*) on the visceral surface probably corresponds in part to that figured for '*Kujdanowiaspis*' (Stensiö 1945, Figure 8B) and more recently termed the 'postocular division of supra-orbital area' (1963*b*, Figure 42C). In *Holonema* the m. levator palatoquadrati had its origin in this depression (p. 177).

Central plate (C, figures 4, 12, 13, 16, 48, 52, 53)

Each central plate is slightly arched transversely, but is flat longitudinally. The external face has an anterior (*apr*), anterolateral (*alpr*) and posterior (*ppr*) process (figures 12B, 13A), although the first two processes are not always distinct (figure 13B). Similar divisions are found in the centrals of other brachythoracids (e.g. *Cocosteus*, Miles & Westoll 1968) and some dolichothoracids (*Anarthraspis*, Denison 1958, Figure 105E), but the posterior process is much longer in *Holonema* than in any other arthrodire. The anterior and posterior processes end in well defined angles (*aa*, *pa*). There are also antero- and posterolateral angles (*ala*, *pla*) which define the extent of the lateral process, and antero- and posteromesial (*ama*, *pma*) angles which define the median margin of the plate. The median suture between the central plates is relatively straight in comparison with other brachythoracids (e.g. Miles 1966*b*, Miles & Westoll 1968), and compares better with that of dolichothoracids (Denison 1958, Figure 105). The mesial overlap

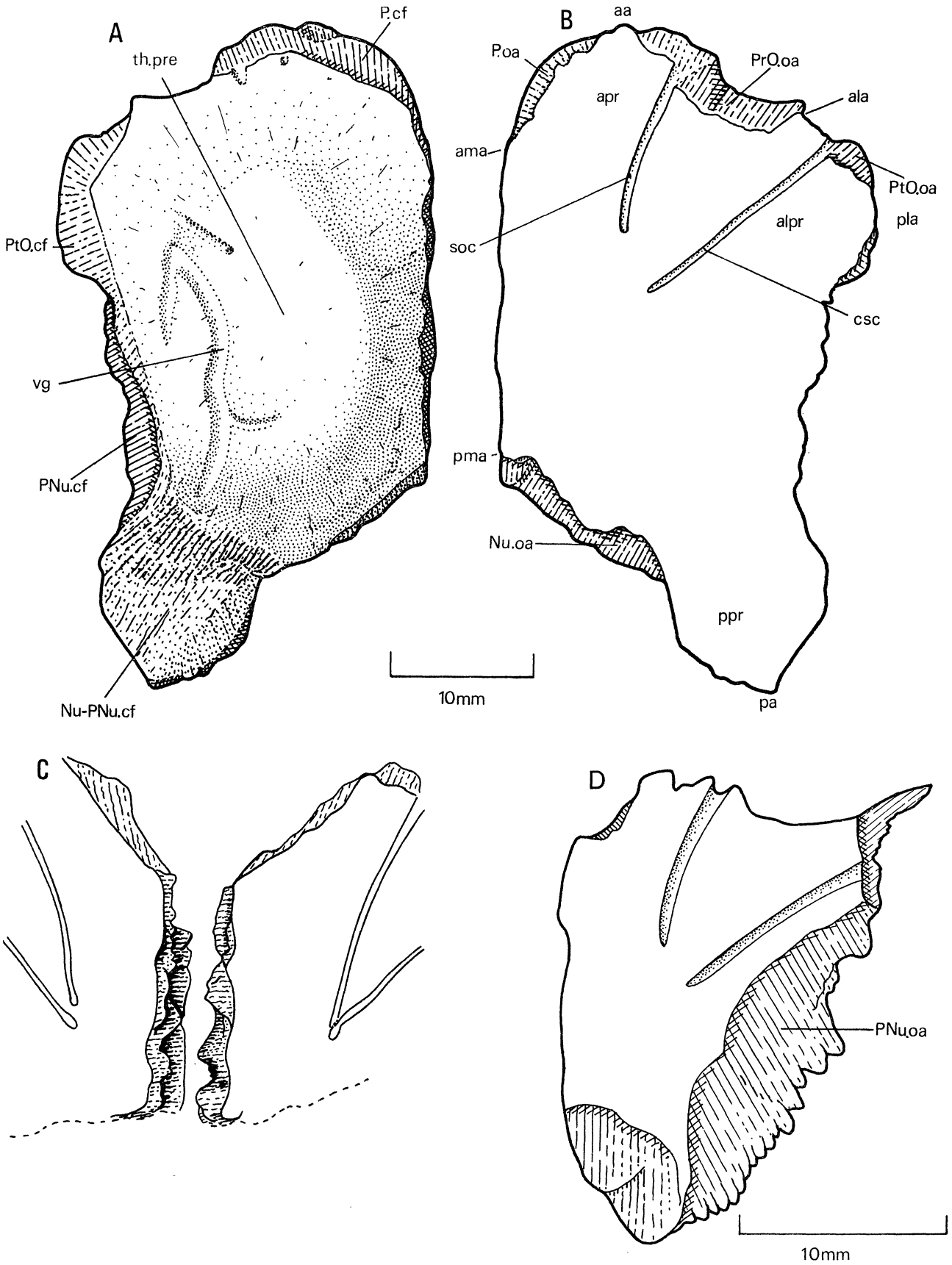


FIGURE 12. *H. westolli* sp.nov. Central plates. A, B, right plate in visceral and dorsal view, based on P.50979; C, mesial margins of left and right plates tilted up towards the middle line to show the overlap surfaces, P.51153; D, right plate in dorsal view, P.50893.

surfaces are not of the usual kind, as the paired centrals are held together by an irregular series of pits and short processes (figure 12C). Overlap areas are present on the dorsal surface for the pineal (*P.oa*), preorbital (*PrO.oa*), postorbital (*PtO.oa*) and nuchal (*Nu.oa*) plates. The first is little more than a slight bevelling of the margin where it forms a tongue which slotted into a groove on the pineal plate. The others are deep, undercut surfaces. In P. 50893 (figure 12D) a broad overlap surface for the paranuchal (*PNu.oa*) is also present. It is unusual in having a pectinate margin. Finally, on the dorsal surface, the laterosensory system is represented by the supraorbital (*soc*) and central (*esc*) lines. Normally the grooves for these lines do not meet, though they may meet on the right central of P. 51153 (figure 12C). This is the only case in the 11 plates available. The presence of the supraorbital canal is a brachythoracid character, as it is not normally present on the central plate in dolichothoracids (Denison 1958). The middle pit-line (*mpl*) is represented by a short series of pits in P. 50962 (figure 13A), but otherwise it is not known. There is never a trace of the posterior pit-line.

There is an extensive pre-endolymphatic thickening (*th.pre*) on the visceral surface, a structure described only for brachythoracids (Stensiö 1963*b*; Miles & Westoll 1968). In P. 50982 it bears a depression for the proximal regions of the vertical semicircular canals (*gr.scc*, figure 53). The centre of ossification of the plate lies at the centre of the pre-endolymphatic thickening. Laterally the thickening is crossed by a broad, vermicular groove (*vg*), which has a single mesial branch. There is also a short, separate, oblique anterior groove. These are possibly neurovascular grooves, comparable with those described for '*Kujdanowiaspis*' (Stensiö 1945, Figure 8B). They have no obvious relationship to the sensory canals on the dorsal surface, although the short oblique groove lies almost under the central sensory line. Perhaps they were for vessels of a subcutaneous vascular plexus, of the type described by Ørvig (1957, Figure 6) in an *Actinolepis*-like dolichothoracid from Spitsbergen. The visceral surface of the posterior process is slightly depressed as a contact face for overlap areas on the nuchal and paranuchal plates (*Nu-PNu.cf*), and a similar contact face is present at either side of the anterolateral angle for the postorbital plate (*PtO.cf*). More strongly depressed contact faces for tongue-and-groove joints are found for the pineal plate (*P.cf*) on the anterior process, and laterally for the paranuchal plate (*PNu.cf*), between the anterolateral and posterior processes.

The paired central plates of P. 50982 bear a deep median pit on the dorsal surface. This pit has a deep inner chamber that penetrates to the basal bone lamina, and a broad upper chamber (*mpt.x*, figure 13A). The floor of the pit is pierced by several large, irregularly placed foramina. Possibly this pit housed sensory organs, as has been suggested for the much smaller pits on the cheek of coccosteids (Ørvig 1960; Miles 1966*b*; Miles & Westoll 1968) and on the skull-roof of *Rhachiosteus* (Miles 1966*a*), but the fact that the pit is not present in other specimens speaks against this interpretation. The pit differs from the lesions which are commonly found on the plates of *Holonema* at Gogo (p. 177) in having a complete lining of smooth bone, covering the spongy middle bone layer. Nevertheless, it may be interpreted as a healed wound, sustained at an early stage of growth.

Marginal plate (M, figures 2, 4, 16, 25, 48, 53)

This plate is not usually completely preserved, but it is well seen in P. 50893 and I have a high level of confidence in the accuracy of the restorations (figures 2, 4, 53). The marginal appears to be an almost flat plate, perhaps slightly curved in the transverse plane. On the upper surface the main lateral-line (*lc*), the otic branch of the infraorbital canal (*ioc.ot*) and the postmarginal

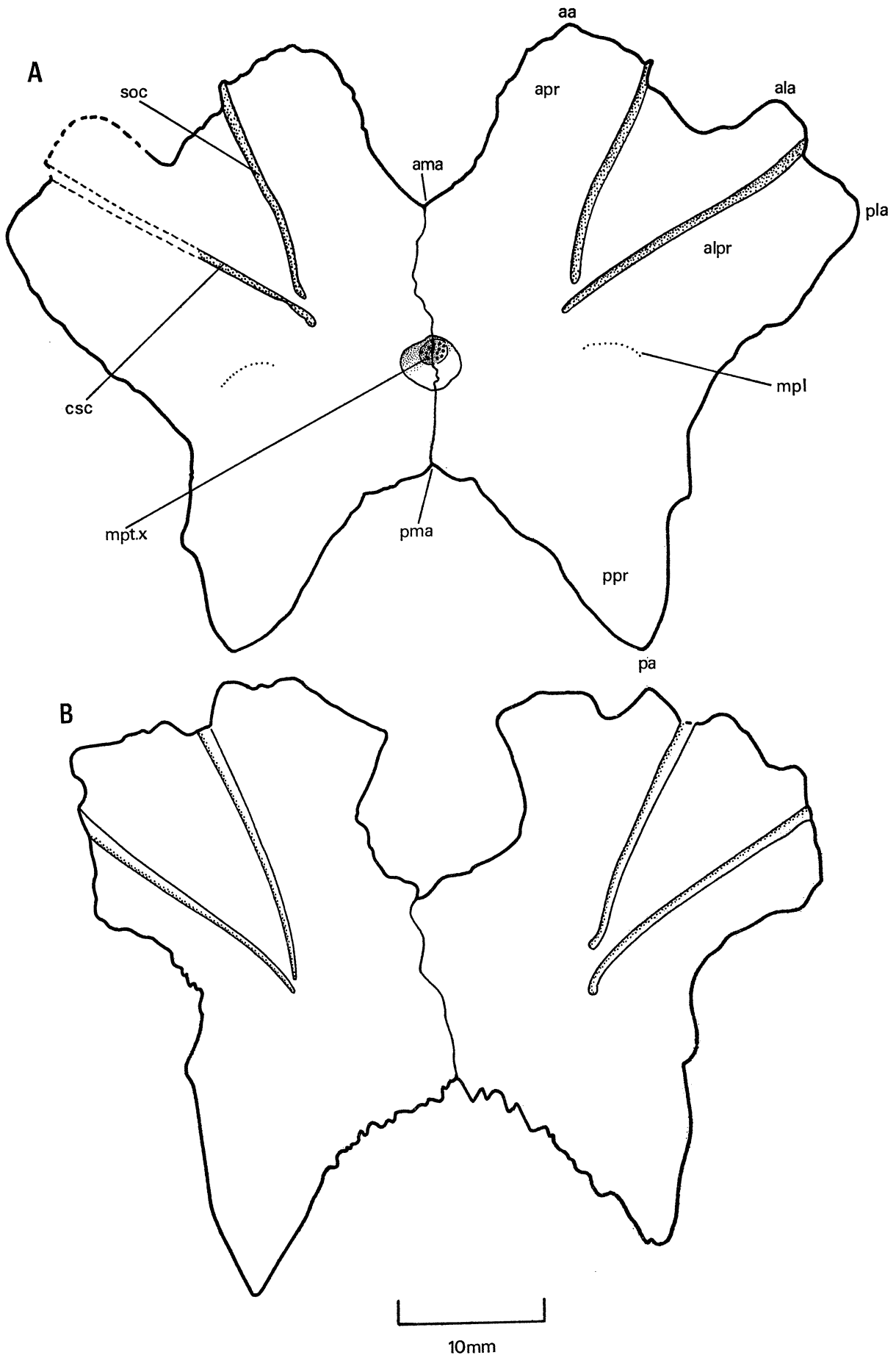
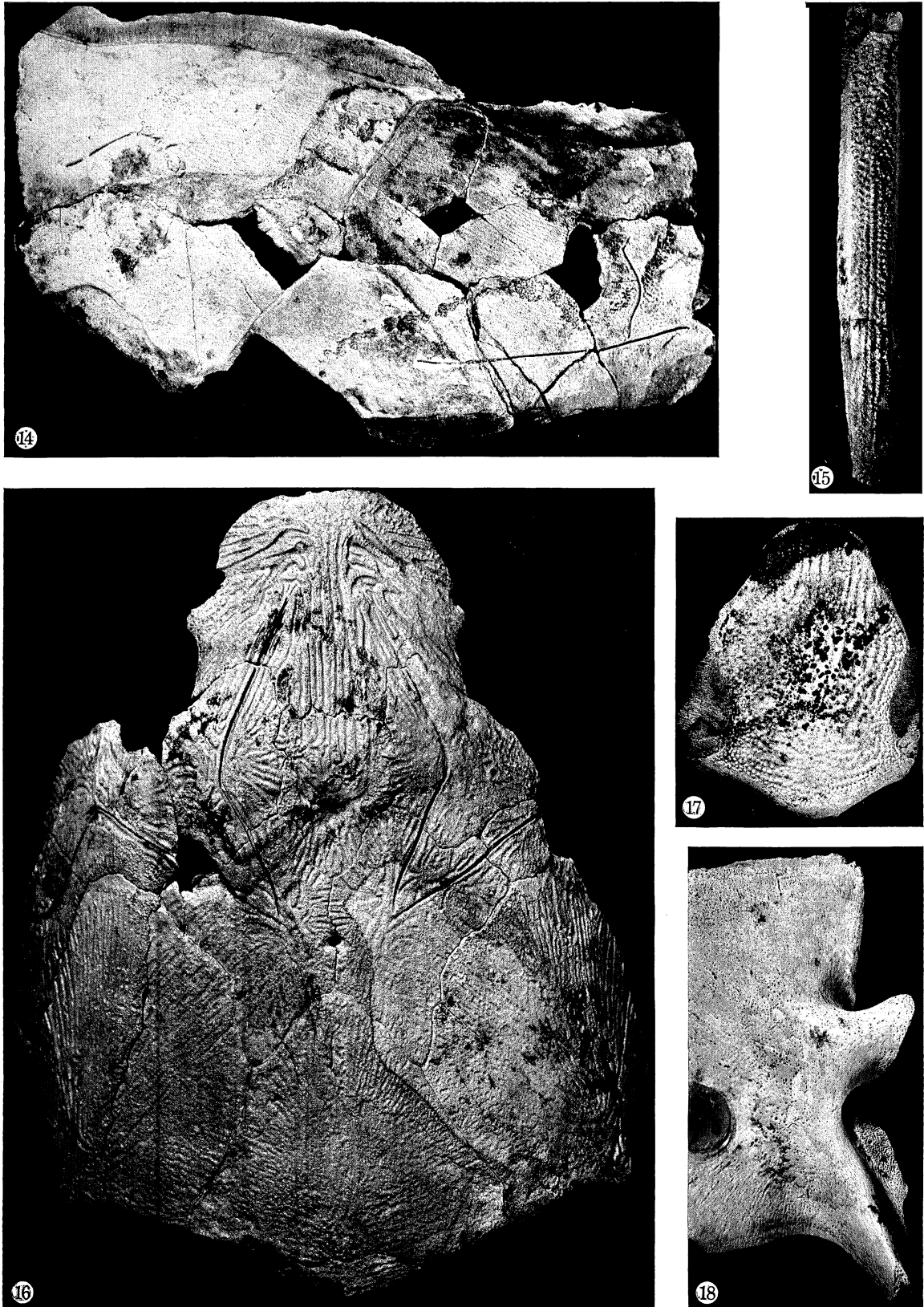


FIGURE 13. *H. westolli* sp.nov. Central plates in dorsal view. A, P. 50982; B, P. 51004.



Holonema westolli sp. nov.

FIGURE 14. Right anterior dorsolateral and posterior dorsolateral plates. P. 51014 ($\times \frac{2}{3}$).

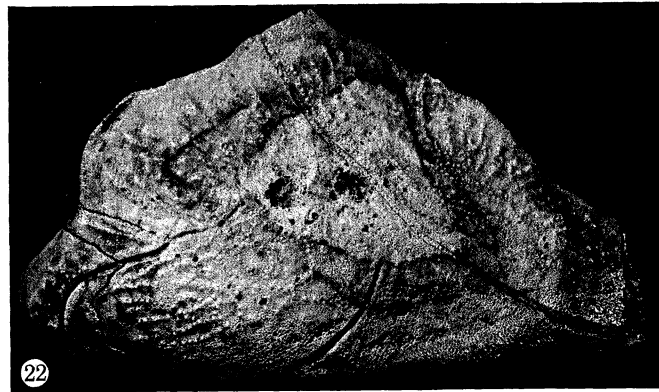
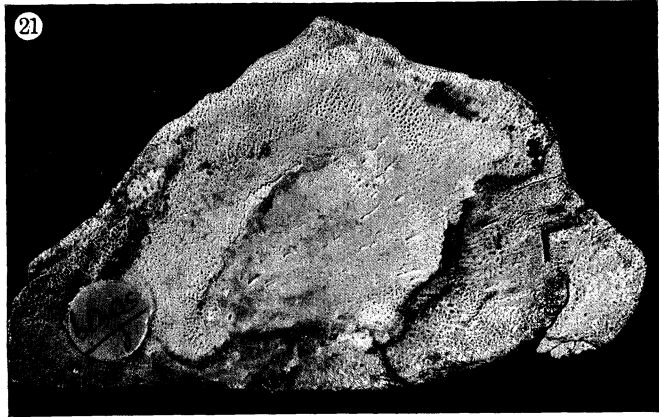
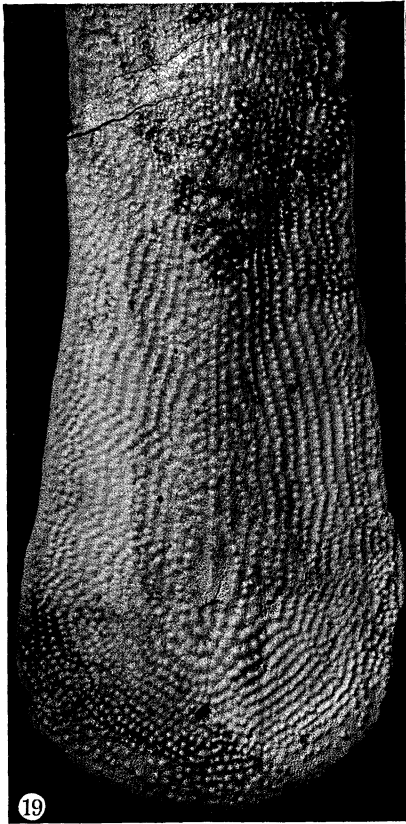
FIGURE 15. Left spinal plate. P. 50988 ($\times 1$).

FIGURE 16. Skull-roof. P. 50982 ($\times 1$).

FIGURE 17. Nuchal plate. P. 50995 ($\times \frac{2}{3}$).

FIGURE 18. Left anterior dorsolateral plate; anterior region of visceral surface. P. 50995 ($\times \frac{2}{3}$).

(Facing p. 122)



Holonema westolli sp.nov.

FIGURE 19. Median dorsal plate. P. 50987 ($\times \frac{4}{3}$).

FIGURE 20. Posterior median ventral plate. P. 50984 ($\times \frac{2}{3}$).

FIGURE 21. Right suborbital, postsuborbital and infrapostsuborbital plates in visceral view. P. 50979 ($\times \frac{4}{3}$).

FIGURE 22. Same specimen as in figure 21, in lateral view.

FIGURE 23. Left palatoquadrate and suborbital plate. P. 51153 ($\times \frac{4}{3}$).

FIGURE 24. Right palatoquadrate and suborbital plate. P. 51153 ($\times \frac{4}{3}$).

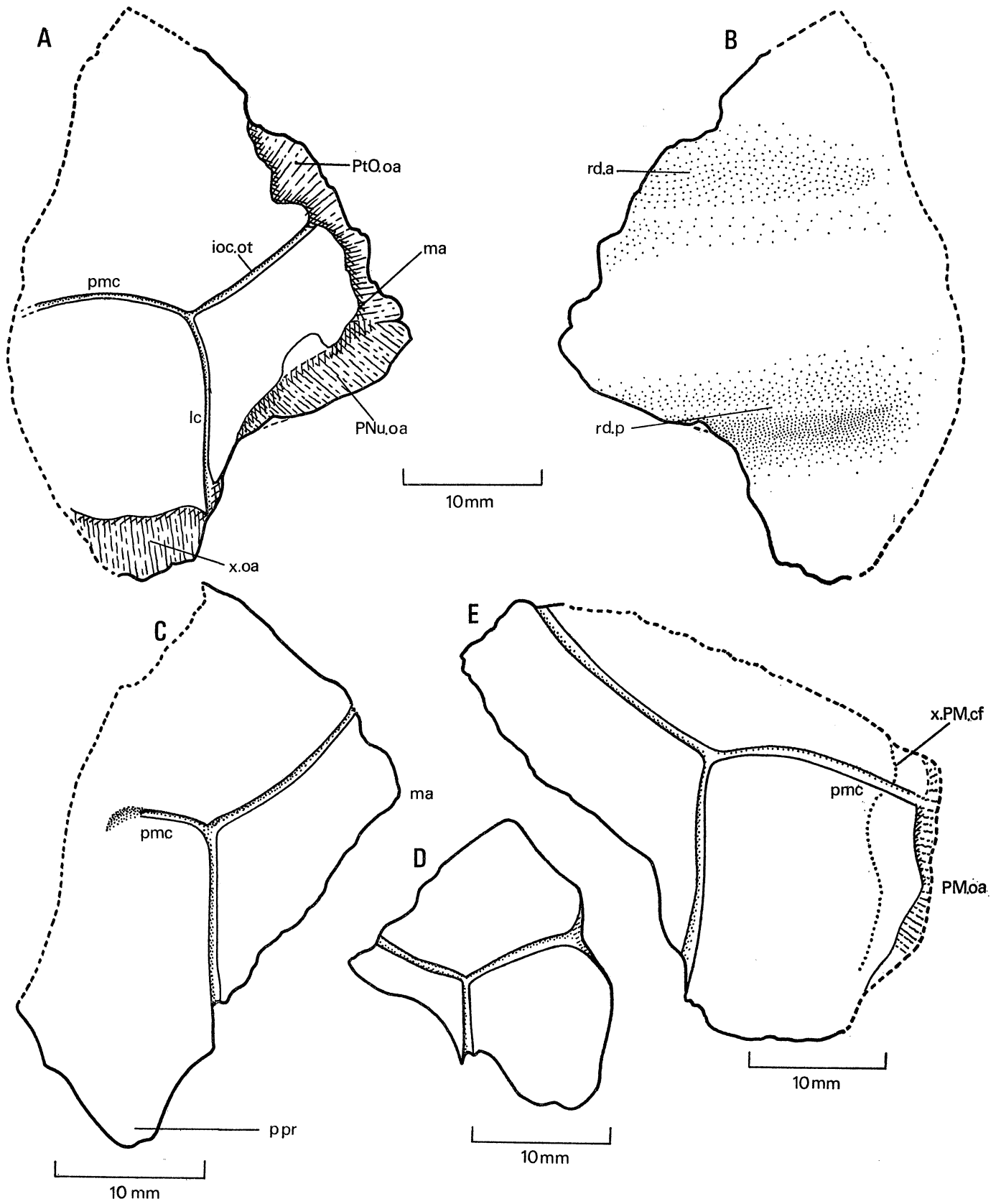


FIGURE 25. *H. westolli* sp. nov. Marginal plates. A, B, left plate in dorsal and visceral view, P. 51153; C, left plate in dorsal view, P. 50982; D, right plate in dorsal view, P. 50893; E, right plate in dorsal view, P. 51152.

canal (*pmc*) meet at the radiation centre. The groove for the postmarginal canal (= preopercular canal *auct*; see Miles & Westoll 1968, p. 456) has only a short extent in *P. 50982* (figure 25 C) and it fades out in a shallow depression well before the margin of the plate. But in three other specimens, *P. 50893*, *P. 51153*, *P. 51155*, this groove runs to the posterolateral margin, where it passes on to the postmarginal plate (figure 25 D, E). *P. 51153* (figure 25 A) shows undercut mesial overlap surfaces for the postorbital (*PtO.oa*) and paranuchal (*PNu.oa*) plates, which merge opposite the mesial angle (*ma*). The same specimen also appears to have a posterior overlap surface (*x.oa*), but this is probably an artefact caused by the weathering of the plate, as other specimens

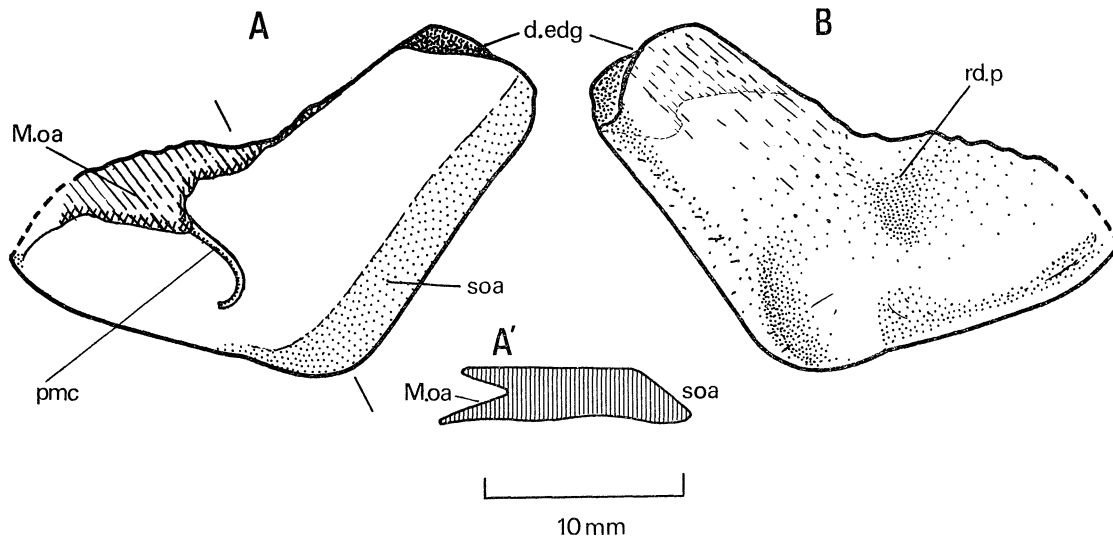


FIGURE 26. *H. westolli* sp. nov. Postmarginal plate, left, in A, lateral and B, visceral view with A', cross-section at indicated level. After *P. 51171*.

are here produced into a posterior process (*ppr*, figure 25 C, D), which is received by a notch in the margin of the paranuchal plate. *P. 51152* and *P. 50893* show that the external edge of the marginal plate is slightly bevelled at either side of the postmarginal canal, where it sutures with the postmarginal plate (*PM.oa*, figure 25 D, E). There is a more extensive contact face for the postmarginal plate on the visceral surface (*x.PM.cf*, figure 25 E). The visceral surface lacks the conspicuous thickenings and stout ridges found on the marginal plate of many brachythoracids (Heintz 1932 *a*; Stensiö 1963 *b*; Miles & Westoll 1968). Two slight transverse ridges (*rd.a*, *rd.p*, figure 25 B) can be seen. The posterior of these seems to correspond to the inframarginal crista of *Coccosteus* (Miles & Westoll 1968) and other brachythoracids.

Postmarginal plate (PM, figures 2, 4, 26, 53)

The left postmarginal of *P. 51171* is the only complete specimen, although in *P. 51014* there is a large fragment from the left side. The dorsally exposed surface is L-shaped, and bears the canal of the postmarginal sensory line (*pmc*, figure 26 A). This line curves forward at the radiation centre and ends abruptly, as in *Coccosteus cuspidatus* (Miles & Westoll 1968, Figure 3 *g*).

The dorsal edge of the plate (*d.edg*) is concave, but its suture with the paranuchal plate is nevertheless best described as a butt joint. The posteroventral edge is steeply cut away to form part of the subobstantic margin of the skull-roof (*soa*); and the thick anteroventral edge sutures with the submarginal plate in a butt joint. The anterodorsal margin bears a deeply undercut

overlap surface for the marginal plate (*M.oa*). The visceral surface shows some relief, which is shown in figure 26B. The posterior transverse ridge of the marginal plate is continued on to the postmarginal (*rd.p*).

Nuchal plate (*Nu*, figures 2 to 4, 16, 17, 27, 28, 48, 53)

The nuchal is essentially a hexagonal plate, as in *H. radiatum* (figure 117; Obruchev 1932, Figure 12; Heintz 1934, Figure 8, as *Coccosteus* sp.) and *H. rugosum* (Case 1931, Plate 4, Figures 1, 2; Wells 1943, Figure 1B). Its dorsal surface has an anterolateral margin which meets the central plate, a lateral margin which meet the paranuchal plate, and a posterolateral margin which enters into the posterior margin of the shield (figure 27A). There is an anterior angle (*aa*) and a bicuspid posterior process (*p.pr*). This process is more pronounced in large specimens (figure 27C, D) than in the small specimen shown in figure 27A, B (P. 50995). Both the anterolateral and lateral margins may be strongly embayed; they are separated by the anterolateral angle (*ala*). The lateral margin bears a lateral process (*l.pr*, figure 28A), which may have distinct lateral (*la*) and posterolateral (*pla*) angles. The posterolateral margins are slightly bevelled where they form the posterior descending lamina (*pdl*) of the skull-roof (Stensiö 1959; Miles 1966*b*; Miles & Westoll 1968). The nuchal has a slightly concave dorsal longitudinal profile anteriorly (figures 2, 28C), and is transversely arched (p. 106; figure 3). Dorsal overlap surfaces are present for the central (*C.oa*) and paranuchal (*PNu.oa*) plates. The first is only a slight depression; the second is a deeper, slightly undercut surface, although it has a raised posterior region (*r.pr*).

Only a small area of the nuchal plate is exposed on the visceral surface of the articulated skull-roof, as this plate is broadly underlapped by the central and paranuchal plates. Separate regions for these plates can be recognized on the lateral contact faces (*C.cf. PNu.cf*, figure 27B). In large specimens (figure 27C, D) the median part of the nuchal thickening (*mn.th*; Stensiö 1963*b*) forms a lamina of smooth bone ascending to the posterior margin of the skull-roof. This lamina forms the roof of the subnuchal levator fossa (*sn.f*, figure 3A; Stensiö 1963*b*; Miles 1969, p. 149), and it is irregularly ridged like the levator fossa of the nuchal plate in the antiarch *Bothriolepis* (Stensiö 1948; Miles 1968). There is a median occipital crest (*moc*) which ends at the two cusps of the posterior process. Sometimes this crest is raised into a median ridge (P. 51152; figure 27C), and in other cases it bears a median groove (P. 50995; figure 27B). Both of these structures received the median vertical septum of the trunk muscles. There is no lateral depression at the side of the crest, as there is in *H. radiatum* (figure 117A) and many other brachythoracids (Stensiö 1963*b*, Figure 54B to D; Miles & Westoll 1968), presumably because of its low, broad form. The smooth ascending lamina of the nuchal is separated from the more coarsely textured anterior region, which was in contact with the dorsal wall of the brain-case, by a distinct transverse occipital crest (*toc*). This crest is equivalent to the 'transversal wall' described by Heintz (1932*a*, 1934) for several brachythoracids, and to the 'transverse ridge posterior to levator fossa' of Stensiö (1963*b*, Figure 112A). Immediately in front of the crest there is a deep transverse fossa (*tf*). In P. 50986 (figure 27D) this fossa continues right across the surface of the plate, but in P. 50982, P. 51152 and P. 50984 (figures 27C, 53) it is interrupted in the middle by the foremost part of the median occipital crest, so that it is a paired structure. The fossa is homologous with the paired pits generally found in brachythoracids (the levator fossa of Stensiö 1963*b*), which received posterior dorsal processes of the braincase (p. 143). In P. 51152 (figure 27C) the fossa is deeply pitted at either side of the occipital crest. In P. 50986 (figure 27D) large nodules

on the anterior wall of the fossa incompletely divide it into median and paired lateral chambers; the median chamber occupies the position of the anterior part of the occipital crest in other specimens. A small specimen, P.50995 (figure 27B), differs from those just described in the relatively larger size of the occipital crest, the small size of the paired cusps on the posterior

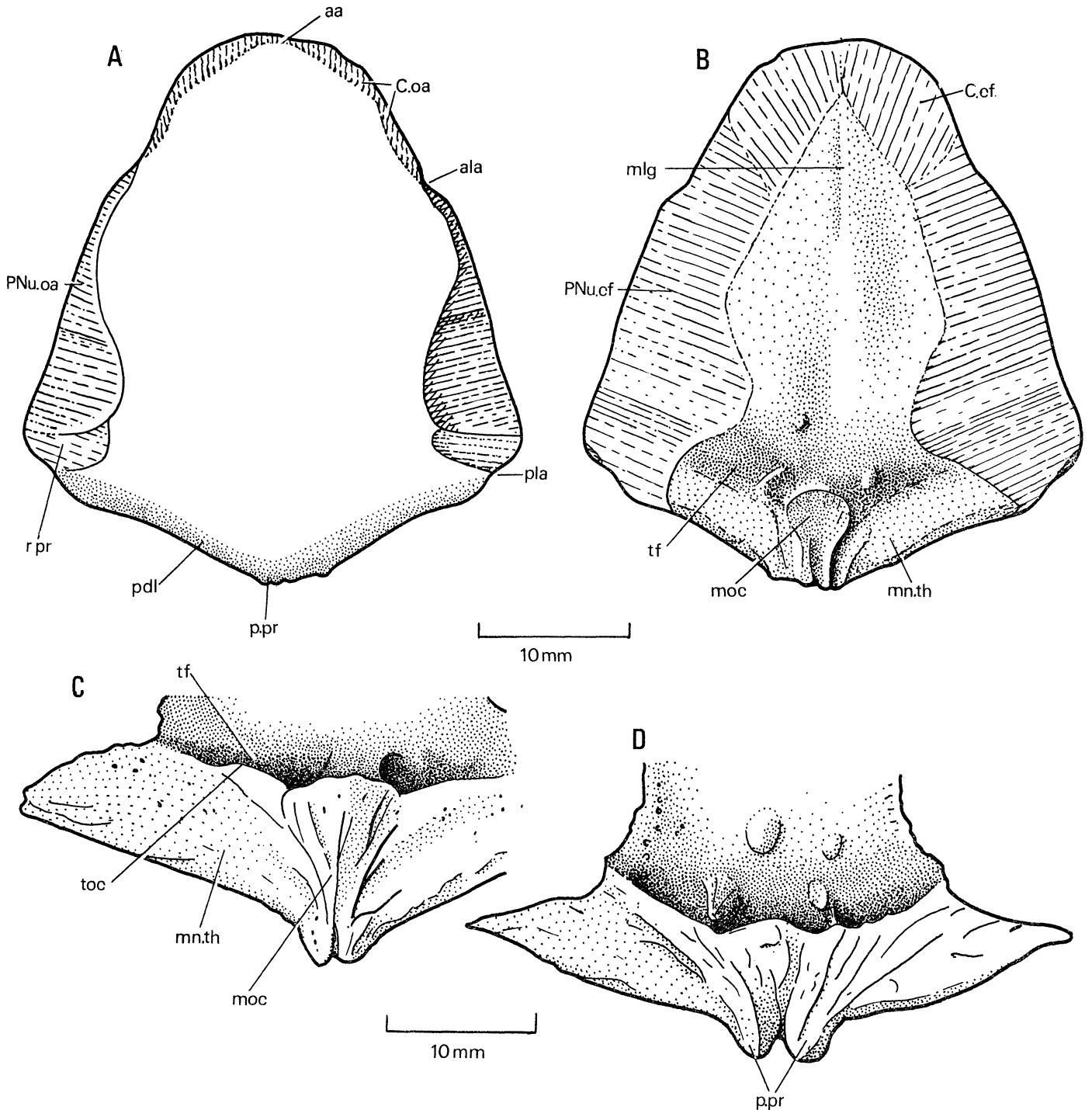


FIGURE 27. *H. westolli* sp. nov. Nuchal plate. A, B, P.50995 in dorsal and visceral view; C, D, posterior region of visceral surface of P.51152 and P.50986 respectively.

process, and the less differentiated condition of the nuchal thickening, transverse occipital crest and transverse fossa. Remaining features of the visceral surface include an anterior, median longitudinal groove (*mlg*, figure 53) and occasional irregular nodules (figure 27B, D). The radiation centre lies just in front of the anterior end of the occipital crest.

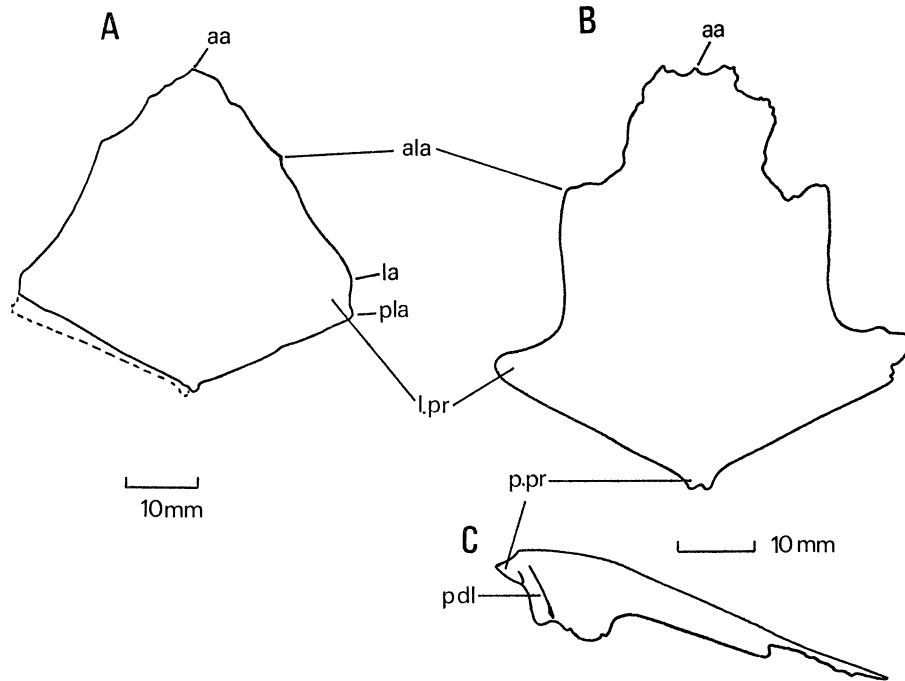


FIGURE 28. *H. westolli* sp. nov. Nuchal plate. A, dorsal view, P.50982; B, C, dorsal and lateral view, P.51152.

Paranuchal plate (*PNu*, figures 2 to 4, 16, 29, 30, 48, 52, 53)

This plate is transversely arched about the dorsolateral axis. The occipital para-articular process (*pap*, figure 29A) is large, with the usual *Siebknochen*-like texture, and it is continued along the edge of the plate (except in P.51004) by a narrow splint of smooth bone, which forms part of the subobstantic margin (*soa*, figure 2). This process and the splint of bone together form a lateral lamina which ends at the lateral angle (*la*). The marginal overlap area (*M.oa*) lies mesially to the lateral angle, and it continues into the substance of the plate as a deep cavity (*M.oac*, figure 30A) which must have received a process from the marginal plate, although this process has not been observed in the specimens. Mesial to the anterior angle (*aa*) lies the shallow central overlap area (*C.oa*), which continues round the plate to the anterior mesial angle (*ama*), where it is replaced by the deeply undercut nuchal overlap area (*Nu.oa*). The posterior margin ends laterally at the distinct posterolateral angle (*pla*). Mesial to this angle the margin is embayed (*ae*) over the lateral articular fossa (*laf*; figures 3, 29B), and still further mesially, it forms the posterior descending lamina of the roof (*pdl*). These two regions of the margin are not separated by a distinct 'upper joint process' (Heintz 1932 *a*, 1934), in contrast to *Dunkleosteus* and *Homostius*. The posteromesial angle is extended to form the postnuchal process (*pnp*), but this process is small in comparison with those of most brachythoracids (Miles 1962, 1969; Miles & Westoll 1968). The main lateral-line (*lc*) curves across the surface of the plate in a deep groove, which however is unusual in that it always ends before the posterior margin. The posterior

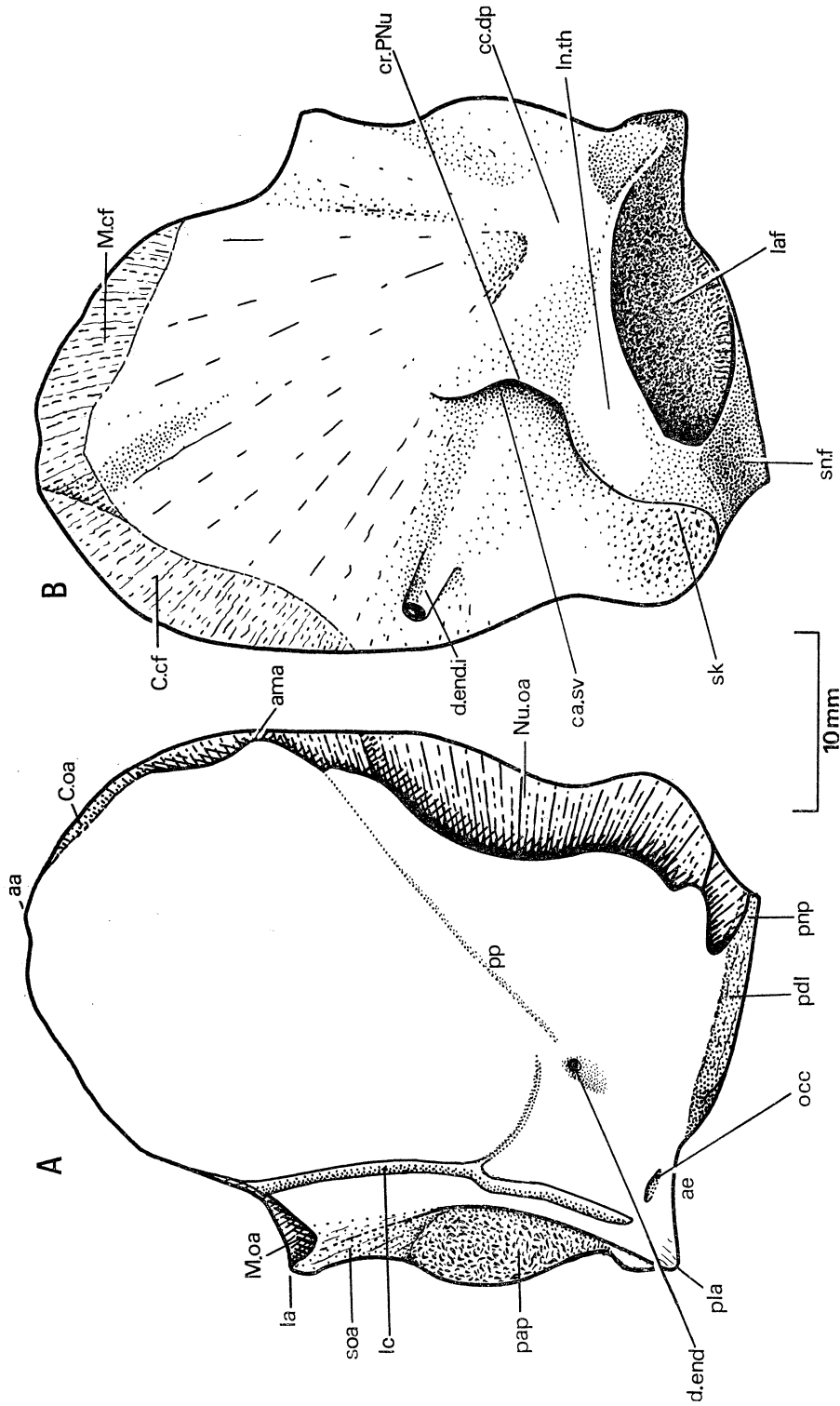


FIGURE 29. *H. westlii* sp.nov. Paranuchal plate, left, in A, dorsal and B, visceral view.
Restoration based on P. 50995.

pit-line (*pp*) leaves the main line and makes the usual posterior curve before crossing the bone obliquely to end at the posterior process of the central plate. The paranuchal-central suture line may be re-entrant at this point (e.g. P. 50982; not in P. 51152). Near the hind margin a short section of the occipital cross-commissure (*occ*) is present. Both the commissure and posterior pit-line are usually represented by shallow grooves, but the latter cannot always be seen distinctly. The course of the posterior pit-line may be unexpectedly irregular (figure 30B), and where it can be seen it seems to be in two sections, an 'anterior' and a 'posterior', as described by Obruchev (1932) for *Holonema ornatum* and *Gyroplacosteus panderi* (figure 125A), and as recorded for some coccosteids (Miles 1966*b*, p. 36). The path of the main lateral-line may also be irregular where the posterior pit-line branches off (figure 29A), and on the right paranuchal of P. 50982

TABLE 3. MEASUREMENTS (IN MILLIMETRES) OF THE LATERAL OCCIPITAL FOSSA IN
HOLONEMA WESTOLLI SP. NOV.

specimen	side	length	height	$h/l \times 100$
P. 50982	right	27	11	41
P. 50986	right	29	12	41
P. 50984	right	28	11	39
P. 51152	right	28	11	39
P. 50995	left	19	7	37
P. 50893	right	19	7	37
				mean 39

Measurements taken as in Obrucheva 1962, Figure 11.

there is a break of some 4 mm in the groove for this line in this region (figure 16). The most anterior section of the posterior pit-line in P. 50982 is represented by a narrow, crack-like fissure in the bone surface. The endolymphatic duct (*d.end*) opens on to the surface in the usual position, and in P. 50995 it opens in a shallow depression (figure 29A). The radiation centre lies lateral to this opening, between it and the main lateral-line canal.

The posterior region of the visceral surface is thickened to form the lateral division of the nuchal thickening (*ln.th*, figures 29B, 53). The posterior face of this thickening takes the shape of a hollow curve dorsomesially, where it completes the lateral region of the subnuchal levator fossa (*sn.f*), as Stensiö (1963*b*, Figure 108) has illustrated for *Brachydeirus? bicarinatus*. Laterally the posterior face bears the elongated, pear-shaped lateral articular fossa (*laf*), which has a *Siebknochen*-like surface texture. The fossa is deepest laterally, where in section it forms an arc of about 140°, but on the whole it is shallow as in *Homostius* (Heintz 1934). The upper and lower margins of the fossa are well defined. Measurements of the fossa in six specimens are given in table 3; the mean breadth/length index is 39. Anteromesially the edge of the lateral division of the nuchal thickening falls steeply to the general level of the visceral surface, and at this edge the bone again shows a *Siebknochen*-like texture (*sk*; figure 29B). Lateral to this area is the distinct paranuchal crista (*cr.PNu*; 'lateral caudal, descending lamina', Stensiö 1963*b*, Figure 43C), beneath which the nuchal thickening is deeply excavated by the supravagal cavity (*ca.sv*) for the supravagal process of the brain-case (figures 29B, 30A). The oblique course of the endolymphatic duct canal through the plate has been cleared in the specimens by acetic acid preparation, and it can be studied in radiographs. The canal is carried away from the visceral surface of the plate in a bony tube, which presumably lay in a dorsal fossa of the brain-case comparable with the endolymphatic groove restored for several pachyosteomorph arthrodires by Stensiö (1963, Figures 88 to 90, 94, 97). Lateral to the paranuchal crista there is a small,

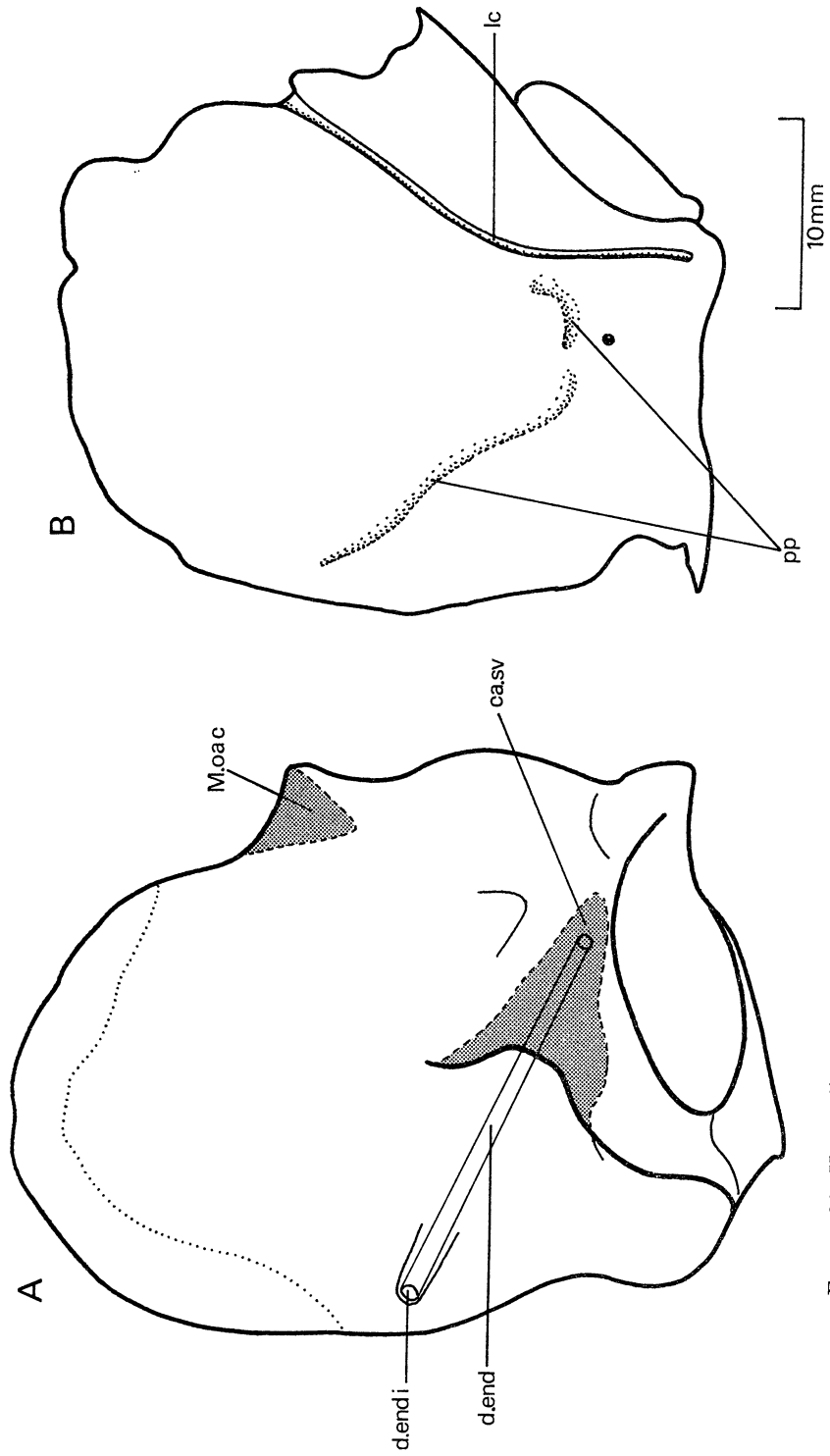


FIGURE 30. *H. westolli* sp.nov. Paranuchal plate. A, diagram to show path of endolymphatic duct and extent of cavities in the bone; B, dorsal view of right plate, P. 50893.

shallow cucullaris depression (*cc.dp*; Stensiö 1945, 1963 *b*) around the radiation centre of the plate. Anteriorly there are contact faces for the central (*C.cf*) and marginal plates (*M.cf*). There is, however, no contact face for the marginal plate just anterior to the lateral angle, such as is found in *H. radiatum* (Obruchev 1932, Figure 13), because of the development of the deep cavity for the posterior process of the marginal (*M.oac*, figure 30A).

Extrascapular plate (*Esc*, figures 31, 63)

The extrascapular plates are separate from the skull-roof, as is normal in brachythoracids (Stensiö 1945, 1963 *b*; Miles 1969; Miles & Westoll 1968). Both members of the pair are preserved in P.50984, although the left plate is incomplete. Other examples are found in P.50893, P.50986 and P.51157. The extrascapular lies against the posterior descending laminae of the

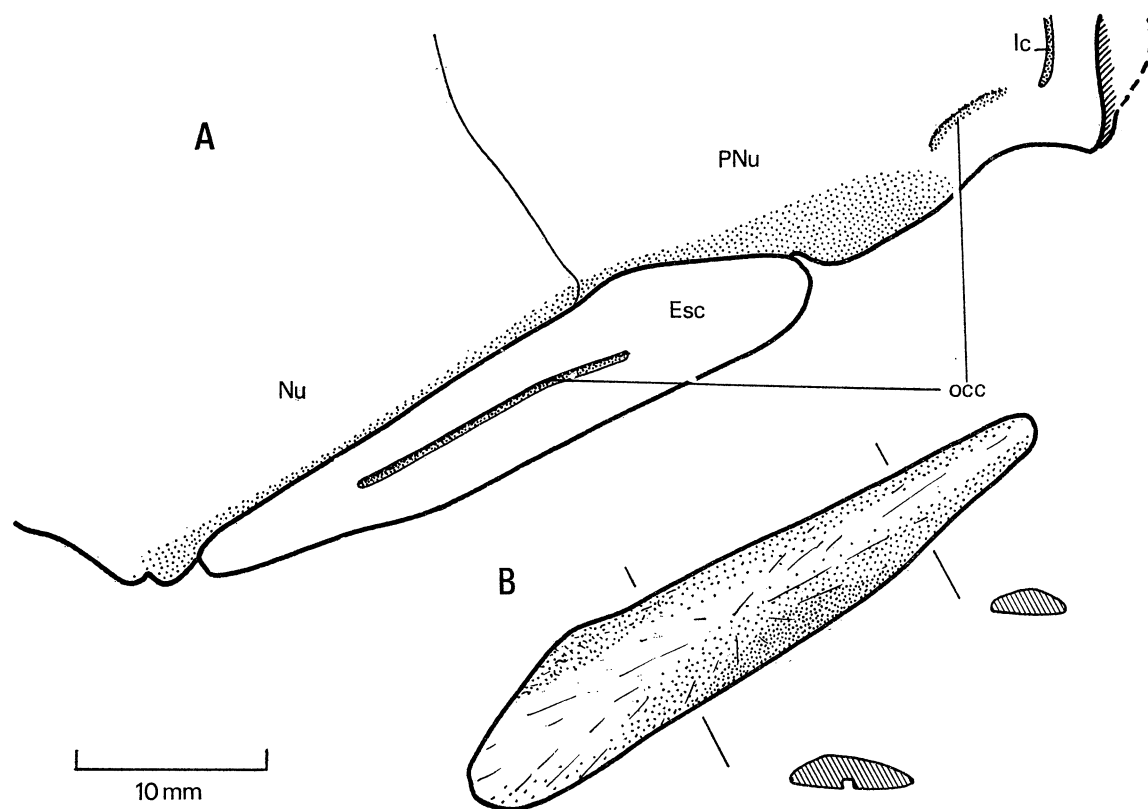


FIGURE 31. *H. westolli* sp.nov. Extrascapular plate, right. A, dorsal view with plate in place on hind margin of skull-roof; B, visceral view with cross-sections at indicated levels.

nuchal and paranuchal plates. Its longest dimension ('breadth') is about five times the maximum of the shortest dimension ('length'). Contrary to the case in coccosteids (Heintz 1938; Miles & Westoll 1963, 1968), the plate appears to be broadest towards its lateral end, but this cannot be confirmed as the specimens are not found *in situ*. The occipital cross-commissure is present as a deep groove (*occ*), which, however, does not extend right across the plate. On the visceral surface the neurovascular grooves show the position of the radiation centre. The plate is more or less triangular in cross-section, with anteroventral, posteroventral and dorsal surfaces. The anteroventral surface contacts the skull-roof.

*Cheek plates, palatoquadrate and opercular cartilage**General features*

The cheek unit is made up of suborbital (*SO*), postsuborbital (*PSO*) and submarginal (*SM*) plates, although their form is unusual. None have been described before for *Holonema*, although Gross (1933, Figure 13) has figured the suborbital of *Rhenonema* (as *H. eifeliense*) as an 'Unbestimmbarer Knochen'. There is a further small plate, not hitherto described in an arthrodire, which will be termed the infrapostsuborbital (*IPSO*). The palatoquadrate is more completely perichondrally ossified in *Holonema westolli* than in other arthrodires. As it tends to be intimately associated with the visceral surfaces of the suborbital and postsuborbital plates, it can best be described with these plates. The opercular cartilage may also be described here, as it is closely applied to the submarginal plate.

Suborbital plate (SO, figures 2, 4, 21 to 24, 32, 33, 81)

This plate is unusual in comparison with the suborbitals of other arthrodires (Denison 1958, Figure 106; Miles & Westoll 1963, 1968; Miles 1966*b*; Stensiö 1969*a*), as it is not divided into distinct suborbital and postorbital laminae, and the orbital emargination is shallow. In addition, there are no distinct laminae on the visceral surface, as there are in typical brachythoracids.

The suborbital is shown in outline in figure 32. The outer surface is gently bowed in longitudinal profile (*d-d*; figure 32C), and tumid in its lower region, as can be seen in the vertical profiles (*a-a*, *b-b*, *c-c*; figure 32A). It has a triangular depression (*td*, figure 32A, 33C) under the middle division of the orbital emargination (*oe_m*, see below) in P. 50979, P. 51153 and P. 51155, though not in other specimens. The following angles are recognized on the margins; the postorbital angle (*poa*), anterior and posterior suborbital angles (*asba*, *psba*), preorbital angle (*proa*) anterior and posterior dorsal angles (*ada*, *pda*), dorsal and ventral anterior angles (*daa*, *vaa*) and dorsal and ventral posterior angles (*dpa*, *vpa*). The plate makes a butt joint with the postorbital plate between the postorbital and anterior dorsal angles, with the submarginal plate between the posterior dorsal and dorsal posterior angles, and with the postnasalo-rostral between the preorbital and dorsal anterior angles (figure 2). The posterior margin, between the dorsal and ventral posterior angles, is variable in form and may be deeply concave. It is deeply and irregularly grooved where it interlocks with the postsuborbital plate (figure 33D), in a joint of similar structure to that between the central plates. The small anterior and the more prominent posterior suborbital angles divide the orbital emargination into anterior, middle and posterior divisions (*oe_a*, *oe_m*, *oe_p*).

The infraorbital sensory line (*ioc*) runs continuously in the surface of the plate as a deep groove. The supraoral line (*sorc*; Miles & Westoll 1968) is well marked for most of its length, although ventrally it either stops abruptly before reaching the margin of the plate (figure 33A), or is transformed into a shallow depression (figure 32A). Dorsally it ends between 1 and 4 mm short of the infraorbital line, in seven of the nine plates in which it can be adequately studied (figure 32A). In the other two plates it anastomoses with the infraorbital groove, about midway along the latter (figure 33A). In the posterior region lies the postsuborbital sensory line (*psoc*, Miles & Westoll 1968), which runs forwards from the postsuborbital plate. This line always ends well short of the infraorbital line, towards which it is directed. It either ends abruptly or fades out in a shallow sulcus (figures 32A, 33A). The presence of a groove for the postsuborbital line on the suborbital plate is unusual in an arthrodire, although this course for the line has been hypothesized by Stensiö (1947, Figure 12C, 'supramaxillary line').

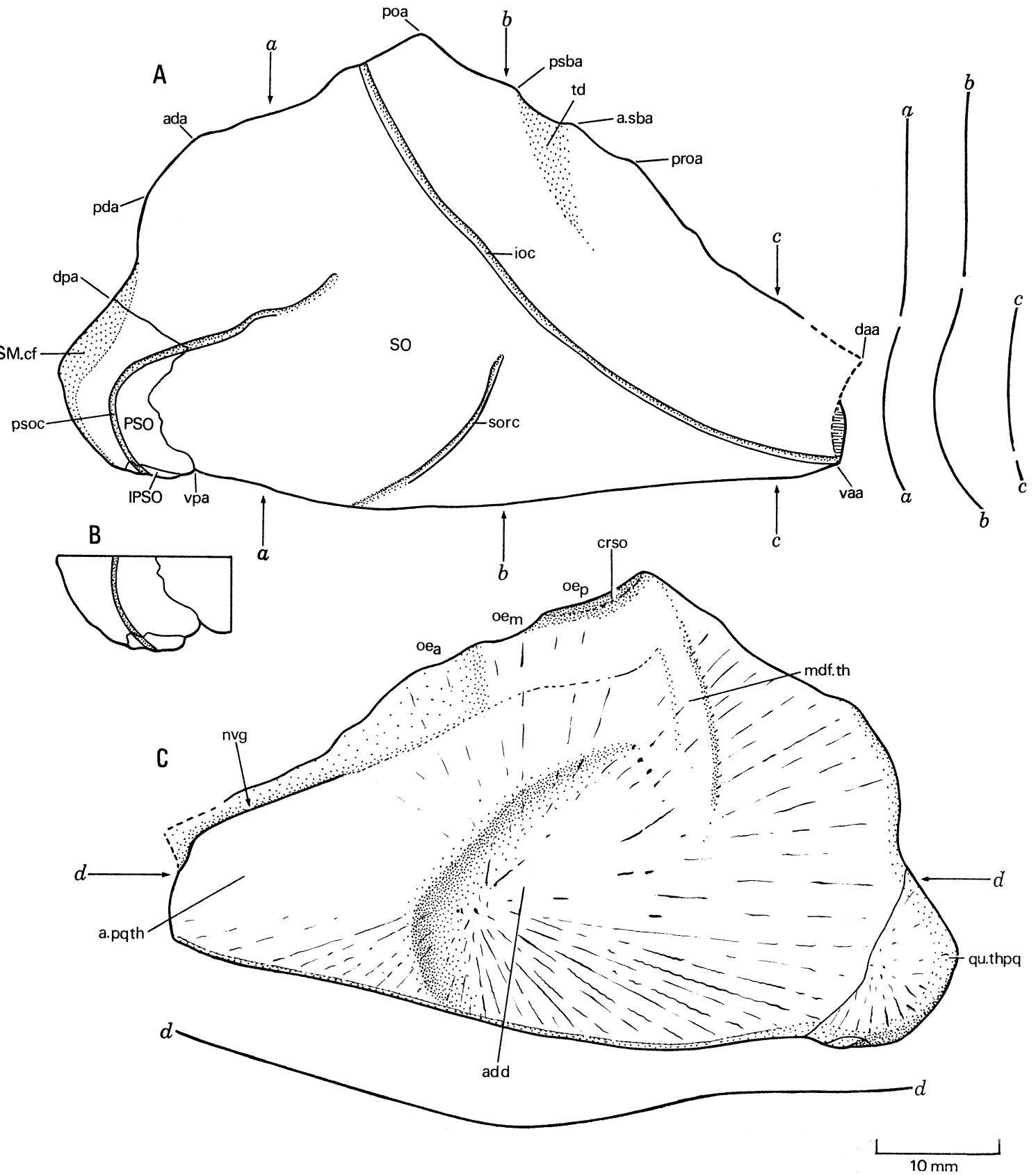


FIGURE 32. *H. westolli* sp.nov. Suborbital, postsuborbital and infrapostsuborbital plates, right, P.50979. A, in lateral view; B, ventrolateral view of posteroventral corner; C, visceral view. Profiles a-a, b-b, c-c and d-d at levels indicated, of outer surface.

The main features of the visceral surface of the plate (figure 32C) include the adductor depression (*add*), which forms the lateral wall of a fossa for the adductor mandibulae muscles (*f.am*, figure 33B); the broad edge of the posterior division of the orbital emargination, which may be termed the suborbital crista (*cr.so*); and the different regions of the palatoquadrate thickening, where the cheek plates were applied to the lateral perichondral wall of the palatoquadrate cartilage. The palatoquadrate thickening is most pronounced in the autopalatine region (*a.pqth*), where it is sharply delimited dorsally by an undercut step in the bone (*nvg*). The space between the palatoquadrate and the upper edge of the plate (*nvsp*, figure 34C) probably carried the n. maxillaris V, the n. buccalis lateralis, and the orbitonasal artery. This agrees with Stensiö's (1963*b*, Figures 39 to 41) restoration of these structures in '*Kujdanowiaspis*' where, however, the cheek and palatoquadrate are unknown. The base of the groove (*nvg*) exhibits large, irregularly spaced foramina, which must principally have transmitted the branches of the n. buccalis lateralis, although other foramina in this region may have transmitted blood vessels (see p. 137). A more posterior, vertical division of the palatoquadrate thickening (*mdf.th*) marks the position of the mandibularis canal (p. 138). The radiation centre of the bone is indicated by the well-marked neurovascular canals on the visceral surface; it lies in the anterior part of the adductor depression (figure 32C).

Postsuborbital plate (PSO, figures 2, 4, 21, 22, 32, 33)

This plate is small relative to the suborbital, even in comparison with other bracythoracid arthrodires. However, Heintz (1962) has shown that the postsuborbital is also relatively small in the dolichothoracid *Arctolepis* (figure 100). The outer surface in *Holonema* is crossed by the postsuborbital sensory line (*psoc*), which continues in a curve from the suborbital down to the ventral edge of the postsuborbital. The posterior margin of the plate is bevelled, and this bevelled edge is continued on the suborbital plate in the articulated cheek unit (*SM.cf*, figure 32A). The submarginal plate lay loosely against this edge (figure 2). A ventral overlap surface (*IPSO.oa*, figure 33A) is for the infrapostsuborbital plate. The visceral surface has a broad posterior rim, which can be regarded as the quadrate division of the palatoquadrate thickening of the cheek unit (*qu.thpq*, figure 32C).

Infrapostsuborbital plate (IPSO, figures 21, 22, 32A, B)

This small plate has not previously been described in an arthrodire. It is found in place in the partially articulated cheek unit of P. 50979, and an overlap surface for its reception is found on the postsuborbital of P. 51154, which suggests that its occurrence in P. 50979 is not an isolated case of a supernumerary bone (or an anamestic bone, *sensu* Westoll 1936). The groove for the postsuborbital sensory line continues across the infrapostsuborbital to the lower edge of the cheek unit. The topographical relations of the infrapostsuborbital to: (1) the mandibular joint, (2) the submarginal plate (= extralateral plate of antiarchs), (3) the postsuborbital plate (= prelateral plate of antiarchs, Westoll 1945) and (4) the postsuborbital sensory line, leave little doubt that this plate is homologous with the infraprelateral plate of the antiarch *Bothriolepis* (Stensiö 1947, Figure 13; 1948, Figures 33, 34; 1969*a*, Figure 134).

Palatoquadrate (pq, figures 23, 24, 33B, C, 34, 55, 57, 58A, B, 106)

The palatoquadrate is a continuous structure in the form of an arch, which includes the autopalatine, middle (or metapterygoid), and quadrate regions of the other arthrodires. These

regions have not been clearly defined (see Stensiö 1963 *b*, 1969 *a*) and there are no distinct boundaries between them in *Holonema*. However, the autopalatine region (*au*) may be said to include the deep anterior part of the palatoquadrate which supports the posterior superognathal (figures 33, 57), and also the more dorsal part which bears a large articular facet (*daf*. figure 33B) for the orbital connexion with the brain-case. The quadrate region (*qu*) bears the articular condyle (*cd.art*) for the mandibular joint. The middle region joins the autopalatine and quadrate regions, and in *Holonema* bears a conspicuous fossa (*f.lpq*) for the insertion of the levator muscles of the palatoquadrate (figure 33B, C).

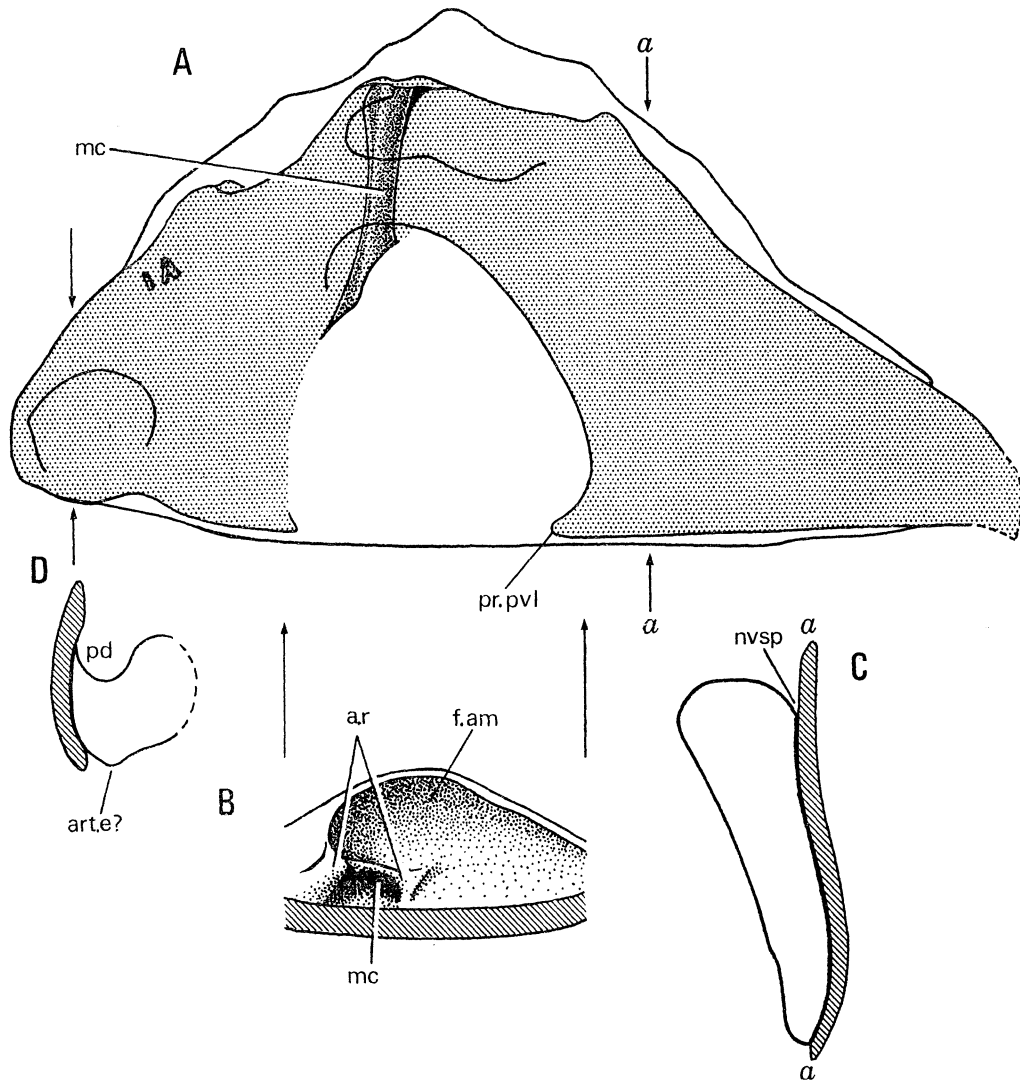


FIGURE 34. *H. westolli* sp.nov. Diagram of suborbital and palatoquadrate in A, mesial view, with B, ventral view of adductor fossa and C, D, cross-sections.

The palatoquadrate is perichondrally ossified on all its faces, including the lateral face which is closely applied to the visceral surfaces of the suborbital and postsuborbital plates. These dermal plates are sometimes found with a smooth, undamaged basal bone surface (figure 21). This indicates that the perichondral bone of the palatoquadrate did not fuse with basal layer of these

plates to the extent normally seen in the quadrate region of brachythoracids (figure 110B; Stensiö 1963 *b*, 1969 *a*; Miles & Westoll 1968). However, in several specimens (P. 51152, P. 51153, P. 51154) the palatoquadrate is intimately associated with, and cannot be separated from, the dermal bones of the cheek, particularly around the adductor fossa (*f.am*, figures 23, 24, 33B, 34B). The inner surface of the perichondral bone layer is raised into a net-work of short, fairly large, anastomosing canals, forming a subperichondral vascular plexus. Histological studies have not been made, but there is no prominent evidence of endochondral bone or subperichondral calcified cartilage. Some larger canals cross the interspace between the sheets of perichondral bones (figure 24), but these also appear to be vascular canals and not endochondral trabeculae (cf. Ørvig 1957, p. 318).

The anterior tip of the autopalatine region is not preserved. However, if the posterior superognathal is placed in its correct position against the palatoquadrate (P. 51153, figures 57, 58A, B), a groove on the outer surface of the tooth-plate (p. 147, figure 56) clearly demonstrates the exact extent and form of the anterior part of the autopalatine region. This region has been restored, therefore, with a high level of confidence in figures 33, 34, 57, 58A, B, and it can be shown to have curved mesially and to have had no anterior connexion with its antimere or with the brain-case. The posterior superognathal lies against the mesial face of the anteroventral part of the autopalatine region, which it almost exactly equals in length (figure 57B). There is no sign of a special facet on the autopalatine region for the reception of the tooth-plate, although one may well have existed, as in other arthrodires (*dp.PSG*, figure 110B; Stensiö 1963 *b*, 1969 *a*). Along the lower edge of the autopalatine region, lateral to the tooth-plate, there is a series of foramina (*v.f*, figures 33B, 58A) which probably transmitted the blood vessels of the subperichondral vascular plexus. Similar foramina are found along the dorsal margin (*df*; figure 33C) and in other regions of the palatoquadrate. There is a groove (*g.ll*) on the lateral face of the autopalatine region, which arises at a foramen (*f.ll*) on the anterior edge of the suborbital plate (figures 33A, 57A, 58A). This groove seems to be related to the forward continuation of the infraorbital sensory line in the skin, from the suborbital plate, and it may have carried a branch of the n. buccalis lateralis.

The articular facet of the palatoquadrate (*daf*, figure 33B, C) is situated between the dorsal and mesial surfaces of the autopalatine region, and faces dorsomesially. The long axis of the facet is slightly arched, so that the facet is deepest most anteriorly, and it is shaped somewhat like a figure of eight. The surface of the facet is lined with smooth perichondral bone, which suggests that the palatoquadrate did not articulate directly with the brain-case, but was connected to it by ligaments. There are no other articular facets or surfaces for a connexion between the palatoquadrate and brain-case. The connexion in *Holonema* clearly corresponds to the orbital articulation in other arthrodires (*orb.art*, figure 110B; Stensiö 1963 *b*, 1969 *a*), which is the only articulation in the region of the subocular shelf for which there is unequivocal evidence. However, in '*Kujdanowiaspis*', Stensiö (1963 *a*, Figures 14, 39, 40) has suggested that there was also a ligamentous basal connexion between the middle region of the palatoquadrate and a tubercle on the ventral surface of the brain-case, a short distance behind the orbital articulation. The shape of the articular facet in *Holonema* makes it possible that it represents both the orbital and basal articular surfaces of '*Kujdanowiaspis*', and this view cannot be seriously contested on the grounds of its morphological relations. Nevertheless, until the basal articulation has been clearly demonstrated in '*Kujdanowiaspis*', it seems best to disregard this possibility. The 'basal articulation' of pholidosteid arthrodires is discussed below (p. 200). Mesial to the hind part of the articular

facet, a perichondrally lined canal, the mandibularis canal (*mc*, figures 33B, 34A, B), passes through the palatoquadrate to open ventrally in the posterodorsal region of the adductor fossa (*f.am*). The lower surface of the palatoquadrate is deeply concave where it forms the roof of the adductor fossa (figure 34B). The fossa is separated from the opening of the mandibularis canal by a stout ridge (*a.r.*). In P. 51153 and P. 51154 the palatoquadrate merges imperceptibly with the suborbital plate where it forms the margins of the adductor fossa. The mandibularis canal clearly transmitted the n. mandibularis V, and probably also the external carotid artery, into the adductor fossa. Finally the posteroventral angle of the ventral edge of the autopalatine region (*pr.pvl*, figure 34A) may be compared with the 'posteroventral palatine process' of *Pholidosteus*, which Stensiö (1963*b*, pp. 232, 237) has homologized with a structure found in certain shark embryos.

The fossa (*f.lpq*) for the m. levator palatoquadrati arises immediately behind the mandibularis canal, and lies on the upper surface of the middle region of the palatoquadrate (*mr*, figure 33B). It is deepest most ventrally, where it ends in a small, distinct pit (*lpq.p*, figure 33C). The quadrate region (*qu*) is not completely preserved (see P. 51152, P. 51153, P. 51154). There is good evidence of a prominent quadrate condyle (*cd.art*; figure 33B), although its mesial wall is not preserved and the exact nature of the mandibular joint cannot be made out. It seems possible, however, that the meckelian cartilage articulated with the lower edge of the condyle (*art.e?*, figure 34D). There is no sign of the detent process found in some other brachythoracids (*pr.det*, figure 110B; Stensiö 1963*b*, 1969*a*). Dorsally around the condyle the surface of the palatoquadrate sinks down into a deep pocket (*pd*), so that the condyle stands away from the general bone surface. This pocket fades out dorsally to a shallow depression on the surface of the middle region, and on the back of the condyle it is transformed into a shallow groove. Further foramina are found on the margin of the palatoquadrate between the levator fossa and the articular condyle. They seem mostly to be variable in occurrence, but one moderately large foramen (*f*, figure 33B) occurs in more or less the same position in all the specimens. Small irregular protuberances are found on this margin, notably in P. 51152 where they are three in number.

Submarginal plate (*SM*, figures 2, 4, 35, 36, 41 to 43)

This plate is large and markedly different in form from that of other brachythoracids (figures 110B, 112C, D). It is similar to that of dolichothoracids (p. 178, figure 100; Denison 1958, Figure 103) and probably close in form and morphological relations to the primitive placoderm type. It is strongly variable in outline and in the relief of the visceral surface. Some difficulty was encountered initially in trying to orientate detached specimens. However, the right submarginal of P. 51154 was preserved in its correct relationship to the suborbital-postsuborbital unit, and this specimen has been used in interpreting other examples and in making the restorations.

The submarginal is pear-shaped (figures 35, 36). The most constant feature of its outline is the posterior embayment in the dorsal margin (*em.PM*), where the plate makes a butt joint with the postmarginal plate. In front of this embayment the dorsal margin makes a butt joint with the marginal plate. It is thus possible to distinguish anterior dorsal (*ada*), dorsal (*da*) and posterior dorsal (*pda*) angles. Anterior ventral (*ava*), ventral (*va*) and posterior ventral (*pva*) angles may also be present (figure 36A), although they are not always well defined. Anteroventrally the outer surface of the plate is arched, so that in the head it follows the curvature of the cheek behind the mandibular joint. On the visceral surface there is a longitudinal ridge (*brd*), below which the

surface slopes away gently in some specimens (figure 35B) and very steeply in others (figure 36B). This sloping face (*paoa*) rested against the infraobstantic lamina of the anterior lateral plate (p. 163) when the head was fully lowered, and it may be termed the paraobstantic area. On the outer surface there may be a groove or depression which corresponds to the longitudinal ridge (P. 50985, P. 51171). This ridge also borders a central area (*ca*), which lacks the prominent

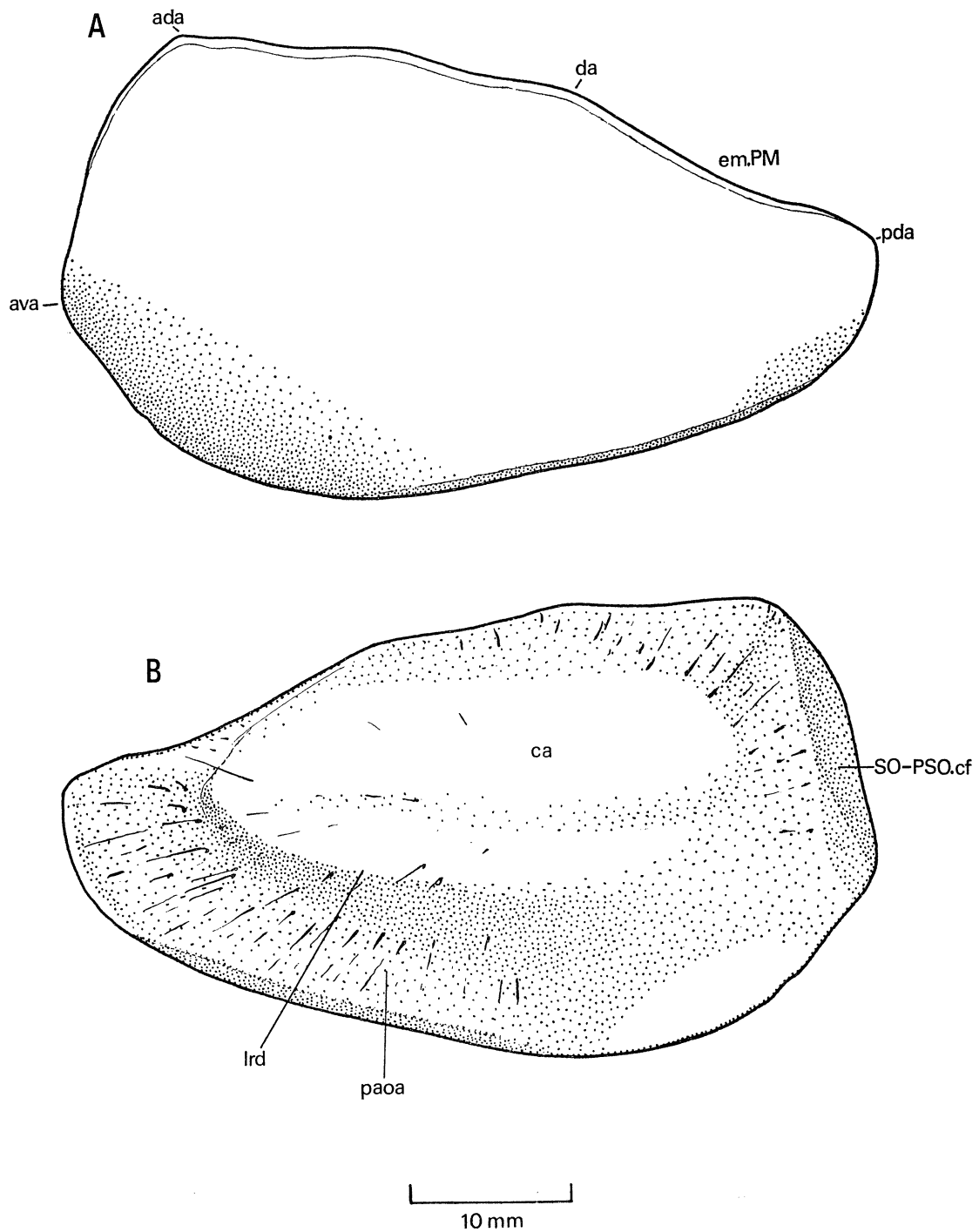


FIGURE 35. *H. westolli* sp.nov. Submarginal plate, left, in A, lateral and B, mesial view; P. 50980.

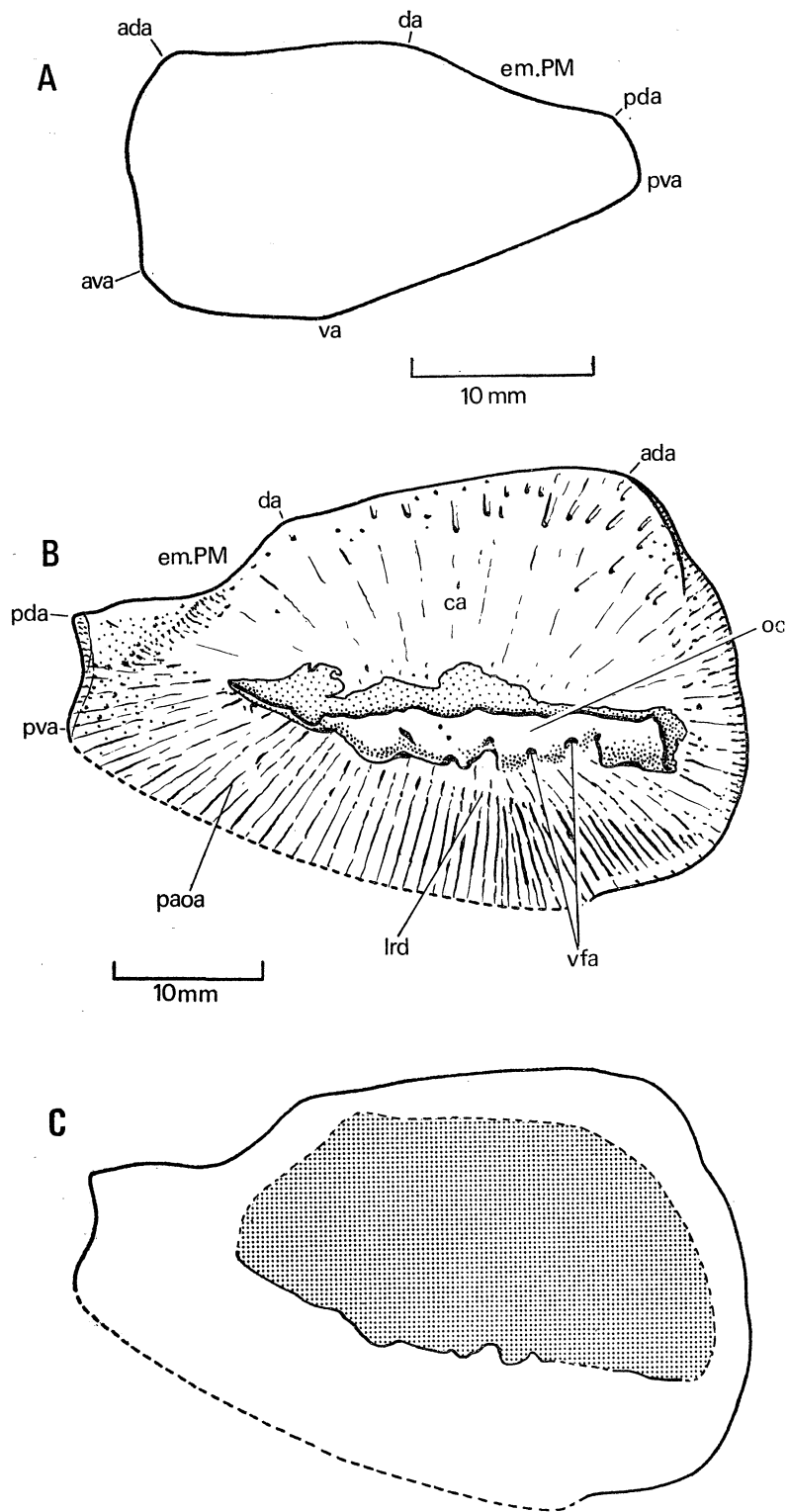


FIGURE 36. *H. westolli* sp. nov. Submarginal plate. A, left plate in lateral view, P. 50893; B left plate in visceral view with opercular cartilage, P. 51153; C as B but with opercular cartilage (regular stipple) restored to its possible original extent.

neurovascular canals that open in the peripheral areas. Anteriorly the visceral surface is bevelled to form a contact face for the suborbital and postsuborbital plates (*SO-PSO.cf*). The dorsal edge is also bevelled in the postmarginal embayment (*em.PM*).

Opercular cartilage (*oc*, figures 36B, C, 43, 55)

The left and right submarginal plates of P. 51153 have the perichondrally ossified lower part of the opercular cartilage preserved in place on the visceral surface, just above the longitudinal ridge (*oc*, figure 36B). The perichondral bone covered the lateral, ventral and mesial faces of the lower part of the opercular cartilage, and was firmly attached (but not fused) to the submarginal plate. The ventral edge bears a series of irregular protuberances, between which open fine foramina (*vfa*), possibly for the blood vessels which served the cartilage and submarginal plate. The original extent of the opercular cartilage can be restored on the assumption that it covered the central area of the dermal bone (figure 36C).

Fenestra orbitalis

The orbital opening is long and narrow, and faces anterodorsolaterally (figures 2, 4, 63). It is margined by the postnasalo-rostral, preorbital, postorbital and suborbital plates, all of which have internal orbital laminae. As in dolichothoracids, the postnasal component of the roof forms the anterodorsal margin of the orbital opening (Stensiö 1945, 1963 *b*). The anterior and posterior suborbital angles of the suborbital plate (*asba*, *psba*, figure 32A) divide the orbital opening into anterior (*o_a*) middle (*o_m*) and posterior divisions, and the anterior divisions is further marked off dorsally by the supraorbital angle of the postnasalo-rostral plate (*soan*, figure 6A). The three divisions of the orbital opening increase in size progressively in the posterior direction. The sclerotic ring (*sc.r*, figure 2) shows that the eye was situated in the posterior division, in apparent contrast to dolichothoracids in which the eye had a strikingly anterior position in the head. Nevertheless, if the markings on the visceral surface of the head-shield have been correctly interpreted in the restoration of the neurocranium, the eye probably occupied the anterior part of the orbital cavity (as defined by Stensiö 1963 *b*, pp. 69, 175, 274 for other arthrodires), i.e. in front of the supraorbital process. As in dolichothoracids, the eye is small and has a thick exoskeletal sclerotic ring (Heintz 1933, 1962).

It is difficult to discuss the nature of the anterior and middle divisions of the orbital opening, particularly in the absence of adequate brain-case material. Three explanations of these divisions have been considered:

(1) They resulted from the regressive development of the exoskeleton and have no morphological significance.

(2) They housed soft tissues of a special nature.

(3) They were external nasal openings (fenestrae exonarinae).

The first explanation has been rejected because *Holonema* is an extensively armoured form with a thick sclerotic ring, and where there has been a regressive development of the exoskeleton in arthrodires in the region of the eye (*e.g.* in many *Wildungen* species, Stensiö 1963 *b*), it takes place equally on all sides of the orbit. The second explanation is suggested by the presence of lymphomyeloid tissue in Recent holocephalans, associated with the orbital sinus. In *Chimaera colliei* the lymphomyeloid tissue 'is present in such quantities at the ventro-anterior corner of the orbit that it bulges laterally in two sizable masses which are visible as soon as the skin is removed

from that area' (Stahl 1967, p. 149). The third explanation is considered below (p. 187) and is favoured, although it is not possible to decide if it is correct. Should it prove to be incorrect, the second explanation is preferred to the first.

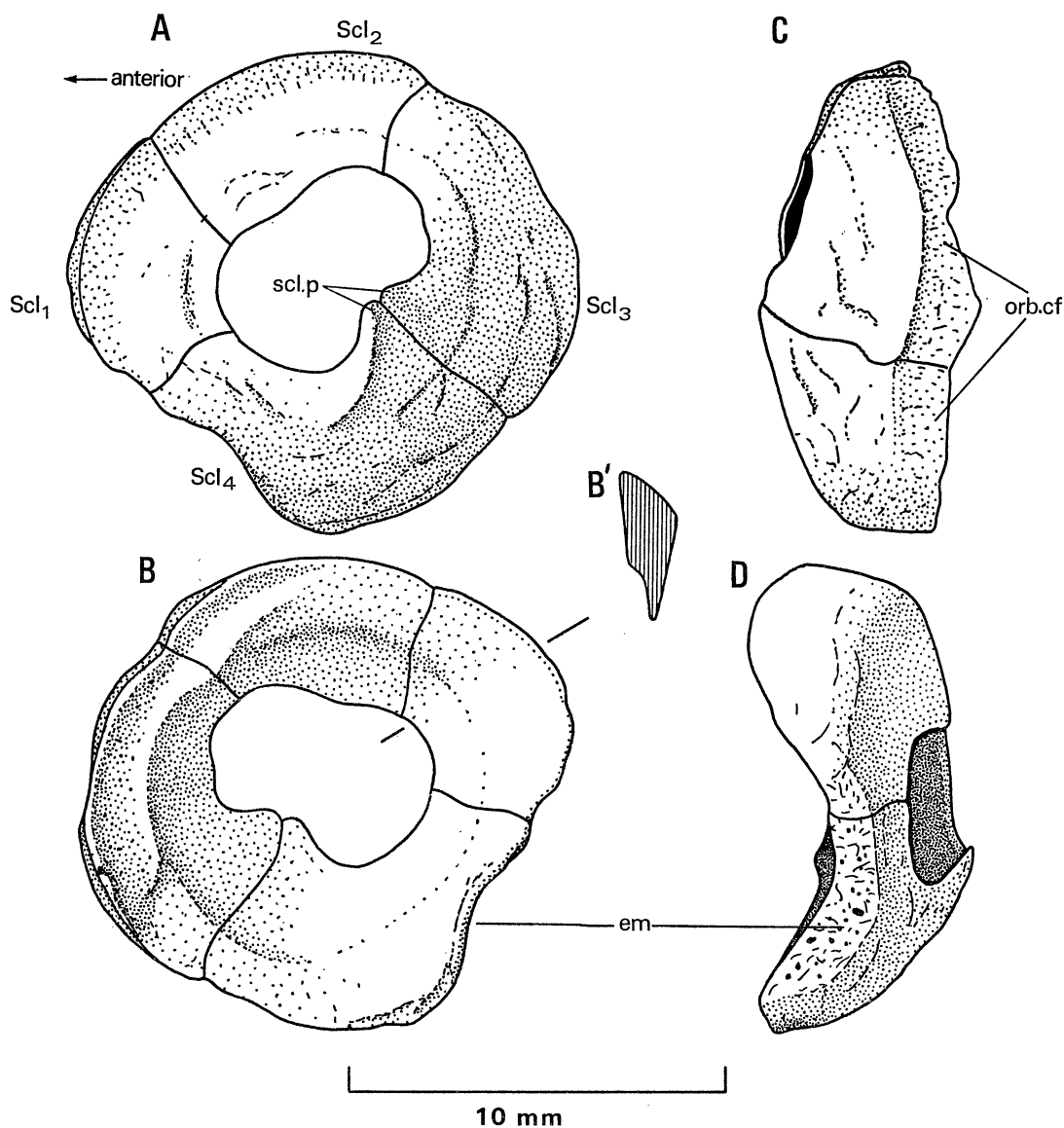
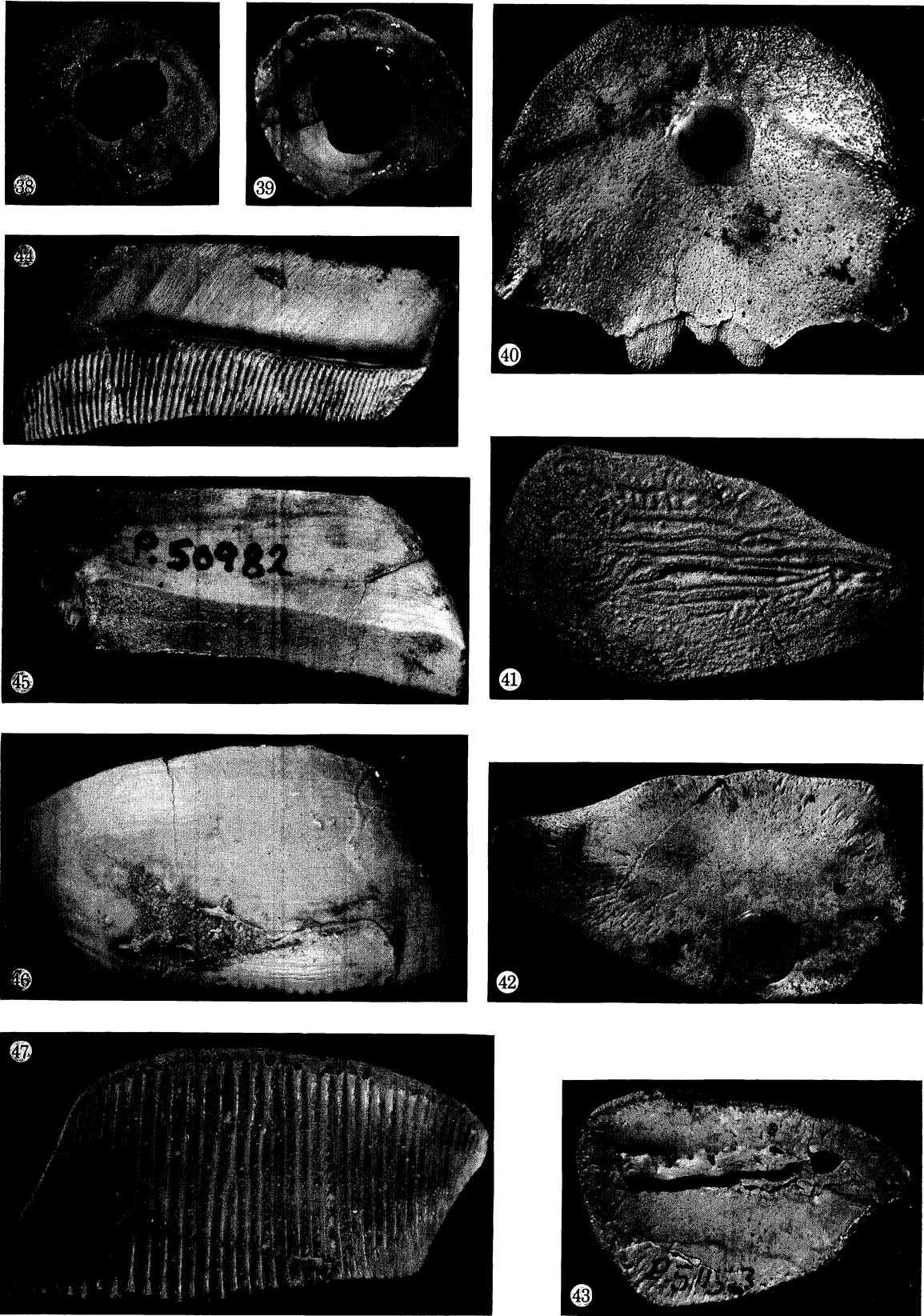


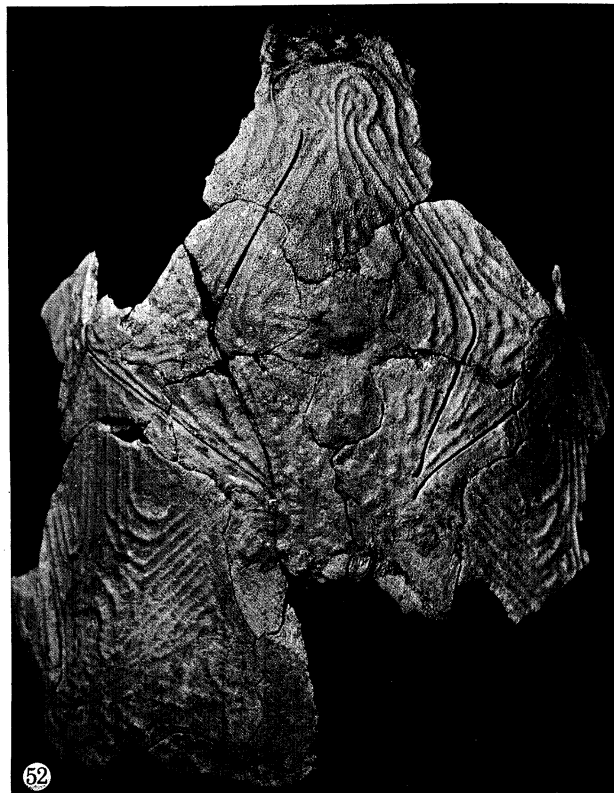
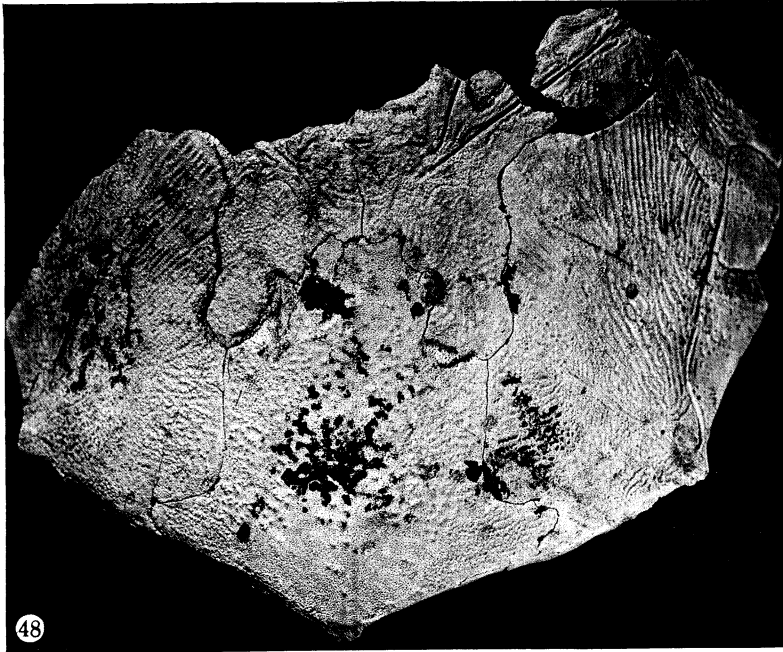
FIGURE 37. *H. westolli* sp. nov. Sclerotic ring, left, P. 51004 in A, lateral; B, mesial; C, anterior; and D, posterior view; with B' cross-section at position indicated.

Sclerotic ring

Detached sclerotic plates are present in P. 50893, P. 50986, P. 51153, P. 51154, P. 51171 and P. 51004. In the last specimen they fit together to form two complete rings of four plates each (figures 2, 4, 37 to 39), the same number as in other arthrodires (Heintz 1962; Stensiö 1963*b*; Miles & Westoll 1968), in contrast to the three in antiarchs (Stensiö 1948; Miles 1968) and ten or more in rhenanids (Stensiö 1950, 1969*a*; Gross 1963). In each ring the plates meet in butt joints, are thick and have a surface ornament. They are dermal bones, strongly bowed in transverse

*Holonema westolli* sp. nov.

- FIGURE 38. Left sclerotic ring in lateral view. P. 51004 ($\times \frac{8}{3}$).
 FIGURE 39. Same specimen as in figure 38 in visceral view.
 FIGURE 40. Postnasalo-rostral plate in visceral view. P. 50979 ($\times \frac{4}{3}$).
 FIGURE 41. Left submarginal plate. P. 50980 ($\times \frac{4}{3}$).
 FIGURE 42. Same specimen as in figure 41, in visceral view.
 FIGURE 43. Left submarginal plate with incomplete opercular cartilage; dorsal edge to the bottom of picture. Specimen damaged subsequent to the preparation of figure 36B. P. 51153 ($\times \frac{4}{3}$).
 FIGURE 44. Left posterior superognathal in aboral view. P. 50982 ($\times \frac{8}{3}$).
 FIGURE 45. Same specimen as in figure 44, in oral view.
 FIGURE 46. Left inferognathal in aboral view; dorsal edge to the bottom of picture. P. 51004 ($\times \frac{8}{3}$).
 FIGURE 47. Same specimen as in figure 46, in oral view.



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- FIGURE 48. Posterior region of skull-roof. P. 51152 ($\times 1$).
 FIGURE 49. Left anterior dorsolateral plate; anterior region. P. 50995 ($\times \frac{1}{3}$).
 FIGURE 50. Right anterior ventrolateral plate. P. 50986 ($\times \frac{2}{3}$).
 FIGURE 51. Left spinal plate, visceral view. P. 50988 ($\times 1$).
 FIGURE 52. Skull-roof. P. 51004 ($\times 1$).

section, and according to their position (figure 37) may be recognized as anterior (*Scl*₁), dorsal (*Scl*₂), posterior (*Scl*₃) and ventral (*Scl*₄) sclerotic plates. The central opening is irregularly oval (cf. Heintz 1962), with its long axis running backwards and upwards. The ring occupies only the posterior division of the orbit, where it fits accurately against the supraorbital, postorbital and suborbital cristae of the preorbital, postorbital and suborbital plates. The dorsal, posterior and ventral sclerotic plates have in consequence a well-defined contact face (*orb.cf*, figure 37C). The posterior and ventral sclerotic plates together bear a short process (*scl.p*) directed towards the centre of the ring. This process has not been described for other arthrodires, and its function is unknown. The anteroventral margin of the ring, with the anterior and ventral plates, is embayed, and large pores of the middle bone layer are exposed on the surface (*em*, figure 37D). This embayment forms the hind wall of the middle division of the orbit. In visceral aspect the sclerotic ring has a deep inner chamber, and a broad, shallow outer chamber.

Neurocranium

The neurocranium was partly invested on all its outer surfaces by a thin layer of perichondral bone, according to the evidence of fragmentary remains in P.50986, P.51153 and P.51171. These fragments give little information about the form of the whole neurocranium, but it seems likely that more complete remains will be found in large, well-ossified individuals. P.51153 shows that the dorsal surface of the neurocranium was raised into a short plug-like process in the pineal region, which filled the pineal pit of the pineal plate (*pi.p*, figures 54, 55). Consequently there was a pineal foramen, and not an extensive orbitotemporal fontanel as in some arthrodires (Stensiö 1963*b*, 1969*a*). The outline of the dorsal wall of the occipital region is given by the well developed paranuchal cristae (*cr.PNu*, figure 53) and lateral and median divisions of the nuchal thickening (*ln.th*, *mn.th*). Otherwise there are only indistinct impressions on the inner surface of the skull-roof to indicate the form of the neurocranium. Nevertheless, it seems worthwhile to attempt an outline restoration of this structure for the light it throws on the structure of the ethmoid region and on the relationships and suspension of the palatoquadrate.

Restorations of the brain-case are given in figures 54, 55. As already noted, the extent of the supravagal process (*Sv*) is indicated by the supravagal cavity of the paranuchal plate. The posterior margin of the dorsal face of the neurocranium confirms that a small process (*d.pr*) fitted into the transverse fossa of the nuchal plate (*tf*, figure 53). This removes any remaining doubt that the homologous pits in other brachythoracids were for processes of the neurocranium and not for ligaments associated with the levator muscles of the head (see Miles & Westoll 1968, p. 400). Also, on the dorsal surface, the pre-endolymphatic depression (*dp.pre*), endolymphatic groove (*gr.end*) and 'endoskeletal part of median dorsal occipital crest' (*ocr*, Stensiö 1963*b*) can be restored from the corresponding structures on the inner surface of the skull-roof. The antorbital (*Ant*) and supraorbital (*SuO*) processes have been restored from the depression on the preorbital plate. If comparisons are made with '*Kujdanowiaspis*' (Stensiö 1945, Figure 9; also 1963*b*, 1969*a*), these processes can be seen to have the same relationship to the orbit and very similar relationships to the preorbital and postorbital plates as in this genus (see also *Arctolepis*, figure 100A). The anterior postorbital process (*APO*) has been restored so that it lies behind the depression on the postorbital plate (*tdp*, figure 53), and its morphological relations are also fundamentally the same as in '*Kujdanowiaspis*' (also *Arctolepis*). There are, however, no means of determining the exact form of this process. The posterior postorbital process presents still greater difficulties, and indeed there is no unquestionable evidence that it was present. In some

advanced arthrodires it may have been absent (Stensiö 1963 *b*). The ridge on the visceral surface of the marginal plate (*rd.p*, figure 53) which has been homologized with the inframarginal crista of *Coccosteus cuspidatus* (Miles & Westoll 1968), adds to the difficulties. In *C. cuspidatus* this ridge

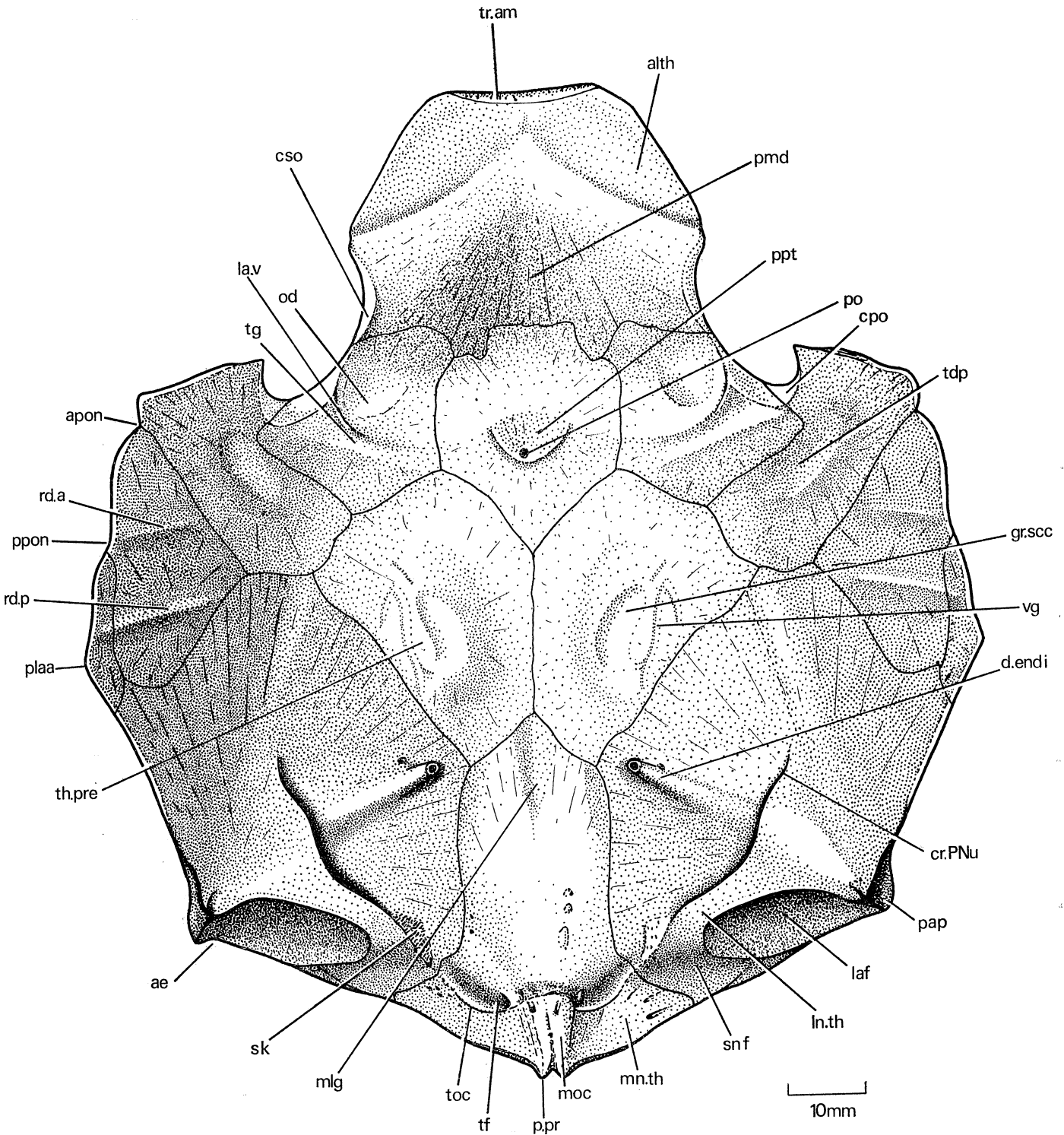


FIGURE 53. *H. westolli* sp.nov. Restoration of skull-roof in visceral view.

occupies the same position as the posterior postorbital process of *Buchanosteus* (White 1952, figure 27), and possibly it represents that process, the dermal ridge having replaced the original endoskeletal structure (Westoll & Miles 1963, p. 150).† This could also be true of *Holonema*, although a short posterior postorbital process is shown in the restorations (*PPO*). The forked

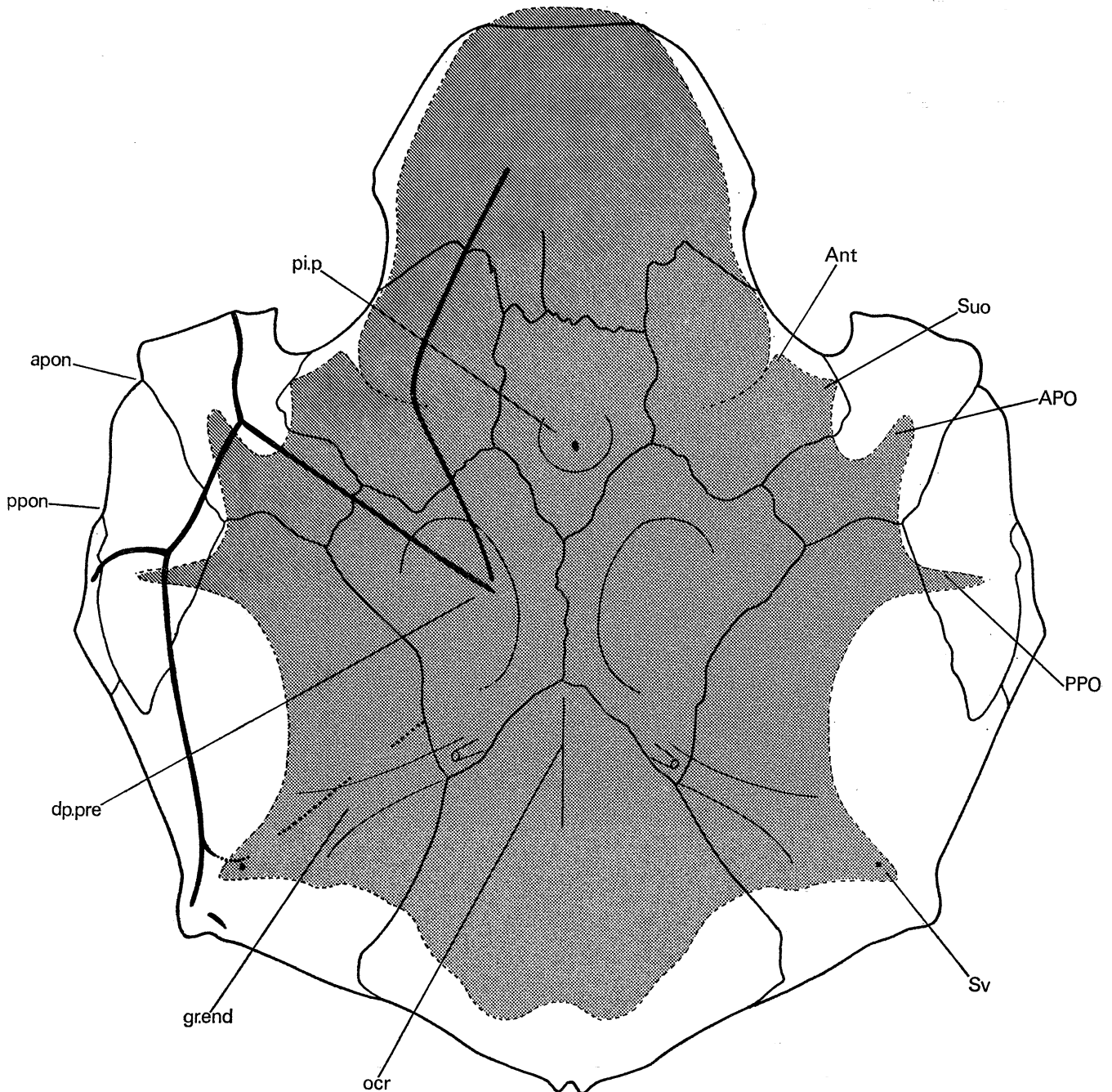


FIGURE 54. *H. westolli* sp.nov. Sketch restoration of dorsal surface of neurocranium (grey stipple).

† I have previously suggested that the posterior postorbital process of *Buchanosteus* was the dermal inframarginal crista (Miles & Westoll 1968, p. 403) but I now believe that this view is incorrect and that White's original interpretation must be accepted. If the inframarginal crista of *Cocosteus* represents the posterior postorbital process, then the restorations of the brain-case in this genus by Miles & Westoll (1968) are incorrect.

posterior postorbital process of '*Kujdanowiaspis*' suggests still another possibility. That is, that the ridge (*rd.p*) in *Holonema* is equivalent to the anterior branch of the process in '*Kujdanowiaspis*', and the posterior branch persisted as an endoskeletal (posterior postorbital) process.

There are no easily interpreted impressions of the ethmoid region, and no identifiable external nasal openings in the head-shield to show the anterior extent of the neurocranium. It is, however, possible to deduce something of the extent of the ethmoid region by considering the possible position of the nasal capsules. This problem is considered below in the section on the comparative morphology of the snout.

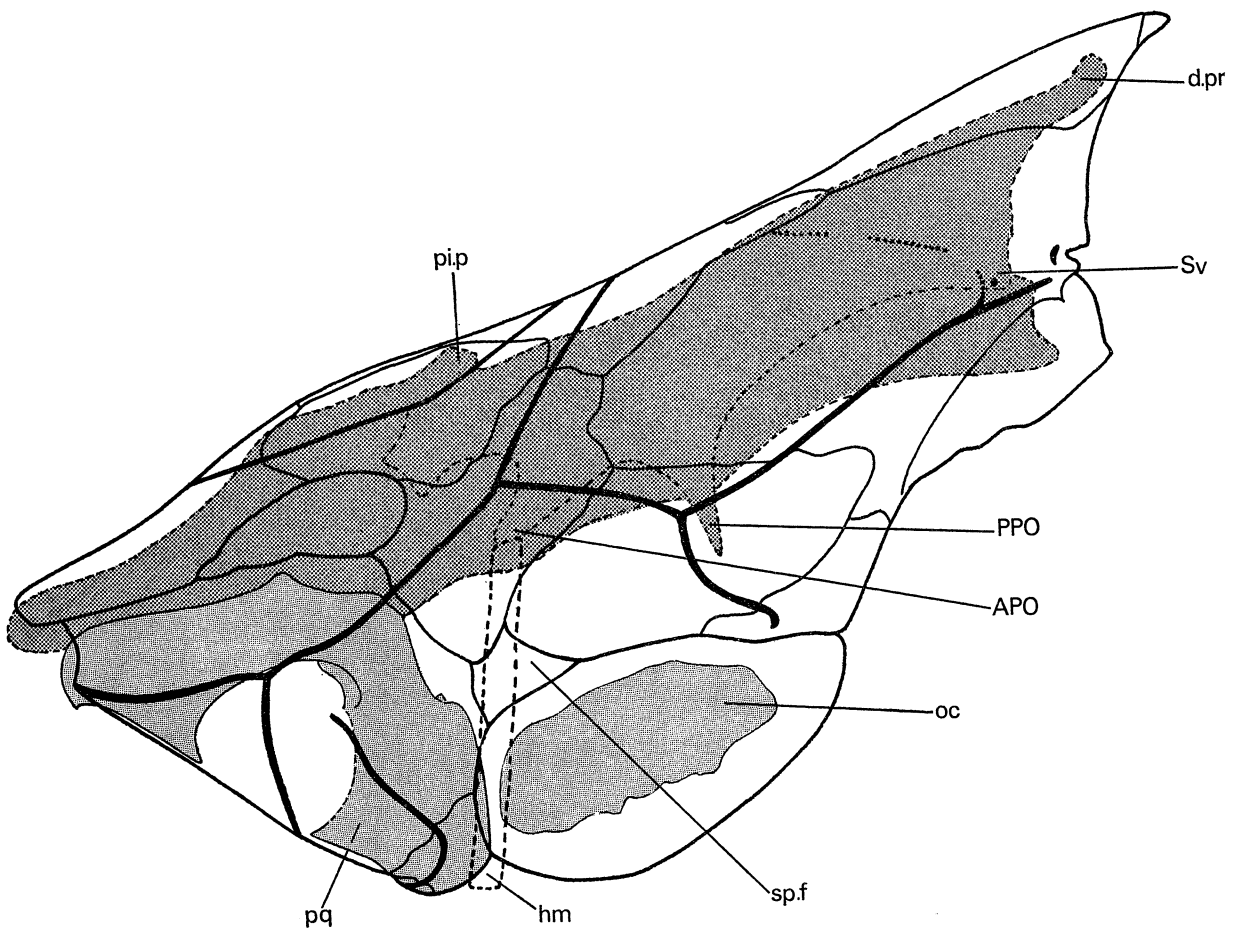


FIGURE 55. *H. westolli* sp.nov. Sketch restoration of neurocranium (dark stipple), palatoquadrate, opercular cartilage (light stipple) and hyomandibula, in lateral view.

Upper tooth-plates

The posterior superognathal is a large element which can be described in detail in *Holonema westolli*. Obruchev (1932, p. 107, Plate 6, Figures 1, 2; Plate 8, Figure 5) has described an incomplete posterior superognathal in *H. radiatum*, although he has misorientated this specimen. There is also evidence of an anterior superognathal in *H. westolli*, but the specimens are not easy to interpret.

Posterior superognathal (PSG, figures 44, 45, 56 to 58, 106)

This element is long and narrow, and curved so that it has a concave oral surface and a convex aboral surface. It is deep and, unlike the posterior superognathal in typical brachythoracids, has no dorsal lamina or process (Stensiö 1963 *b*; Miles & Westoll 1968). The aboral surface bears a prominent ornamentation in its lower half, comprising fine pipe-like ridges in a vertical series. There is a slight tendency for the ridges to anastomose in some specimens (e.g. P.51153, P.51154), and they tend to break up into elongated nodes and tubercles at the an-

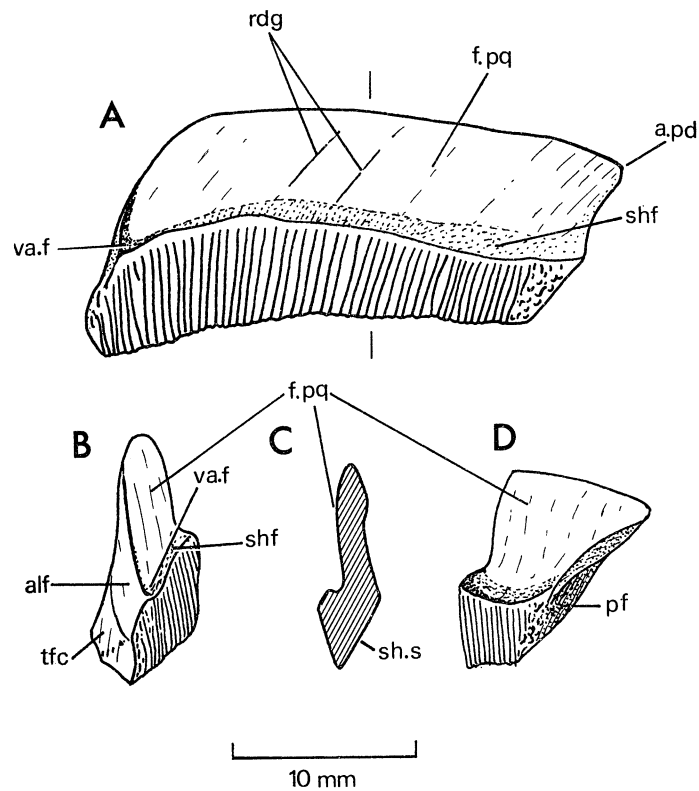


FIGURE 56. *H. westolli* sp. nov. Posterior superognathal, left, in A, aboral, B, 'anterior' and C, 'posterior' view, with section at indicated level; P.50982.

terior and posterior ends of the series. The ridges seem to be slightly more resistant to wear than the tissue between them, so that their projecting ventral ends tend to give the plate a denticulate lower edge, particularly in the anterior region of the plate. Although unworn specimens are not available, analogy with other arthrodires suggests that young individuals would have had posterior superognathals with a completely denticulate lower edge. Above this ornamented region the posterior superognathal is faceted where it was applied to the inner surface of the palatoquadrate (*f.pq*, figure 56). Anteriorly the facet ends in a distinct ventral angle (*va.f*), and in P.50982 and P.51155 the facet becomes more marked towards the posterior end of the plate. The surface of the palatoquadrate facet is formed mostly of smooth bone, with one or two slightly oblique ridges (*rdg*). However, the narrow shelf of bone between the facet and the ornamented region (*shf*), which was applied to the lower edge of the palatoquadrate, has an open bone texture.

The inner face of the posterior superognathal is divided into a lower shearing surface (*sh.s*,

figures 56 C, 57 B, 58 A, C) which worked against the outer edge of the lower tooth-plate, and an upper, depressed area of smooth bone. The shearing surface shows very little sign of the polished and scored areas usually found on brachythoracid gnathals. The tooth-plate also has anterior and posterior surfaces. The posterior surface (*pf*) is well marked and faces posteromesially. It bears an ornament of small scattered tubercles. The transition area between the inner and posterior faces forms a vertical ridge which rises to a well-marked posterior dorsal angle (*a.pd*) on the upper edge of the plate. This angle may be raised into a distinct posterodorsal process

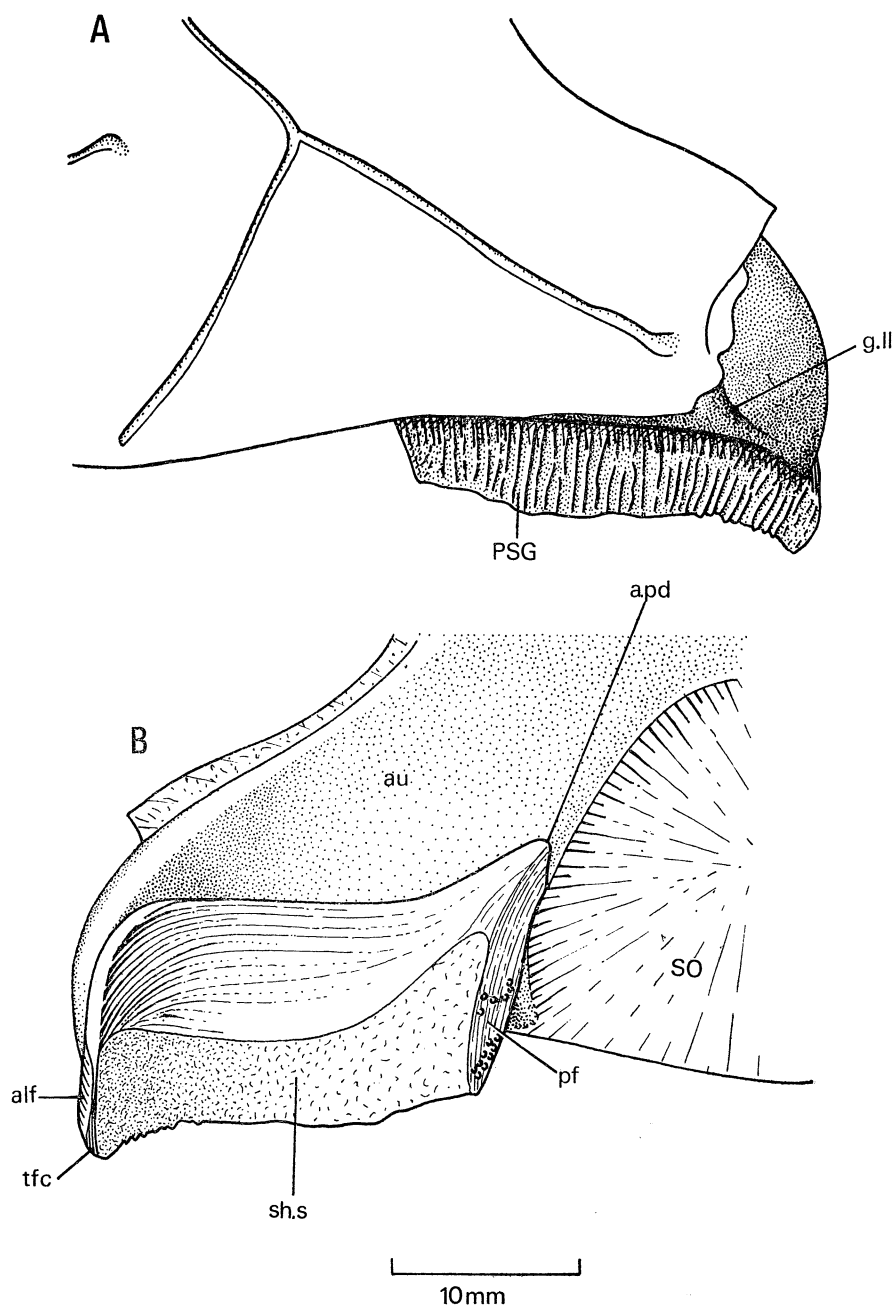


FIGURE 57. *H. westolli* sp.nov. Restoration of anterior region of right suborbital plate and palatoquadrate, with posterior suprognathal in place. A, lateral and B, mesial view. After P.51153.

(figure 57B). The shearing surface of the plate extends upwards on the ridge at the root of this process. The anterior surface of the plate is mostly devoid of feature; it is, however, divided into an upper anterolateral face (*alf*) and a lower terminal face (*tfc*, figures 56B, 57B). In a small specimen, P. 50893 (length of gnathal, 17 mm) the tubercles on the posterior surface are arranged in vertical rows, and appear to represent successive generations formed during the growth of the element (figure 58C). In other specimens as well (figure 45), there are clearly defined growth lines on the upper depressed area of the aboral surface. P. 50893 also has the lower edge

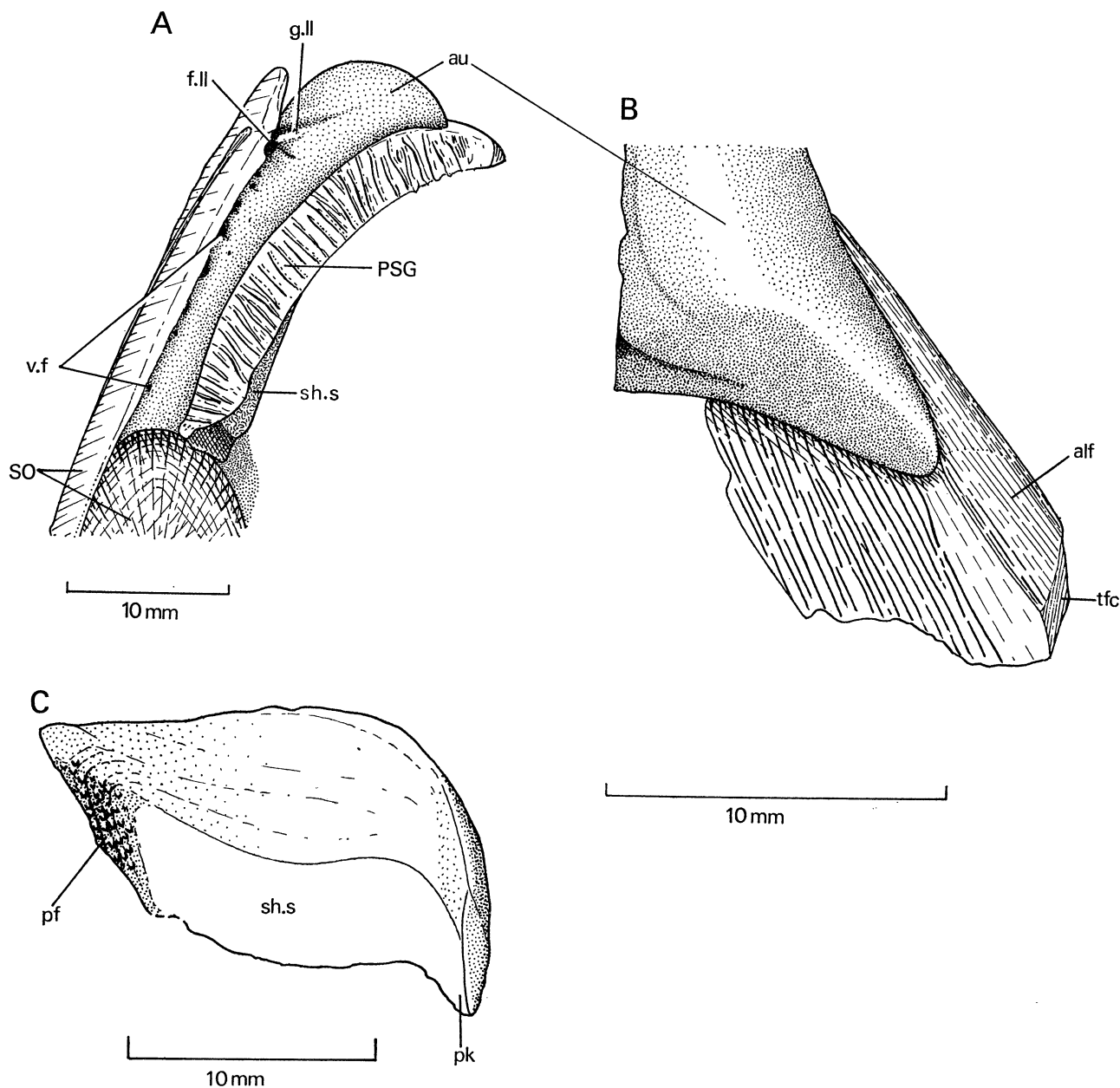


FIGURE 58. *H. westolli* sp. nov. A, Restoration of anterior region of right suborbital plate and palatoquadrate with posterior superognathal in place, ventral view. After P. 51153. B, restoration of right palatoquadrate and posterior superognathal in 'anterior' view. After P. 51153. C, posterior superognathal, left, in oral view, P. 50893.

of the tooth plate produced into an anterior cusp (*pk*, figure 58 C). There are indications of this cusp in other specimens, although it is always worn down.

Anterior superognathal (ASG, figure 59)

In P. 51155 the left and right inferognathals with their supporting meckelian cartilages, and the left posterior superognathal, are preserved in virtually their natural relationships. The small tooth-plate, which is here identified as the anterior superognathal, was found close to the anterior margin of the posterior superognathal, and it was subsequently freed from the specimen during preparation. One other example of this tooth-plate has been found in P. 50893; it is closely similar to that of P. 51155.

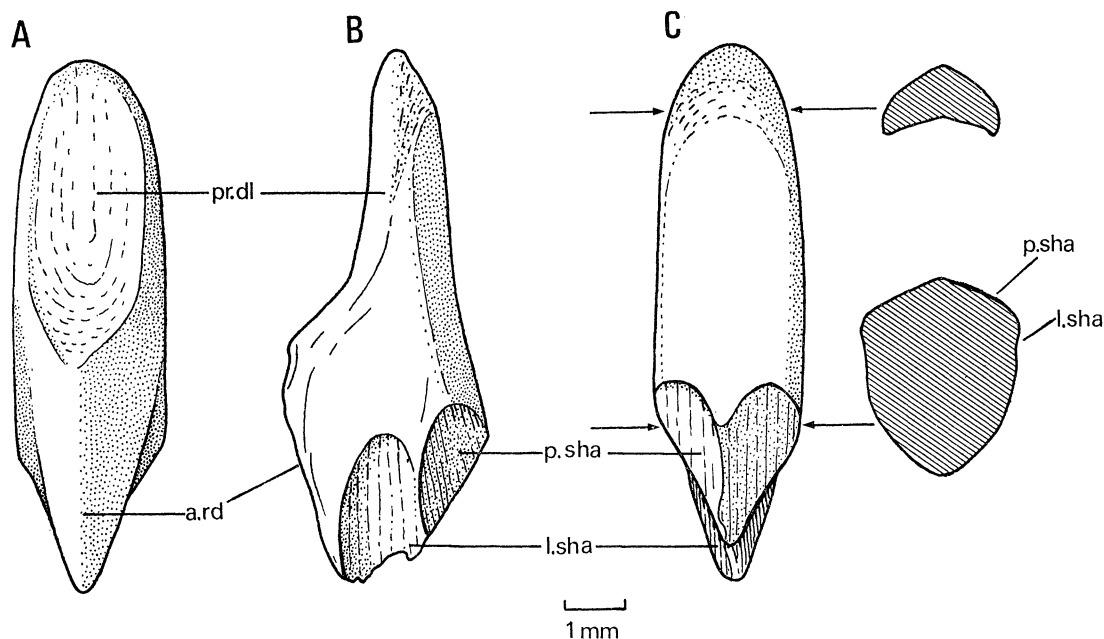


FIGURE 59. *H. westolli* sp. nov. Anterior superognathal in A, anterior, B, lateral and C, posterior view, with sections at levels indicated; P. 51155. The lower section is to a slightly larger scale than the other figures.

It has proved difficult to orientate this peg-like gnathal, but as the inferognathal normally shears against the oral surfaces of the superognathals in arthropods, the shearing surfaces have been assumed to be on the posterior and lateral surfaces of the bone. As can be seen in figure 59, there is a stout dorsal process (*pr.dl*) with a slightly hollowed anterior face; below this process the anterior (aboral) face of the bone forms a projecting ridge (*ard*). Ventrally there is a paired lateral shearing area (*l.sha*), followed immediately by a further paired shearing area on the posterior (strictly the oral) face (*p.sha*). There is no sign of a dorsal lamina such as is found in typical brachy thoracid anterior superognathals (Stensiö 1963 *b*; Miles & Westoll 1968), nor can this bone be compared with the transversely elongated anterior superognathal of the dolichothoracid '*Kujdanowiaspis*' (P. 18278; Stensiö 1963 *b*, Plate 62). The anterior superognathal has, however, a superficial similarity to those of the advanced brachy thoracids *Paraleiosteus diensti* Stensiö and *Brachyosteus dietrichi* Gross (Stensiö 1963 *b*, Figure 118 I, K). Perhaps the most remarkable feature of the anterior superognathal in *Holonema westolli* is its almost perfect bilateral symmetry. This symmetry makes it difficult to regard the tooth-plate as a paired structure strictly comparable with the anterior superognathal of other arthropods. Perhaps the presence

of lateral and posterior shearing surfaces, enclosing between them an angle of about 100° , can be explained by assuming that the shearing relations with the anterior end of the inferognathal varied, because the cheek-palatoquadrate-lower jaw complex was laterally mobile. But the presence of paired lateral and posterior shearing surfaces would clearly seem to indicate that the anterior superognathal was an unpaired median element. It is not clear whether the lateral surfaces of the tooth-plate were contiguous with the anterior faces of the posterior superognathals, and its relationships to the ethmoid region of the brain-case are not known (p. 189).

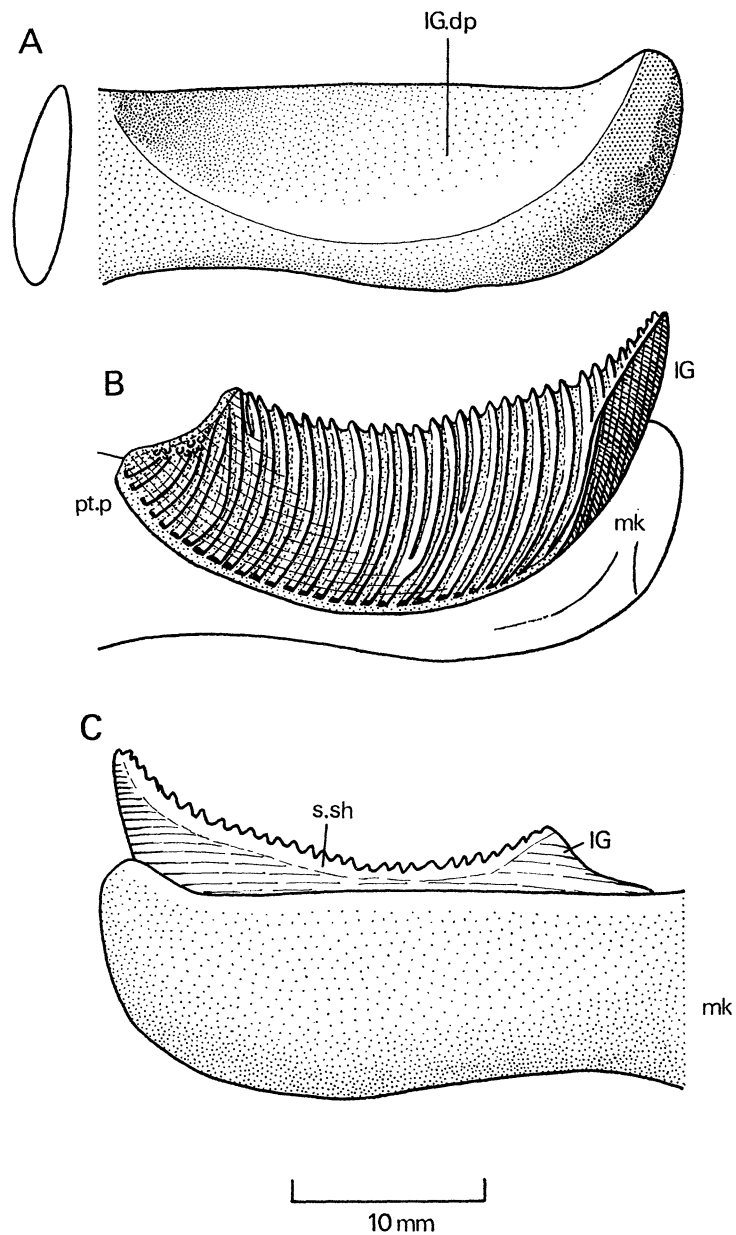


FIGURE 60. *H. westolli* sp. nov. A, meckelian cartilage, left, anterior region in mesial view, with end section; B, C, inferognathal, left, in place on meckelian cartilage, in mesial and lateral view. Restoration after P. 51004 and P. 51155.

Lower jaw

The lower jaw is represented by the inferognathal tooth-plate and the perichondrally ossified anterior part of the meckelian cartilage. The inferognathal is a short bone, comparable only with the biting or functional division of the inferognathal in typical brachythoracids. There is no sign of the blade which lies mesial to the meckelian cartilage in other brachythoracids. An inferognathal of similar short extent is known in some dolichothoracids (Denison 1958, Figure 101A to E), although it is not closely comparable with that of *H. westolli*. The ossified region of the meckelian cartilage is comparable with the mentomandibular ossification in other brachythoracids (Stensiö 1963*b*; Miles & Westoll 1968), which lies ventral and mesial to the biting division of the inferognathal.

Inferognathal (IG, figures 46, 47, 60B, C, 61A to C)

This tooth-plate is a thin, delicate structure in comparison with the posterior superognathal, against which it sheared. It is arched in both longitudinal and transverse profiles, and has a

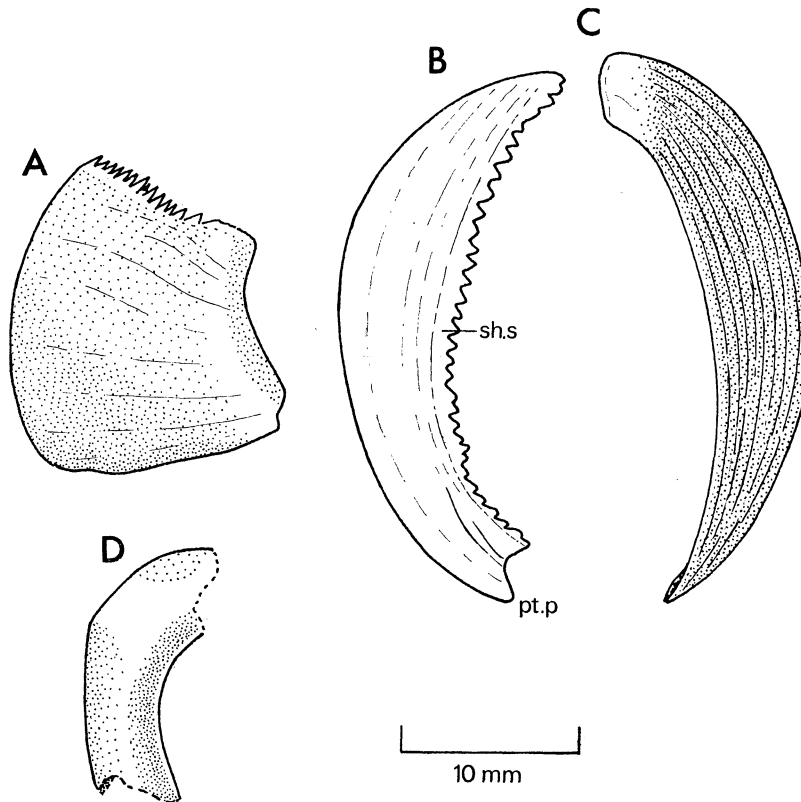


FIGURE 61. *H. westolli* sp. nov. A-C, inferognathal, left, in A, 'anterior', B, dorsal and C, ventral view. D, meckelian cartilage, right, anterior region in ventral view, P.51154.

strongly convex, aboral surface and a concave oral surface. The aboral surface is formed of smooth bone, with a worn, poorly defined shearing surface dorsally (*sh.s*). It exhibits a series of parallel, faint growth lines. The posteroventral angle of the plate is drawn out into a short process (*pt.p*). The oral face of the inferognathal bears a series of ridges comparable with those on the aboral face of the posterior superognathal. The ridges shown a slight tendency to branch,

and they tend to break up into a few small tubercles near the posterior edge of the plate (figure 60B). The ridges are open ventrally and appear to be hemicylindrical tubes, but dorsally each is produced into a solid tip so that the inferognathal has a denticulate upper edge. Thin sections of the tooth-plate have been prepared in the British Museum (Natural History) and by Dr T. Ørvig in the Swedish Museum of Natural History. They show that the ridges are composed partly of semidentine, and the body of the tooth-plate is composed of bone. There are no hyper-mineralized hard tissues.

Meckelian cartilage (mk, figures 60, 61D)

The perichondral bone investing this structure is very thin. It is incomplete at the tip of the meckelian cartilage, as well as more posteriorly, so the nature of the mandibular symphysis is unknown. The bone, however, makes a strong mesial bend anteriorly, and there is no doubt that it was connected to its antimere either by ligaments or through a basimandibular element. The most prominent feature of this ossification is the well-defined depression (*IG.dp*, figure 60A) on its mesial surface for the inferognathal plate.

Trunk-shield

General features

The trunk-shield includes the usual plates that are found in phlyctaenaspid- and coccosteo-morph-level arthrodires. There are no anteroventral plates as there are in actinolepid-level species, and no 'normal' member of the armour is suppressed, as is the case in some pachyosteo-morph-level families. The plates are large and thin in comparison with those of the head-shield, and generally have simple overlapping sutures. The terminology of the overlapping surfaces that is used for the skull-roof can be used for the trunk-shield, and the remarks made above on the radiation centres of the plates also apply. In most specimens the plates have drifted out of their natural relationship, and they tend to be too damaged after preparation for the shield to be reconstructed bone by bone. However, the dorsal and flank plates are preserved in their correct relationship in P. 51157 and P. 50893 (figures 62, 82) and the dorsal plates and part of the ventral shield have been restored in P. 50984 (figure 73) and P. 50995 (figures 92, 93) respectively. The graphic restorations (figures 63 to 65) have been based mainly on these four specimens.

The armour is long and more box-like than in most arthrodires. The flank plates are extensive, although the postpectoral wall is narrow. There is a long, low pectoral fenestra (*p.fen*) and a long spinal plate (*sp*), both of which are carried well above the base-level. The dorsal and ventral walls of the armour are tumid with transversely and longitudinally arch profiles. There are no dorsolateral or ventrolateral 'edges' or 'keels', although the flank is arched so that it presents dorsolateral and lateral faces. Anteriorly the anterior dorsolateral and anterior lateral plates jointly give rise to an obstantic process (*pro*). The ventral wall of the shield has a posterior median notch. The visceral surface of the trunk-shield and other structures, including the articular condyle, are described below in the accounts of the individual plates.

The shield is broadest across the posterior tips of the ornamented surfaces of the spinal plates. From the restorations, it appears that the maximum length of the shield is slightly greater than its maximum breadth (breadth/length index about 94), and the maximum height of the shield is equal to slightly less than one-half of its maximum length. The individual plates may now be described.

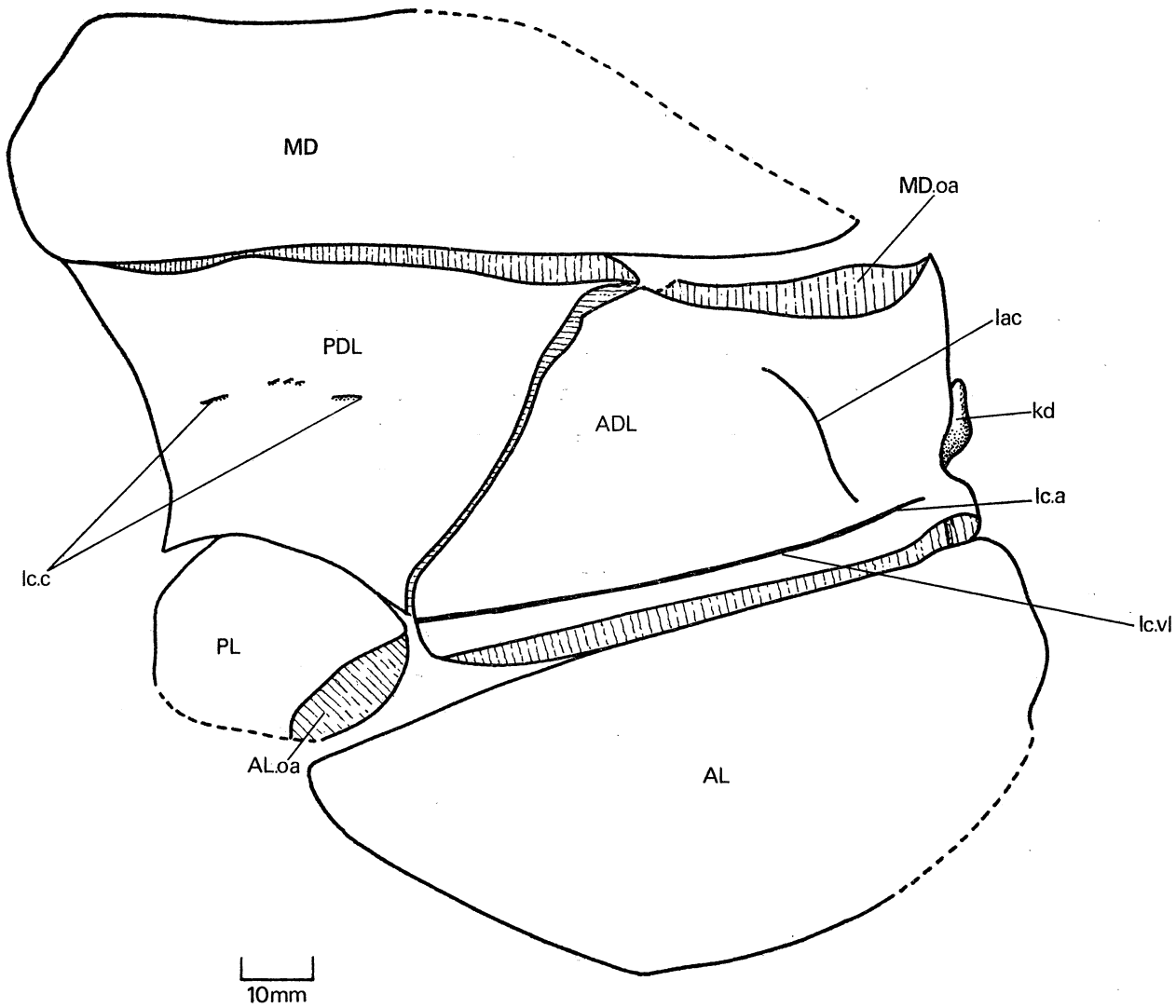


FIGURE 62. *H. westolli*. sp.nov. Sketch of right flank plates, as preserved, P. 50893.

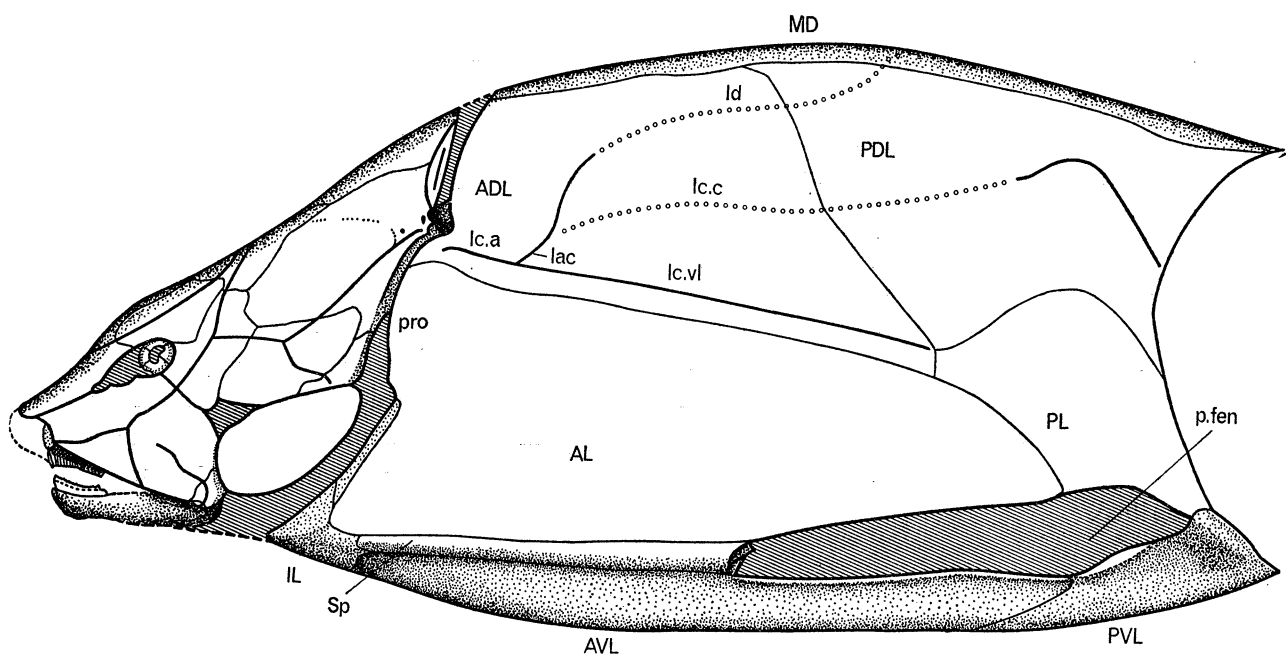


FIGURE 63. *H. westolli* sp.nov. Restoration of head and trunk shields in lateral view. Hypothetical sensory lines represented by rows of small circles.

Median dorsal plate (MD, figures 19, 62 to 64, 66, 67, 73, 82)

This plate is of the usual long, slender shape for *Holonema*. Unfortunately no specimens are completely preserved, but the estimated breadth/length index in the holotype (P. 50984) is 31. The plate is arched in both its transverse and longitudinal profiles. The shape of the margins vary, but the anterolateral (*ala*), first lateral (*la*₁) and posterolateral (*pla*) angles are consistently present, and in P. 50984, P. 50983 and P. 50987 there is also a second lateral angle (*la*₂, figure 66).

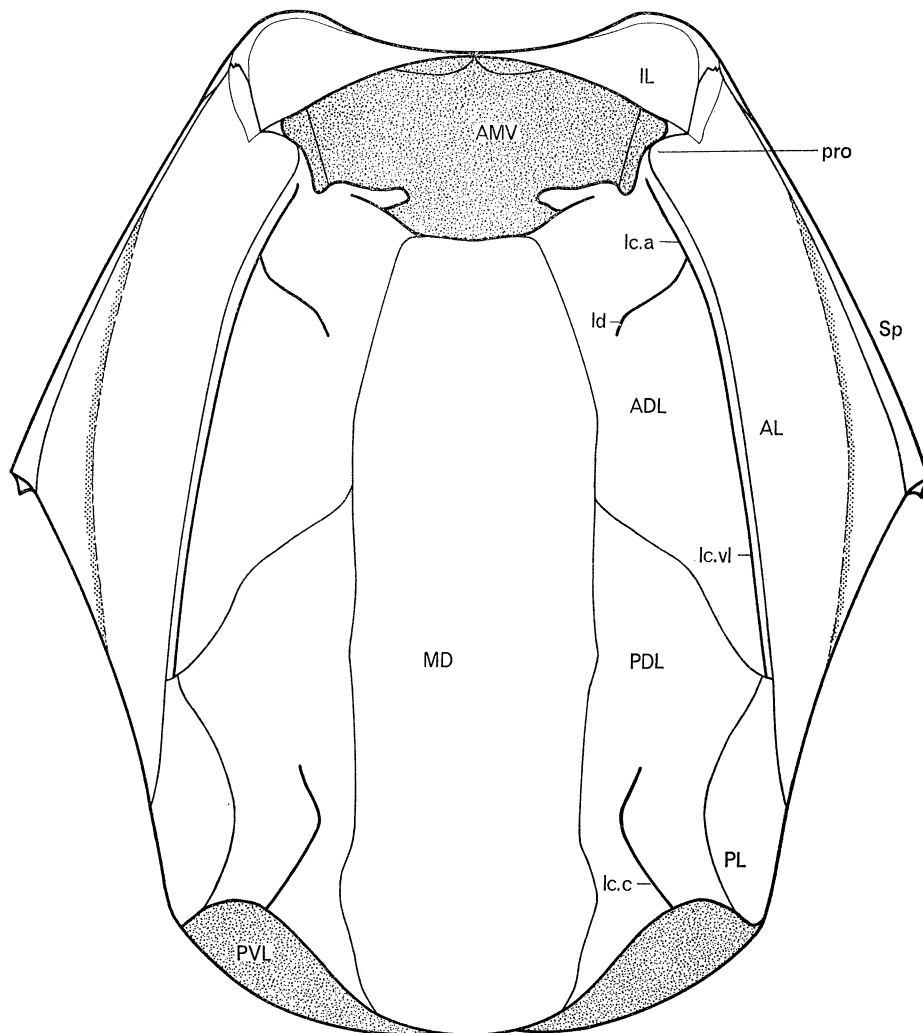


FIGURE 64. *H. westolli* sp.nov. Restoration of trunk-shield in dorsal view.

The anterior margin is slightly concave. In P. 50984 (figure 66) it is possible that a small plate (*fp*) has partly fused with the anterior margin; it is delimited by a small foramen to the left and a notch to the right of the middle line, and by a vestigial suture on the visceral surface reminiscent of that found on the postnasalo-rostral plate. No other specimens show this plate. It might possibly be regarded as an extrascapular element that has fused with the median dorsal plate, but this seems unlikely as normal extrascapulars are found in this specimen (p. 131). The degree of convexity of the posterior margin varies, but there is never a distinct posterior median angle or process (figures 66, 67 A). The upper edges of the median dorsal are slightly bevelled, particularly

in the larger specimens (*b.d.e.*, P. 50989, P. 50984). The radiation centre is posteriorly situated, and may be preceded by a short, median dorsal ridge (*mdr*), although this structure is always ill-developed (it is part of the structure in the ornamentation termed the 'club', p. 175; Wells 1942). There are no sensory lines on the surface.

The visceral surface has a short, paired contact face for the anterior dorsolateral plate (*ADL.cf*), and a long, paired contact face for the posterior dorsolateral plate (*PDL.cf*). These

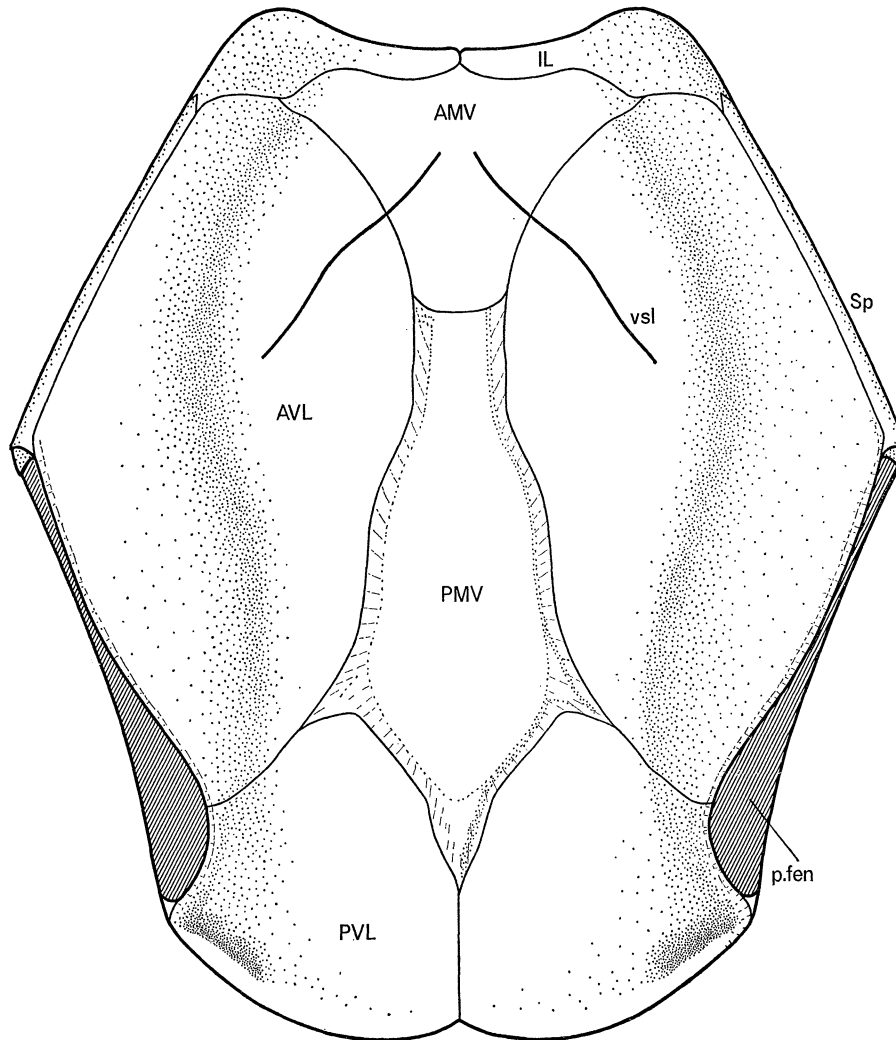


FIGURE 65. *H. westolli* sp. nov. Restoration of trunk-shield in ventral view.

contact faces are relatively broader in small individuals than in large ones. Thus in P. 50987 (estimated length of plate 110 mm) the maximum width of the posterior dorsolateral contact face is equal to about one-third of the maximum width of the plates, whereas in P. 50987 (estimated length of plate 215 mm) the maximum width of the contact face is equal to slightly less than one-quarter of the maximum width of the plate. In all specimens there are prominent neurovascular foramina along the margins of the contact faces. In the middle line there is not a single, deep keel, as in typical brachythoracids (Miles 1969), but a series of three structures. Anteriorly there is a short, ill-defined thickening, the 'anterior keel' (*a.th*; cf. *H. radiatum*,

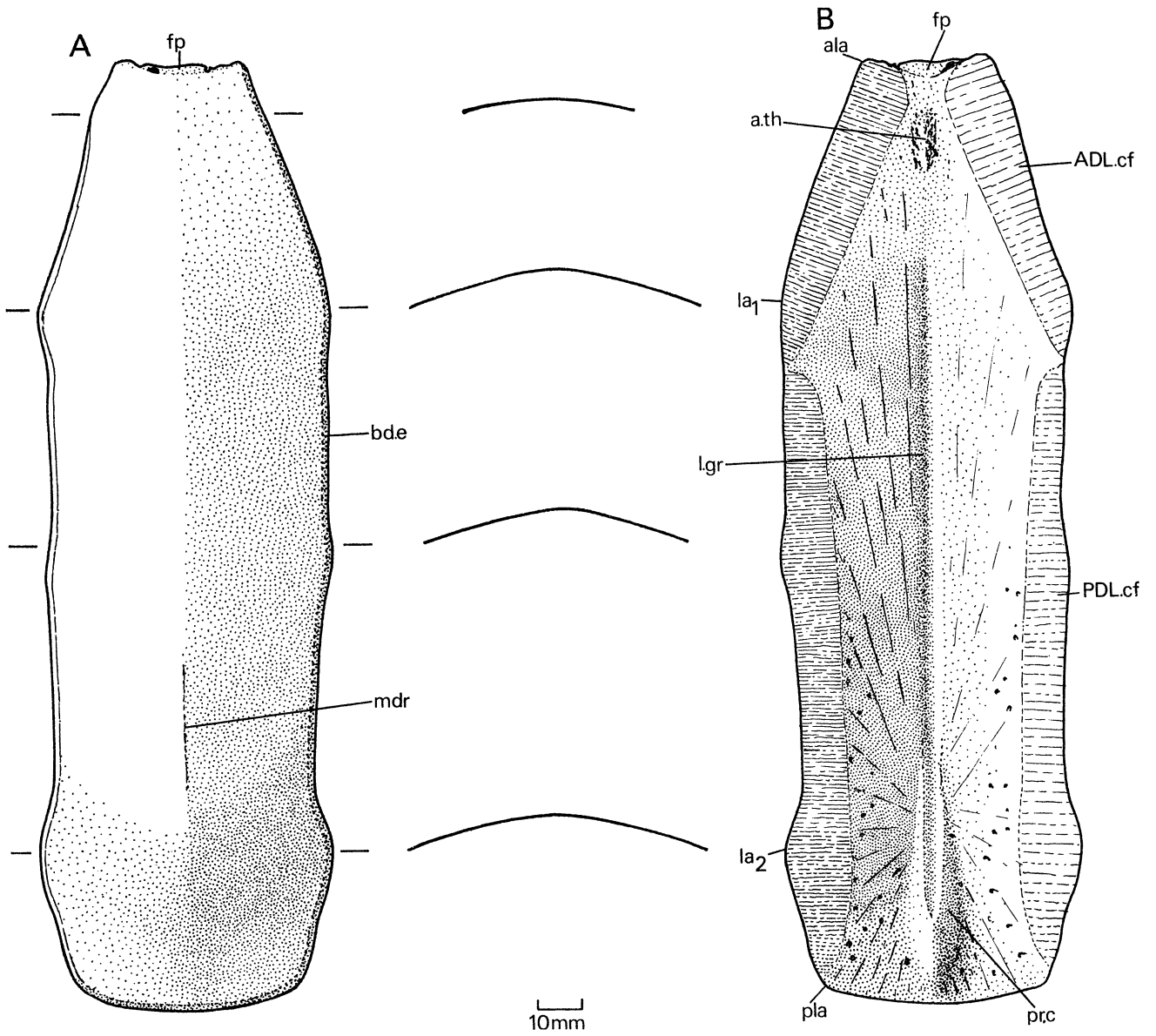


FIGURE 66. *H. westolli* sp.nov. Median dorsal plate in A, dorsal and B, visceral view, with profiles at levels indicated. After P. 50984.

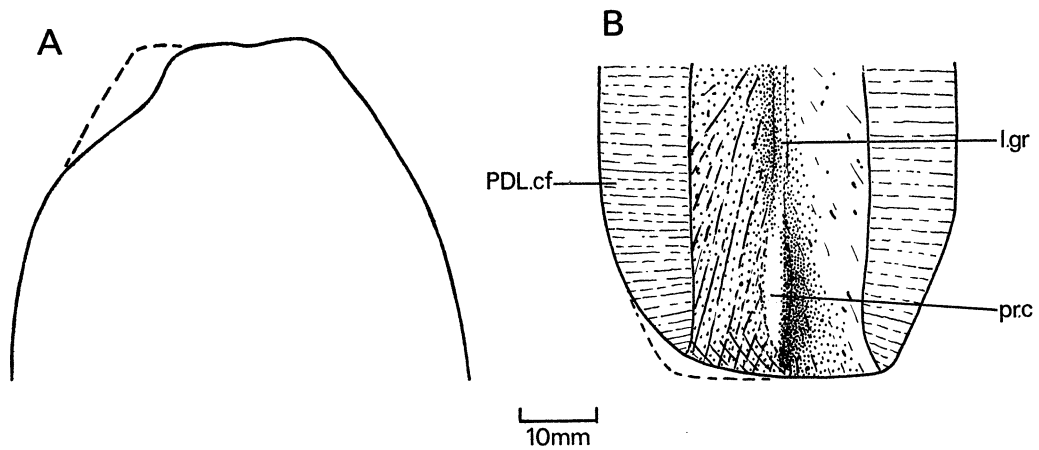


FIGURE 67. *H. westolli* sp.nov. Median dorsal plates. A, anterior region in outline, P. 51221; B, posterior region in visceral view, P. 50989.

Obruchev 1932, Figure 5); in the middle a long, well-defined groove (*l.gr*), and posteriorly a small process, the 'posterior keel' (*pr.c*). The groove in the middle of the series extends posteriorly on to the anterior edge of the 'posterior keel' where it fades out. The 'posterior keel' is variable in its development, although there is no apparent correlation between its form and the size of the individual. In P. 50984 (figure 66B) it is broad and low, but well-defined; in P. 50987 it is little more than an ill-defined thickening of the bone surface; whilst in P. 50989 (figure 67B), P. 50893 and P. 51225 it is narrow and moderately deep.

Anterior dorsolateral plate (ADL, figures 14, 18, 49, 62 to 64, 68 to 70, 73)

This is one of the most robust plates of the trunk-shield, and it is particularly thick at the root of the articular condyle (*kd*, figure 68). It is dorsoventrally arched, but the axis of fold is difficult to define and there is no distinct dorsolateral 'edge' between dorsolateral and lateral laminae. Dorsally, on the outer surface of the plate, there is a distinct overlap surface for the median dorsal plate (*MD.oa*), and ventrally there is an overlap surface for the anterior lateral plate (*AL.oa*). Anteriorly, the anterior lateral overlap surface increases in depth, and it is grooved (*gr.pbl*) for the uppermost part of the postbranchial lamina of the anterior lateral plate. Prominent features of the margins are the antero- and posterodorsal angles (*a.ad*, *a.pd*), and the antero- and posteroventral external angles (*a.av*, *a.pv*). The anterodorsal angle is borne on a postnuchal process (*pn.pr*), but unlike the postnuchal angle of antiarchs, it is devoid of ornament. The anteroventral angle lies at the tip of a small obstantic process (*pro*). The lower edge of this process bears a postobstantic notch (*pon*), just above the groove *gr.pbl* on the anterior lateral overlap surface.

The principal lateral-line groove (*lc.a*, *lc.vl*) arises shortly behind the obstantic process and runs posteriorly roughly parallel with the external ventral margin of the plate. The groove may extend to the posterior margin, as in P. 50995 and P. 51124, but in other specimens it ends well short of this margin (figure 68A). It is interpreted as having housed the anterior part of the main lateral-line plus the ventrolateral line (p. 191). The anterior dorsolateral line (Stensiö 1969*a*) is also represented by a groove (*ld.a*). The configuration of this groove varies (cf. Ørvig 1969) and its interpretation is discussed below (p. 193).

The articular condyle arises on the visceral surface just in front of the radiation centre of the plate. The root of the condyle extends over the bone surface in powerful dorsal (*d.kdr*) and ventral (*v.kdr*) ridges, the latter lying under the groove *gr.pbl* on the overlap surface for the anterior lateral plate (figure 68B). These ridges correspond to the 'ridge supporting condyle' and the 'condyle basis' respectively, of Heintz's (1932*a*, Figure 47) account of *Dunkleosteus*. The dorsal ridge delimits the 'upper joint fossa' (*ujf*) as in *Dunkleosteus* (Heintz 1932*a*, Figure 71). The condyle is transversely elongated and narrows mesially so that it is somewhat pear-shaped. Its articular face has a *Siebknochen*-like texture, and this face is separated from the smooth posterior face by slight supra- and infra-articular ridges (*sar*, *iar*, figure 69). The long axis of the condyle is about $2\frac{1}{2}$ times as long as the maximum height of the articular area in P. 50986 and P. 51014, and about twice as long in the small specimen P. 50995. It is, however, difficult to define the lateral edge of the condyle and therefore it is difficult to make exact measurements. The long axis of the condyle encloses an angle of about 45° with the outer surface of the dorsolateral lamina of the plate. Below the condyle on the inner surface of the obstantic process, lies a prominent pad of bone with a *Siebknochen*-like texture, which corresponds to the subglenoid 'process' of other brachythoracids (Heintz 1932*a*; Miles & Westoll 1968). This pad worked against

the large occipital para-articular process of the skull-roof, and will be termed the para-articular face of the anterior lateral plate (*paf*). The para-articular face is connected to the ventrolateral corner of the articular condyle by a neck of bone, again with a *Siebknochen*-like texture (*n.Sk*; figure 69).

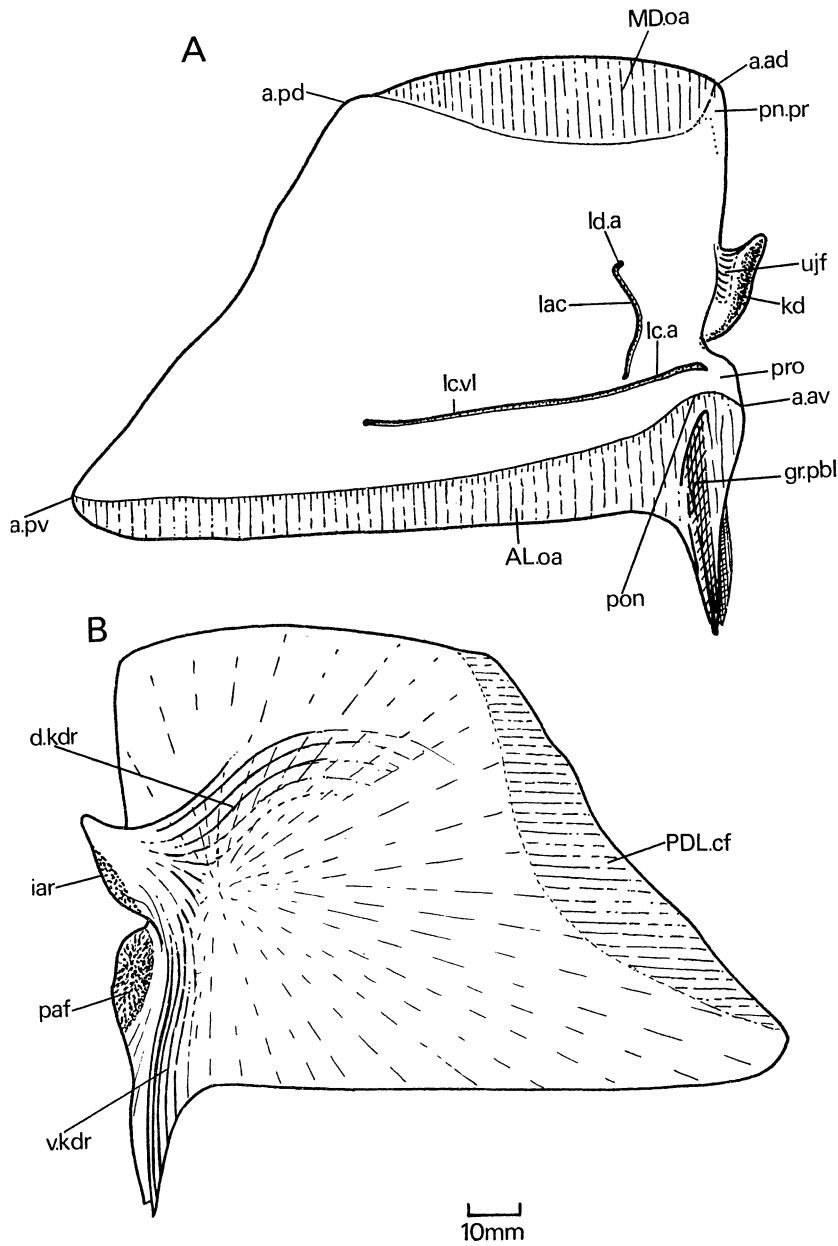


FIGURE 68. *H. westolli* sp.nov. Anterior dorsolateral plate in A, lateral and B, visceral view. Based on P. 51014.

Along the posterior margin of the anterior dorsolateral there is a broad contact face for the posterior dorsolateral plate (*PDL.cf*).

Posterior dorsolateral plate (PDL, figures 14, 62 to 64, 71 to 73)

This large plate is fairly completely preserved in several specimens and it is possible to found an accurate restoration on P. 51014 (figure 71). The surface of the plate is dorsoventrally curved,

but as in the case of the anterior dorsolateral, it is not possible to recognize a dorsolateral 'edge' separating the dorsolateral and lateral laminae. The outer surface bears well-defined overlap areas dorsally, anteriorly and ventrally, for the median dorsal (*MD.oa*), anterior dorsolateral (*ADL.oa*) and posterior lateral (*PL.oa*) plates respectively. There is no contact with the anterior

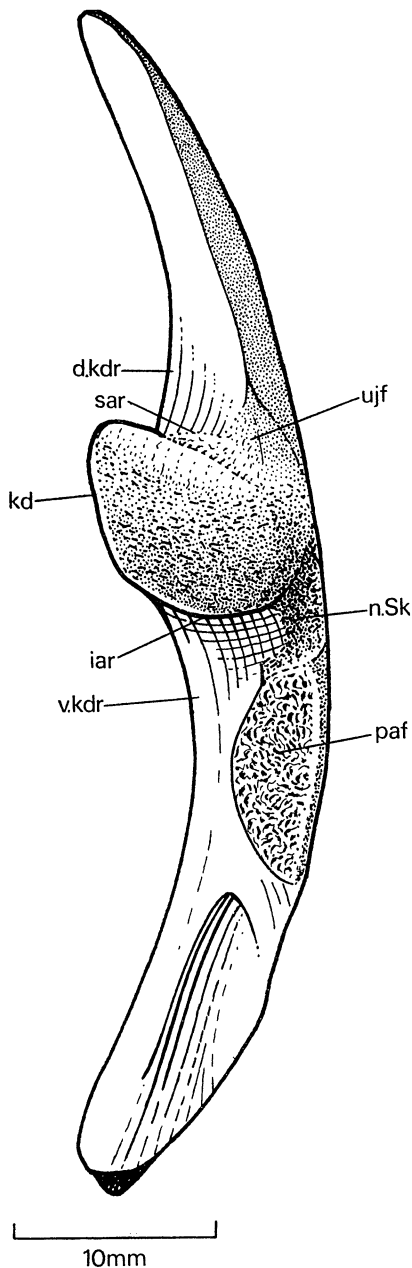


FIGURE 69. *H. westolli* sp.nov. Anterior dorsolateral plate; anterior face in anteromesial view; P. 50995.

lateral plate, as there is in many dolichothoracids (Denison 1958, Figure 109), and in this respect *Holonema* resembles many brachythoracids (Heintz 1932*a*; Miles & Westoll 1968). The overlap areas are delimited by distinct antero- and posterodorsal angles (*ad.an*, *pd.an*) and antero- and posteroventral (*av.an*, *pv.an*) external angles. These angles are drawn out into small, distinct processes. The main lateral-line canal (*lc.c*) is represented as a groove in the posterior

half of the bone surface. This groove may extend to the posterior margin (figure 72B), but in most specimens it stops short of this margin. In P.50987 it is a continuous, smoothly arched structure, as depicted in the reconstructions (figures 63, 64), but in five other specimens it is broken up into a variable number of differently oriented short sections (figures 71A, 72). The overall arched path of the line is matched on the posterior dorsolateral plates in some dolichothoracids (Denison 1958; Gross 1962*b*, Figure 6B). The posterior dorsolateral is thicker in the region of the growth centre, posterior to which there is a slight depression on the visceral surface (*pdp*, figure 71B).

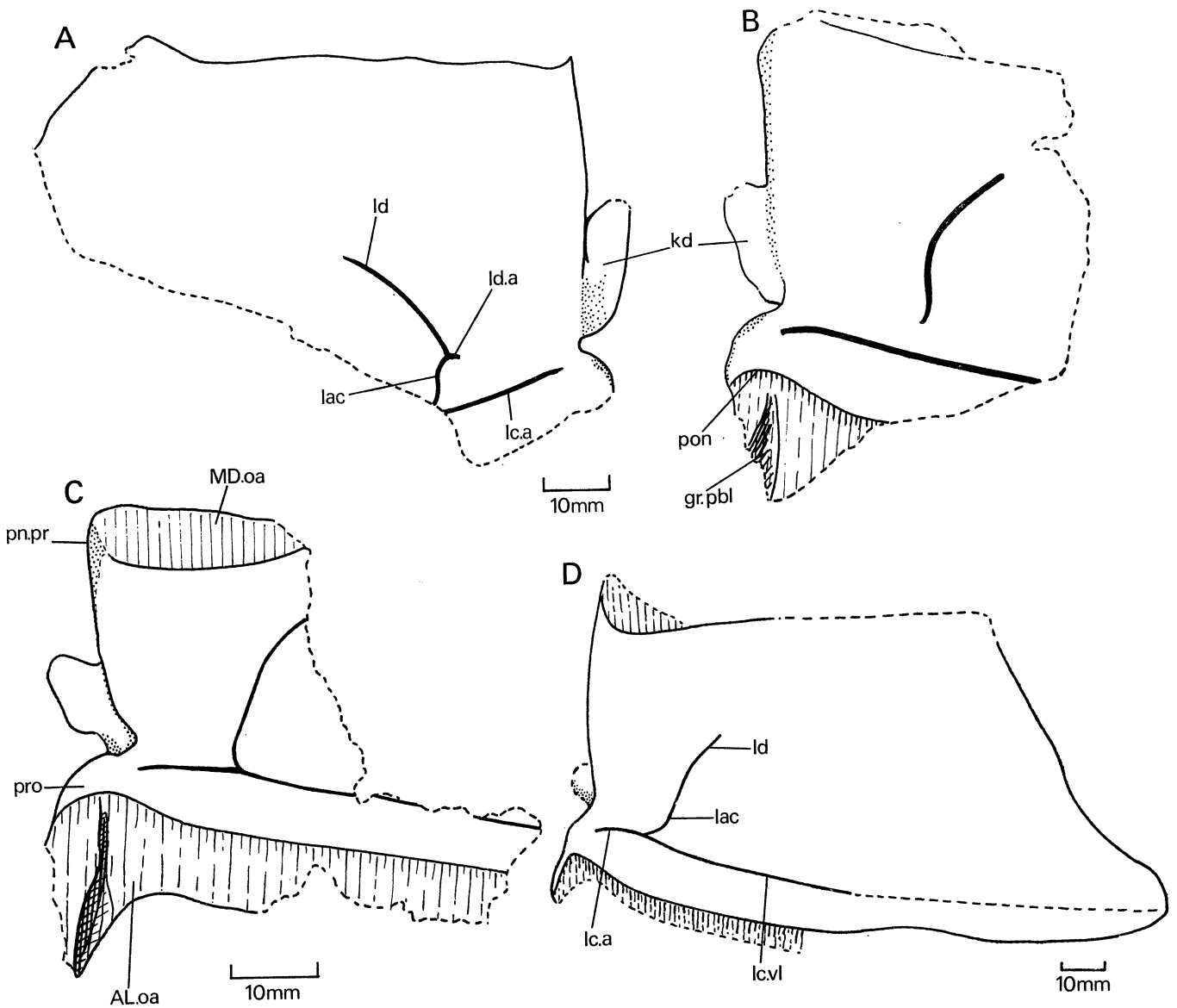


FIGURE 70. *H. westolli* sp.nov. Anterior dorsolateral plates. A, right plate P.50984; B, left plate P.51014; C, left plate, P.50995; D, left plate, P.51157.

Anterior lateral plate (AL, figures 62 to 64, 74, 75, 82, 83)

The anterior lateral plate is long and laterally bowed. The suprascapular (or ventral) margin is about $1\frac{1}{2}$ times as long as the suprapectoral (posteroventral) margin, and the lower part of the plate which carries these margins is flared out about an ill-defined line, as indicated in figure 64. The suprascapular and suprapectoral margins meet at the posteroventral angle (*pv.ae*, figure 83), and the suprapectoral and posterodorsal margins meet at the posterior angle (*p.ae*). There are also posterodorsal and anteroventral angles (*pd.ae*, *av.ae*). The upper part of the anterior margin

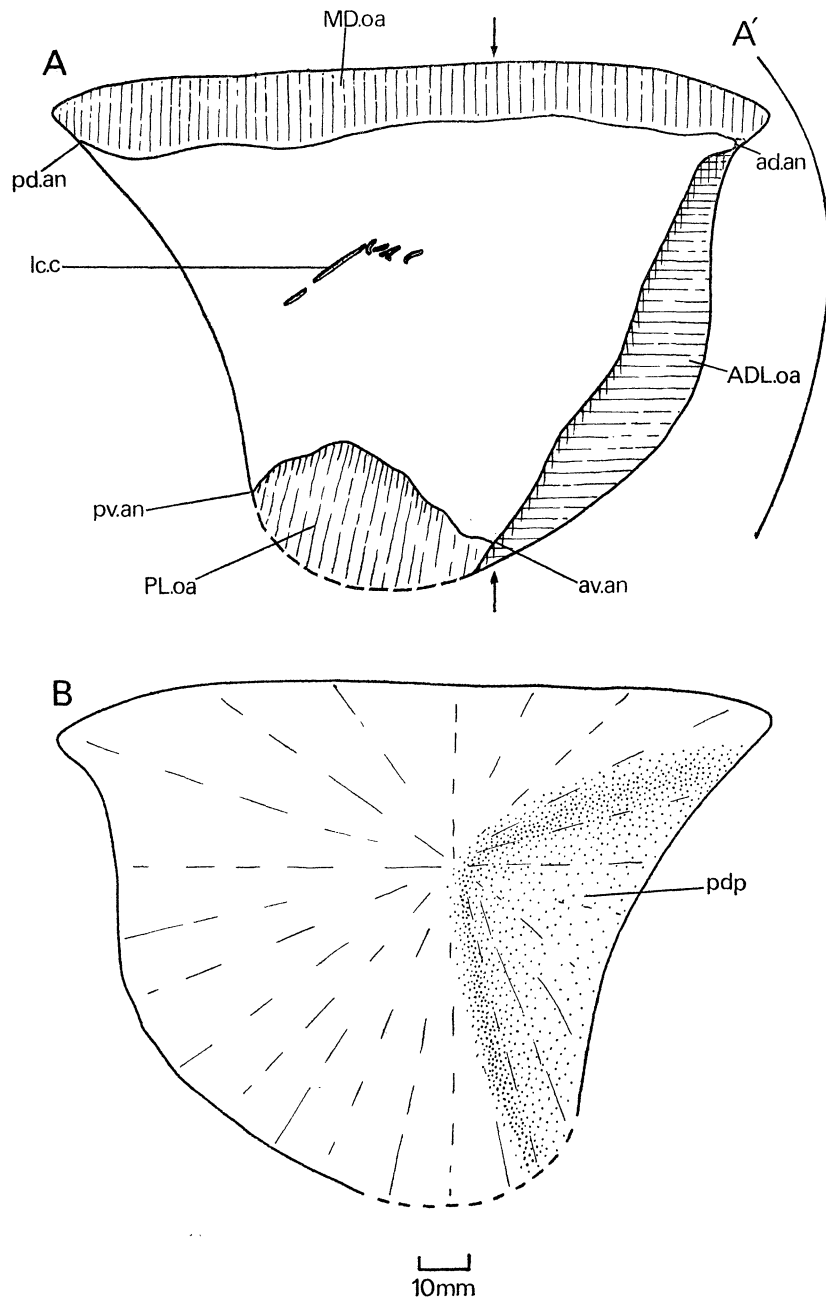
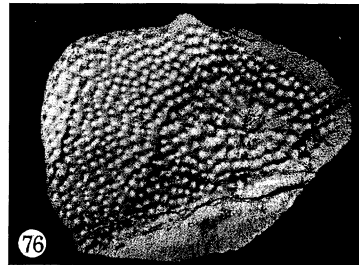


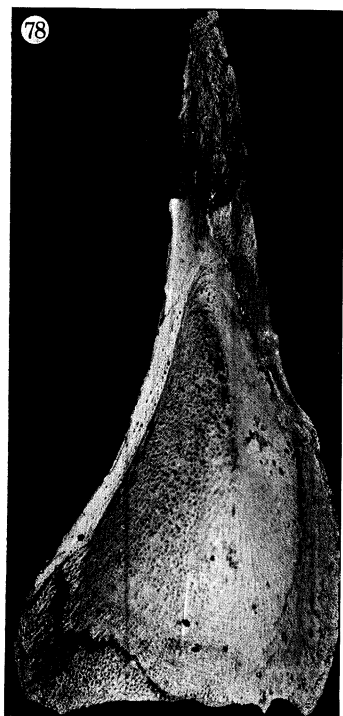
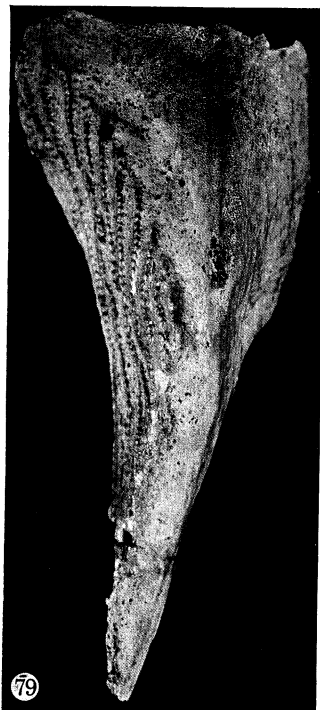
FIGURE 71. *H. westolli* sp. nov. Posterior dorsolateral plate, left, in A, lateral and B, visceral view, with A', profile at level indicated. Based on P.51014.



Holonema westolli sp.nov.

- FIGURE 73. Dorsal plates of trunk-shield. Holotype, P. 50984 ($\times \frac{2}{3}$).
 FIGURE 74. Left anterior lateral plate in lateral view. P. 51152 ($\times \frac{2}{3}$).
 FIGURE 75. Same specimen as in figure 74, but in visceral view.
 FIGURE 76. Left posterior lateral plate. P. 50987 ($\times \frac{4}{3}$).
 FIGURE 77. Left posterior ventrolateral plate. P. 50987 ($\times \frac{4}{3}$).

(Facing p. 162)



Holonema westolli sp. nov.

FIGURE 78. Interolateral plate in posterior view. P. 51171 ($\times \frac{4}{3}$).

FIGURE 79. Same specimen as in figure 78, but in anterior view.

FIGURE 80. Anterior median ventral plate. P. 51152 ($\times \frac{4}{3}$).

FIGURE 81. Left suborbital plate. P. 51154 ($\times \frac{4}{3}$).

FIGURE 82. Flank plates with injected gravel *in situ*. Specimen subsequently prepared with acetic acid. P. 50893 ($\times \frac{2}{3}$).

is produced in a prominent obstantic process (*pro*) which is contiguous with the obstantic process of the anterior dorsolateral plate. The convex dorsal margin of the obstantic process is received by the postobstantic notch in the external surface of the anterior dorsolateral plate. Below the obstantic process, the anterior margin is obliquely cut away in a hollow, unornamented face (*l.io*), the infraobstantic lamina, over which lay the paraobstantic area of the submarginal plate when the head was fully lowered. This face seems to be homologous with the thickening 'y' of

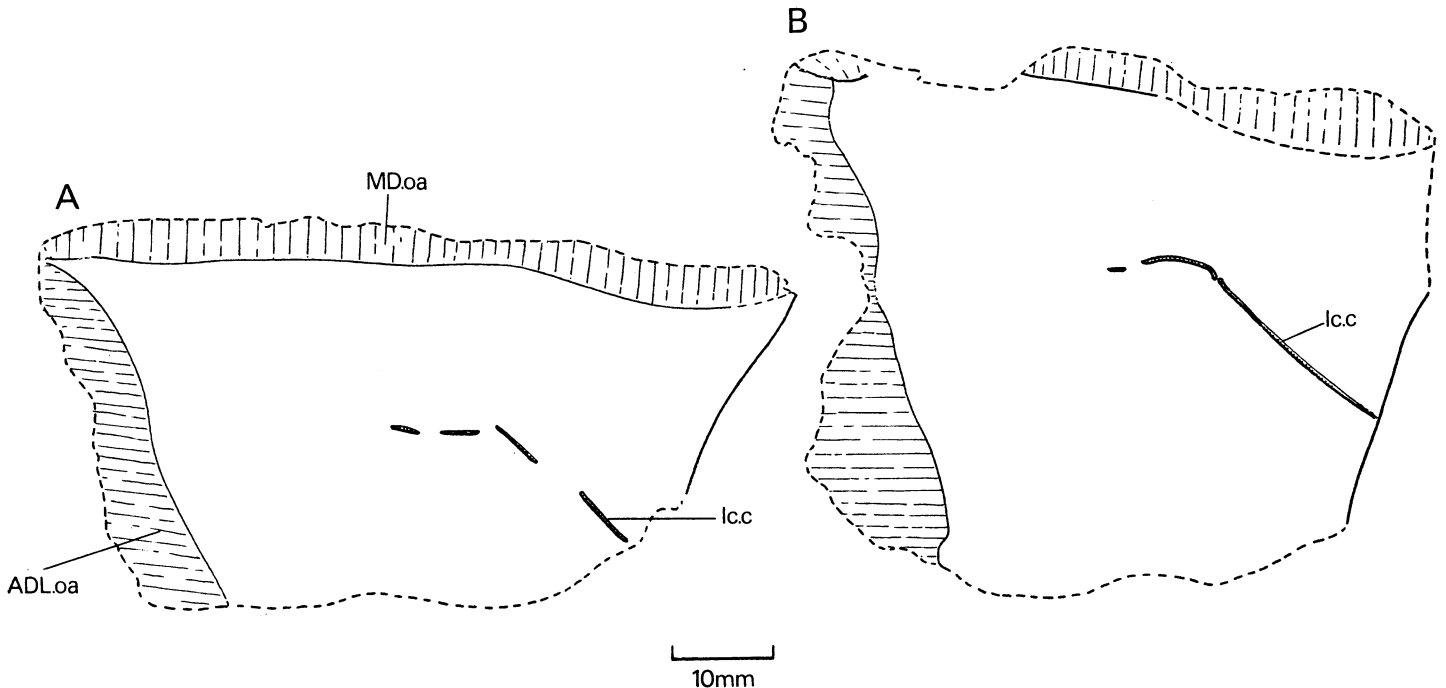


FIGURE 72. *H. westolli* sp.nov. Posterior dorsolateral plates. A, left plate P. 50893; B, left plate P. 50995.

Heintz's (1934, Figures 38, 39) account of *Homostius*. There may be a distinct postbranchial notch (*pbn*) separating the obstantic process and infraobstantic lamina, as in P. 51224, P. 50893 and P. 50989. However, this notch is not distinct in P. 51152.

On the visceral surface there are spinal (*S.cf*), posterior lateral (*PL.cf*) and anterior dorsolateral (*ADL.cf*) contact faces; the last two areas meet at the posterodorsal angle. Anteriorly the anterior dorsolateral contact face extends ventrally over the upper part of the postbranchial lamina (*pbla*), where this lamina fits into the groove *gr.pbl* on the anterior dorsolateral plate. The postbranchial lamina arises on the visceral surface. Its lower half is divided into two distinct regions, an anteromesially facing region of smooth bone, and an anteriorly facing overlap area for the interolateral plate (*IL.oa*). The ventral margin of the postbranchial lamina is not well preserved, but P. 50995 has suggested the tentative outline given in figure 83C. Finally, there is a distinct pit (*pbp*) a few mm above the interolateral overlap area, which corresponds in position to a prominent thickening in *Dunkleosteus* (Heintz 1932a, Figure 53). The radiation centre of the anterior lateral plate is anteriorly situated, as shown in figure 83B; and none of the specimens has a distinct supra-scapulocoracoid lamina inside the suprapectoral margin. The postbranchial lamina is completely devoid of ornamentation.

Posterior lateral plate (PL, figures 62 to 64, 76, 82, 84)

This is a relatively large plate, gently arched in the dorsoventral plane. It is preserved in only a few specimens and is subject to some surprising variations in form. In P.50893 and P.50995, in which the plate has an anteroposterior length of at least 40 mm, it bears a large posteroventral, suprapectoral process (*pr.sp*, figure 84), which is without ornament and was

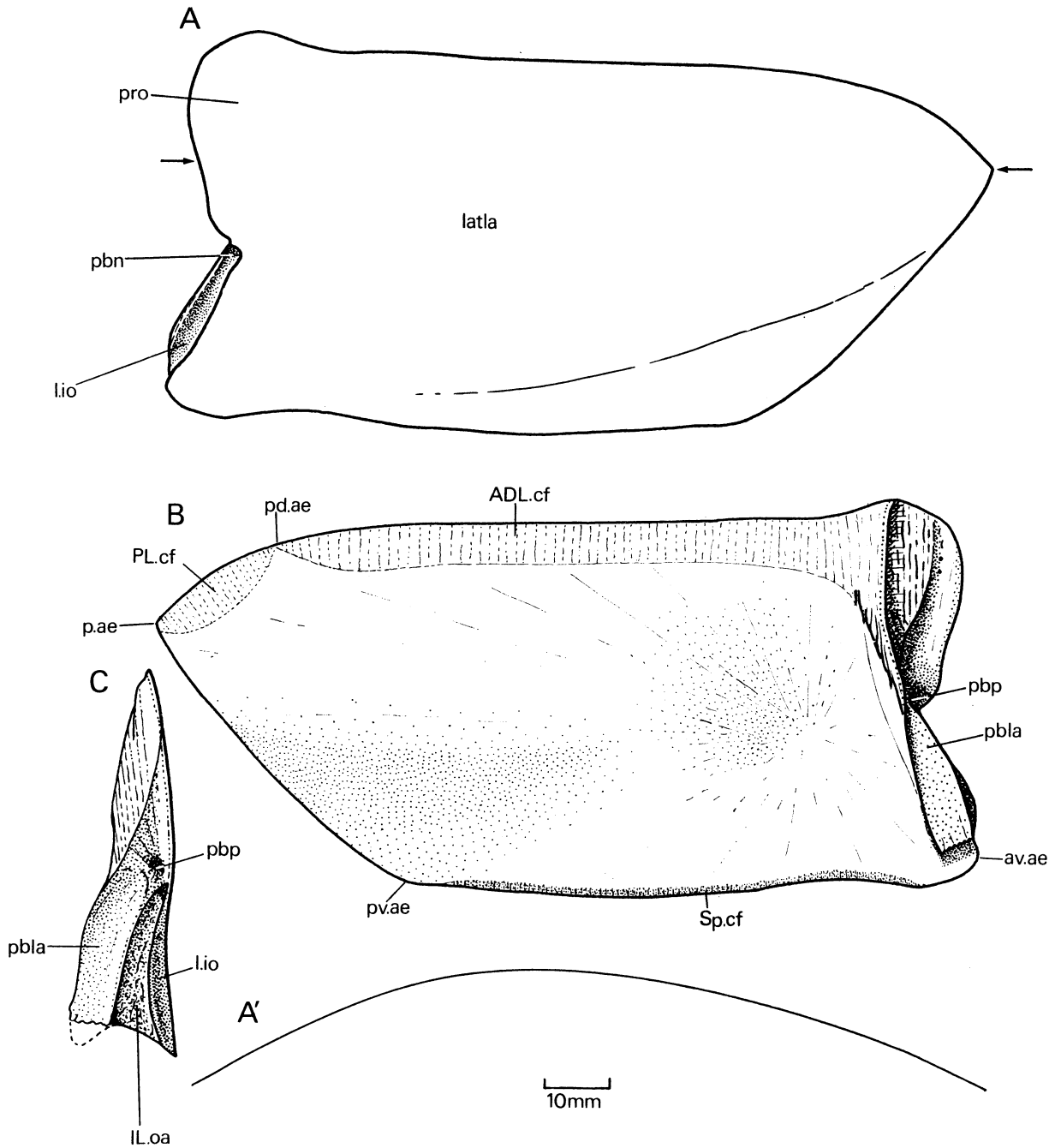


FIGURE 83. *H. westolli* sp.nov. Anterior lateral plate, left, in A, lateral, B, visceral, C, anterior view, with A', profile at level indicated. Based on P.50893 and P.50989 with information from other specimens.

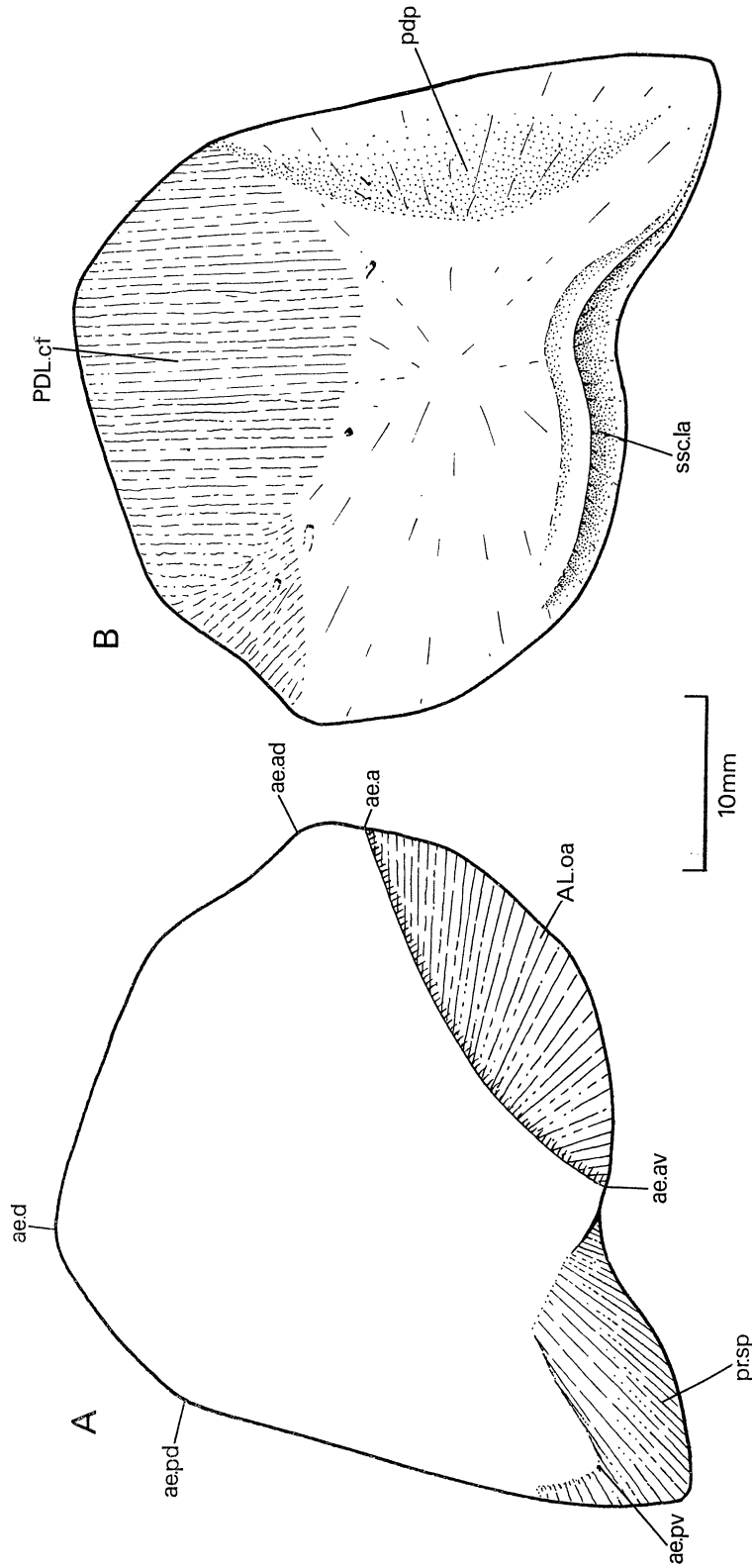


FIGURE 84. *H. westolli* sp.nov. Posterior lateral plate, right, in A, lateral and B, mesial view; P. 50893.

partly overlapped by the posterior ventrolateral plate. The ornamented surface ends at a distinct external posteroventral angle (*ae.pv*), and the anterior edge of the suprapectoral process forms a suprapectoral margin. Other features include the anteroventral (*ae.av*), anterior (*ae.a*), anterodorsal (*ae.ad*), dorsal (*ae.d*) and posterodorsal (*ae.pd*) angles. An extensive overlap surface for the anterior lateral plate (*AL.oa*) lies between the anterior and anteroventral angles, and the plate makes a butt joint with the anterior dorsolateral plate between the anterior and anterodorsal angles. On the visceral surface there is a broad contact face for the posterior dorsolateral plate (*PDL.cf*), between the anterodorsal and posterodorsal angles. There is also a distinct suprascapulocoracoid lamina (*ssc.la*) bounded by a low ridge, and a posterior depression (*pdp*) which is in line with the posterior depression of the posterior dorsolateral plate. The position of the radiation centre is indicated in figure 84B.

The posterior lateral plate of P. 50987 (figure 76) differs from those described above in the poor development of the suprapectoral process, the poor development of the suprascapulocoracoid lamina, and the absence of the external posteroventral angle. Presumably the posterior lateral made a butt joint with the posterior ventrolateral plate in this specimen. However, the overlap surface for the anterior lateral plate is well developed. P. 50987 is a small individual (maximum length of the posterior lateral plate about 30 mm), so the differences between it and larger specimens may be due to juvenile characters.

Spinal plate (*SP*, figures 15, 51, 63 to 65, 85, 92, 93)

This is a long, slender plate of hemicylindrical cross-section. Unlike the spinal plates of most placoderms, therefore, it did not enclose a lateral prepectoral process of the scapulocoracoid in a central cavity. In this respect it is like the spinal plate of *Dunkleosteus*, which Stensiö (1959, p. 20) has designated as a secondary 'pseudo-spinal'. A variety of 'pseudo-spinals' are found in the

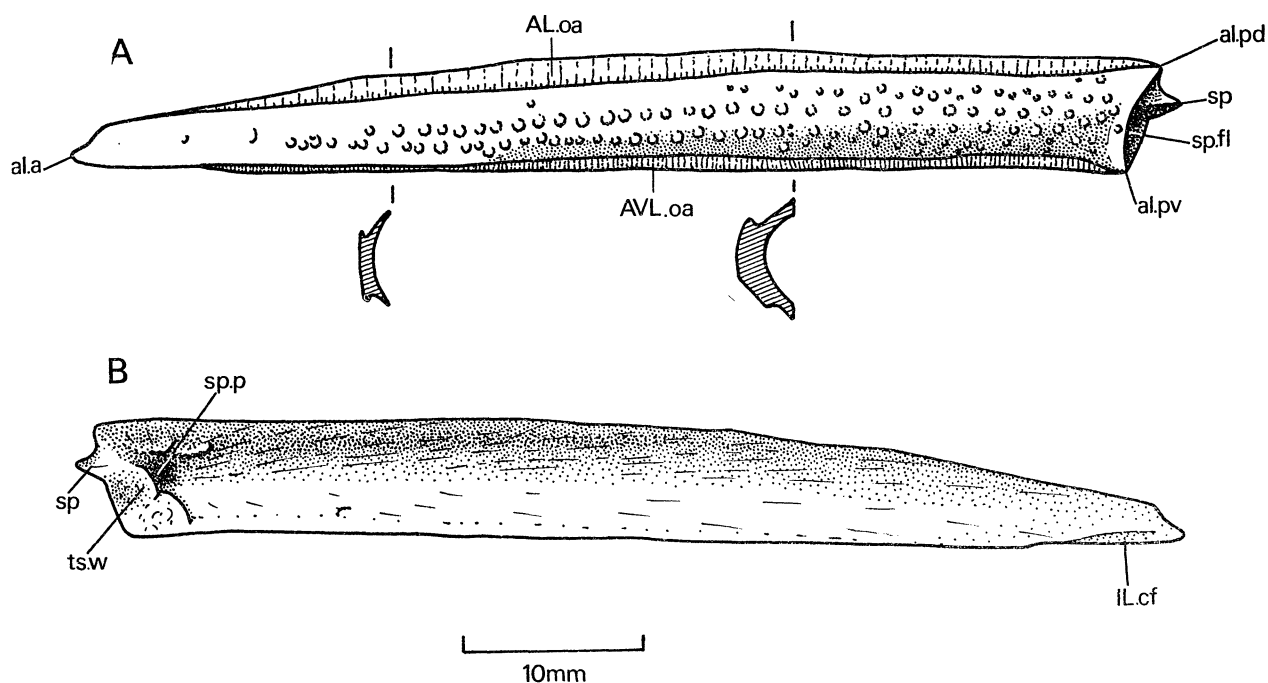


FIGURE 85. *H. westolii* sp. nov. Spinal plate, left, in A, lateral and B, mesial view, with sections at levels indicated; P. 50893.

advanced coccosteomorph-level and pachyosteomorph-level arthrodires from Gogo, and I regard them as representing stages in the reduction of true spinal plates, in which the posterior spine is lost (see also Mark-Kurik 1963; Heintz 1968).

The spinal is well preserved in a number of specimens, notably in P. 50893, P. 50986, P. 50988, P. 50989, P. 50995 and P. 51014. It reaches its maximum external width posteriorly, between the posterodorsal and posteroventral angles (*al.pd*, *al.pv*, figure 85), and is about 10 times as long as it is wide. Anteriorly it tapers to a distinct anterior angle (*al.a*). There is a dorsal overlap area for the anterior lateral plate (*AL.aa*), and a ventral overlap area for the anterior ventrolateral plate (*AVL.aa*). These areas tend to be undercut, particularly towards the anterior end of the plate. Posteriorly there is an unornamented flange of bone (*sp.fl*), the upper part of which is crossed by a ridge which continues over the posterior end as a small angle (*sp*) in most specimens (figure 15), but forms a short spine in P. 50893 (figure 85). This structure is homologous with the posterior (pectoral) spine of the spinal plate in other arthrodires, e.g. *Coccosteus cuspidatus* (Miles & Westoll 1968, Figure 38 d to k). In visceral aspect the spinal plate appears as a long trough which becomes shallow in its anterior third and is bounded posteriorly by a thick transverse wall (*ts.w*). At the base of this wall, at the radiation centre, there is a well-defined pit (*sp.p*), which can be regarded as a last vestige of the spinal cavity. The lateral surface of the prepectoral region of the scapulocoracoid lay against the visceral surface of the spinal plate, and posteriorly this surface of the spinal tends to bear irregular ridges and nodes of smooth bone (figure 51). This is particularly true of the larger specimens such as P. 50986, P. 50988, both of which have an estimated length of more than 90 mm. There is a slight contact face anteriorly (*IL.cf*), where the plate fitted against the interolateral plate.

Interolateral plate (*IL*, figures 63 to 65, 78, 79, 86, 87)

Both the ascending postbranchial and the ventral lamina of this plate are well developed. Laterally the ventral lamina is anteroposteriorly extensive, where it forms a broad lateral lamina (*la.l*, figures 86 C, 87) in the terminology of coccosteomorph-level arthrodires (Stensiö 1959; Miles & Westoll 1968). The lateral lamina is relatively much longer anteroposteriorly in P. 51171 (figure 86 C) than in P. 51154 (figure 87), although the specimens are of the same order of size. The lateral margin of the ventral lamina is divided into an anterior free division, and a posterior division (*Sp.m*) which was slightly overlapped by the spinal plate. These divisions are bounded by anterolateral (*al.ale*), lateral (*l.ale*) and posterolateral (*pl.ale*) angles. There is a narrow overlap area along the posterior margin of the ventral lamina. It is divided into a lateral area for the anterior ventrolateral plate (*AVL.aa*) and a mesial area for the anterior median ventral plate (*AMV.aa*). As the interolateral also overlaps the anterior median ventral, it is clear that there was a deep tongue-and-groove joint between these two plates. An external posterior angle (*p.ale*) marks the boundary between the two overlap areas. The anterior face of the ascending lamina can be divided into three regions for description. There is an upper, slightly hollowed, anterodorsally facing region with a prominent ornamentation of rows of contiguous tubercles (*or*). Below this there is a smooth band of bone which faces anteroventrally in its mesial half and anteriorly in its lateral half (*sm.r*). Lateral to this last division there is a triangular area of smooth bone (*f.pb*) which is continuous with the infraobstantic lamina of the anterior lateral plate. The ascending lamina of *Holonema* is unusual in that its anterior face is predominantly convex, particularly in its lateral regions, rather than concave as is usual in brachythoracid arthrodires (e.g. Miles & Westoll 1968, Figure 42 a).

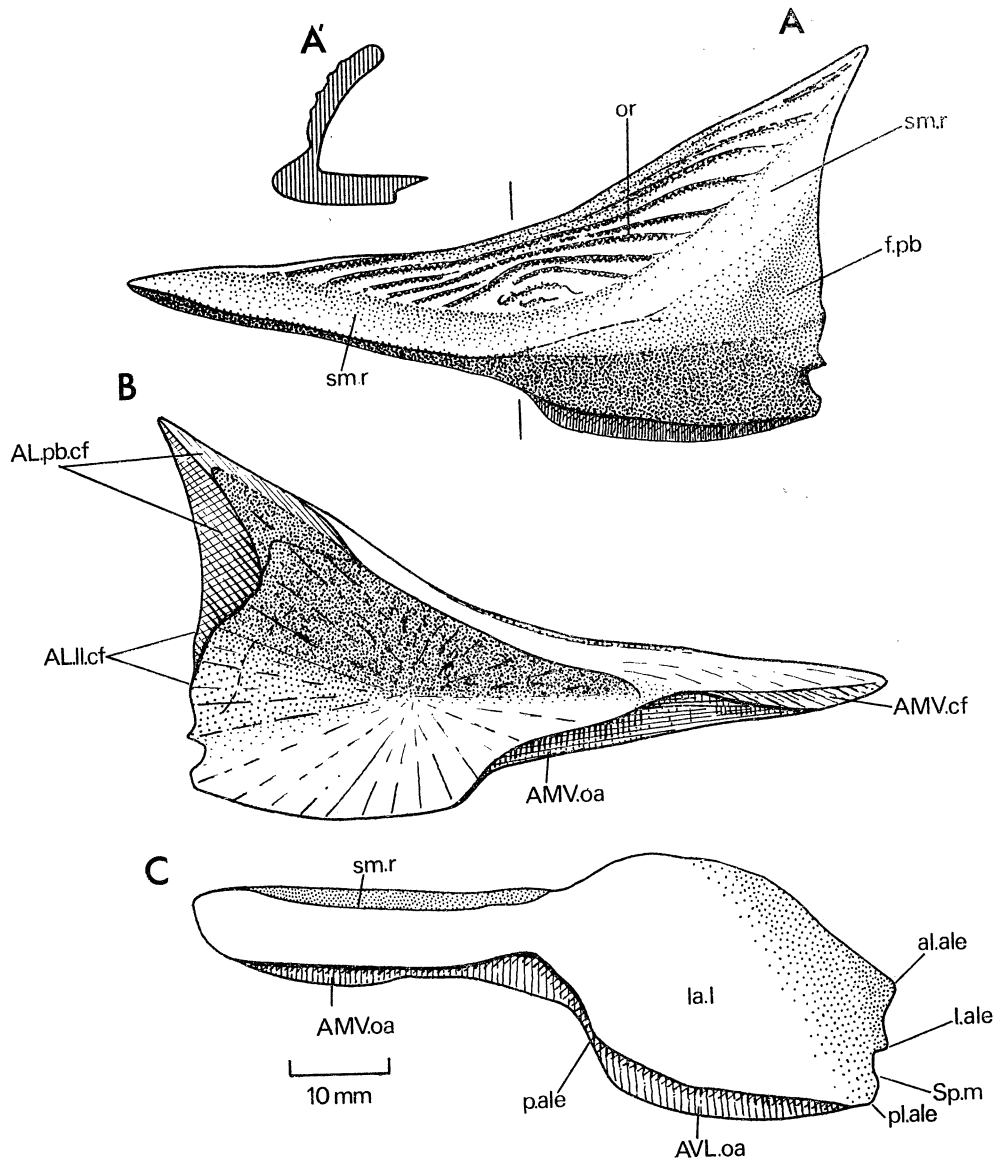


FIGURE 86. *H. westolli* sp.nov. Interolateral plate, left, in A, anterior, B, posterior and C, ventral view, with A', section at level indicated. Based on P.51171.

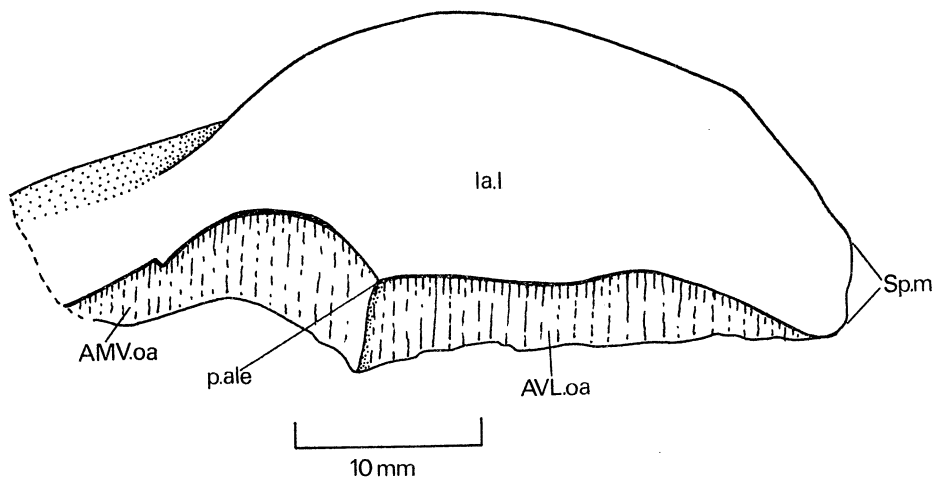


FIGURE 87. *H. westolli* sp.nov. Interolateral plate, left, in ventral view; P.51154.

The visceral surface of the interlateral (figure 86B) comprises a deeply concave lateral region which was probably filled by the scapulocoracoid (mostly the coracoid process) except where it was overlapped by the anterior lateral plate, and a short, dorsally facing mesial region with a posterior contact face for the anterior median ventral plate (*AMV.cf*). The lateral and dorsal contact faces (*AL.pb.cf*) mostly received the postbranchial lamina of the anterior lateral plate. However, the most ventral part of the lateral face (*AL.ll.cf*) appears to have received the lower edge of the anterior margin of the lateral lamina of the anterior lateral plate.

Anterior ventrolateral plate (AVL, figures 50, 65, 88, 92, 93)

This plate is rostrocaudally elongated in comparison with most other arthrodires, and is the largest member of the ventral shield. Unfortunately it is a thin, easily damaged plate, and not completely preserved in any one specimen. Restorations can, however, be based on moderately complete specimens such as P. 50986 and P. 50995 (figures 50, 92, 93). The length of the spinal division (*Lsp*, figure 88; also Miles 1964*a*, Figure 3) is equal to about one-half of the total length (*Lt*) of the plate (*Lt/Lsp* index, 51). Both the spinal (*Sp.m*) and subpectoral (*sbp.m*) margins are

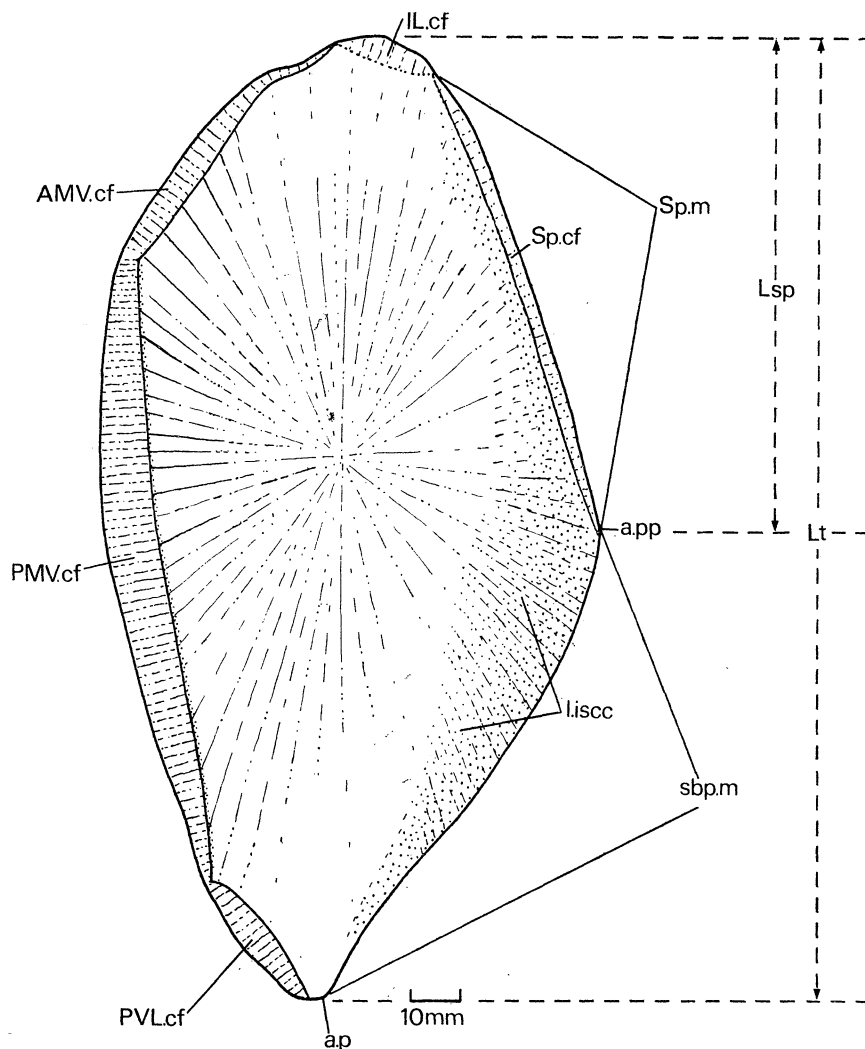


FIGURE 88. *H. westolli* sp. nov. Anterior ventrolateral plate, right, in visceral view. Based on P. 50986.

relatively long, and together occupy about three-fifths of the length of the ventral shield. The extent of the subpectoral margin is defined by distinct prepectoral (*a.pp*) and posterior (*a.p*) angles. The plate is arched in cross-section and both the spinal and subpectoral margins are raised above the base-level, particularly anterior and posterior to the prepectoral angle. It is not possible, however, to speak of a distinct infraspinal lamina. The ventral sensory line ('umbilical line', Stensiö 1969*a*) is represented by a well-defined groove which arises at the radiation centre and runs anteromesially on to the anterior median ventral plate (*vsI*, figure 65). On the visceral surface there are contact faces for the spinal (*Sp.cf*), interolateral (*IL.cf*), anterior median ventral (*AMV.cf*), posterior median ventral (*PMV.cf*) and posterior ventrolateral (*PVL.cf*) plates. A broad infrascapulocoracoid lamina (*l.iscc*) is present mesial to the subpectoral margin, although it is not well defined. The pitted surface of this lamina, due to the presence of numerous fine neurovascular foramina, runs anteriorly by the side of the spinal contact face. It marks the area which received the lower edge of the scapulocoracoid.

Posterior ventrolateral plate (PVL, figures 63, 65, 77, 89, 92, 93)

The posterior ventrolateral is relatively small, transversely arched plate. There are differences in structure between P. 50987 (maximum rostrocaudal length about 52 mm) and two larger specimens P. 50989 and P. 50995 (length over 55 m). (Cf. posterior lateral plate, p. 166). In the two larger specimens there is a distinct lateral, postpectoral lamina (*la.pp*, figure 89C) which overlapped the posterior lateral plate; it has a distinct contact face on its visceral surface (particularly P. 50995). In contrast to this, P. 50987 has only a slight convex margin in the position of the postpectoral lamina, and it apparently met the posterior lateral plate in a butt joint (figure 89A, B, D). All three plates have a broad ventral lamina with a rounded posterior margin, and an anterolateral overlap area (*ALV.oa*) for the anterior ventrolateral plate, which extends between the anterior and anterolateral angles (*a.an*, *al.an*). Between the antero- and postero-mesial angles (*am.an*, *pm.an*) the plate meets its fellow in the middle line. There is no well-defined overlap between the plates, and they appear to meet in a butt joint, despite a slight bevelling of the mesial edges. The posterior margin of the ventral shield is notched between the posterior ventrolaterals. The lateral lamina has postpectoral (*pp.an*) and posteroventral (*pl.an*) angles, and between the postpectoral and anteroventral angles there is the subpectoral margin (*sbp.m*), which may also be slightly bevelled.

On the visceral surface there is a contact face for the posterior median ventral plate, between the anterior and anteromesial angles (*PMV.cf*), and an infrascapulocoracoid lamina (*l.iscc*) along the subpectoral margin. In P. 50989 and P. 50995 there is a transverse ridge under the postpectoral lamina. The position of the radiation centre is indicated in figure 89D.

Anterior median ventral plate (AMV, figures 65, 80)

The anterior median ventral is represented by two incomplete examples: P. 51152, a detached bone, and P. 51159, a weathered intaglio. These specimens show that the ventral sensory line groove crossed the surface of the plate in the direction of the radiation centre, although it did not meet its fellow in the middle line. P. 51152 also has part of the interolateral overlap surface preserved, which confirms that a deep tongue-and-groove joint was formed between the anterior median ventral and interolateral plates (see p. 167).

The outline of the external face of the anterior median ventral plate can be obtained from the restoration of the ventral shield (figure 65). In this restoration the plate is closely similar to that

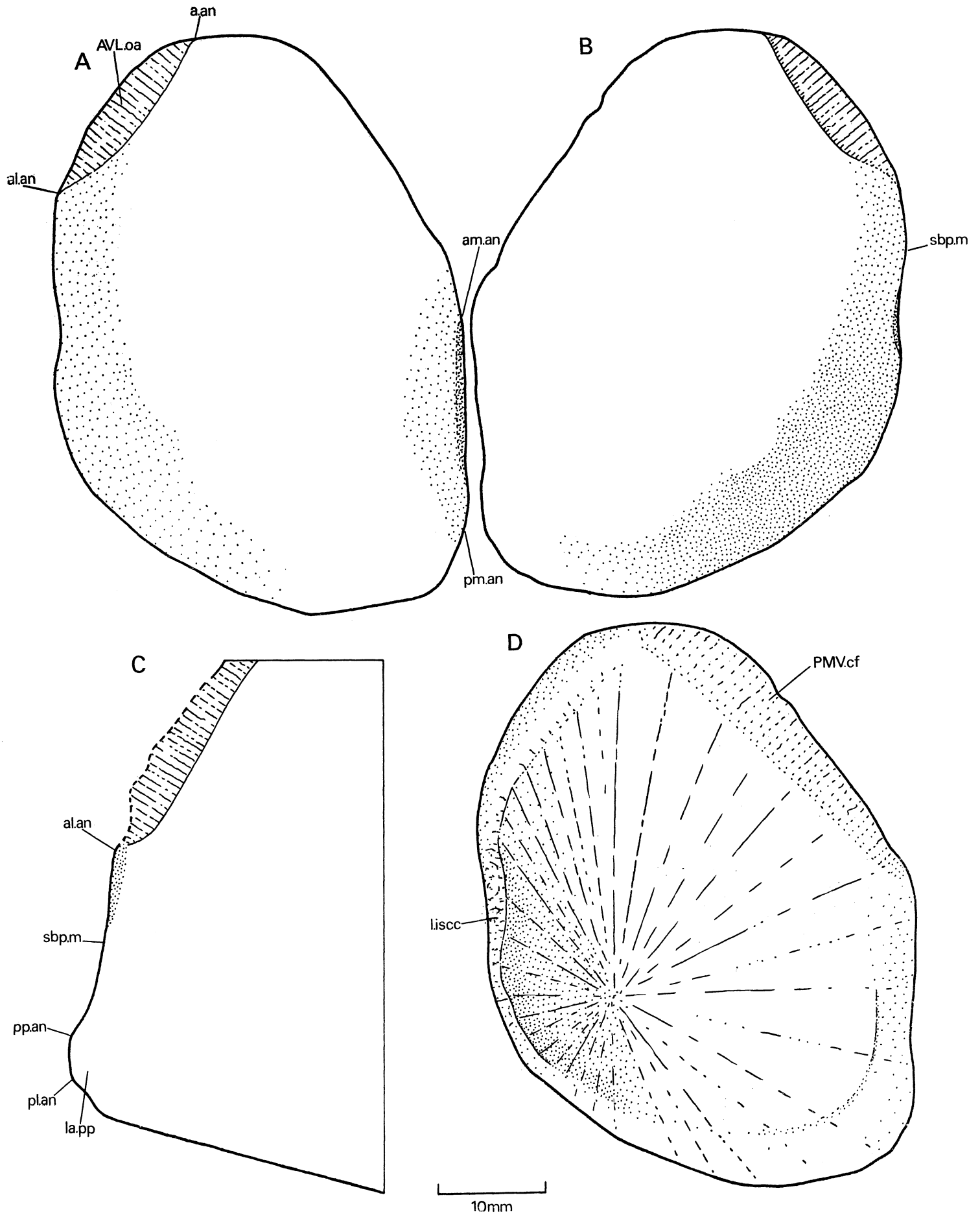


FIGURE 89. *H. westolli* sp.nov. Posterior ventrolateral plates. A, B, right and left plates in ventral view, P. 50987; C, right plate, marginal region in ventral view, P. 50989; D, left plate in visceral view, P. 50987.

of *Holonema radiatum* (Obruchev 1932, Figures 2, 3), with an anterior median angle and pronounced lateral angles.

Posterior median ventral plate (PMV, figures 20, 65, 80)

This is an elongated, pentagonal plate with anterolateral (*all.a*, figure 90A), lateral (*ll.a*) and posterior (*pr.a*) external angles. It is slightly arched in both longitudinal and transverse directions, and is fringed by overlap surfaces for the anterior median ventral (*AMV.oa*), anterior ventrolateral (*AVL.oa*) and posterior ventrolateral (*PVL.oa*) plates. The visceral surface is

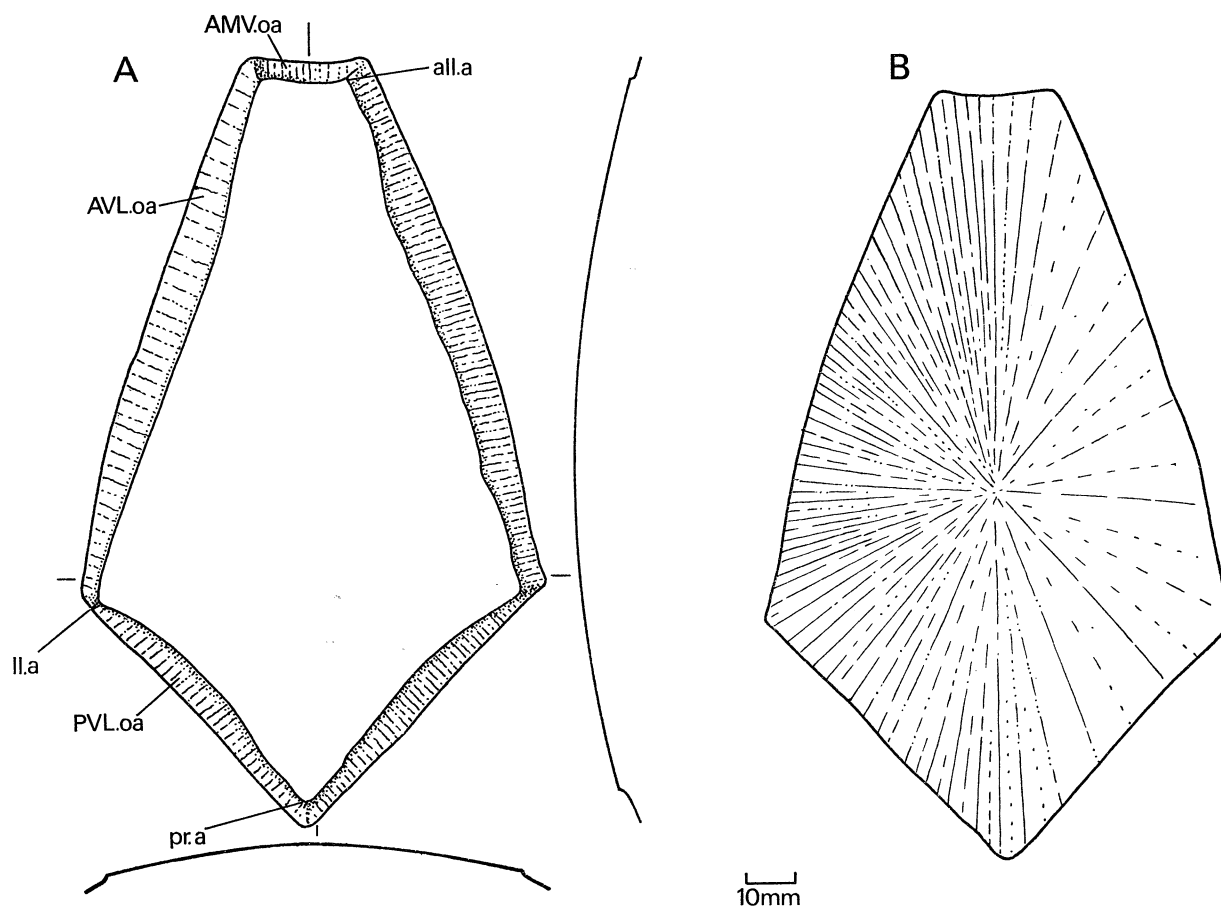


FIGURE 90. *H. westolli* sp.nov. Posterior median ventral plate in A, ventral and B, visceral view, with longitudinal and transverse profiles at levels indicated. Based on P. 50984.

devoid of prominent features; the radiation centre is situated in the middle of the plate (figure 90B).

No examples of the plate are completely preserved, and it is not possible to obtain accurate breadth/length ratios. Nevertheless, there is a suggestion that the proportions of the plate are strongly variable. The external surface appears to be more than twice as long as it is broad in P. 50893 and P. 50995, both of which are less than 100 mm long; and less than twice as long as it is broad in P. 50984 and P. 50986, both with a length of at least 150 mm. The lateral and posterior angles tend to be extended into poorly defined processes, particularly in small individuals such as P. 50893 and P. 50995. Both the presence of scattered tubercles on these processes, and

attempts to reconstruct the ventral shield plate by plate, indicate that the lateral and posterolateral overlap surface were not perfectly overlapped by the anterior and posterior ventrolateral plates in small individuals, and there may have been a considerable gap between the external surfaces of these plates and the posterior median ventral plate (figure 65).

Endoskeletal shoulder-girdle

Determinable fragments of the perichondrally ossified scapulocoracoid are preserved in P.50984, P.50986 and P.51173. The first of these specimens is a fragment from near the

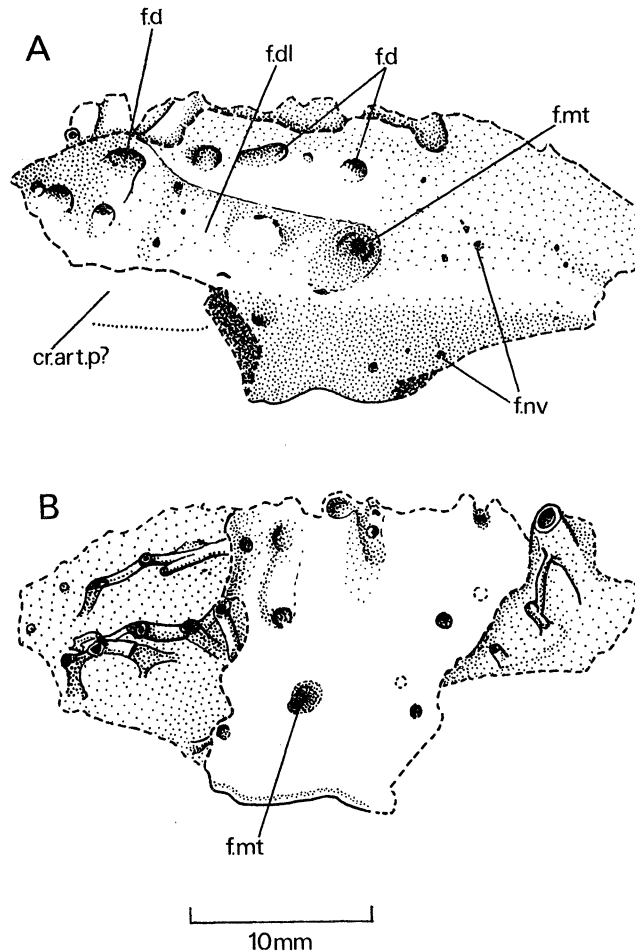


FIGURE 91. *H. westolli* sp.nov. Incomplete scapulocoracoid in A, lateral and B, mesial view; P.51173.

posterior end; the second is apparently a piece from the anterior end of the fin-bearing region plus a part of the prepectoral region, but the whole is squashed against the inner surface of the spinal plate and cannot be interpreted with certainty; and the third is a piece from the posterior end somewhat better preserved than the other two specimens. The scapulocoracoid is considerably better preserved in some other Gogo arthrodires, and it is hoped to discuss this structure in more detail on a later occasion. The fragments belonging to *Holonema* stand to make little contribution to our understanding of arthrodire structure and relationships. I shall, therefore, limit this account to a few notes to accompany sketches of P.51173 (figure 91), in which the terminology of Stensiö (1959) is used without prejudice.

P.51173 is a fragment from the posterior part of the fin-bearing region of the left scapulocoracoid. The margin is only complete over a short distance of the ventral edge. As in the forms described by Stensiö, both the outer and inner surface and the canals for blood vessels and nerves are lined with perichondral bone. It is clear that the scapulocoracoid of *Holonema* was a long, low structure. This confirms the form of the pectoral fenestra restored in the drawings (figures 63, 65). There is no sign of the articular crest, but the possible position of its most caudal part is indicated in figure 91A (*cr.art.p?*). Apparently most of the specimen lies behind the crest. A dorsal depression on the outer surface (*f.dl*) was presumably for the origin of fin muscles, and there is a series of large foramina for dorsal pterygial nerves and blood vessels (*f.d.*). A large foramen (*f.mt*) near the posterior end of the depression (*f.dl*) is possibly the metapterygial foramen. The canals that lead from these foramina branch and anastomose within the scapulocoracoid, to open as distinct foramina on the inner face (figure 91B). A few smaller dorsal and ventral nerve foramina (*f.nv*) are also present, particularly near the posterior end of the specimen.

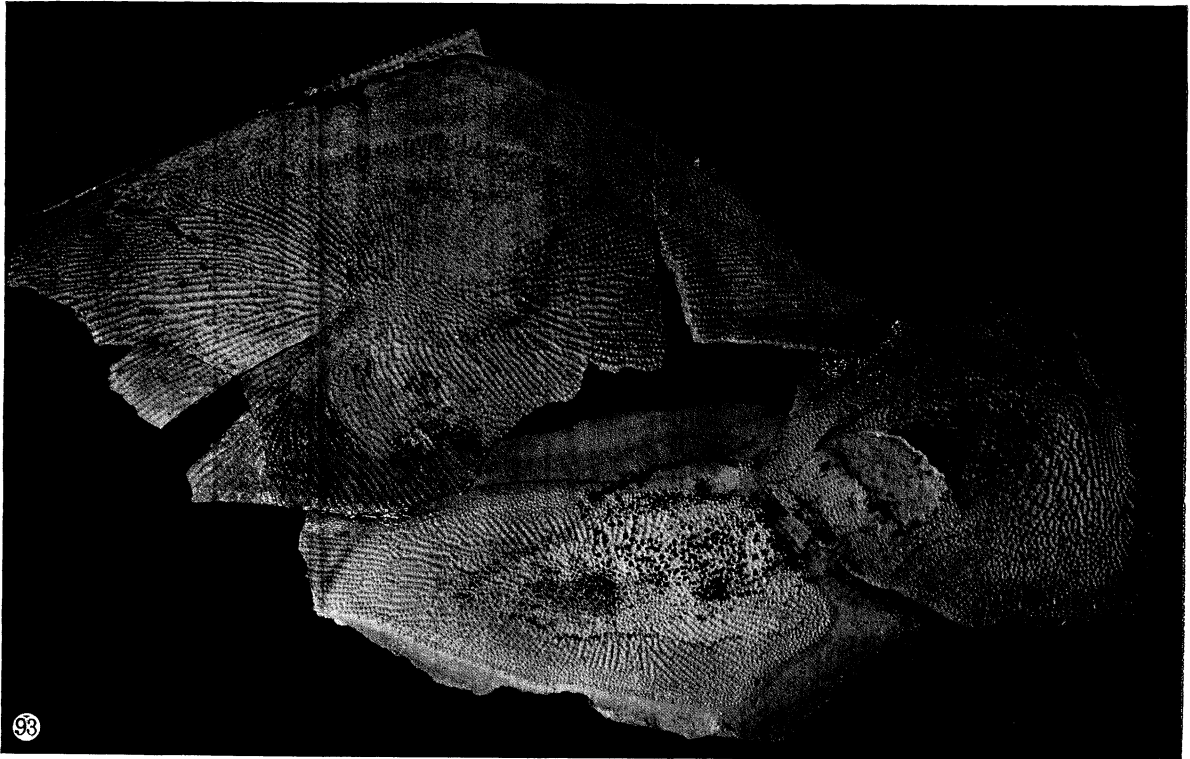
Dermal ornamentation

The dermal bones of *Holonema* comprise three layers, as in many other placoderms. There is a superficial layer forming the tubercles and ridges of the dermal ornamentation; a middle cancellous layer; and a basal lamellar layer (Obruchev 1932; Bystrow 1967). These layers are formed of cellular bone. The characteristic arthrodiran tissue semidentine (Ørvig 1967) is not present in the superficial layers of the dermal shields, but is restricted to the outer layers of the ridges on the inferognathal and posterior superognathal. The superficial layer of the shields grew by the apposition of new generations of tubercles and ridges, and may show evidence of the resorption of older generations. It is traversed by vascular canals from the middle layer, which open on the surface of the bone. Bystrow (1957, Figure 24) has described numerous coarse canals for vertically oriented Sharpey's fibres in the superficial layer in *Holonema radiatum*, but I have only been able to match this condition in a section of the sclerotic plate in *H. westolli*.

The superficial ornament of *Holonema* is usually described as a series of ridges, and Obruchev's (1964, p. 142) definition of the genus includes, 'Armour covered with radial crests connected by bars, separated by deep grooves. Crests forming a network in the middle of the bones and bearing 1-3 rows of small tubercles'. However, the extensive material of *H. westolli* shows that the ornamentation is variable, and Obruchev's description cannot be accepted without reservation. It also suggests that the ornamentation is a poor criterion for defining species of holonematids. In *H. westolli* the character of the ornamentation changes during growth, it varies from individual to individual, and it varies from one region of the armour to another. An additional problem encountered in the study of *H. westolli* is the tendency for the outermost layer of the ornament to chip off, to expose earlier generations of tubercles and ridges.

The ornamentation of *Holonema westolli* is best comprehended through the photographs (figures 14 to 17, 19, 20, 22, 38, 41, 44, 47, 48 to 50, 52, 73, 74, 76, 77, 79 to 82, 93). The following remarks are made to draw attention to the main features; they do not cover all the minor variations in pattern that occur. The approximate sizes of all the specimens mentioned in this section can be obtained from the legends to the figures.

The ornamentation in small individuals is overtly tubercular. The tubercles have stellate bases and they are usually arranged in well-spaced rows. On the median dorsal (figure 19) the rows have a concentric arrangement around the radiation centre, in the posterior half of the plate, as they also have around the margins of a small nuchal plate (figure 17). However, over



Holonema westolli sp. nov.

FIGURE 92. Left spinal, anterior ventrolateral, posterior ventrolateral and posterior median ventral plates in visceral view. P. 50995 ($\times 1$).

FIGURE 93. As figure 92, in ventral view.

(Facing p. 174)

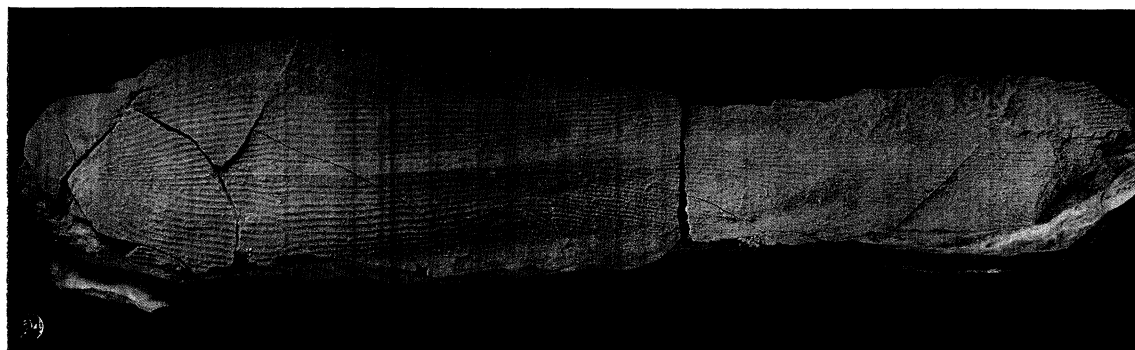


FIGURE 94. *Holonema* sp. Middle Devonian, near Thuin, Hainaut, Belgium. Median dorsal plate. Cast P. 43505.

FIGURE 95. *Holonema* sp. Middle Devonian, near Thuin, Hainaut, Belgium. Right posterior dorsolateral plate. Cast P. 43504.

FIGURE 96. *Holonema* sp.? Upper Devonian, Upper Plattenkalk, Bergisch-Gladbach, Germany. Right posterior lateral plate. S.M.N.H. P. 5421.

FIGURE 97. *Holonema* sp. Upper Devonian, Upper Plattenkalk, Bergisch-Gladbach, Germany. Left posterior superognathal. S.M.N.H. P. 5420.

FIGURE 98. *Holonema* sp. Upper Old Red Sandstone, Redheugh, Berwickshire, Scotland. Impression of undetermined plate. Cast P. 52915.

FIGURE 99. *Holonema* sp. Upper Devonian, Pickwell Down Sandstone, Woolacombe Bay, Devon, England. Undetermined fragment. P. 12397.

the greater part of the nuchal and in the anterior half of the median dorsal, the rows have a radiating arrangement, which is much more typical of the armour as a whole. The radial disposition of the ornament is well seen on the anterior ventrolateral, posterior median ventral and anterior lateral plates (figure 93). In each case the rows converge on the radiation centre. However, immediately around the radiation centre the tubercles have a more haphazard arrangement. The regular arrangement of the rows may also be broken around the margins of the plates (figure 93). In P. 50893, short rows of tubercles lie at right angles to the margins of the medial dorsal, anterior lateral and posterior lateral plates (see also description of large median dorsal, below). A similar disposition of the peripheral ornament is found in the antiarch *Bothriolepis* (Stensiö 1948; Miles 1968), and it probably marks an area of recent growth by marginal addition. The strongly tubercular ornamentation of the posterior lateral and posterior ventrolateral plates demands special mention (figures 76, 77). The closely packed tubercles appear to have an irregular arrangement, although this may have been superimposed on a fundamentally concentric pattern.

In large specimens the ornamentation is predominantly one of continuous ridges, which anastomose and frequently have an irregular, radiating arrangement. The most notable exception is provided by the spinal plate (figures 15, 92, 93), which retained a tubercular ornamentation throughout life. Unfortunately the specimens cannot be arranged into a 'growth series' to show the transformation of the rows of tubercles into ridges. The ridges, however, show clear signs of comprising rows of fused tubercles (e.g. figures 16, 81). They may be topped by a single row of tubercular nodes, or, as in very large specimens in which the ridges appear flat to the naked eye (e.g. figure 20), they may be randomly strewn with numerous, exceedingly fine tubercles. Wells (1942, Plate 97, Figure 4) has illustrated this last condition well in *Holonema rugosum* (Claypole). In very large specimens the apparently flat topped ridges are much broader than the interspaces. Here the ornamentation appears as a system of short narrow grooves (figure 73). The progressive broadening of the ridges may eventually result in the virtual suppression of the ornamentation, although under the microscope the granular texture of the bone is still obvious.

The head-shield demonstrates some of the features of interspecific variation. In P. 50982 (figure 16) the anterior region and sides of the skull-roof are coarsely ornamented with irregular, anastomosing ridges, each bearing fine tubercles. The ridges are smaller in the middle of the roof, and in the posterior median region they are modified into a series of short, delicate structures with nodes, the whole system still bearing numerous granular tubercles. This specimen may be contrasted with P. 51004 (figure 52), which is of the same order of size. Here all the preserved regions of the skull-roof are covered by widely spaced, anastomosing, sharp ridges. Where these ridges are undamaged, i.e. where older generations of the ornamentation are not exposed, there is virtually no sign of tubercles of any size. Comparable variations are found in the ornamentation of the cheek plates (e.g. figures 22, 41, 81).

The ornamentation of large median dorsal plates (e.g. figure 73) conforms to that described for *Holonema rugosum* and *H. haiti* Denison (see also *H. farrowi* Stevens 1964). Denison's (1968, p. 282) description of the pattern in *H. haiti* can be applied directly to *H. westolli*: '(1) a long central ridge, the 'club' of Wells; (2) concentric ridges posterior and lateral to 1; (3) lateral zones of ridges mainly at right angles to the edge, but showing many irregularities and sinuositities; (4) anterior fanned ridges; (5) also a posterior zone of fanned ridges, not developed in *H. rugosum*'.

In a series of stylized drawings of *Holonema radiatum*, Obruchev (1932) has illustrated the

radiating pattern of the ridges on the anterior median ventral, posterior median ventral, anterior dorsolateral, nuchal, paranuchal and marginal plates. These patterns are matched closely in *H. westolli*, and can be seen from the photographs without further comments.

As is usual in arthrodires, the postbranchial lamina of the interolateral plate is strongly ornamented (see, for example, Miles & Westoll 1968, p. 440, with references). In *H. westolli* (figure 79) the ornament comprises triangular, downwardly directed tubercles, which are fused at their bases into long, subparallel, bead-like rows. These rows run obliquely across the lamina, as in figure 86A. The tubercles have no subsidiary cusps, as for example in *Coccosteus cuspidatus* (Miles & Westoll 1968, Figure 38c).

The ornamentation of the tooth-plates has already been described, and that of the sclerotic plates noted.

Restoration and mode of life

The restorations in figures 63 to 65 have been constructed graphically by scaling together drawings of undistorted plates from several specimens. The most notable features of the restorations are the small size of the head-shield relative to the trunk; the box-like construction of the trunk-shield; the long, low pectoral fenestra; the short postpectoral wall; the extensive prepectoral wall with the long spinal plate; the large size of the anterior ventrolateral relative to the posterior ventrolateral plate; and the tumid dorsal and ventral walls.

The nuchal gap is small, but the head could rotate about the well-developed external (cranio-thoracic) neck joint through some 15°. When the head rested in the fully lowered position, the occipital para-articular process lay inside the para-articular face of the anterior dorsolateral plate, the subobstantic margin of the head-shield lay inside the obstantic process of the trunk-shield, and the paraobstantic area of the submarginal plate lay outside the infraobstantic lamina of the anterior lateral plate. These relationships between the head and trunk shields are highly characteristic of arthrodires, and provide a check on the proposed reconstructions. They are particularly valuable in confirming the relative sizes of the head and trunk shields.

A large fossa is present in the exoskeleton of the restored head between the postorbital, marginal, suborbital and submarginal plates (*sp.f.*, figures 2, 4). A consideration of the relationship of the palatoquadrate, hyomandibular and m. levator palatoquadrate to the spiracle in certain sharks (*Heptanchus*, Goodrich 1909, Figure 59a; *Chlamydoselachus*, Allis 1923, Plates 5, 11, Figure 22; Plate 20, Figure 55) leads to the conclusion that this fossa is the exoskeletal spiracular opening. However, as a spiracle is not otherwise known in arthrodires, this must be regarded as a speculative conclusion.

Holonema is unquestionably an arthrodire (*sensu* Miles 1969; cf. Stensiö 1969a, b). It is, however, a transfigured arthrodire which shows a notable degree of convergence to antiarchs, particularly *Asterolepis* (Gross 1931, Figure 11; Karatajute-Talimaa 1963, Figure 35). This is manifest in the proportions of the head to the trunk, the long, box-like trunk-shield, the small orbital openings and heavily ossified sclerotic ring, the (possible) posterior position of the nasal openings away from the rim of the head-shield, the form of the upper gnathals and their anteromesial position under the rim of the head-shield, and the feeble development of the inferognathal. Other similarities include the large opercular plates (the submarginal in *Holonema*, the extralateral in antiarchs), and the presence of an infrapostsuborbital in *Holonema*, which is the homologue of the infraprelateral in *Bothriolepis*. These last two similarities are, however, probably not the result of convergence, as a large submarginal is seemingly a primitive placoderm

character (p. 196), and the infrapostsuborbital may also have been present in other arthrodires. It should not be overlooked that *Holonema* frequently occurs with *Bothriolepis*, as at Gogo. Evidently the holonematid and antiarch adaptive subzones did not seriously overlap (see Miles 1969 on placoderm adaptive zones).

The extensive trunk-shield probably encased almost half of the trunk musculature, so that a relatively small proportion was available for use in swimming. *Holonema* would thus seem to have been a poorly swimming, benthic fish. The large pectoral fenestra nevertheless indicates that the pectoral fins were large with a broad muscular base, which is unexpected in a benthic arthrodire (cf. rhenanids and stensioellids). Probably, however, the pectoral fins functioned principally as props, to support the fish as it rested on the bottom, like the pectoral appendages of antiarchs. They differ strongly from these last structures, however, in both form and position on the flank.

The new observations on the musculature of the head suggest no serious changes in earlier restorations of arthrodire myology (e.g. Miles & Westoll 1968), but some points may be clarified. The m. levator palatoquadrati took origin on the dorsal surface of the middle region of the palatoquadrate and inserted on the lateral wall of the neurocranium, in front of the anterior postorbital process and on an adjacent depression in the visceral surface of the skull-roof. The m. adductor mandibulae took origin on the palatoquadrate, and possibly on the adjacent surface of the suborbital plate, in the adductor fossa, and inserted on the lateral surface of the mandible (on the meckelian cartilage in *Holonema*, but on the blade of the inferognathal in most brachythoracids).

The adductor mandibulae muscles were short in *Holonema* and the small size of the subnuchal muscle fossa, together with the convex form of the hind margin of the skull-roof, suggests that the levator muscles of the head were only moderately large. These conclusions, taken together with the feeble development of the inferognathal and short gnathal margins, suggest that the gape was small and the bite weak in comparison with the majority of contemporary arthrodires (see Miles 1969). Probably the mouth opening was small.

It seems likely that *Holonema* was a scavenger, feeding on carrion and small invertebrates in the bottom mud. Within the articulated trunk plates of P. 50893 (figure 82) there is a quantity of gravel, of a type not found in the nodules enclosing other Gogo fishes. It comprises smooth pebbles of shale and sandstone up to 10 mm in length with rounded edges, and angular fragments of quartz up to 8 mm in length. Almost certainly these small stones were taken in with the food, along with bottom mud. Whether the gravel contributed to the death of the fish, or was injected in normal feeding, cannot be decided; it shows no unequivocal signs of gastric etching, and it seems highly improbable that it comprises specially collected gastroliths.

A possible example of a healed wound has already been described on the central plates of P. 50982 (p. 121), although the cause of this wound is unknown. Superficial scars are also found (e.g. figures 76, 77) where small areas of the tuberculated layer seem to have been replaced independently of the normal growth processes. These scars are characterized by the wide openings of the ascending vascular canals and the markedly stellate bases of the tubercles. They are found on the dorsal and lateral plates as well as on the ventral shield, and it is unlikely that they had a simple mechanical cause. Finally, lesion-like areas in which the middle layer of the bone is deeply eroded are commonly found on the outer surfaces of the plates (e.g. figures 50, 79). These areas show no sign of healing and are almost certainly due to post-mortem damage, the cause of which is, however, unknown.

3. COMPARATIVE MORPHOLOGY

Several topics of general interest in the field of placoderm comparative morphology will be discussed in this section, following either as a direct result of the description of *Holonema westolli*, or as an aid in the interpretation of this species. They are concerned with the snout, lateral-lines, jaws and gill-covers. No attempt will be made to make an exhaustive comparative study of the structure of *Holonema* for its own sake. A more general analysis of the character complex of *Holonema* is included below in the discussion of its affinities (pp. 227–229).

Arctolepis from Spitsbergen

In the description of the cranial morphology of *Holonema westolli*, both dolichothoracid- and brachythoracid-like characters have been noted. As some points in the structure of the dolichothoracid head-shield are badly understood, the small collection of *Arctolepis decipiens* (Woodward) from Spitsbergen described by Heintz in 1962, has been borrowed and restudied, to provide a broader base for comparisons with *Holonema*. I am indebted to Professor Heintz for the opportunity to prepare and study this material (P.M.O. A 28629, A 28636–28639 counterparts, A 28637, A 28603). The outline of the skull-roof in A 28637 is comparable with that shown by Ørvig in a restoration of an undetermined Spitsbergen neurocranium (in Stensiö 1963 *b*, Figure 15). The neurocranium in A 28637 has been prepared sufficiently to show that it is of the same type as in Ørvig's restoration, and this evidence has been used in the restoration.

The new restoration of the skull-roof (figure 100) establishes that there is a single large plate at the anterior end of the head-shield (rostral plate, Heintz 1962), and that the supraorbital sensory lines continue on to this plate from the preorbitals. Accordingly this plate is here termed the postnasalo-rostral (*PNR*; see below). Heintz's (*PN?*, 1962, Figure 2) independent postnasal plate has proved on preparation to be part of the suborbital lamina of the suborbital plate (*sol*, figure 101). The suborbital lamina is much longer than shown in Heintz's restoration (1962, Figure 8). It is broad, but in lateral aspect it appears to be narrow because the lower quarter of the outer surface of the plate is turned in under the head at about 90° (cf. *Phlyctaenius acadicus* (Whiteaves), Heintz 1933, Figure 1; Plate 1, Figure 4). The relationship between the anterior tip of the suborbital and the lateral angle of the postnasalo-rostral cannot be determined. On the ventral surface of the snout, the nasal cavity and internasal wall are as shown in Ørvig's drawing (figure 103B).

Heintz (1962, Figures 2, 4, 8) has shown that the postsuborbital is a small plate, closely applied to the hind margin of the suborbital. Stensiö (1969 *a*) has wrongly reinterpreted this plate as the submarginal ('middle preopercular'). A large space between these plates and the skull-roof must have been filled by the true submarginal plate. The right submarginal is partly preserved in A 28637, and both left and right plates are preserved *in situ* in A 28639 (see *Mg*, Heintz 1962, Plate 1, Figure 2), although they are not well seen. Mr D. Goujet (Paris) informs me that the submarginal plate lies partly outside the marginal plate in dolichothoracids, as he will show in a forthcoming study of certain Spitsbergen species. This condition is shown in the tentative restoration in figure 100. Further evidence on the submarginal is provided by three plates from the Lower Devonian of Utah (Denison 1958, Figure 103), which can now be safely determined, although I have previously considered one to be a postsuborbital (Miles 1969, p. 144, Figure 9D).

The extent of part of the neurocranium is indicated in figure 100A, after Ørvig. The relations of the regions of the neurocranium to the dermal plates and the sensory line grooves are the

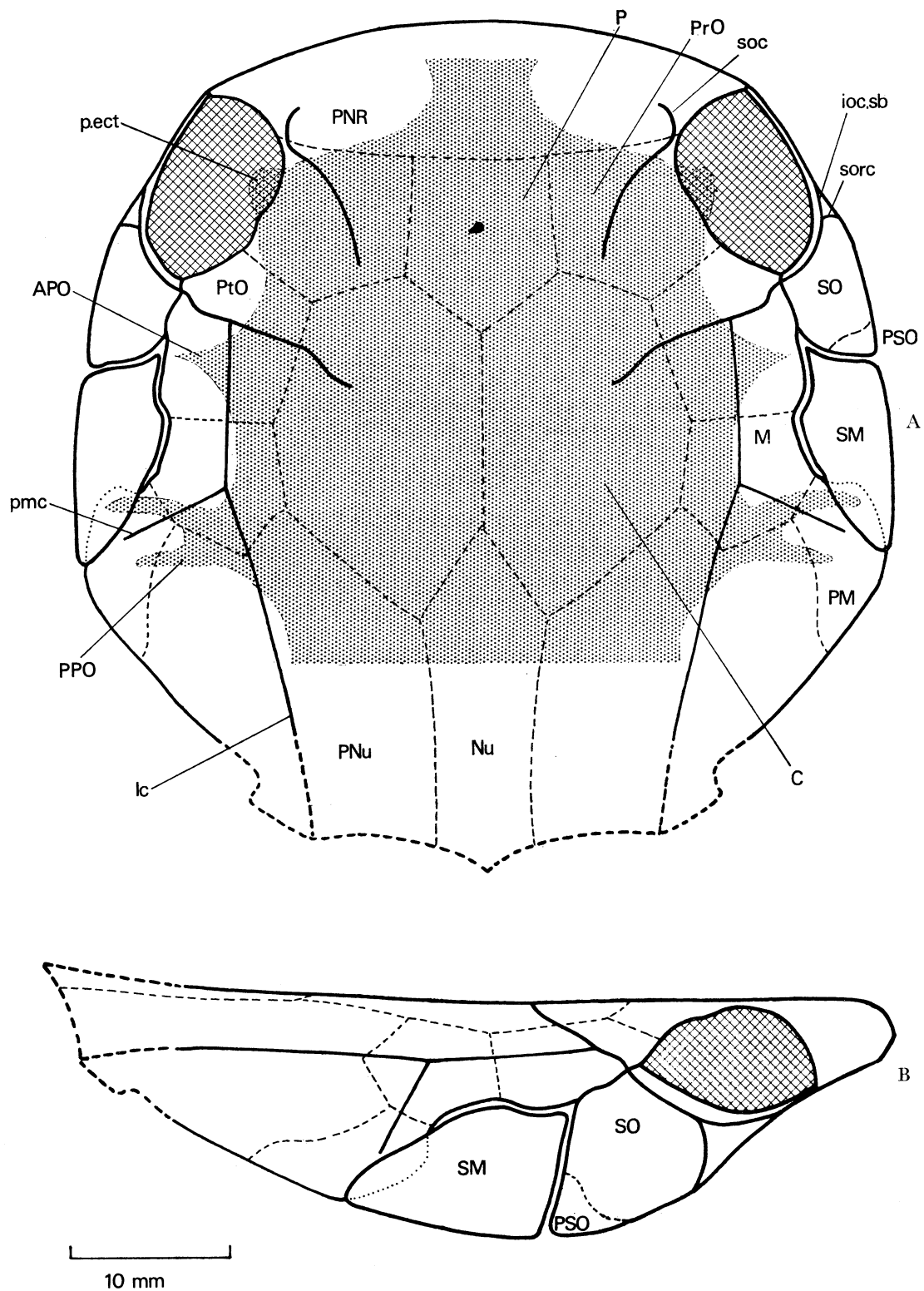


FIGURE 100. *Arctolepis decipiens* (Woodward). Restoration of head-shield in A, dorsal and B, lateral view. Extent of neurocranium partly shown in A by regular stipple. Based on P.M.O. A28637 and A28639.

same as in '*Kujdanowiaspis*' (Stensiö 1945, 1963*b*, 1969*a*). The position of the cheek plates relative to the anterior postorbital process (*APO*) is interesting, for it shows that the palatoquadrate must have been situated almost entirely in front of this process (see p. 199).

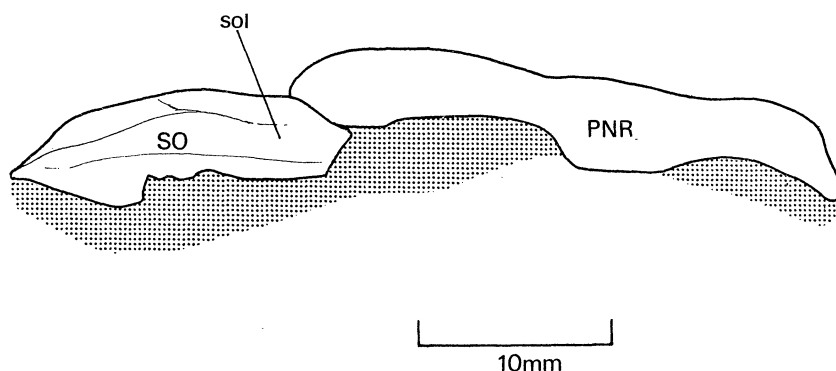


FIGURE 101. *Arctolepis decipiens* (Woodward). Sketch of head-shield P.M.O. A 28637 in anterolateral view to show suborbital lamina of suborbital plate.

The snout

The snout of *Holomena* has proved difficult to interpret in two main respects: (1) the homologies of the dermal bones and the significance of their variable development, (2) the position of the nasal sacs and nasal openings. These subjects may be considered separately on a comparative basis.

Dermal bones

In brachythoracid arthrodires the dorsal and anterior faces of the snout are usually covered by a median rostral and paired postnasal plates. The latter generally lie above the external incurrent nasal openings, although in some species they are each provided with a ventral interfrenal process which bounds the lower edge of the opening (e.g. *Coccosteus cuspidatus*; Miles & Westoll 1968). The conditions in dolichothoracids are less clear, mainly because adjacent dermal bones in the skull tend to fuse with each other, with the complete obliteration of the sutures. The restudy of Heintz's (1962) material of *Arctolepis decipiens* has confirmed that this species has a single broad ossification stretching from side to side at the front of the skull-roof, which enters into the anterior margins of the orbits. This plate has been named the postnasalo-rostral above, principally after the analysis of *Holomena* that follows, and Heintz's suggestion that small separate postnasals existed has been discounted. It is noteworthy that the supraorbital canals (*soc*) turn anteriorly towards the single, median radiation centre of this plate, at least in some individuals.

There is a compound postnasalo-rostral plate in most specimens of *H. westolli* (p. 110), but there is some variation in the snout bones. Two aspects require further comment. (1) The evidence for the compound nature of the postnasalo-rostral is not that which is usually held to be the most satisfactory, i.e. the presence of two or more centres of radiation (Parrington 1949, 1956; White 1965). (2) The relationship of the postnasal component of the postnasalo-rostral plate to the paired postnasal plate of brachythoracids, and the nature of the bones in the rostral region of dolichothoracids.

The postnasalo-rostral plate is shown to be a compound plate by the presence of a vestigial suture around its rostral component, and this interpretation is confirmed by the existence of an

independent rostral plate in one specimen. A *paired* postnasal component is assumed to be present on general grounds of comparative placoderm morphology. Regardless of whether the rostral plate exists separately or is fused with the postnasals, it does not appear to have a discrete radiation centre. I specifically exclude the possibility that the rostral plate had its own radiation centre at an early stage of skeletogenesis, and that this was lost once the rostral fused with the postnasals due to the resorption and remodelling of the bone, because this degree of remodelling is unknown in placoderms.

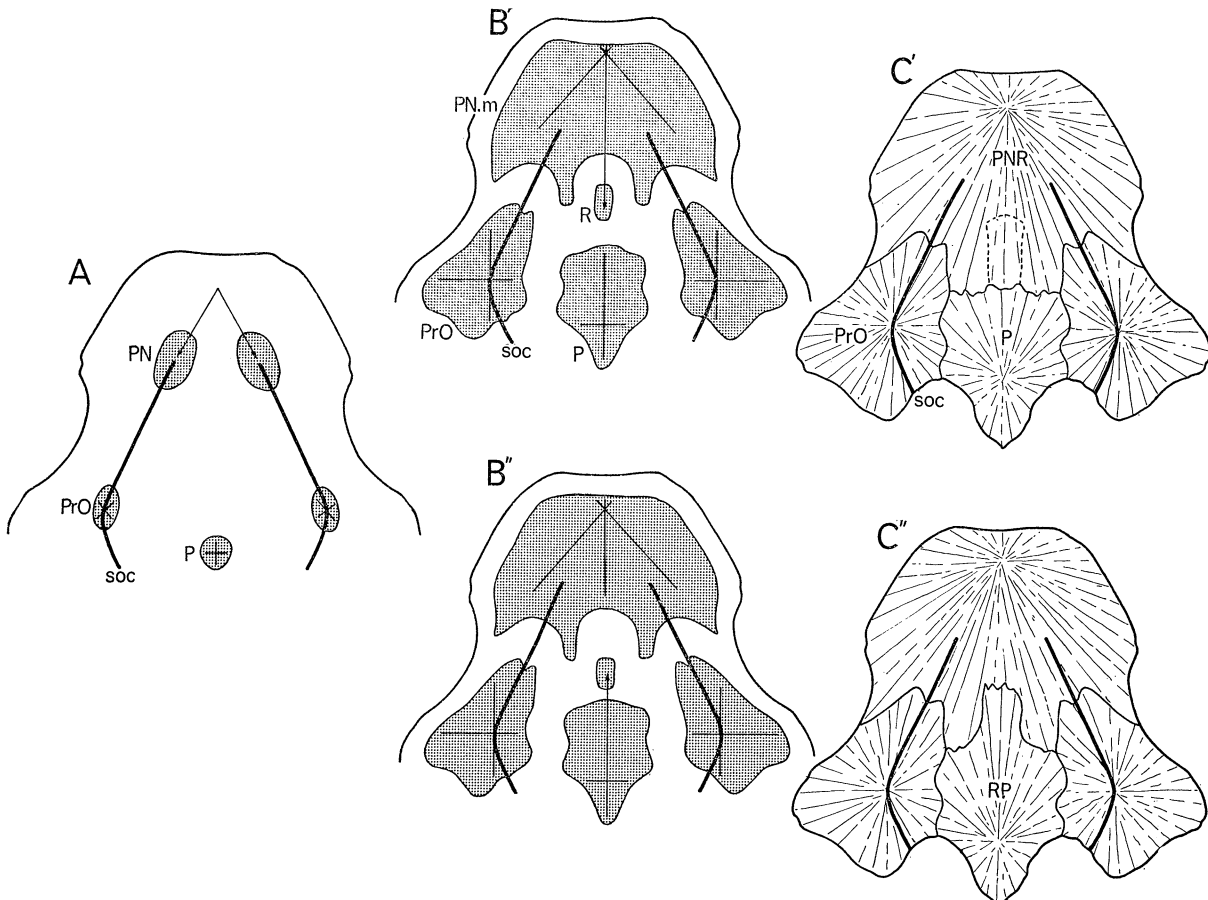


FIGURE 102. *H. westolli* sp. nov. Alternative developmental pathways of plates in rostral region of skull-roof, A-B'-C'; A-B''-C''. In A, B' and B'' the primordia are related to the outline of the fully developed exoskeleton, and the supraorbital canal is shown in its definitive course.

An ontogenetic explanation of the structure of the postnasalo-rostral plate may be proposed. First it must be noted that the centre of growth of a plate is not necessarily the same as its centre of radiation (Devillers 1947, p. 76, footnote 2). As commonly used in placoderm studies, the term radiation centre means the focus of the neurovascular grooves and canals in the bone tissue, and it is used in this sense throughout this work.

It may be assumed (figure 102A) that the paired postnasal (*PN*) and preorbital (*PrO*) primordia developed at an early stage of skeletogenesis, and were associated with the supraorbital sensory lines (*soc*). The postnasal primordia apparently received their neurovascular supply from a median, anteriorly situated centre. The primordium of the pineal plate may also have developed at an early stage, its position being fixed by the pineal body. At a later stage (figure 102B')

the rostral primordium (*R*) appeared. The rostral plate can be regarded as an anamestic bone in *Holonema*. Usually it received its neurovascular supply from the same centre as the developing postnasals, which at this stage of ontogeny had merged into a large, median structure. Skeletogenesis then continued (figure 102C') until the developing rostral became incorporated into the same plate as the postnasals; the three components continued to share the same radiation centre. Finally in large, well ossified individuals, the rostral component tended to lose its identity. An alternative path of development is shown in figure 102B", C", to account for the condition in P. 51155 (figure 8). Here it is assumed that the rostral primordium received its neurovascular supply from the pineal centre, and that subsequently it fused with the developing pineal to give a compound rostralo-pineal plate. A compound rostralo-pineal plate has been assumed to occur widely in primitive arthrodires (Denison 1958; White 1968) and petalichthyids (Ørvig 1967, Figure 5), but only on topographical grounds.

Thus in specimens of both *Holonema* and *Arctolepis decipiens* the rostral is fused with the postnasal plates, and the resulting structure has a single median radiation centre, towards which the supra-orbital canal may be directed. In general, however, the conditions in dolichothoracids are not well known. In many species it has been assumed that paired postnasals with discrete radiation centres are present, with the supraorbital canal of each side passing through the postnasal radiation centre (Denison 1958, Figure 105). '*Kujdanowiaspis*' is one such form. It has been carefully studied by Stensiö (1942, p. 13), and it illustrates well the difficulties encountered in interpreting material with extensive bone fusions. Stensiö records that 'the centre of radiation of the postnasal is so obscure that its exact position cannot be ascertained', and he is forced to assume that 'it must...be situated in the ventralmost part of the bone'. Alternatively, of course, '*Kujdanowiaspis*' may have a postnasalo-rostral plate of the same type as *Arctolepis decipiens* (cf. Heintz 1962). That some dolichothoracids should have postnasals with separate radiation centres is not surprising in view of the situation in brachythoracids. If this condition exists, as assumed by Denison (1958) and Stensiö (1942, 1963*b*, 1969*a*), then the postnasals probably fused with the rostral plate at a much later stage of ontogeny than in *Arctolepis decipiens* and *Holonema*.

It seems likely that the presence of a compound postnasalo-rostral plate with a single radiation centre is a primitive character for adult arthrodires, and the condition may be widespread in dolichothoracids. If this is the case, the separate postnasals of adult brachythoracids may be regarded as the products of paedomorphosis.

Nasal capsules and nasal openings

Before considering *Holonema* it is necessary to review the structure of the snout in some other arthrodires.

'*Kujdanowiaspis*' (Stensiö 1942, 1963*b*) is the best known form. The snout (figure 103A) comprises a discrete skeletal unit, with a rostral exoskeletal capsule enclosing the endoskeletal nasal capsules (rhinocapsular bones). The rostral capsule includes the pineal, rostral, paired postnasal (see above) and internasal (*IN*; 'prerostral', Stensiö 1963*b*) bones. It covers the dorsal, anterior, ventral and lateral sides of the ethmoid region, and has posterolateral orbital faces. The paired fenestra exonarina communis (*fec*) is completely surrounded by dermal bone, and is incompletely divided by an interfenestral process ('of the postnasal') (*pr.if*) into an anterior incurrent (*fe.i*) and a posterior excurrent opening (*fe.x*). These openings are extensively lined with small tubercles. The posteroventral margin of the capsule is formed by the paired subnasal

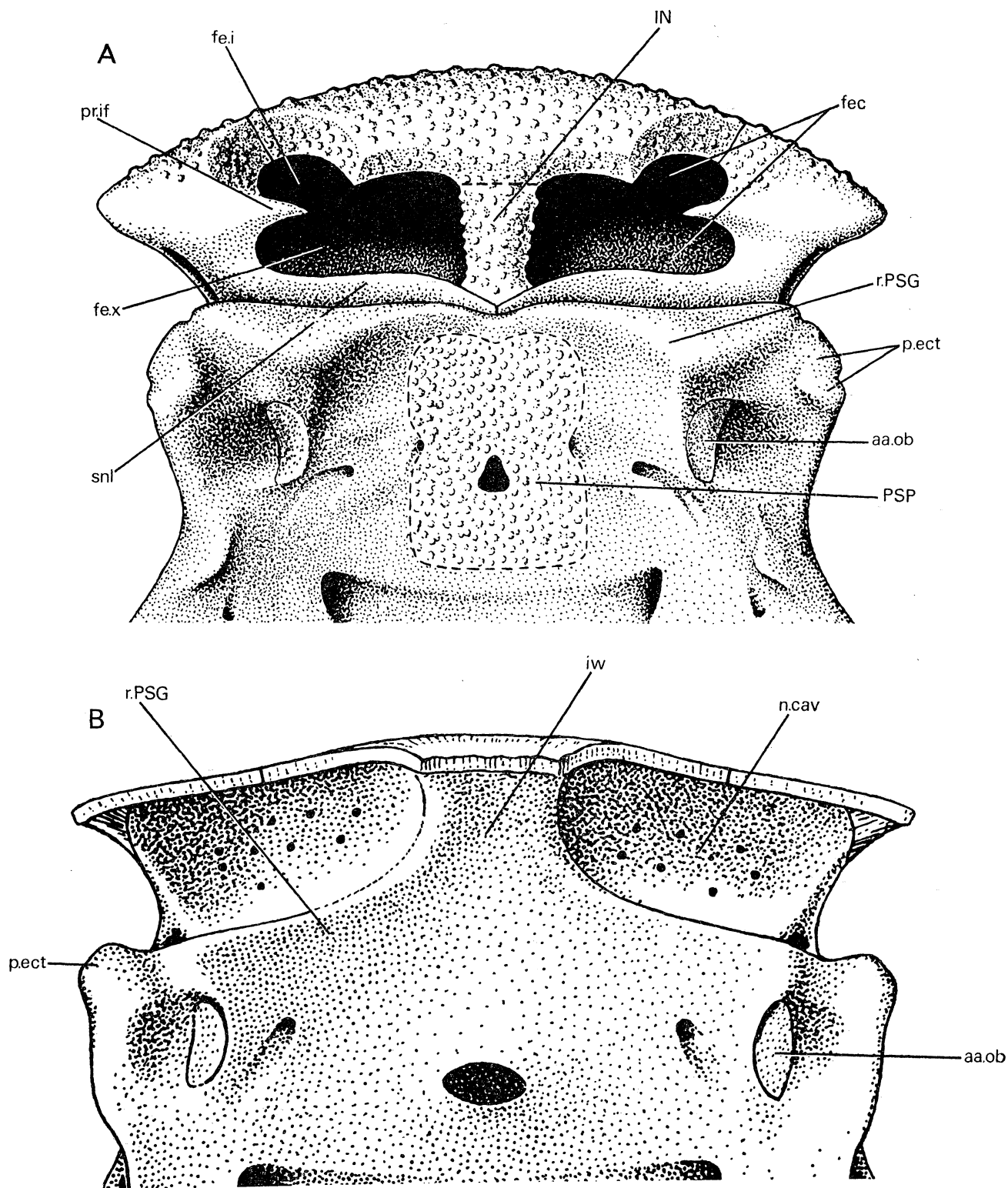


FIGURE 103. A, '*Kujdanowiaspis*' sp. Anterior part of neurocranium with dermal rostral capsule, in ventral view. B, undetermined dolichothoracid from Spitsbergen. Anterior part of neurocranium in ventral view. After Stensiö.

lamina ('of the postnasal') (*snl*), which meets its antimere in the middle line immediately behind the internasal bone (*IN*). This lamina lies anterior to the parasphenoid (*PSP*) and the paired ridge (*r.PSG*) on the lower surface of the subnasal shelf which supported the anterior superognathals. The paired nasal capsule, within the rostral capsule, consists of a rhinocapsular ossification which lined the nasal cavity and stretched back to enclose the olfactory bulb and foremost part of the olfactory tract. It was completely separated from the postethmo-occipital ossification, and from its fellow of the other side. The precise relationship of the nasal capsule to the dermal bones has not been described.

Further information about the snout of dolichothoracids is provided by an undetermined form from Spitsbergen, described as having an endocranium of 'type A' (Stensiö 1963*b*). This type of endocranium is found in *Arctolepis decipiens* (p. 178). In 'type A' (figure 103B) the rostral exoskeletal capsule is incorporated in the skull-roof and the nasal capsules are co-ossified with the postethmo-occipital region of the neurocranium. The internasal bone, interfenestral process and subnasal lamina are all absent. There is, however, a broad, solid internasal wall (*iw*), which widely separates the nasal cavities (*n.cav*), and the postnasal wall is extended laterally into an ectethmoid process (*p.ect*) which lies posterolateral to the ridge for the anterior superognathal (*r.PSG*). Again the nasal capsule comprises a thin sheet of bone which lined the nasal cavity. It opens ventrally through an extensive fenestra endonarina communis, and its roof is said to be pierced by fine foramina for the fila olfactoria.

In his 1942 paper on the snout, Stensiö recorded a number of elasmobranch characters in arthrodires. These include the relationship of the nasal capsules to the ethmoid region and the mouth; the position of the nasal openings on the rostrum; the relationship of the sensory canals on the snout to the nasal openings; and the position of the lower face of the ethmoid region, 'at a somewhat higher level than the lower face of the postethmoid part of the endocranium just as it is in several Selachians'. He also suggested that arthrodires may have had selachian-like nasal flaps, as there is no ornament on the interfenestral process. Building on these elasmobranch-like features, Stensiö (1963*b*) later restored an extensive annular cartilage (*ala nasalis*) in both '*Kujdanowiaspis*' and the undetermined species ('type A') from Spitsbergen. Stensiö supposed that the annular cartilage completed the lateral and ventral nasal walls, and divided the fenestra endonarina communis into an anterolateral incurrent and a ventral excurrent opening.

A number of points are raised by Stensiö's interpretation of the snout. Westoll (1945, p. 395) has already pointed out that while the nasal capsules and their external nasal openings in dolichothoracids and elasmobranchs 'may show considerable likeness...their mutual arrangement and the general character of the whole endocranium are not remarkably alike, and it is possible that Stensiö is relying on characters that may prove to be rather generalized and primitive than truly restricted characters of immediate use in phylogenetic studies'. The nasal capsules in the Spitsbergen form ('type A') lend some support to this view, if de Beer (1937, p. 395) is correct in supposing that the nasal capsule primitively had no floor. Jarvik (1942, p. 251, footnote 1) has taken de Beer (1937, p. 456) to task for the alleged assertion that the nasal *cavity* in sharks has no floor, claiming that 'this is untenable from a morphological point of view'. But the absence of a cartilaginous floor in the nasal *capsules* of elasmobranchs is a tangible fact, and if this is the primitive condition it is not a reason for restoring the nasal structure of placoderms strictly after an elasmobranch model. It may also be noted that there are no markings on the nasal capsule or dermal skeleton to show that an annular cartilage was present, and it is hardly necessary to restore such a structure in '*Kujdanowiaspis*' in which the nasal openings are so closely delimited by

dermal bone. We may note Westoll's (1967, p. 97) more recent suggestion, 'that in Euarthrodira the dermal elements surrounding the nasal capsule may readily be recognized as the fore-runners of important parts of the cartilaginous secondary nasal capsule of elasmobranchs'. In so far as I can follow Holmgren's account of the embryological development of the nasal capsule in elasmobranchs, e.g. in *Etmopterus spinax* (1940, p. 139), the secondary nasal capsule comprises wholly or mostly the annular cartilage. Westoll's suggestion is, therefore, incompatible with the presence of an annular cartilage in arthrodires and it contradicts Stensiö's interpretation. Final

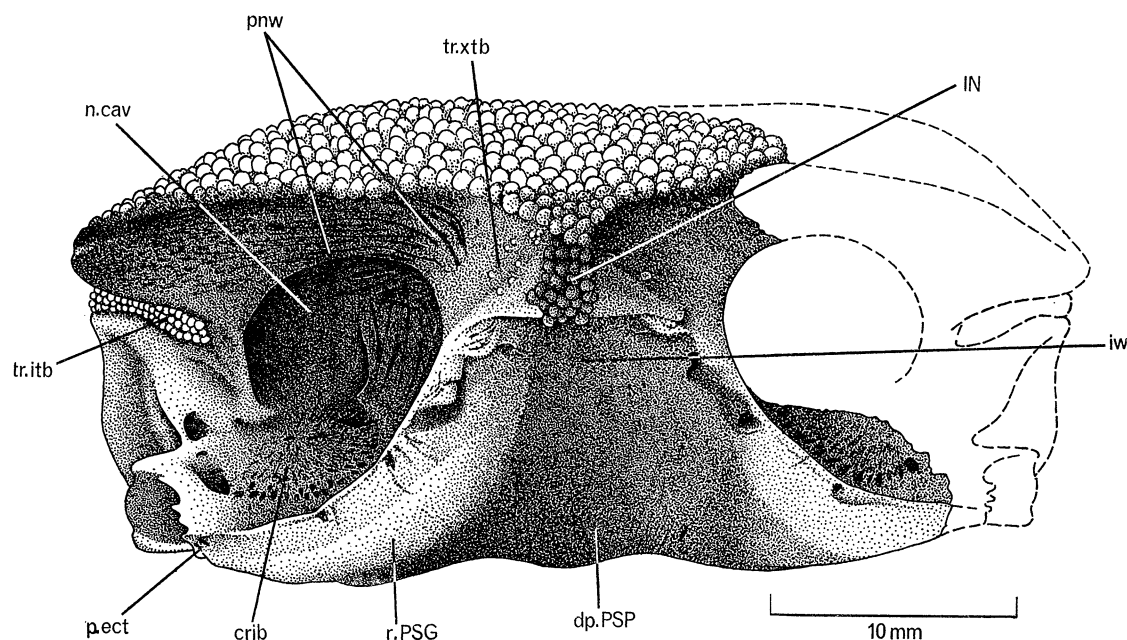


FIGURE 104. *Buchanosteus* sp. Rostral capsule in ventral view. P. 33612. Lower Devonian, New South Wales.

acceptance of Westoll's suggestion (yet to be published in detail) must, however, be withheld, for it seems to demand a much closer phylogenetic relationship between elasmobranchs and arthrodires than at present seems likely.

A specimen of the rostral capsule of *Buchanosteus* sp. (P. 33612) throws important new light on the structure of the snout in arthrodires. This specimen will be described by Dr E. I. White, to whom I am indebted for the opportunity to make these comments, and my account will be limited to some points which aid in the interpretation of *Holonema*. *Buchanosteus* is the only brachythoracid known to have a discrete rostral capsule. In P. 33612 (figures 104, 105) it comprises the pineal, rostral and internasal bones, although the sutures are not distinct. Postnasals were probably present in life, but have become detached and separated from the specimen. The ethmoid region of the neurocranium is intimately associated with the dermal bones of the rostral capsule, its dorsal perichondral wall having coalesced with the basal bone layer of the exoskeleton. No sutures separate the dermal and cartilage bones, and it is not always clear where they merge with one another. The endoskeleton is more extensive than that associated with the rostral capsule in '*Kujdanowiaspis*', as it reaches back to include the subnasal shelf of that form, as well as a broad internasal wall. The dermal internasal bone (*IN*) is situated in front of the triangular internasal wall (*iw*), where the latter merges with the prenasal wall (*pnw*) in the divisio prenasalis communis. The internasal wall was filled with cartilage in life

(cf. the neurocranium of 'type A'; Stensiö 1963 *b*), and there was certainly no cavum precerebrale. The median internasal wall merges with the paired postnasal wall, which runs out laterally to form a prominent ectethmoid process (*p.ect*). Mesial to the ectethmoid process the floor of the neurocranium is thickened where it supported the anterior superognathal (*r.PSG*), and mesial to this thickening the floor is depressed where it was covered by the anterior part of the parasphenoid (*dp.PSP*). The cribrosal division of the postnasal wall (*crib*) is well defined and

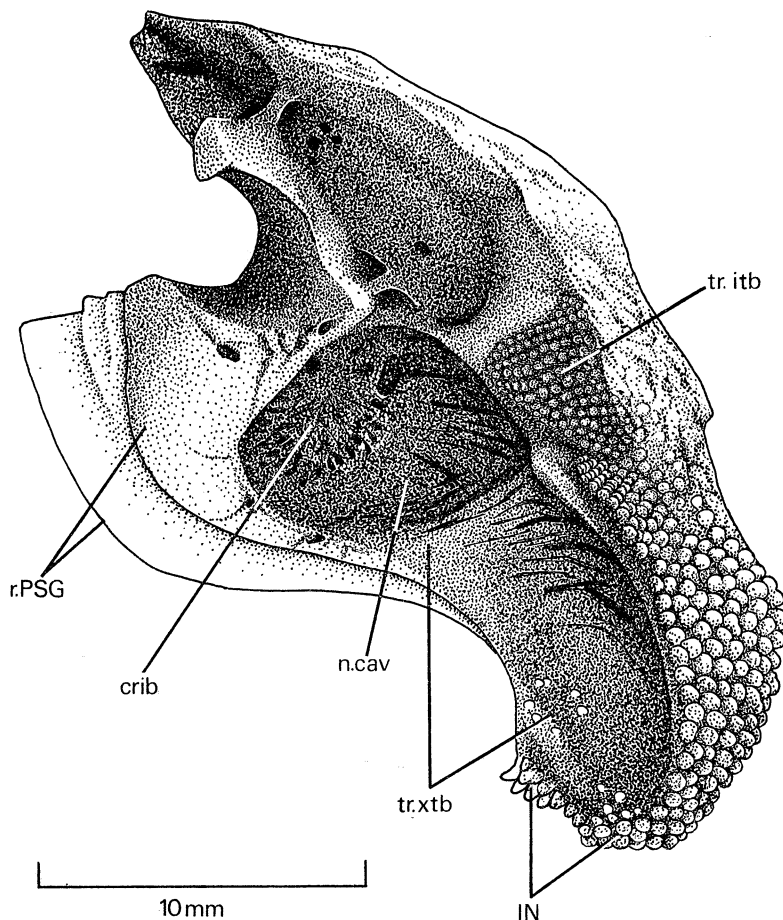


FIGURE 105. *Buchanosteus* sp. Rostral capsule in lateral (and slightly ventral) view. P. 33612. Lower Devonian, New South Wales.

immediately comparable with the cribrosal ossification of other brachythoracids (Stensiö 1963 *b*; Miles & Westoll 1968). In front of the cribrosal division lies the distinct nasal cavity (*n.cav*). As in '*Kujdanowiaspis*' and 'type A', it is clear that the nasal capsule did not have a skeletal floor, and that its lateral wall was incomplete. The ventral edge of the internasal bone is ornamented with prominent tubercles. From this edge, at each side, a thin sheet of smooth dermal bone with a few fine tubercles, sweeps up to merge with the more coarsely textured, somewhat striated bone that lies in front of the nasal cavity, and it also extends posteriorly as far as the anteromesial region of the nasal cavity. The boundary between dermal and cartilage bone is not clear. This smooth sheet of dermal bone delimits a wide path (*tr.xtb*) which leads from the (*excurrent*) fenestra exonarina posterior to the nasal sac. A distinct notch on the edge of the rostral plate, with an inflected triangular area bearing fine tubercles, marks the position of the

(incurrent) fenestra exonarina anterior. In life, this fenestra was presumably completed by the postnasal plate. Again the boundary between the exoskeleton and endoskeleton is not distinct, but the tuberculated area leads almost to the edge of the nasal cavity, and it apparently marks a path (*tr.itb*) leading to the nasal sac.

If we put aside the elasmobranch model that is frequently used to interpret placoderm structures, the most obvious interpretation of the nose in *Buchanosteus* is as follows. The nasal sac communicated with the outside by a short, laterally directed anterior nasal tube and a long, anteroventrally directed posterior nasal tube. These tubes led to the incurrent and excurrent nasal openings respectively. The nasal sac seemingly fitted closely into the nasal cavity; there is no good evidence of accessory nasal sacs or nasal diverticulae, although it is just possible that there was an anterolateral diverticulum. There is no evidence of any other endoskeletal elements in the snout other than those already mentioned, and it must be assumed that the fenestra endonarina communis was divided into incurrent and excurrent openings by a nasal bridge of soft tissues.

With regard to other brachythoracids, it may be noted that the external nasal openings of coccosteids and dinichthyids can be interpreted closely after the conditions in '*Kujdanowiaspis*' (Miles & Westoll 1968), and there is no suggestion that the nasal cavities differed in any fundamental way from those of *Buchanosteus*. In some of the Wildungen pachyosteorhynchid-level brachythoracids, however, Stensiö (1963*b*) has argued for a somewhat different interpretation, basing his case mostly on *Trematosteus fontanellus*, in which the 'rhino-interorbital' ossification is preserved. In such deep-headed forms, Stensiö suggests that there was an anterodorsally situated fenestra endonarina communis, divided into incurrent and excurrent openings by an annular cartilage. The foramen in the expected position of the excurrent endoskeletal nasal openings on the ventral face of the snout, immediately in front of the anterior superognathals, is interpreted as the opening of a subnasal sinus. The information now available leads, however, to a more satisfactory interpretation. The 'subnasal sinus' communicates with the nasal cavities through a pair of foramina, separated by the internasal wall, which may be determined as the excurrent endoskeletal nasal openings. The single pair of nasal openings on the anterodorsal face of the dermal skeleton may be determined as the incurrent fenestrae exonarinae anteriores. The distance between the incurrent and excurrent nasal openings, which cannot be explained if an annular cartilage is assumed to be present, presents no problem if it is assumed that the nasal sacs were provided with nasal tubes as in *Buchanosteus*.

It is now possible to consider the snout of *Holonema*. The difficulties in interpreting this form arise because there are no obvious nasal notches or dermal nasal openings on the rostrum, and no indisputable impression of the ethmoid region of the brain-case. I have considered three possible arrangements of the nasal capsules and nasal openings:

- (1) Both the capsules and nasal openings were situated in front of the dermal head-shield.
- (2) The capsules were situated under the anterior region of the postnasalo-rostral plate, with the nasal openings in front of the dermal head-shield.
- (3) The capsules were situated under the postnasalo-rostral plate, and the nasal openings occupied the anterior and/or middle division(s) of the fenestra orbitalis.

The first arrangement maintains the 'correct' relationships between the nasal capsules and the superognathals, as seen for example in '*Kujdanowiaspis*' and *Buchanosteus*. It implies that the capsules were situated in a soft rostrum, such as restored by Stensiö (1969*a*, Figures 22A, 23) for *Macropetalichthys*, and the nasal openings may have been dorsal, lateral or ventral in position.

This arrangement must, however, be discounted, because restorations of the head-shield with the palatoquadrate and gnathals in position (figure 106) show that the skull is too shallow anteriorly to have been continued forwards in a long, soft rostrum. It will be shown below that the peculiar development of the gnathals in *Holonema* support an alternative interpretation of the snout.

The second arrangement (figure 107A) is suggested by a comparison with *Buchanosteus*. It may be supposed that the nasal capsules (*ncp*) lay under the anterolateral thickenings of the postnasalo-rostral plate, and that the posteromesial ridges (*r.pm*) which delimit these areas

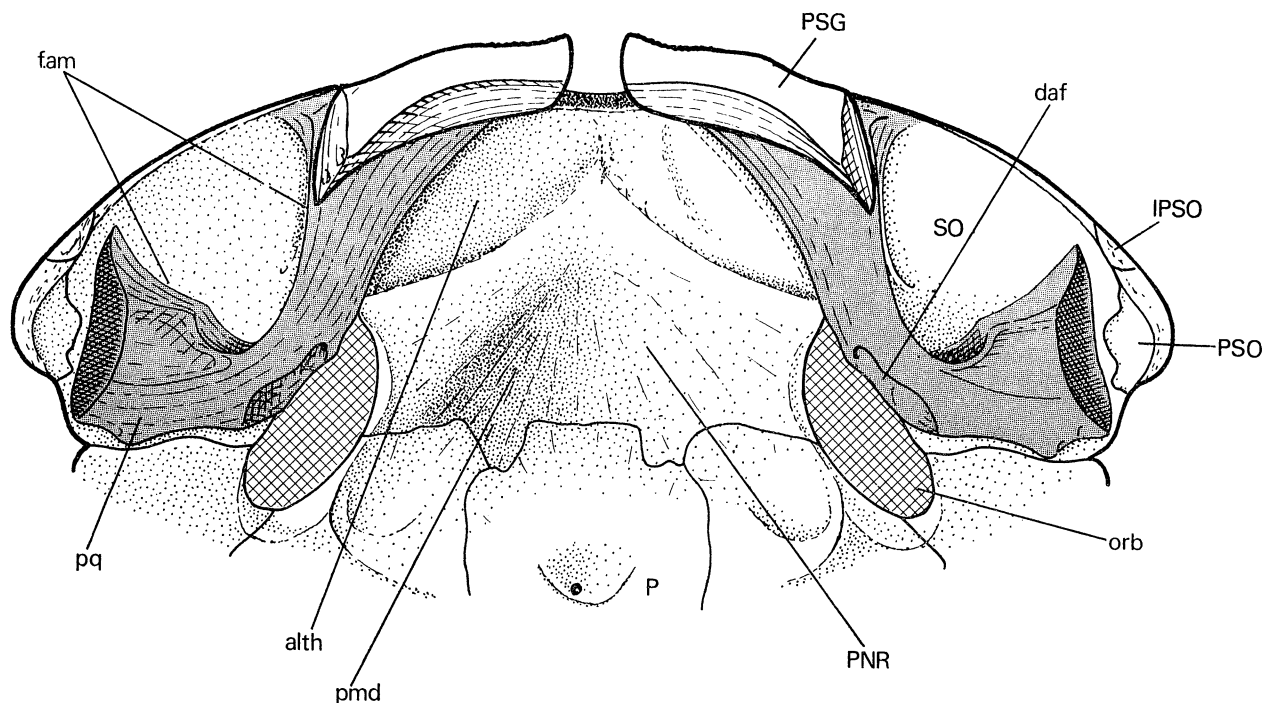


FIGURE 106. *H. westolli* sp. nov. Restoration of upper jaws in ventral view; anterior superognathal omitted.

mark the position of the continuous postnasal-internasal wall (see also the neurocranium 'type A'). The nasal sac was provided with incurrent and excurrent nasal tubes (*nt.i*; *nt.x*) which opened on the snout in front of the dermal skeleton, either dorsally, laterally or ventrally. Unfortunately this interpretation meets with the same objections as the first one. Although it is possible to show the nasal sacs in this position in a diagram, there does not seem to be room either for the nasal capsules or for the forward passage of the nasal tubes in a three-dimensional reconstruction, with the palatoquadrate and superognathals in place.

The third interpretation (figure 107B) is thought to be correct. It may be assumed that the nasal capsules (*ncp*) lay close together under the posteromedian depression of the postnasalo-rostral plate, and that each nasal sac was served by laterally directed incurrent and excurrent nasal tubes (*nt.i*; *nt.x*). The anterior and middle divisions of the fenestra orbitalis may be identified as the incurrent and excurrent dermal nasal openings respectively. However, because the anterior division of the orbit is small, it is just possible that the middle division was for the fenestra exonarina communis.

If this last interpretation of the snout is correct, *Holonema* has paralleled antiarchs to a considerable extent (see p. 176). The nasal capsules have moved backwards and upwards from the presumed primitive placoderm condition seen in dolichothoracids, and have come to lie close

together about the middle line, and the principal upper tooth-plates lie at the rostral margin of the head-shield (figure 106). The nasal openings have, however, come to lie in front of rather than between the orbits. A similar comparison can be made with rhenanids, although these placoderms lack tooth-plates. Primitively in placoderms, the anterior superognathal lies immediately behind the nasal cavity, supported by the postnasal wall (e.g. '*Kujdanowiaspis*', *Buchanosteus*). It is particularly interesting to note, therefore, that in groups with a modified snout such as the antiarchs, ptyctodontids and rhenanids, in which the postnasal wall is no

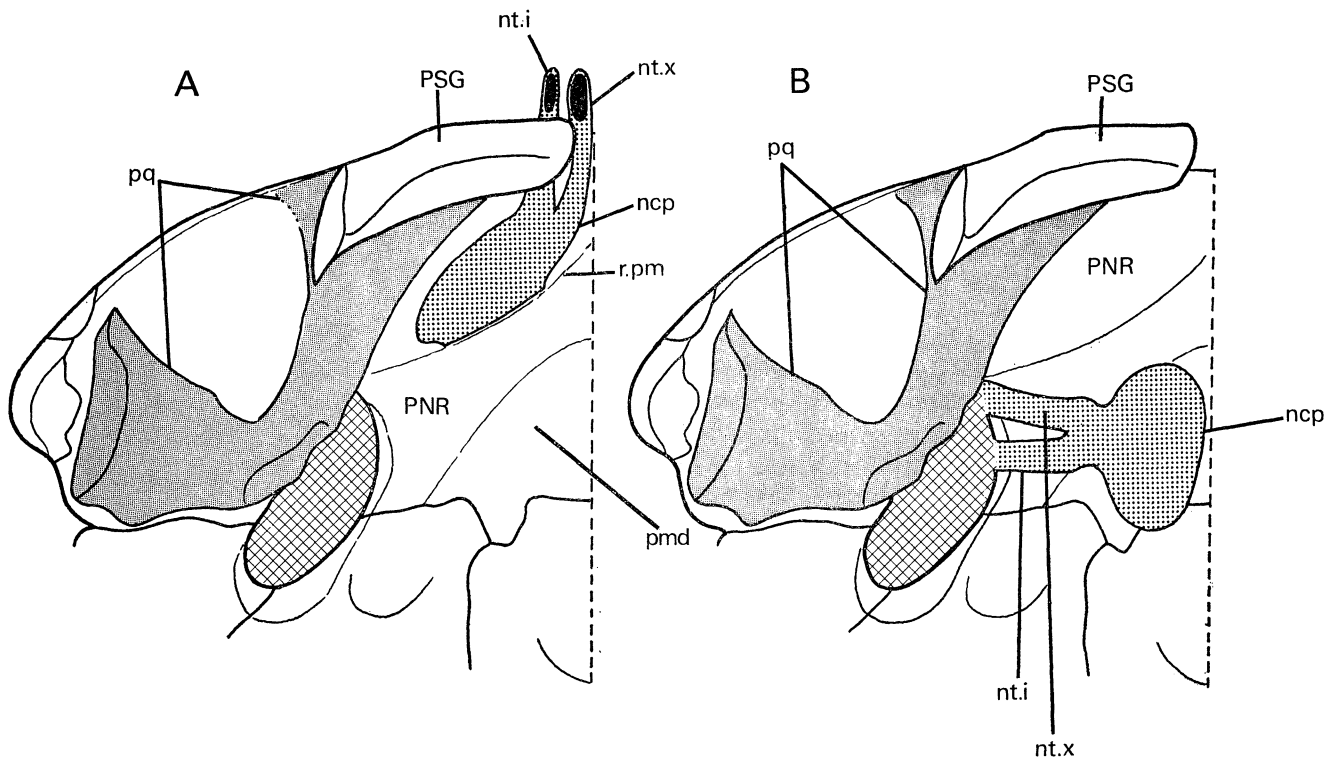


FIGURE 107. *H. westolli* sp.nov. Two possible interpretations of the nasal sacs using same base drawing as in figure 106. Right side shown only.

longer available as a supporting structure, the anterior superognathal has been lost or has fused with the posterior superognathal. The vestigial condition of the anterior superognathal in *Holonema* is therefore consonant with the modified condition of the snout, and may be used in support of the third interpretation. It is true that the anterior superognathal is a small element in some advanced brachythoracids with a long mandible and a wide gape, but this condition is correlated with the organization of the jaw mechanism (Miles 1969) and has no connexion with the conditions discussed here. This leaves the question of the truncated anterior margin of the postnasalo-rostral plate. An internasal bone which could have abutted against this surface has not been found, and if the nasal capsule and openings were as suggested above, it is unlikely that this bone was present. It is possible, however, that it had fused with the postnasalo-rostral. The truncated anterior margin may be interpreted as a surface that was continuous with the soft tissues that capped the snout.

Lateral-line system

The lateral-lines in *Holonema* are represented by grooves of varying depth in the bone surface which have on the whole a typically arthrodiran arrangement (see, for example, Stensiö 1947, 1963*b*, 1969*a*; Denison 1958; Miles & Westoll 1968). They have been described above for *H. westolli*. It remains to discuss some points of more general interest in the lines on the snout, cheek and flank.

Lateral-lines of the snout

The supraorbital grooves end anteriorly on the dorsal surface of the snout, on the fused postnasal components of the exoskeleton. They are directed towards the median radiation centre of the postnasals, but end posterior to this point. It is possible that the supraorbital lines were continued forwards as superficial pit-lines, to a median anastomosis at the radiation centre. If so, these pit-lines can be regarded as forming a rostral commissure and can be compared with the dorsally situated rostral (prenasal) commissure of holocephalans (Holmgren 1942) and dipnoans (White 1962; Panchen 1967). However, as a rostral commissure has not otherwise been described in arthrodires, more evidence is required before this point can be accepted.

There is no doubt that the supraorbital canal did not anastomose with the infraorbital canal. This compares with the hypothetical primitive condition for vertebrates, and is also shown by Recent dipnoans (Panchen 1967; Jollie 1969). In arthrodires, the supraorbital canal usually passes off the lower edge of the postnasal plate, and it is plausibly regarded as having anastomosed with the infraorbital line in the soft tissues of the snout. This anastomosis is definitely present in rhenanids (Gross 1963; Stensiö 1969*a*). Thus the absence of the anastomosis in *Holonema* may not be a primitive feature, but a secondary character that can be correlated with the modified condition of the snout (p. 188). The infraorbital canal (*ioc*) either passes off the anterior margin of the suborbital plate or ends a few mm short of this margin (figures 32A, 33A). In the latter condition it probably continued forwards as a superficial pit-line. Whether or not it was connected to its fellow in an ethmoid commissure is not clear. This commissure is usually thought to be present in arthrodires (e.g. Stensiö 1963*b*, 1969*a*), and it is clearly seen in rhenanids (Gross 1963). However, it is possible that it had been lost in *Holonema* as a result of the modification of the snout.

Lateral-lines of the cheek

The cheek-line grooves are unusually well developed in *Holonema*. This is particularly true of the postsuborbital canal ('posterior part of supramaxillary line', Ørvig 1960) which dorsally extends forwards from the postsuborbital on to the suborbital plate. Stensiö (1947) originally restored the hypothetical posterior part of the supramaxillary line in arthrodires as passing anteroventrally across the submarginal, postsuborbital and suborbital plates, from near the 'preopercular' line to the supraoral line ('anterior division of supramaxillary line'), but more recent discoveries (Ørvig 1960; Miles & Westoll 1968) have shown that this is wrong. It is particularly noteworthy that the postsuborbital line (*psoc*) has never been found on the submarginal plate, and I believe that the dorsal extension of the postsuborbital canal on to the suborbital plate in *Holonema* (figures 32A, 33A) represents the primitive condition. Although this canal always ends posterior to the infraorbital canal, it is possible that the two lines were joined in life by a superficial section of the postsuborbital line. Evidence that the cheek canals have

primitive disposition in *Holonema* is provided by a suborbital of *Buchanosteus* (P. 50416) now being studied by Dr E. I. White. In this specimen, the postsuborbital canal extends on to the suborbital exactly as in *Holonema*. Also the patterns of the cheek sensory canals in *Homostius* (Heintz 1934, Figure 22) and possibly *Titanichthys clarki* Newberry (Dean 1909, Plate 40) are most readily interpreted as modifications of the type of arrangement seen in *Holonema*.

The sensory pit which is situated behind the infraorbital line on the suborbital plate of coccosteids (figure 110A; Ørvig 1960; Miles & Westoll 1968) may possibly be a vestige of the primitive anterior part of the postsuborbital canal. However, the presence of a similar pit in front of the postsuborbital line on the postsuborbital plate weakens this explanation.

The postmarginal canal of the above account (also Miles & Westoll 1968), on the marginal and postmarginal plates, is the preopercular canal of Stensiö (1947, 1963*b*, 1969*a*). Reasons for rejecting the term 'preopercular line' have been given by Miles & Westoll (1968, pp. 456–457), but some additional points can now be made. The preopercular line (*sensu* Stensiö 1947) of chondrichthyans and osteichthyans continues ventrally on to the lower jaw, as the mandibular line, yet the postmarginal line manifestly does not have this course in *Holonema* (*pmc*, figure 2), nor in *Coccosteus cuspidatus* (Miles & Westoll 1968, p. 456). If, therefore, a homologue of the preopercular line exists in arthrodires, it might better be sought in the postsuborbital line. Anteriorly this line has a similar relationship to the postorbital part of the infraorbital line as the preopercular line of crossopterygians, dipnoans and some acanthodians (those with the *Euthacanthus* arrangement; Stensiö 1947). Unfortunately, the anterior position of the postsuborbital line, lateral to the mandibular joint at the angle of the jaw, speaks against this homology, as does its position in *Coccosteus* sp., anteroventral to the hyomandibula (figure 110). On the other hand, the relationship between superficial lateral-lines in open grooves and deeper structures may have been quite variable in forms with a thick armour. Also it is clear that the postmarginal line continued ventrally on to the lower jaw across the infrapostsuborbital plate in *Holonema*, and it makes sense to regard its ventral continuation as the mandibular line, the oral line arising as a continuation of the more anteriorly situated supraoral canal on the suborbital plate.

Lateral-lines of the flank

The lateral-lines of the flank in arthrodires have proved difficult to interpret, particularly in coccosteids where they may be exceptionally completely represented by grooves in the surface of the bone (e.g. Miles & Westoll 1968, p. 457). Recently, Ørvig (1969) has drawn up a scheme for the description and interpretation of the lines by combining in one drawing all the lines that have been found in coccosteids.† Ørvig has also interpreted the lines of holonematids by reference to this scheme. Stensiö (1969*a*, pp. 659–667) has introduced a new terminology for the sensory lines of the trunk.

If we substitute Stensiö's new terms for the old names, Ørvig's scheme for the flank canals is as follows (figure 108). The main lateral-line can be divided into three parts, with the anterior (*lc.a*) and middle (*lc.b*) parts on the anterior dorsolateral plate, and the posterior part (*lc.c*) on both the anterior dorsolateral and posterior dorsolateral plates. The ventrolateral sensory line (*lc.vl*) diverges from the main line at the junction of its anterior and middle sections, to run obliquely back (posteroventrally) across the anterior dorsolateral plate. Ørvig suggests that the ventrolateral line continued ventrally across the posterior lateral and posterior ventrolateral

† Ørvig writes of 'coccosteids and *Millerosteus*' (also Stensiö 1963*b*, 1969*a*), but there is no doubt in my mind that *Millerosteus* is a coccosteid.

plates, usually as a superficial line which has left no grooves in the bone surface (*lv.v*). Near the junction of the anterior and middle sections of the main line, the anterior dorsolateral line (*ld*) diverges to run back across the posterior dorsolateral plate and on to the median dorsal plate, where it meets its antimere. Finally, an accessory twig (*lac*) on the anterior dorsolateral plate joins the anterior dorsolateral and ventrolateral lines.

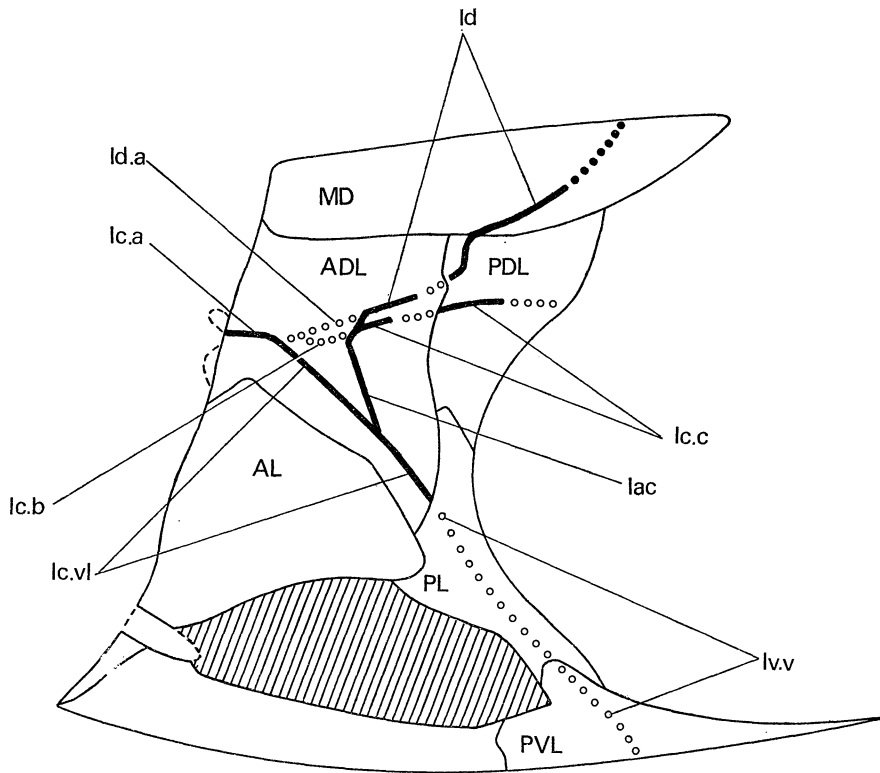


FIGURE 108. Hypothetical scheme of sensory line canals on the flank in a coccosteid. Canals not normally represented by grooves indicated by rows of small circles. After Ørvig.

The system of lines on the flank does not occur *in toto* in any one individual. In particular, it may be noted that the anterior part of the anterior dorsolateral line (*ld.a*) and the middle part of the main line (*lc.b*) have not been observed (but see below), and Ørvig remarks that in life they may not have existed, having been replaced by the secondary development of the accessory twig (*lac*). Alternatively I suggest that the accessory twig might comprise the deflected anterior part of the dorsolateral line and/or the middle part of the main line. Despite these points, Ørvig's scheme provides a basis for the description of new material, and it may now be applied to *H. westolli*.

The deep groove crossing the anterior dorsolateral plate (figure 63) corresponds to the deep, oblique groove in coccosteids and *Rhachiosteus* (Miles 1964*a*, 1966*a*; Miles & Westoll, 1963, 1968). This groove has usually been termed the main lateral-line (cf. Stensiö 1959, 1969*b*), but it can now be regarded as having housed the anterior part of the main lateral-line plus the ventrolateral line (*lc.a*, *lc.vl*). As in coccosteids, it is directed posteriorly towards the posterior lateral plate, but it may end before the posterior margin of the anterior dorsolateral plate, and there is no evidence that the sensory line turned ventrally to cross the surfaces of the posterior lateral and posterior

ventrolateral plates. The groove for the accessory twig (*lac*) is well developed, although it does not always anastomose with the groove for the combined anterior part of the main and the ventrolateral lines (figures 68A, 70B). Ventrally the accessory twig may turn in either the anterior or posterior direction. The posterodorsal continuation of the accessory twig (*ld*) has been regarded as the anterior dorsolateral line ('dorsal branch of main line') in *H. radiatum* (Ørvig 1969, Figure 2B), and this must also be the case in *H. westolli*, although the groove ends well away from the posterior and dorsal margins of the anterior dorsolateral plate. There is no groove on the median dorsal plate in *H. westolli*. The disjointed groove which arises midway along the posterior dorsolateral plate (*lc.c*, figures 63, 64, 71A, 72) and turns posteroventrally to run off about midway down the posterior margin of that plate (although it does not always reach this margin, p. 161), is the posterior part of the main line. Clearly it would be more satisfactory to assume that the dorsally placed grooves on the anterior and posterior dorsolateral plates housed the same lateral-line, than that they housed the anterior dorsolateral line on the former and the main line on the latter. But this interpretation would make it difficult to account for the groove on the median dorsal of some holonematids (figures 114A, 115A, 116; Wells 1943; Stevens 1964; Denison 1968), and it must, therefore, be rejected. Further, there is now evidence for the path of the anterior dorsolateral line on the posterior dorsolateral plate in the form of a groove in an undetermined species of *Holonema* from Belgium (p. 218, figure 123).

A short, anteriorly directed groove arises at the anastomosis of the anterior dorsolateral line and the accessory twig in P. 50984 and P. 51014 (*ld.a*, figures 68A, 70A), and is also found in a specimen of *H. radiatum* (p. 213, figure 119). This groove can be regarded as having housed the anterior part of the anterior dorsolateral line, and it is the first evidence that the anterior part of the main line was distinct from and could co-exist with the accessory twig. However, the position of the groove in P. 51014 (figures 68A) indicates that the anterior part of the anterior dorsolateral line was in a vestigial condition, and did not always anastomose with the anterior part of the main line. Possibly it was present in only a small percentage of individuals (28% of the existing sample) and was very variable. It must be assumed that a superficial line, which has left no trace in the form of a groove, connected the posterior part of the main canal on the posterior dorsolateral plate with the middle part on the anterior dorsolateral plate (figure 63).

The principal groove on the flank thus carried the anterior part of the main line and the ventrolateral line in holonematids, coccosteids and *Rhachiosteus*. In all these forms the line passes back posteroventrally and is directed towards the posterior lateral plate. This may be contrasted with the usual condition in arthrodires (see, for example, Miles 1966*a*; Stensiö 1969*a*), in which the principal groove on the flank was for the main lateral-line, which passed back more or less horizontally across the anterior and posterior dorsolateral plates. Holonematids also resemble coccosteids in the presence of dorsally situated grooves on the flank plates for the anterior dorsolateral line, but all these similarities seem to be the result of parallel evolution (p. 227).

Endoskeleton of jaw apparatus and gill-cover

At the present time, any discussion of the upper jaw, the suspensorium and gill cover in placoderms, must be based on the rhenanid *Jagorina pandora* Jaekel. Although the rhenanids are highly specialized fishes with protrusible jaws, *Jagorina* is the only placoderm in which all these structures have been described, and in which their relationships to the neurocranium are known (figure 109; Stensiö 1969*a*). Even so, the interpretation of the jaw apparatus in rhenanids has been the subject of some controversy (summarized in Miles 1969, p. 140; see Watson 1951;

Gross 1963; Westoll 1963; Stensiö 1969*a*). I now accept that Stensiö has correctly identified the palatoquadrate and meckelian cartilage in *Jagorina*.

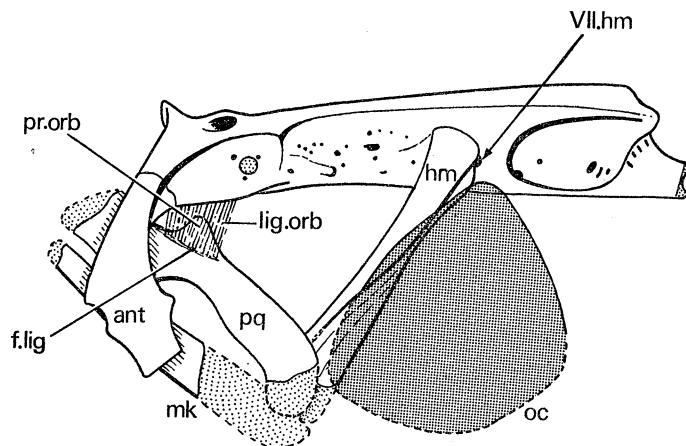


FIGURE 109. *Jagorina pandora* Jaekel. Neurocranium and jaw apparatus in lateral view. After Stensiö.

Palatoquadrate

The palatoquadrate (*pq*) of *Jagorina* is a single bone, although capped with cartilage at each end (Stensiö 1969*a*, Figures 155, 158), and the palatoquadrate of *Holonema* is also a single bone. It would appear that the palatoquadrate was primitively a continuous unit (see p. 135), because of the great distance in relationship between *Jagorina* and *Holonema*, and because the general trend of change in arthrodires is towards the reduction of the middle region of the palatoquadrate, until all connexion is lost between the autopalatine and quadrate ossifications. There is no evidence to show that the autopalatine and quadrate divisions of the palatoquadrate were separate at a pre-placoderm stage. My earlier discussion of the primitive arthrodire palatoquadrate (Miles 1969, pp. 144, 145) was based on the erroneous determination of a dolichothoracid plate (a submarginal, p. 178) from the Lower Devonian of Utah as the postsuborbital-quadrate complex, and is vitiated by the new evidence presented here.

The palatoquadrate is closely applied to the visceral surface of the suborbital and postsuborbital plates in *Holonema*, as it is in brachythoracids, although the perichondral bone of the quadrate region does not fuse with the basal bone layer of the postsuborbital (Stensiö 1963*b*; Miles & Westoll 1968). In *Jagorina* the protrusible palatoquadrate has lost all connexion with the dermal head-shield. This appears to be true also of *Gemuendina*, where however a recognizable suborbital plate is retained in the skull (Gross 1963). In *Jagorina* the suborbital plate is replaced by the antorbital cartilage-bone (*ant*, figure 109), which articulates with the ectethmoid process of the neurocranium (Stensiö 1950, Figure 7A; 'processus antorbitectethmoidien', Stensiö 1969*a*). The apparent phylogenetic replacement of the suborbital by the antorbital cartilage has been accounted for by the operation of the ontogenetic process of delamination (Westoll 1967, p. 96). However, another possibility, which does not preclude a skeletogenetic relationship between the antorbital and suborbital, is that the antorbital is the autopalatine ossification, which has become detached from the rest of the palatoquadrate, whilst maintaining its normal or near normal relationship with the neurocranium (the palatoquadrate articulates with the ectethmoid process in petalichthyids; Stensiö 1969*a*). The rostral part of the palatoquadrate must then be composed of the palatine process, as in elasmobranchs

(Holmgren 1943, p. 63). In arthrodires the palatine process is apparently incorporated in the floor of the neurocranium, as it is in holocephalans and teleostomes (Stensiö 1963*b*, 1969*a*), and there is no rostral symphysis between the palatoquadrates. This interpretation of *Jagorina* is not used in the following parts of this paper.

Stensiö recognizes a dorsal orbital process of the palatoquadrate in *Jagorina* (*pr.orb*), and just lateral to this process a facet for the attachment of a ligament (*lig.orb*) running to the suborbital shelf of the neurocranium. A similarly placed orbital connexion has been suggested for '*Kujdanowiaspis*', on the evidence of a facet on the floor of the neurocranium (*aa.ob*, figure 103B; Stensiö 1945, 1963*b*). A prominent facet for the orbital articulation is also found on the palatoquadrate of *Holonema*. Whether the palatoquadrate articulated directly with the neurocranium, or was connected to it by ligaments cannot be determined, although the latter is thought to be the most likely (p. 137). There is no orbital process situated mesially to this facet in *Holonema*. The position of the orbital articulation is closely similar to that in '*Kujdanowiaspis*', in relation to the dermal skeleton.

It is important to note that in neither *Holonema* nor *Jagorina* is there an otic connexion between the palatoquadrate and the anterior postorbital process of the neurocranium (p. 199). The quadrate region is incompletely preserved in *Holonema*, but it appears to have borne an ill-defined condyle for the mandibular joint, much as in other arthrodires (Stensiö 1963*b*; Miles & Westoll 1968). In both *Holonema* and *Jagorina* then, there is only one connexion between the palatoquadrate and neurocranium, the orbital articulation.

Opercular cartilage

In *Jagorina* the opercular cartilage (*oc*, figure 109) is perichondrally ossified, and intimately associated with the basal surface of the submarginal plate (Westoll 1967, p. 89; 'ventral preopercular ("postsuborbital") plate', Stensiö 1963*b*, Figure 78D; 1969*a*, Figure 148D). Conditions are very similar in *Holonema* (p. 141, figure 55), except that the cartilage is apparently less completely ossified. In both forms the perichondral lining is pierced by foramina, probably mainly for the vascular supply of the submarginal plate and the cartilage itself. Stensiö suggests that they were for nerve branches serving the preopercular (= postmarginal, p. 191) sensory line, but there is no evidence that this line crossed the plate in either *Holonema* or rhenanids (see *Gemuendina*, Gross 1963).

It seems to be beyond question that the submarginal plate, and therefore any underlying cartilage, lay primitively in the gill-cover in placoderms, as in *Holonema* and rhenanids. Stensiö (1969*a*, p. 388) has termed the opercular cartilage of *Jagorina* the symplectic (earlier the postspiracular plate, 1963*b*, p. 234), for the following reasons: 'Comme l'a montré Holmgren (1940, 1943), les rayons branchiaux mandibulaires postspiraculaires des Élasmobranches sont en général fusionnés à l'hyomandibulaire formant la partie antéro-ventrale, latérale de celui-ci, mais qu'exceptionnellement (chez deux Rajiformes) ils persistent comme éléments séparés. Comme Holmgren (1943) l'a aussi montré, le composant mandibulaire postspiraculaire de l'hyomandibulaire des Élasmobranches correspond au symplectique des Actinoptérygiens. Dans ces conditions, la plaque ou les plaques mandibulaires, postspiraculaires des Arthrodires, peuvent aussi être correctement appelées symplectique.'

This argument is based explicitly on the assumption that the gill-cover of placoderms is a mandibular arch structure (Stensiö 1934, p. 32). I have discussed the evidence for this view elsewhere (Miles 1969, p. 139), and found it to be weak.

I suggest that the opercular cartilages of *Holonema* and *Jagorina* should be compared in the first place with the opercular cartilages of chimaeroids (Garman 1904, Plate 1, Figure 2, Plate 11; Goodrich 1909, p. 171, Figure 134), the hyomandibular branchial rays of sharks such as *Chlamydoselachus* (Allis 1923, Plate 7) and *Heptanchus* (Daniel 1934, Figure 48) and the opercular cartilage of the lung-fish *Neoceratodus* (Goodrich 1909, Figure 206; Devillers 1958, p. 671). In all of these living fishes these structures belong to the hyoid arch, and are situated in a hyoidean gill-cover with a constrictor hyoideus musculature, innervated by the facial nerve. The relations of the opercular cartilage to the jaws and gill-arches are essentially the same in *Holonema* as they are in chimaeroids and *Neoceratodus*; and the opercular cartilage has a similar position relative to hyomandibula (or epihyal) in *Jagorina*, chimaeroids and *Neoceratodus*. The opercular cartilage does not touch the mandibular arch in either *Holonema* or *Jagorina*, and it appears to be more closely associated with the hyoid arch in both of these fishes (figures 55, 109). A large opercular plate is found in antiarchs (the extralateral, Stensiö 1948; Watson 1961), ptyctodontids (footnote, p. 203; the 'postsuborbital' Ørvig 1960; Miles 1967*a*), petalichthyids (the 'postmarginal', Gross 1961), stensioellids (the 'postsuborbital', Gross 1962*a*) and a still undescribed form possibly related to the phyllolepid (Ritchie 1969, Figure 2*b*), as well as in arthrodires and rhenanids. Thus there is strong evidence that the presence of a large opercular plate (the submarginal) is a primitive character for placoderms, and it is reasonable to assume that it was normally associated with a large opercular cartilage.

From the evidence presented above, I suggest that the gill cover of placoderms must be regarded as a hyoid arch structure, most readily compared with that of holocephalans, but also with the dorsal region of the operculo-gular membrane of teleostomes (Jarvik 1963).

Hyomandibula

The hyomandibula is not preserved in *Holonema*, but it is necessary to consider this element in placoderms in order to discuss the suspension of the upper jaw. It is restored for this genus in figure 55 (*hm*). The hyomandibula of *Jagorina* (*hm*, figure 109; Stensiö 1963*b*, 1969*a*, Figures 7, 157, 158, 163, 179) articulates dorsally with the side of the neurocranium immediately in front of a foramen believed to have transmitted the ramus hyomandibularis facialis (*VII.hm*). Its relationships to the palatoquadrate and meckelian cartilage are not known exactly, because it is incompletely ossified ventrally, but Stensiö restores it in contact with both of these elements, and widely separated from the ceratohyal. Because of the apparently anomalous position of the proximal hyomandibular articulation in front of the foramen for the hyomandibular nerve, Westoll (1963; see also Allis 1928, p. 206) has suggested that the hyomandibula of *Jagorina* (also *Gemuendina*, Gross 1963) should be reinterpreted as a mandibular arch structure: 'the relations are those of the elasmobranch processus oticus internus palatoquadrati. This develops as a blastema (in which the spiracular cartilage(s) chondrify), extending from the palatoquadrate to the lateral commissure. The importance of this embryonic structure in elasmobranchs is probably of phylogenetic significance.'

There is no question of the similarity between the hyomandibula of *Jagorina* and this blastema in some elasmobranchs (Holmgren 1940, e.g. Figures 55, 81, 86, 118, 126, 128, 130, 133, 136, 140, 156, 162, 171, 178), and the similar relations of these structures to the hind end of the palatoquadrate. However, in so far as the relationship of this blastema to the lateral commissure is involved, the whole subject is complicated by enduring disagreement over the nature of this last structure. Holmgren (1943, pp. 149, 150; also Allis 1914) regarded the commissure as the

persisting processus oticus internus, in both elasmobranchs and actinopterygians, but later workers have regarded it as a hyoid arch or neurocranial structure. Thus Jarvik (1954, pp. 73, 74, 81) believes the lateral commissure to be the supratharyngohyal element in *Eusthenopteron*, and Bjerring (1967, p. 262) also finds this to be the case in *Squalus acanthias*. Bertmar (1959, 1963) concludes that the lateral commissure of *Neoceratodus* is formed from the top of the hyoid arch, but that it is a neurocranial structure in actinopterygians (also de Beer 1926). If the lateral commissure is a hyoid arch structure, it is noteworthy in connexion with the hyomandibula of *Jagorina*, that the hyomandibular nerve leaves the neurocranium behind the lateral commissure in crossopterygians (see, for example, Bjerring 1967, Figure 12).

Against the interpretations of Jarvik, Bjerring and Bertmar, however, may be set the opinion of Nelson (1968, 1969, p. 523), that separate infra- and supratharyngobranchials probably never existed in the pro-otic arches, and that 'independent supratharyngobranchials arose as secondary modifications associated with the crowding together of the gill arches under the cranium . . .'. The only safe conclusion at present is that the hyomandibula cannot be interpreted by reference to the lateral commissure of Recent fishes, as the relationships between cranial structures of supposed mandibular and hyoid arch origin are still imperfectly understood.

A more direct approach to the hyomandibula problem in *Jagorina*, not involving the embryology of Recent forms, is possible through a consideration of the innervation. There is a prominent groove on the hyomandibula which runs down the posterior and then the lateral surface. This groove carried the nerve which issued from the lateral surface of the neurocranium immediately behind the hyomandibula articulation. If Westoll is correct in regarding the hyomandibula as a mandibular arch structure in *Jagorina*, this nerve should be a branch of the trigeminal. Fortunately the endocast is well known in *Jagorina* (Stensiö 1963*a*, 1969*a*, Figures 52, 64, 55) and this hypothesis can be tested. According to Stensiö, the n. maxillaris V, n. mandibularis V, n. hyoideomandibularis VII, and n. acusticus (VIII) left the brain closely together, as in elasmobranchs (see, for example, Goodrich 1909, Figures 7, 8; Daniel 1934, Figure 200), and the n. hyoideomandibularis diverged to run posterolaterally through the thick lateral wall of the neurocranium immediately in front of the labyrinth. As there is no other canal which could have transmitted the visceral trunk of the facialis, and as the morphological relations of this nerve in Stensiö's account are correct with respect to the labyrinth, his interpretation would seem to be incontestable. Thus the hyomandibula of *Jagorina* carried a branch of the facial nerve in a prominent groove. The hyomandibula must therefore be a hyoid arch bone, and it is reasonably interpreted as a true hyomandibula comparable with that of Recent fishes.

Stensiö (1969*a*, Figure 164) has described a bone which is traversed by a narrow vertical canal in its upper third, as the hyomandibula of the ptyctodontid '*Ramphodontus tetrodon?* Jaekel' (= *Rhynchodus eximius* Jaekel, 1919, Figure 16). The canal is said to have transmitted the hyomandibular nerve. However, I now believe that this bone is an ossification of the palatoquadrate (cf. Miles 1969, p. 140), possibly the quadrate, and the canal may be compared with that in *Holonema* which gave passage to the n. mandibularis and external carotid artery. This ossification is not in any sense comparable with the hyomandibula of *Jagorina*.

It has been suggested that the submarginal plate of the arthrodire *Coccosteus*, which has a broad groove on its visceral surface, was associated with a dorsal element of the hyoid arch (the epihyal, Miles & Westoll 1968, p. 398, Figure 50; Miles 1969, p. 140, Figure 7*c*), in the same way that the dermohyal bone is associated with the lateral face of the hyomandibula in some

actinopterygians (Nielsen 1942). This suggestion has been confirmed by an excellently preserved specimen of '*Coccosteus*' sp.† from Gogo (P. 50917), which I hope to describe in detail in a later paper. In this specimen the head of the endoskeletal element is preserved *in situ* on the visceral surface of the submarginal plate (figure 110B). On its upper surface the endoskeletal element (figure 111) has a well-defined articular surface (*ah*), which can be shown to have articulated against the *anteroventral* edge of the anterior postorbital process (see *dp.APO*, figure 110A). The

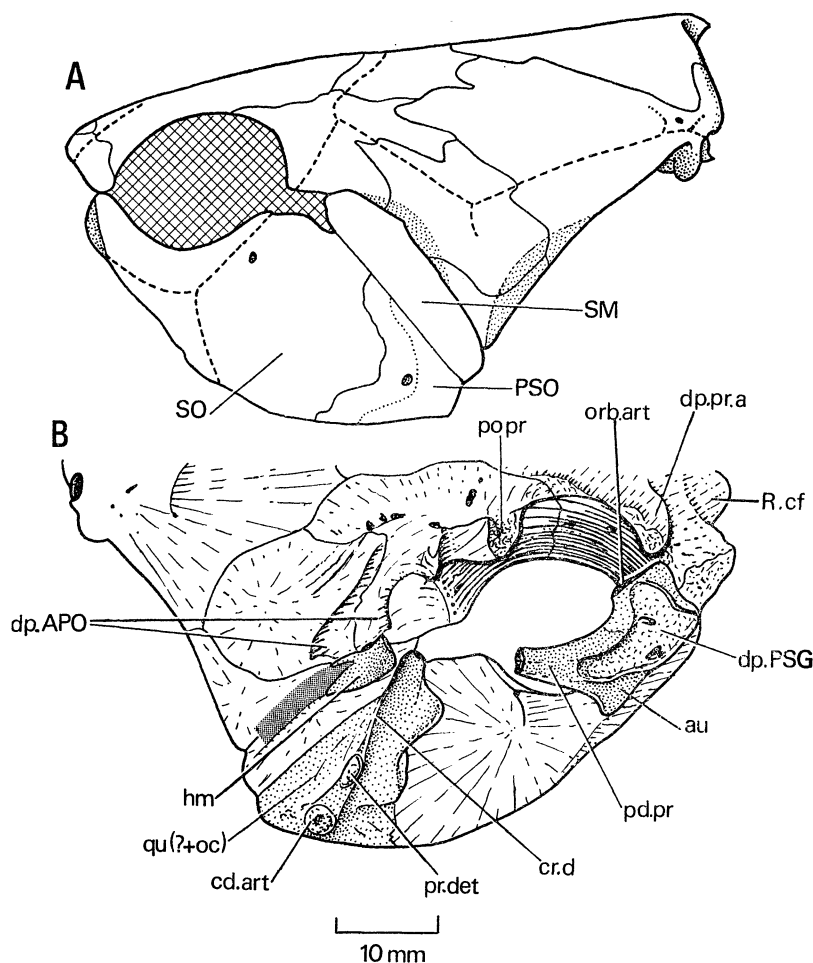


FIGURE 110. '*Coccosteus*' sp. Upper Devonian, Gogo, Western Australia. A, restoration of head-shield in lateral view; B, sketch of inner surface of cheek and adjacent region of skull-roof; restored shank of hyomandibular represented by regular stipple. P. 50917.

function of this element was clearly to hinge the cheek plate-palatoquadrate complex on the skull-roof-brain-case unit. My earlier opinion that the cheek was rigidly fixed to the roof in *Coccosteus* and similar forms (Miles 1967*b*, 1969) is shown to be incorrect by this specimen and by several other forms from Gogo (see also Stensiö 1947, 1963*b*; Denison 1958). The relationship of the endoskeletal element to the submarginal plate would seem to suggest that it must be the opercular cartilage, as in *Holonema* and *Jagorina*. Nevertheless, this explanation is unconvincing in view of its articulation with the neurocranium and its suspensory function. Instead it is confidently

† This specimen is congeneric with that described by Øravig (1960, p. 304, Figure 3A) as *Coccosteus*? sp. Dr Øravig will describe further material of this form from Bergisch Gladbach under a new generic name, in a forthcoming account.

determined as the hyomandibula, homologous with that of *Jagorina*. The hyomandibula lies immediately mesial to the anterior end of the submarginal-opercular cartilage complex in *Jagorina*, and may be imagined to have a similar position in *Holonema* (figure 55). In *Coccosteus*, and other unspecialized brachythoracids, it appears that the hyomandibula has become more intimately associated with the submarginal plate, concomitant with the reduction in size and closer incorporation in the head-shield of this plate (between the skull-roof and the suborbital and postsuborbital plates). This change can be understood as a correlative of the evolution of the jaw-gill-cover mechanism in arthrodires (see p. 202). It probably also entailed the loss of

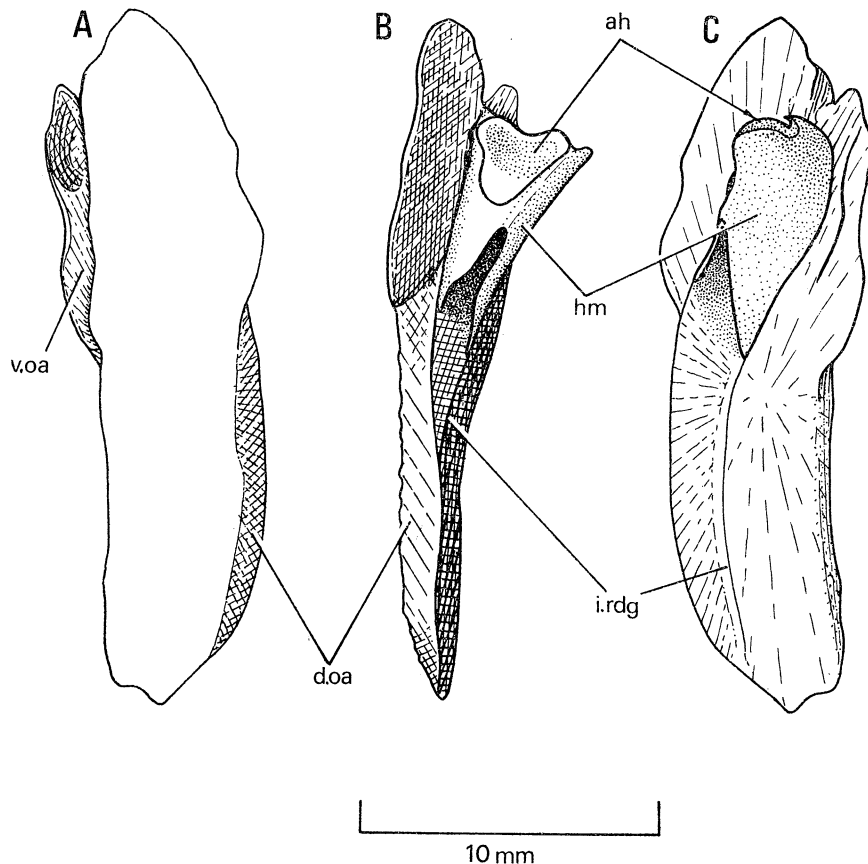


FIGURE 111. '*Coccosteus*' sp. Upper Devonian, Gogo, Western Australia. Left submarginal plate and head of hyomandibula. P.50917. A, lateral, B, dorsal and C, mesial view.

the opercular cartilage, although Stensiö (1963 *b*, 1969 *a*) has suggested that the latter merged with the quadrate ossification of the palatoquadrate (to form the 'quadrato-spiracular' or 'quadrato-symplectique'), which is coalesced with the visceral surface of the postsuborbital. Attempts to restore the visceral skeleton of '*Coccosteus*' suggest that the distal end of the hyomandibula became far removed from the ceratohyal and out of alignment with the epibranchials of the gill arches, as a result of these changes.

In '*Coccosteus*' sp. from Gogo (figure 110B), the palatoquadrate does not articulate with the anterior postorbital process of the neurocranium. Instead the quadrate ossification is directed anteriorly towards the subocular shelf of the neurocranium, as it is in other Gogo coccosteomorphs, *Holonema* and *Jagorina*. In *Arctolepis decipiens* (figure 100) as well, the palatoquadrate cannot have articulated with the anterior postorbital process, as the suborbital and postsuborbital

plates are situated in advance of the anterior postorbital process (p. 180). It may be concluded that primitive placoderms did not have an otic connexion between the palatoquadrate and the neurocranium, and there is no evidence that this connexion ever evolved in arthrodires or rhenanids. It may be present as a secondary modification in ptyctodontids (but see p. 203).

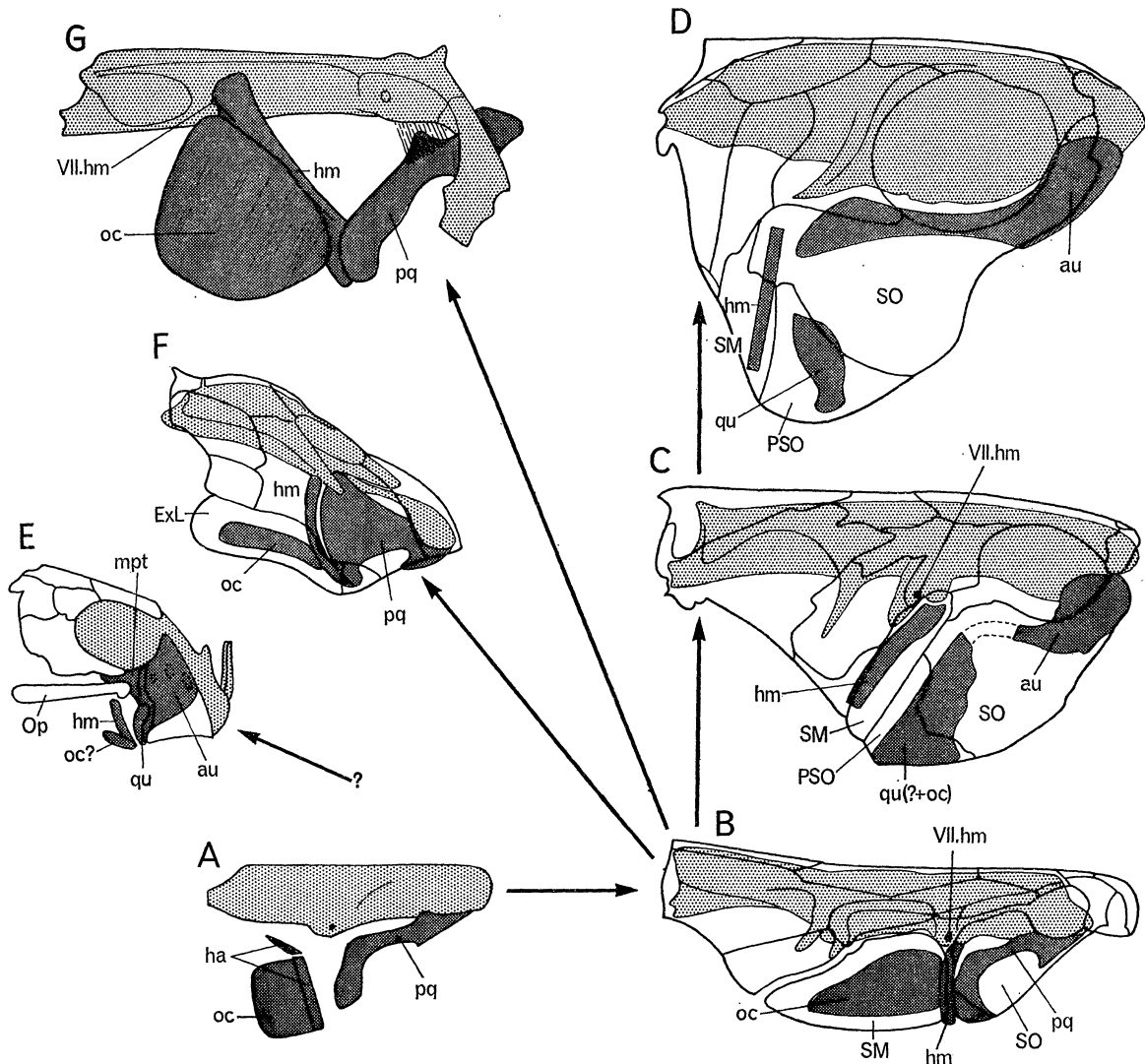


FIGURE 112. Upper jaw apparatus in some placoderms. A, hypothetical primitive condition; B, primitive arthrodire; C, moderately advanced arthrodire; D, advanced arthrodire; E, ptyctodont; F, antiarch; G, rhenanid. After Miles, Stensiö & Ørvig.

In '*Kujdanowiaspis*' (Stensiö 1963*b*, Figures 16, 17) there is an area on the anteroventral edge of the anterior postorbital process without perichondral bone, which Stensiö has interpreted as a surface for the attachment of the otic process of the palatoquadrate. It can now be suggested that this area received the hyomandibula, which has an articular head similar to that found in '*Coccosteus*' sp. (figure 111B). In *Tapinosteus* and *Pholidosteus* (Stensiö 1963*b*, Figures 46, 48, 49) the hyomandibula probably articulated against the 'basipterygoid process' (= anterior division of anterior postorbital process, cf. Miles & Westoll 1968, p. 402). The true palatobasal

articulation, if it existed, must have been ligamentous and more anteriorly situated. Finally, in *Macropetalichthys*, the clearly defined 'aire articulaire pour le processus otique du palatocarré' (Stensiö 1969*a*, Figures 22, 23) was also probably for the hyomandibula.

In all the examples cited above, the articulation of the hyomandibula is against the anterior edge of the anterior postorbital process, in front of the foramen for the hyomandibular (VII) nerve, as in *Jagorina*. This appears to be the normal relationship between the nerve and the hyomandibula in placoderms. The posterior face of the anterior postorbital process of '*Kujdanowiaspis*' (see also *Macropetalichthys*) is without perichondral bone, and Stensiö has identified it as the site of the hyomandibular articulation. However, as previously noted, this surface does not have the character of a hyomandibular articulation (Miles 1969, p. 140). It may have been an attachment surface for the pharyngobranchial of the first branchial arch.

Summary of jaw suspensions in placoderms

The main results of the above discussion may now be drawn together in a brief review of jaw suspensions in placoderms (figure 112).

Primitive placoderms (figure 112A) are believed to have had a continuous palatoquadrate (*pq*) which ossified in a single piece, and had a single, orbital connexion with the neurocranium. The palatoquadrate was not fused with the dermal skeleton of the head, which was in a primary micromeric condition (Ørvig 1968; Nelson 1970*a*).

The different relations of the suspensory hyomandibulae to neighbouring blood-vessels and nerves have been used to demonstrate that the hyomandibula evolved independently in chondrichthyans and osteichthyans (de Beer & Moy-Thomas 1935; de Beer 1937). In view of the unique relations of the head of the hyomandibula to the hyomandibular nerve in placoderms, this argument can now be extended to demonstrate the independent origin of the hyomandibula in placoderms. If we accept that the elasmobranchiomorphs comprise two collateral groups, the chondrichthyans (with elasmobranchs and holocephalans) and placoderms (Miles 1971*b*), and that the primitive condition of the hyoid arch for chondrichthyans is shown by the holocephalans, it is likely that the holocephalan, non-suspensory condition of the arch was found in primitive placoderms. That is to say there was no hyomandibula, and the suspension of the upper jaw answered most closely to the autodiastyly of de Beer & Moy-Thomas (1935).

Some other possible features of ancestral placoderms have been considered elsewhere (Miles 1967*b*, p. 67), although parts of that discussion now require revision. It is possible that there was a series of elasmobranch-like gill-clefts, each opening independently to the outside, and that the hyoid gill-cover was only moderately enlarged.

In primitive arthrodires (figure 112B) the dermal skeleton has become consolidated into a macromeric plate armour, the palatoquadrate is still a single unit, and it is closely associated with the cheek plates which are independent of the skull-roof. The hyoid arch includes a suspensory hyomandibula (*hm*) which has a proximal articulation with the anterior postorbital process, in front of the foramen for the hyomandibular nerve (*VII.hm*). Distally the hyomandibula is closely associated, perhaps contiguous, with the quadrate region of the palatoquadrate and opercular cartilage (*oc*), and probably bound to the former by ligaments. The hyomandibula thus hinges the dermal bone-palatoquadrate cheek unit on the neurocranium; the only other contact between these structures is through the orbital articulation, as in primitive placoderms. The jaw suspension may thus be described in functional terms as hyostylic (Huxley 1876), although Stensiö (1969*a*, p. 392) refers to this condition as amphistylic, following de Beer's

classification (1937). The primitive arthrodire condition is shown by *Holonema* and presumably by most dolichotheoracids.

In more advanced arthrodires the trends of change include the reduction in size and closer incorporation in the cheek unit of the opercular (submarginal) bone, the separation of the palatoquadrate into autopalatine and quadrate ossifications, and the coalescence of the quadrate ossification with the postsuborbital plate. The opercular cartilage may also have fused with the quadrate, although I think this is improbable (p. 199). If it has, its connexion with the mandibular arch is secondary, and cannot be cited as evidence for the mandibular nature of the gill-cover. The hyomandibula may also become closely associated with the submarginal plate (p. 197). In coccosteids (figure 112C) and dinichthyids the two ossifications of the palatoquadrate were still connected by cartilage, but in leiosteids (*Pachyosteidae*) they were probably not connected (Stensiö 1963*b*). In all of these forms, and in primitive trematosteids, the submarginal (SM) is a slender plate between the skull-roof and the postorbital and postsuborbital plates; the skull-roof and cheek are therefore still discrete units, and the hyomandibula (*hm*) presumably played an important role in hinging the cheek unit on the cranium. Following Huxley (1876) we may still term this type of suspension hyostyly.

Finally in some of the Wildungen arthrodires, the skull-roof and cheek plates became firmly interlocked (figure 112D), so that independent movement of the latter was impossible. The autopalatine (*au*) and quadrate (*qu*) regions were probably connected by a cartilaginous middle region in some forms (e.g. pholidosteids), but not in others, and in all species the quadrate is fused to the postsuborbital plate (*PSO*). It is likely that the opercular cartilage was completely reduced, and that the hyomandibula (*hm*) had lost its suspensory role. The jaw suspension was therefore a form of autostyly in which the quadrate gained support by fusing with the dermal skeleton (cf. 'pareia-autostylic' and 'tecto-pareia-autostylic' suspension, Stensiö 1963*b*).

Among other placoderms, the jaw suspension in gemuendinoid rhenanids is most closely comparable with that of primitive arthrodires (figure 112G). The gemuendinoids are, however, divergently specialized, with a more flexible cheek, no connexion between the palatoquadrate and the dermal skeleton, the presence of a palatine process of the palatoquadrate, and a symphysial connexion between the palatine processes. These features may be correlated with the development of protrusible jaws. The significance of the tessarated dermal armour has been disputed. Westoll (1967) has argued strongly that it is in a secondary micromeric condition, and if so there may be a correlation between the state of the dermal skeleton and the mobile jaw apparatus. In *Jagorina*, Stensiö (1969*a*, Figures 157, 158, 179) restores the ventral end of the hyomandibula in contact with the meckelian cartilage and widely separated from the ceratohyal. The ceratohyal articulates proximally with a pseudohyal, so that the whole arrangement is strikingly ray-like. The value of this restoration is, however, uncertain.

The cheek and jaws are hardly known in the more primitive palaeacanthaspoid rhenanids (Gross 1958*a*, 1959), but they were probably close to those of primitive arthrodires as there is no suggestion that the jaws were protrusible.

The endoskeleton of the head is almost completely unknown in antiarchs. Nevertheless, Stensiö (1969*a*, Figures 41, 42, 135) has given a restoration of the neurocranium and visceral skeleton in *Bothriolepis*, which in principle I find acceptable. I can, however, see no reason for assuming either the presence of a palatine process or for classing the palatoquadrate as 'un type élasmobranchoïde'. In this restoration (figure 112E) the palatoquadrate is short and deep with a single (orbital) connexion with the neurocranium, and the opercular bone (*ExL*, the extra-

lateral) is closely applied to an opercular cartilage (*oc*, 'symplectique'; Stensiö 1969*a*). The palatoquadrate and hyomandibula are contiguous at the angle of the jaw in my slightly modified version of Stensiö's figure, and the opercular cartilage is contiguous with the hyomandibula. This arrangement and the hinged cheek unit invite comparison with *Holonema*, and it seems that the jaw suspension and visceral skeleton in antiarchs were organized essentially as in primitive arthrodires.

The palatoquadrate of ptyctodontids is best known in *Ctenurella* (figure 112E), although other forms appear to be built on fundamentally the same plan (Ørving 1962; Miles 1967*a*; Stensiö 1969*a*). There are three separate ossifications joined by cartilage, the autopalatine (*au*), metapterygoid (*mpt*) and quadrate (*qu*). The metapterygoid is drawn out posteriorly into a process which has been compared with the otic process of holocephalans (Ørving 1962, p. 54). However, in view of the structure of the palatoquadrate in other placoderms and the general lack of an otic connexion with the neurocranium, it is quite possible that this is an orbital process. The mesial face of the autopalatine bears three surfaces where the palatoquadrate was attached to the neurocranium (shown as broken rings in figure 112E). Stensiö regards the two anterior areas as jointly representing the orbital connexion of other placoderms, and the posterior area as the otic connexion, but it is doubtful whether significant comparisons can be made with other groups, and these areas may represent new connexions without homologues in other placoderms.

The hyoid arch of ptyctodontids is unknown (see p. 197; cf. Stensiö 1969*a*). The gill-cover was a flexible, scale-covered structure (Miles 1967*a*), with dorsally a slender opercular plate (*Op*) homologous with either the postsuborbital or submarginal of arthrodires.† Stensiö (1969*a*, Figure 173) has restored a 'symplectic' cartilage in *Ctenurella* (*Oc?*, figure 12E), although this element has yet to be described. Apparently there is an articular area on the articular ossification of the meckelian cartilage in *Rhynchodontus eximius* (Stensiö 1969*a*, Figure 152) for this element, but here, as in arthrodires, the connexion between mandibular arch and opercular structures must be regarded as secondary. Stensiö (p. 443) also suggests that there could have been a second, more dorsal 'symplectic' supporting the opercular ('preopercular') plate.

In ptyctodontids the jaw cartilages have lost all connexion with the dermal skeleton and have gained support through extensive articulation with the neurocranium. This is a special form of autostyly, if we assume that the hyomandibula played no part in the suspension of the jaws (cf. Miles 1969; Stensiö 1969*a*), which Stensiö has termed endocranio-autostylic suspension. It is probably correlated with the reduction of the cheek plates (Miles 1967*a*, p. 116). Nevertheless, there is sufficient evidence to show that the jaws and gill-cover are built on the same basic plan as in other placoderms, and the ptyctodontid condition could have been derived from either the primitive placoderm or primitive arthrodire condition. Well preserved material of the hyoid arch might enable us to decide between these alternatives.

The jaw bones and cheek plates are not known in phyllolepid or petalichthyids, and although found in stensioellids they are too poorly preserved for a satisfactory interpretation (Gross 1962*a*; Stensiö 1969*a*). However, in all placoderm groups in which these structures are known, their arrangement can be interpreted as variations of a single plan, which is fundamentally the same as the plan in other gnathostome fishes.

† The position of this plate in the gill-cover suggests that it is the submarginal, as in *Holonema* and other placoderms (Westoll 1967). It is, however, crossed by a sensory line, which would be unusual for a submarginal, but is some evidence of its homology with the arthrodiran postsuborbital (Ørving 1962).

On largely theoretical grounds, Stensiö (1969*a*, pp. 391–392) has suggested that primitively in placoderms the palatoquadrate and neurocranium were joined in orbital, basal and hyo-mandibular connexions, representing attachments to the cranium of the premandibular, mandibular and hyoid arches respectively. This is termed triastylic suspension. No evidence in favour of this view has been found in this study.

4. REVIEW OF THE HOLONEMATIDAE

In this section an attempt will be made to define the family Holonematidae, and to review briefly all the known members in the light of the structure of *Holonema westolli* (defined on p. 104). Certain other genera which have been regarded as close relatives of *Holonema* are also considered. *H. westolli* is the only well-known species, and it must be used as a standard of comparison in considering other members of the family. Unfortunately other holonematids are so poorly known that it is virtually impossible to provide satisfactory definitions for them, and much work remains to be done to put the family in good systematic order. The following is presented as a first step towards the study of the phylogeny and zoogeography of the family.

Family HOLONEMATIDAE Obruchev, 1932

Definition. Brachythoracid arthrodires at the primitive coccosteomorph level of organization; with the head-shield equal to about two-thirds of the length of the median dorsal plate; the pre-orbital region occupies more than one-quarter of the length of the skull-roof; the anterior superognathals are greatly reduced, and the posterior superognathal and the inferognathal have a pipe-like ornamentation; the pectoral spine is vestigial; and the pectoral fenestra is greatly elongated.

Remarks. The cases for classifying the holonematids in the Brachythoraci and for placing them at the primitive coccosteomorph level of organization are given in the final section of this paper. It is possible that the structure of the snout and position of the nasal openings are characteristic of holonematids, but these characters have been omitted from the definition pending their better understanding.

Genus HOLONEMA Newberry, 1889

Definition. Holonematids in which the posterior margin of the nuchal plate is markedly convex and bears a well-developed median posterior process; the nuchal thickening is well developed; the condyle and fossa of the cranio-thoracic joint are more than twice as long as they are high; the postnasal plates are fused together and may be fused with the rostral plate; the median dorsal plate has anterior and posterior 'keels'; the spinal plate is long and slender; the ornamentation comprises tubercles and ridges with narrow interspaces, and the ridges often bear small tubercles.

Type species. *H. rugosum* (Claypole 1883).

Remarks. Although *H. westolli* has provided a wealth of new anatomical facts, the other holonematids are so poorly known that the taxonomic value of most of them cannot be judged. They are, therefore, unavailable for use in framing a definition of the genus. The above definition is deliberately short, and does not differ greatly from that given in Obruchev (1964, p. 142).

Holonema rugosum (Claypole, 1883)

PTERICHTHYS RUGOSUS (Claypole 1883, p. 666)

PTERICHTHYS? *RUGOSUS* sp.nov. (Claypole 1883, figure on p. 667)

HOLONOMA RUGOSA Claypole, sp. (Newberry 1889, p. 93, Plate 17, Figures 1 to 4)

Pterichthys (*Both.*) *rugosus* or *Holonema rugosum* (Claypole 1890, p. 257, Figure on p. 256)

Holonema rugosum (Woodward 1891, p. 315)

non *Holonema rugosa* (Cope 1891, p. 456, Plate 30, Figure 7; = *Bothriolepis nitida* Leidy)

H. rugosa Clayp. (Cope 1892, p. 221, Plate 7, Figure 2)

H. rugosa Claypole (Williams 1893, p. 286, Figure 2)

H. rugosum (Traquair 1908, p. 324, Figure 3)

H. rugosum (Claypole) (Hussakof & Bryant 1918, p. 104, Plate 32, Figure 1)

non *Holonema* cf. *rugosum* Newberry (Hills 1929, pp. 183, 197; = *Phyllolepis* sp.)

Holonema (Case 1931, Plate 4, Figures 1, 2)

Holonema sp.nov. (Wells 1942, Plate 97, Figure 4)

H. rugosum (Claypole) (Wells 1943, p. 4, Figure 1B, Plate 1)

H. rugosum (Stevens 1964, p. 170, Figure 1B, E)

Definition. A large species with a broad trunk-shield; nuchal plate with a monocuspid posterior process.

Occurrence. Middle Devonian (Erian) of Michigan and Wisconsin; Upper Devonian (Senecan) of New York and Pennsylvania.

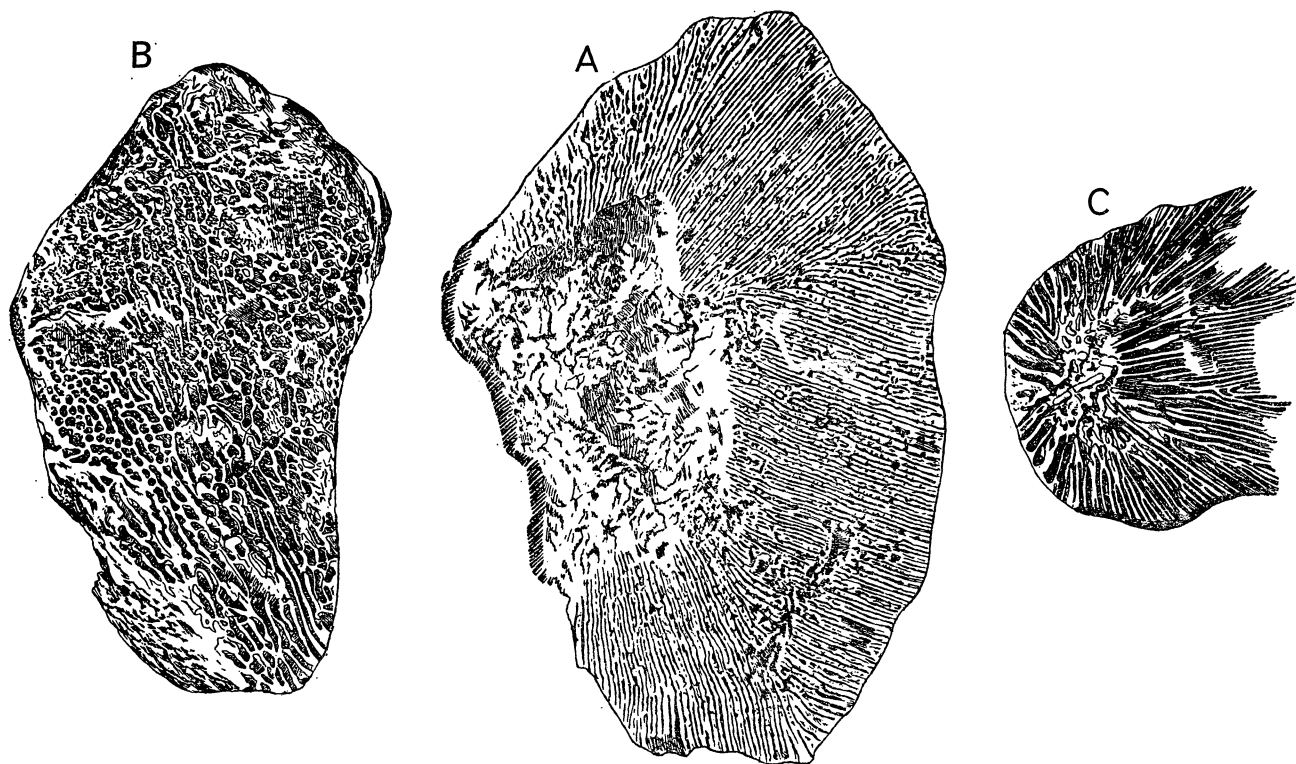


FIGURE 113. A, *H. rugosum* (Claypole); right anterior ventrolateral plate. B, *H. horridum* Cope; right anterior ventrolateral plate. C, '*Holoptychius*' *filosus* Cope = ?*Holonema horridum* Cope; postnasalo-rostral plate. After Cope.

Remarks. It is unfortunate that the type species of *Holonema* is so poorly known. Previous accounts are listed in the synonymy. A cast (P. 50014) of the nuchal and right paranuchal plates figured by Case has been studied. Wells (1943, p. 6) concluded that Case's Middle Devonian specimens from Michigan are identical with Upper Devonian specimens of *H. rugosum* in ornamentation and in the form of the paranuchal plate, and that there are no 'criteria for species discrimination'. Whether more extensive material will uphold this view is open to doubt, but Wells's conclusion must be accepted for the time being. Paranuchal, median dorsal, anterior dorsolateral, anterior ventrolateral, anterior median ventral and posterior ventrolateral plates are known from Upper Devonian deposits, in addition to other bone fragments.

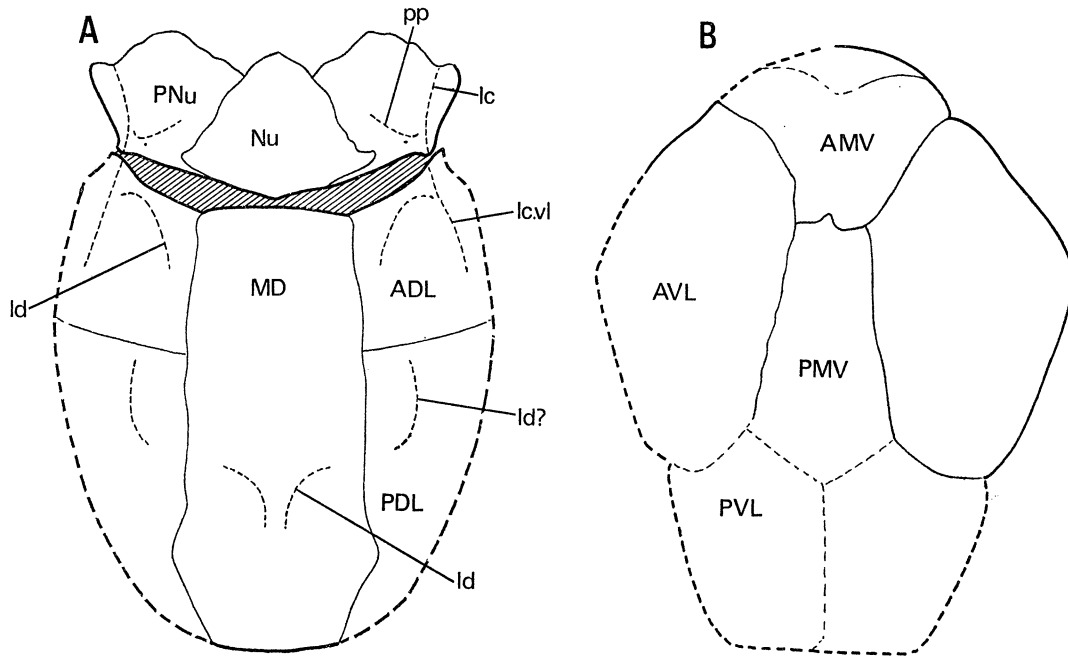


FIGURE 114. *Holonema rugosum* (Claypole). A, dorsal wall of trunk-shield and posterior plates of skull-roof; B, ventral wall of trunk-shield. After Wells and Williams.

The holotype posterior median ventral plate is 230 mm long, and the nuchal plate in Case's specimen is about 95 mm long. The nuchal is posteriorly broad in Wells's (1943, Figure 1A) restoration, with a monocuspid posterior process, and this is confirmed by P. 50014, but the plate is otherwise similar to the nuchal of *H. westolli* (figure 114). The posterior pit-line (*pp*) is a single groove on the paranuchal plate, but it does not join the main lateral-line groove (*lc*). The median dorsal plate does not narrow anteriorly in Wells's restoration, as it does in other species, but this region of the specimen is missing and the figure (114A) may be incorrect. The posteriorly arched path of the anterior dorsolateral sensory line on the median dorsal plate (*ld*) has been considered to be characteristic of this species, but a similar condition is found in *H. farrowi* and *H. haiti* (figures 115, 116). The path of the anterior dorsolateral line on the posterior dorsolateral plate in Wells's restoration (figure 114A) is hypothetical, yet nevertheless probably essentially correct (p. 193); it appears to be based on a misinterpretation of the main lateral-line canal of *H. radiatum*. The ventral plates of the trunk-shield show no unusual features, if it is assumed that Williams erred in his restoration of the anterior median ventral plate (figure

114B). The posterior median ventral is accurately depicted by Claypole (1890). The ornamentation (figure 113A) consists of prominent ridges, generally diverging from the radiation centre of the plate, with some fragmentation and anastomosis; it is never tubercular. The ridges are broader than the interspaces. Wells (1943, p. 5) has distinguished zones in the ornamentation of the median dorsal plate (p. 175).

Comparisons. Although it is closely similar to *H. westolli*, this species differs primarily in the relatively broader trunk-shield, on the evidence of the proportions of the median dorsal plate. It also has a relatively broader nuchal plate, with a single posterior cusp.

Holonema horridum Cope, 1892

HOLONEMA HORRIDA sp.nov. (Cope 1892, p. 222, Plate 7, Figure 2)

(?)HOLOPTYCHIUS FILOSUS sp.nov. (Cope 1892, p. 228, Plate 7, Figure 3)

Holonema horridum Cope (Eastman 1907, pp. 21, 156)

H. horridum Cope (Stevens 1964, p. 172)

H. horridum Cope (Denison 1968, p. 284)

Definition. A species with a very coarse ornamentation of ridges.

Occurrence. Upper Devonian (Senecan) of Pennsylvania.

Remarks. Cope's type specimen (figure 113B) is an anterior ventrolateral plate, obtained from the same horizon as plates of *H. rugosum*. The ornamentation is said to run longitudinally, unlike that of *H. rugosum* which has a radiating disposition. However, *H. westolli* now clearly demonstrates that the ornamentation varies from region to region of the armour, and this difference may not be significant. Otherwise the specimen shows no important features. Cope's type specimen of *Holoptychius filusus* (figure 113C) is a coarsely ornamented postnasalo-rostral plate of a holonematid, which is here assigned to *Holonema horridum* on the character of the ornamentation, although alternatively it may belong to *H. rugosum*. This plate compares closely with that of *H. westolli*. It measures about 65 mm between the posterolateral angles.

Denison (1968, p. 284) has suggested that *H. horridum* does not belong in the genus *Holonema*. However, if the postnasalo-rostral plate is correctly assigned, there is now good evidence for Cope's determination. This species may be conspecific with *H. rugosum*, but more evidence is required to decide this point.

Holonema farrowi Stevens, 1964

Holonema farrowi sp.nov. (Stevens 1964, p. 163. Figures 1 C, F, Plates 1, 2)

H. farrowi Stevens (Denison 1968, p. 282)

Definition. 'A large arthrodire, the ventral shield of which is composed of rather thin, simple, oval antero-ventrolateral plates and small thin, subtriangular postero-ventrolateral plates' (Stevens 1964, p. 164).

Occurrence. Middle Devonian (Erian) of Michigan.

Remarks. Stevens has described the anterior ventrolateral, posterior ventrolateral, anterior median ventral and median dorsal plates of this large species (figure 115). The median dorsal has an estimated length of about 200 mm. The original 'diagnosis' includes: 'Ornamentation can be distinguished from all other species of *Holonema* in that it consists of nonstellate tubercles arranged in beadlike rows, and these tuberculate rows never fuse to form a ridge. These rows are

either concentric, radial, or longitudinal, depending on the position they occupy on the plates.' However such attributes cannot now be regarded as characteristic, particularly as they are based on a small number of plates, although for the present they serve to separate *H. farrowi* from other N. American species.

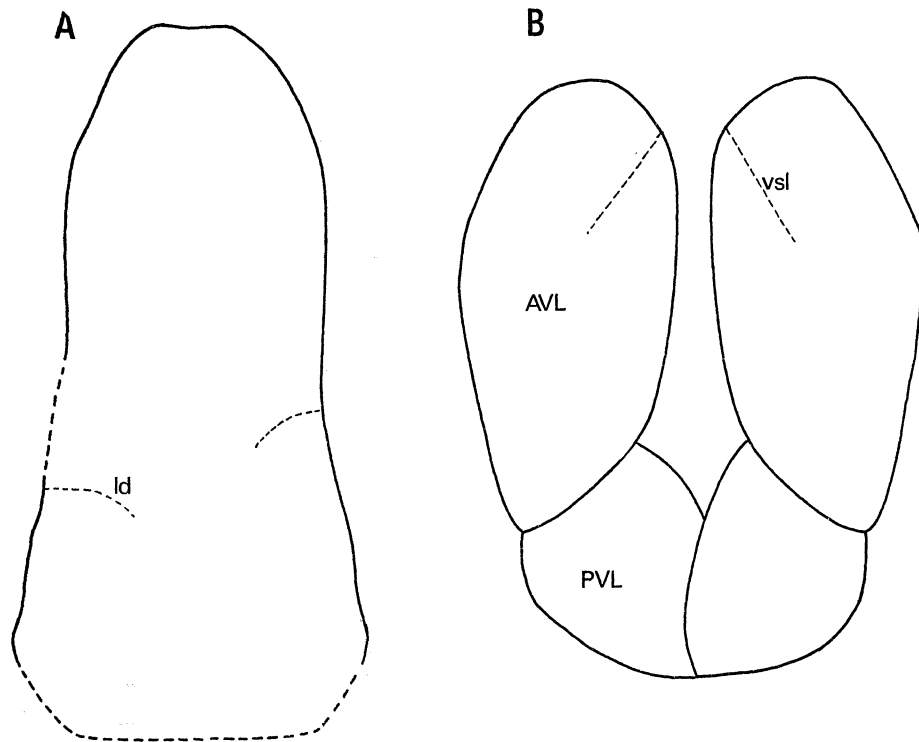


FIGURE 115. *H. farrowi* Stevens. A, median dorsal plate; B, lateral plates of ventral wall of trunk-shield. After Stevens.

The anterior ventrolateral plate has a relatively short spinal margin (Lsp/Lt index is approximately 38). The only median dorsal plate broadens posteriorly to a greater extent than in any other species (figure 115A). Unfortunately the posterior margin of this plate is not preserved and its proportions are unknown. The anterior dorsolateral sensory line grooves (*ld*) curve across the surface as in *H. rugosum*, with the right groove situated anterior to that of the left.

Comparisons. *H. farrowi* can be separated from other species by the form of the anterior ventrolateral and median dorsal plates.

Holonema haiti Denison, 1968

Holonema haiti, sp.nov. (Denison 1968, p. 282, Figure 10)

Definition. 'The median dorsal plate is proportionately longer and narrower than in other species of this genus, with an estimated ratio of width/length of 0.28. It is also more strongly arched than in other species, having a median angulation of about 90° near the anterior end' (Denison 1968, p. 282).

Occurrence. Middle Devonian (Jefferson formation) of Idaho.

Remarks. This species is known only by the holotype median dorsal plate (figure 116). The ornamentation is mainly of ridges which are slightly broader than the interspaces, and with occasional anastomoses. It is divided into five zones (p. 175). The anterior dorsolateral sensory line groove (*ld*) is present on one side.

Comparisons. This species can be separated from others by the characters given in the definition. It has no close relatives among the better known species of *Holonema*.

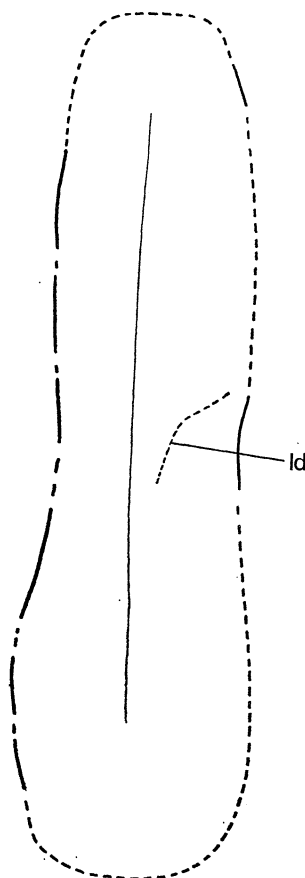


FIGURE 116. *H. haiti* Denison. Median dorsal plate. After Denison.

***Holonema radiatum* Obruchev, 1932**

Coccosteus megalopteryx (partim) (Trautschold 1880, Plate 9, Figures 10, 11)

Holonema rohani (nomen nudum) (Obruchev 1931 *a*, p. 94)

H. radiatum (nomen nudum) (Obruchev 1931 *b*, pp. 287, 295)

H. radiatum (Obruchev 1932, pp. 100–107, Figures 2 to 17, 26, 27 *a*, Plate 5, Figures 2 to 5, Plate 6, Figures 1, 2, 5, Plate 7, Figure 3, Plate 8, Figures 1, 3 to 5)

Coccosteus sp. (Heintz 1934, Figure 8)

non? *Holonema* cf. *radiatum* (Obruchev) (Heintz 1935, pp. 115–121, Plate 1)

H. radiatum Obruchev (Bystrow 1957, pp. 267–269, Figure 24)

non? *H. radiatum* Obruchev (Kulczycki 1957, pp. 329–331, Plate 10, Figure 2 *a*, *b*)

H. radiatum Obruchev (Obruchev 1964, Plate 2, Figure 4)

Definition. A species with a relatively broad trunk-shield in which the estimated breadth/length index of the median dorsal plate is about 40; nuchal plate with monocuspid median posterior process.

Occurrence. Upper Devonian (Shelon beds) of the Leningrad and Donetz basins, U.S.S.R.

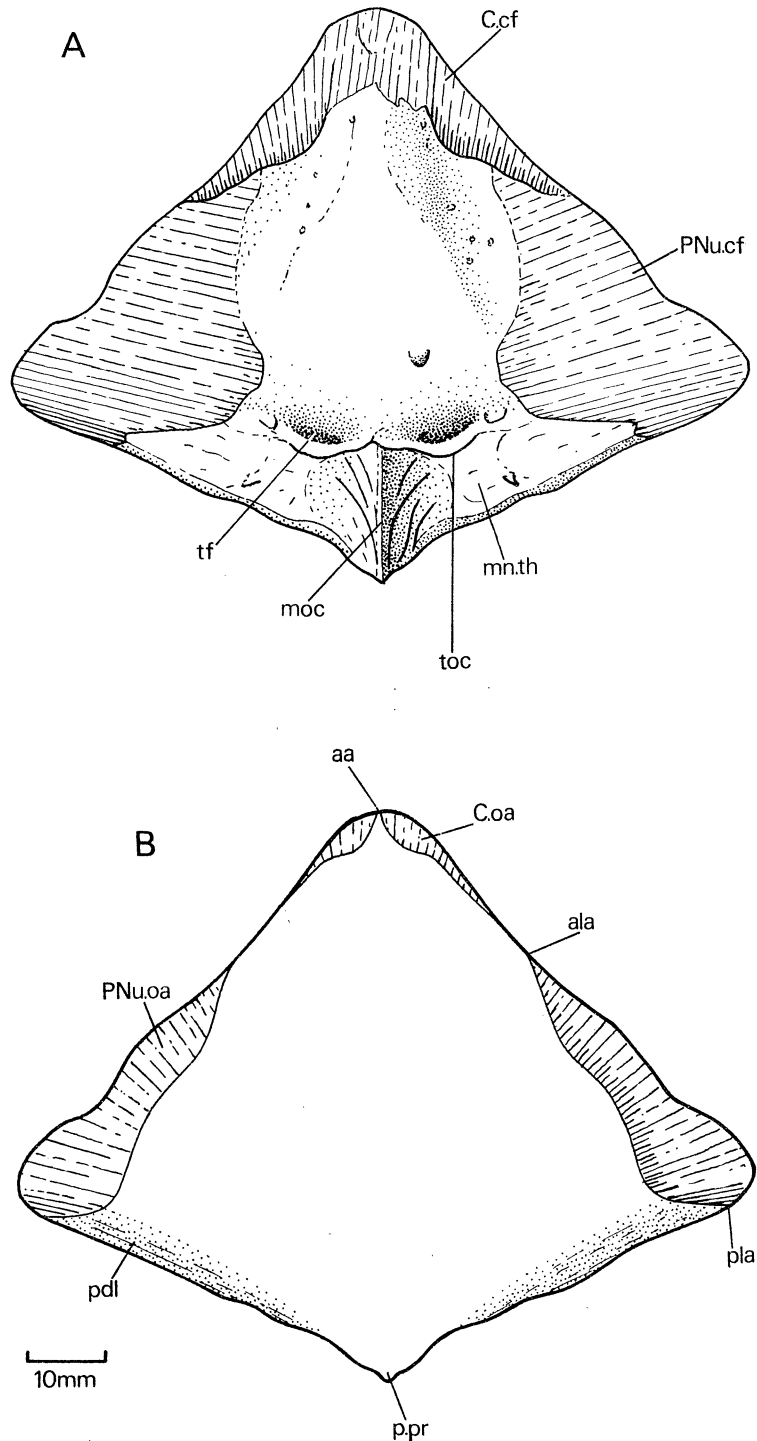


FIGURE 117. *H. radiatum* Obruchev. Restoration of nuchal plate, slightly flattened, in A, visceral and B, dorsal view. After R.S.M. 1902.72.16. Upper Devonian, R. Sjass, U.S.S.R.

Remarks. Previously this had been the best known holonematid (Obruchev 1932). The following remarks are based on Obruchev's paper, five specimens in the Royal Scottish Museum and one in the British Museum (Natural History). *H. ornatum* is known from detached, abraded bone fragments of the posterior region of the head-shield and the trunk-shield. Obruchev's (1932, figure 26) restoration of the posterior part of the skull-roof errs in showing the marginal plate too large and the paranuchal plate too small relative to the nuchal plate. The nuchal plate (figure 117) can be restored after R.S.M. 1902.72.16, to confirm the main points in Obruchev's (1932, Figure 12) sketch of the outer surface and Heintz's (1934, Figure 8) sketch of the visceral surface. The overlap surfaces, contact faces and angles correspond closely with those of *H. westolli*.

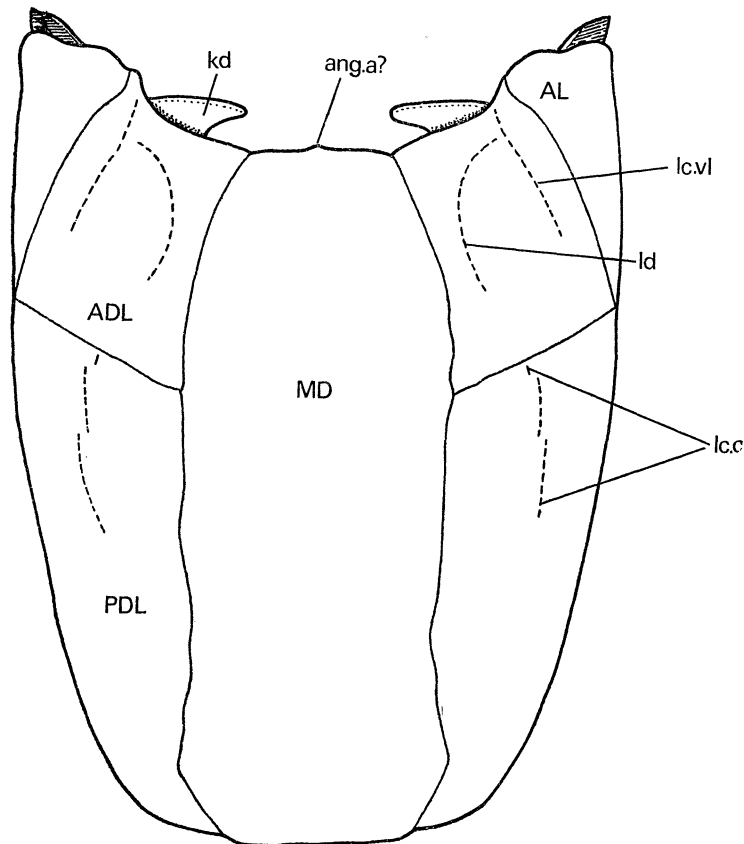


FIGURE 118. *H. radiatum* Obruchev. Dorsal wall of trunk-shield. After Obruchev.

There is, however, no sign of the median longitudinal groove on the visceral surface; the median occipital crest (*moc*) is a narrow, sharp-edged structure, and the median posterior process (*p.pr*) is monocuspid. The transverse fossa is divided into widely separated pits (*tf*) and there is a distinct transverse occipital crest (*toc*). The paranuchal plate (Obruchev 1932, Figures 13 to 15) is closely similar to that of *H. westolli*. It has a broad lateral occipital fossa, large occipital para-articular process and deep supravagal cavity (R.S.M. 1891.42.9). There is, however, a contact area for the marginal plate, which has not been seen in *H. westolli*. Obruchev figures the posterior pit-line as a series of five disconnected short sections, directed towards the nuchal plate. This path is probably an individual variation, and in other specimens the line may have been directed towards the central plate, as in other arthrodires (e.g. *H. westolli*). Obruchev (1932, Figure 16) appears to have correctly determined the marginal plate, but his incomplete

specimen is difficult to interpret. Whether the incomplete 'suborbital' (Obruchev 1932, Figure 17) is correctly determined is not clear, as the specimen shows no sensory canals. The posterior superognathal (Obruchev 1932, Plate 6, Figures 1, 2) is correctly determined, but it is misorientated so that the ventral edge is placed dorsally. Again the specimen compares well with the corresponding element in *H. westolli*. The outer surface bears a dorsal fossa for the reception of the palatoquadrate, and a ventral ornamented area with vertical ridges which dissolve posteriorly into a mass of small tubercles. The inner surface bears an extensive shearing area which posteriorly extends upwards, exactly as in *H. westolli*.

The dorsal wall of the trunk-shield (figure 118) has been restored in a form that is shorter and broader than in *H. westolli*. The median dorsal plate has a breadth/length index of about 40.

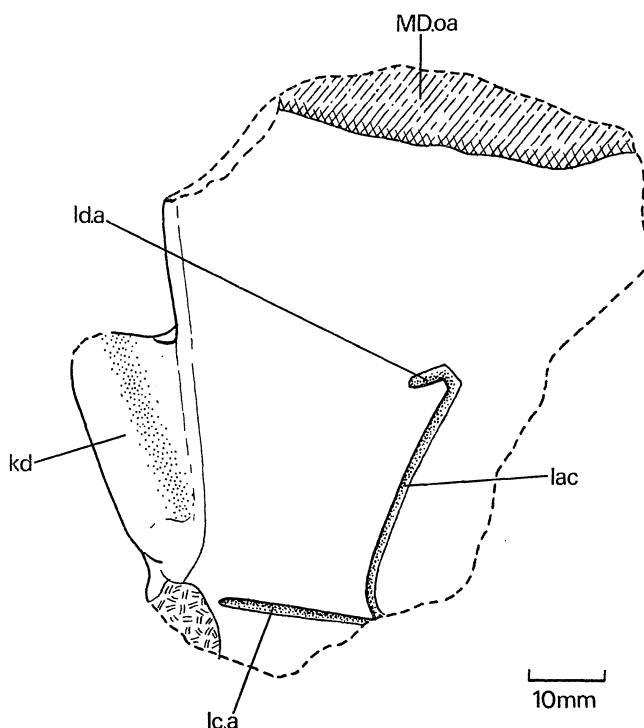


FIGURE 119. *H. radiatum* Obruchev. Incomplete left anterior dorsolateral plate in lateral view. P.6726. Upper Devonian, R. Sjass, U.S.S.R.

Obruchev (1932, Figure 5) has restored the median dorsal plate with a median anterior process (*ang.a?*), so that it has a bow-shaped anterior margin. This is probably incorrect. Otherwise the angles, contact faces, and structures in the middle line on the visceral surface are closely similar to those of *H. westolli*. The anterior part of the anterior dorsolateral plate has been figured by Trautschold (1880, Plate 9) and Obruchev (1932, Figures 7, 8). Obruchev's restoration of the dorsal shield (figure 118) is wrong, however, in that it shows the anterior dorsolateral with a short antero-posterior extent and the posterior dorsolateral as an extensive plate. Obruchev's figure of the anterior dorsolateral plate clearly shows the articular condyle, par-articular area, obstantic process and subobstantic notch. According to Obruchev the long axis of the condyle encloses an angle of about 30° with the upper surface of the anterior dorsolateral plate, but R.S.M. 1902.72.18 and P.6726 show that the angle is much closer to that of *H. westolli* (about 45°). These two specimens show the visceral surface, and demonstrate that the

root of the articular condyle is drawn out into dorsal and ventral ridges. P. 6726 (figure 119) is of further interest because the anterior part of the anterior dorsolateral line (*ld.a*) is represented by a short groove, as in some individuals of *H. westolli*. This condition probably only occurs as a rare variation. The posterior dorsolateral plate (figure 118; Obruchev 1932, Figure 9) has the groove for the main lateral line (*lc.c*) in its anterior half, unlike specimens of *H. westolli* in which the groove is posteriorly situated. As in most specimens of *H. westolli*, the line is broken up into a series of disjointed sections. Obruchev (1932, Figure 11) figures a supposed posterior lateral plate with an extensive ventral overlap surface for the posterior ventrolateral plate and a section of a sensory line groove. This plate is quite unlike the posterior lateral plate of *H. westolli*, and it might be a fragment of the posterior dorsolateral plate. The anterior lateral plate is too small in his restoration. The postbranchial lamina and contact face for the anterior dorsolateral plate (Obruchev 1932, Figure 10) are, however, much as in *H. westolli*. The anterior median ventral plate (Obruchev 1932, Figures 2, 3) is more completely preserved than in *H. westolli*, although it appears to be essentially the same in both species (p. 170). The posterior median ventral and anterior ventrolateral plates are both incomplete (Obruchev 1932, Figure 4, Plate 5, Figures 3, 4).

The ornamentation of *H. radiatum*—forming ridges with one, two or more rows of tubercles—has been described from abraded plates of large individuals, and is of limited value in defining this species.

Heintz (1935) has described some fragments, including part of an anterior dorsolateral plate, from the lowermost Upper Devonian of Spitsbergen (Fiskekløfta Formation, Mimersdalen Series). He refers them to *Holonema* cf. *radiatum*, but they are too incomplete for a safe determination. Kulczycki (1957, pp. 329–331, Plate 10, Figure 2a, b) has described the anterior part of an anterior dorsolateral plate from the Frasnian of the Holy Cross Mountains, Poland. The specimen is said to be almost identical with the corresponding region of *H. radiatum* in shape and size, but with equal justification this might now be said in comparison with *H. westolli*. Kulczycki's determination must, therefore, be regarded as uncertain.

Comparisons. *H. radiatum* can be separated from *H. westolli* by the characters singled out in the definition. It is still a relatively poorly known arthrodire, and extensive comparisons are not justified. There can be no doubt that *H. radiatum* and *H. westolli* are closely related species, and they appear to differ from *H. rugosum* in the more slender shape of the trunk-shield.

***Holonema obrutshevi* Mark, 1953**

Holonema obrutshevi sp.nov. (Mark 1953 *a*, pp. 382–390, Figures 1 to 6, 8, Plate 1)

H. obrutshevi sp.nov. (Mark 1953 *b*, pp. 825–826, Figures 1, 4)

H. obruchevi Mark (Denison 1968, p. 284)

Definition. A 'middle size' species with the median dorsal plate bearing a dorsal, horn-like process.

Occurrence. Middle Devonian (Arakula horizon) near Tartu, Estonia.

Remarks. This species is known by detached plates of the trunk-shield. Mark's original definition includes a number of characters, such as the weak development of the median dorsal keels and the form of the anterior dorsolateral and anterior lateral plates, which are probably found in all holonematids. The salient features of the species are shown in figures 120, 121. The restoration probably errs in representing the posterior dorsolateral as a very deep plate and in omitting the posterior lateral plate. The breadth/length index of the median dorsal plate is about 33.

The median dorsal, anterior dorsolateral and anterior lateral plates are built much as in *H. westolli*, apart from the horn-like median dorsal process (*pr.MD*). The fragments figured as spinal plates (Mark 1953 *a*, Plate 1, Figures 4 to 6) do not compare well with the spinal plate of *H. westolli*, and are probably incorrectly determined. The ornamentation comprises broad radiating grooves, each with one or two rows of tubercles, and narrow interspaces.

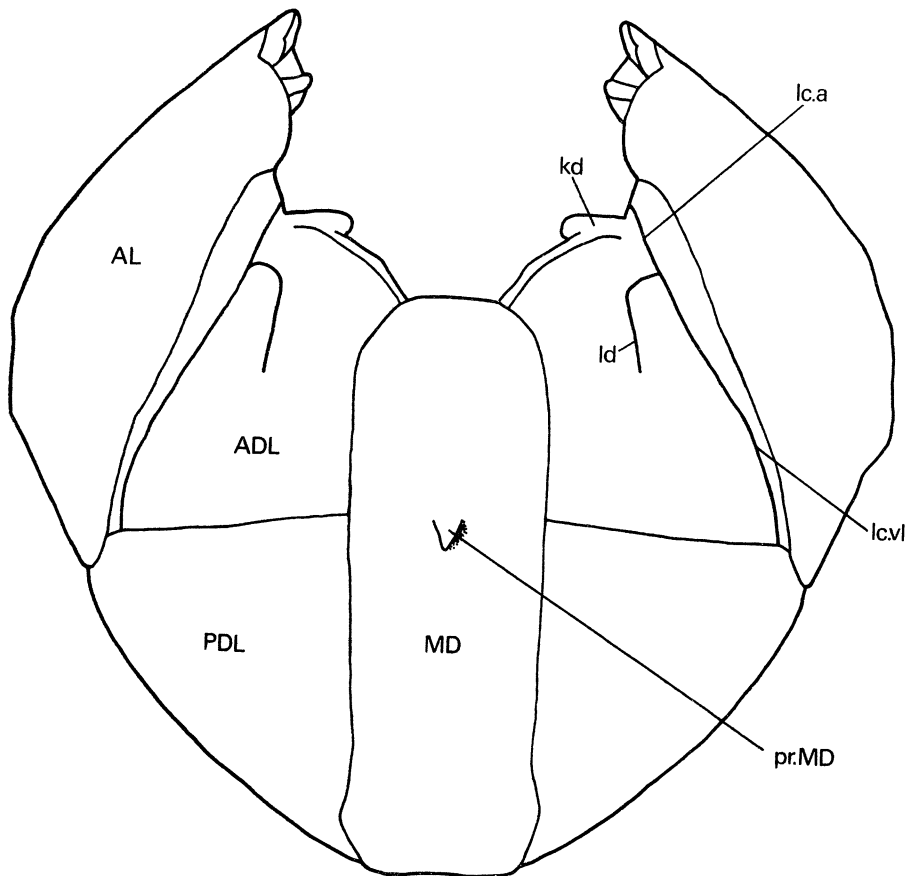


FIGURE 120. *H. obrutshevi* Mark. Dorsal plates of trunk-shield. After Mark.

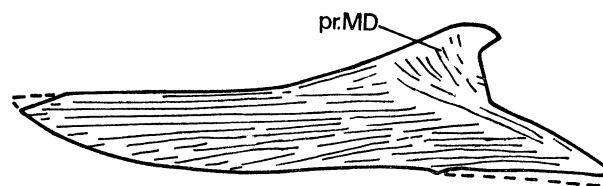


FIGURE 121. *H. obrutshevi* Mark. Median dorsal plate in lateral view, anterior region. After Mark.

Comparisons. This is a singular species, readily separated from other species of *Holonema* by the median dorsal process. Denison (1968) has stated that it does not belong in this genus, but I can find no convincing evidence on which this view might be based.

***Holonema harmae* Mark, 1953**

Holonema harmae sp.nov. (Mark 1953 *a*, pp. 390–393, Figure 7, Plate 2, Figures 7 to 9)

H. harmae sp.nov. (Mark 1953 *b*, p. 826, Figure 2)

Definition. A large species; the anterior lateral plate is low anteriorly; the spinal and subpectoral margins of the anterior ventrolateral plate meet at almost a right angle.

Occurrence. Middle Devonian (Burtnicki horizon) near Tyrva, Estonia.

Remarks. This species is known only by the anterior lateral and anterior ventrolateral plates. Mark has stressed the relative proportions of the margins of the anterior ventrolateral plate in her definition. This plate (figure 122) is usually broad across the prepectoral angle (*a.pp*), and the infrascapulocoracoid lamina (*l.iscc*) is broad and well defined. The *Lsp/Lt* index is about 64. The postbranchial lamina of the anterior lateral plate is said to be of simpler construction than that of *H. obruchevi*, but in both species the lamina is probably essentially the same as in *H. westolli*. The ornamentation comprises ridges with from three to five rows of tubercles.

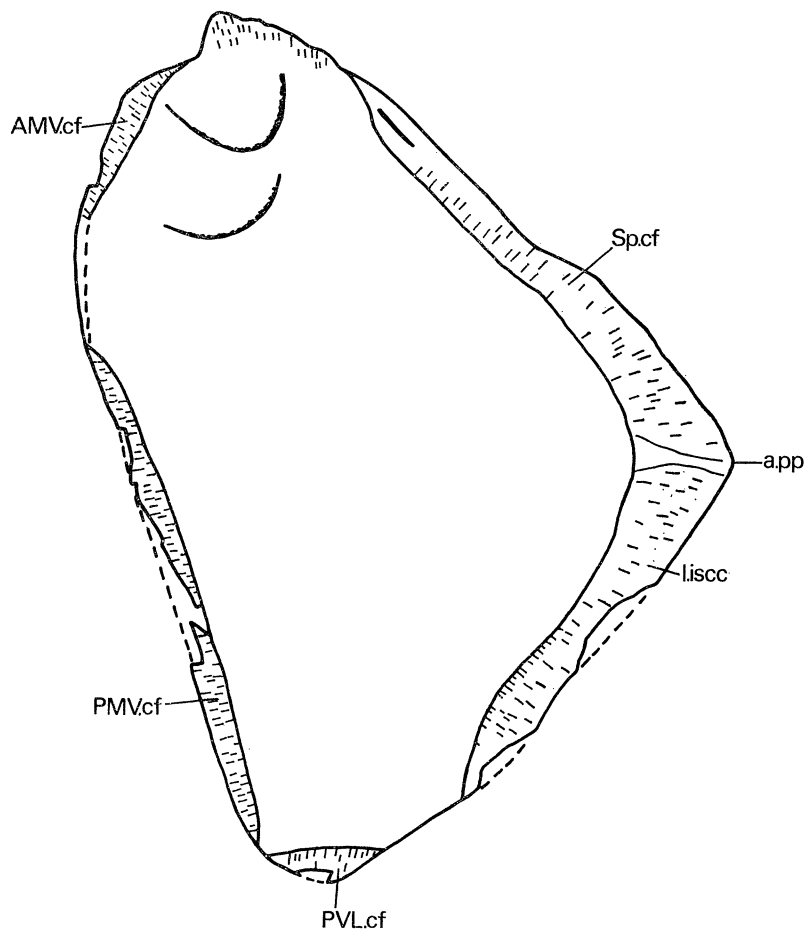


FIGURE 122. *H. harmae* Mark. Visceral surface of right anterior ventrolateral plate. After Mark.

Comparisons. This species may be separated from others, where the known plates allow a direct comparison (*H. rugosum*, *H. farrowi*, *H. westolli*, and to some extent *H. radiatum*), by the form of the anterior ventrolateral plate. It also appears to be distinct from *H. obruchevi*, although a wider range of plates is required to confirm this point.

Holonema ornatum Traquair, 1908

Holonema ornatum sp.nov., Traquair (Traquair 1908, pp. 327–328, Plate 2)
non? *Holonema* cf. *ornatum*, Traquair (Woodward 1919, p. 102)

Definition. A species in which the radiating ridges around the margins of the plate each bear a row of small tubercles.

Occurrence. Upper Middle Devonian (Bressay Flags) of Shetland.

Remarks. This species is known from large fragments of thin plates, of uncertain position in the armour. They have a central ornamentation of anastomosing ridges in a radiating pattern, and a broad marginal zone of parallel ridges at right angles to the margin.

Woodward (1919) has described some poorly preserved fragments (P. 12397, 8) from the Upper Devonian Pickwell Down Sandstone of Woolacombe Bay, N. Devon as *Holonema* cf. *ornatum*. I have examined these remains (figure 99) and find that they are not determinable, although they are probably of a holonematid.

Traquair's reference of the Shetland material to *Holonema* seems reasonable. Wells (1943, footnote 4) and Denison (1968, p. 284), however, have stated that *H. ornatum* does not belong in this genus, and Wells further suggests that it is not a holonematid. Better material is required to settle this point. Woodward (1919) claimed that the Devon plates are similar to *Psammosteus* and *Drepanaspis* in microstructure, and therefore different from the true bone of arthrodires, but an examination of his thin section (of P. 12397) shows that this is incorrect, and that the plates are typically holonematid.

Holonema sp. 1

Material with surface grooving bearing great resemblance to *Holonema* (Dineley & Rust 1968, p. 796, Plate 3, Figure 15, Plate 4, Figures 16 to 18)

Occurrence. In the late Cretaceous or Tertiary Idlorak Formation (derived locally from former outcrops of Upper Devonian rocks) of Somerset Island, Arctic Canada.

Remarks. This record is based on some 12 fragments (Dineley & Rust 1968) which may reasonably be referred to *Holonema* on the evidence of the ornamentation. They are otherwise indeterminate.

Holonema sp. 2

Holonema sp. (Miles 1968, p. 13)

Occurrence. Upper Old Red Sandstone (Redheugh beds) of Berwickshire, Scotland.

Remarks. A single incomplete plate (R.S.M. 1967.49.16C) with a typical holonematid ornamentation of narrow, radiating ridges, is the basis of this record (figure 98). It is indeterminate, but may provisionally be referred to *Holonema*.

Holonema sp. 3

Holonema? (Ørvig 1962, p. 50)

Occurrence. Frasnian (Upper Plattenkalk) of Bergisch Gladbach, Germany.

Remarks. This record is based on an incomplete posterior superognathal (figure 97) of a species at least as big as *H. westolli* and *H. radiatum*. The plate shows the characteristic pipe-like ornamentation, which, however, does not break up into tubercles posteriorly as in these other species. The shearing area and posterior ridge on the aboral surface are formed exactly as they are in *H. westolli*. Another plate (figure 96) may be the posterior lateral. It has a deeply impressed overlap surface, possibly for the posterior ventrolateral plate, and a faint ornamentation of rows of low tubercles. If this plate is correctly determined as the posterior lateral, it is lower and more elongated than the corresponding plate in *H. westolli*.

Conclusion. It seems possible that these specimens represent a new species of *Holonema*, but as they do not give sufficient information for the construction of a satisfactory definition they must be left unnamed.

Holonema sp. 4

Un bouchier céphalique de *Ptérictys* ou d'un genre voisin (Gosselet 1888, p. 572)

Holonema (Dutertre 1929, p. 81)

Holonema sp. (Dutertre 1930, pp. 573–574, plate 59, Figure 10 a, b)

Occurrence. Lower Givetian (Poudingue de Gaffiers) of Boulonnais, France.

Remarks. This form is represented by a single large fragment with a fine ornamentation of anastomosing, beaded ridges.

Comparisons. Dutertre compared this plate with those of *H. ornatum* from Shetland and *Holonema* sp. from the Pickwell Down Sandstone, Devon (p. 216), but there is not enough evidence to establish a relationship. The ornamentation is unusually fine, and it may prove to be sufficiently characteristic for the erection of a new species, once more material is available. Gross (1933, p. 47) suggested that it might belong to *H. eifeliense* (= *Rhenonema eifeliense*), but the ornamentation makes this unlikely.

Holonema sp. 5

Occurrence. Middle Devonian (Calcaire de Givet), approximately 5 km Southwest of Thuin, Hainaut, Belgium.

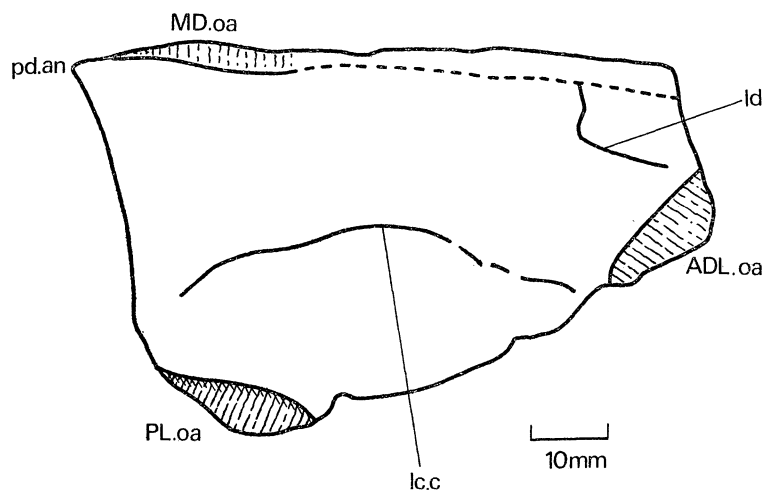


FIGURE 123. *Holonema* sp. Sketch of right posterior dorsolateral plate. Middle Devonian, near Thuin, Hainaut, Belgium. Cast P. 43504.

Remarks. Under this heading may be described casts of two specimens, both unfortunately incomplete; a median dorsal plate, I.R.Sc.N.B. U.B. 2. (cast P. 43505); and a posterior dorsolateral plate, I.R.Sc.N.B. U.B. 1. (cast P. 43504). The median dorsal (figure 94) appears to have been a long, slender plate. It is angled in its posterior half so that the sides meet at about 135° , and there is a slight dorsal ridge around which the ornamentation runs in concentric ridges. There is, however, no 'club' (p. 175). Anteriorly the plate is flattened and the ridges have a radiating disposition. The anterior dorsolateral sensory line groove is present on both sides, but it is more posteriorly situated on the left than on the right, as in *H. farrowi*. It is also arched, as in this last species, *H. rugosum* and *H. haiti*. The posterior dorsolateral plate (figures 95, 123) has a distinct posterodorsal angle (*pd.an*) and shows parts of the median dorsal, anterior dorsolateral

and posterior lateral overlap areas (*MD.aa*, *ADL.aa*, *PL.aa*). It is clear that the plate is close to that of *H. westolli* in its form and proportions. The sensory lines grooves are of particular interest. That for the main lateral-line (*lc.c*) runs in a curve from almost the anterior to the posterior margin, but anteriorly it is somewhat interrupted, and short sections of it are slightly misaligned. Higher up, the anterior dorsolateral line (*ld*) makes a sharp bend across the anterodorsal corner of the plate. The anterior dorsolateral line must cross this region of the posterior dorsolateral plate in other species of *Holonema*, as it passes from the anterior dorsolateral to the median dorsal plate, but this is the first specimen in which the line is represented by a groove (cf. figure 63).

The ornamentation is best seen on the median dorsal plate, where it comprises sharp-edged ridges separated by broad interspaces. There are no tubercles in the interspaces (cf. *Deirosteus abbreviatus*). The possible relationship of these specimens to *Deirosteus omaliusii* is discussed below (p. 220). Because their relationships are uncertain they are not here named.

Holonema sp. 6

Holonema sp.ind. (Obruchev 1961, p. 562, Plate D-89, Figure 1)

Occurrence. Middle Devonian of the Altai-Sayan Region, U.S.S.R.

Remarks. Obruchev has figured an incomplete plate from the trunk-shield. It is ornamented with radiating ridges and appears to be correctly determined as *Holonema*. A specific determination is impossible at the present time.

Holonema sp. 7

A species of *Holonema* (Gupta 1966, pp. 95, 96, Figure 1)

Occurrence. Middle Devonian of the Anantnag District of Kashmir, India.

Remarks. Gupta has determined a single specimen as the median dorsal of *Holonema*. His photograph is, however, too poor to show the characters of the plate. A note published a little later on the Kashmir material (Gupta & Denison 1966) makes no mention of *Holonema*, and it is possible that the original determination was erroneous.

Holonema sp. 8

Holonema sp.indet. (Rade 1964, p. 929, Plate 149, Figure 7)

Occurrence. Devonian (Lower or Middle?) of the Mt Jack area, N.S.W., Australia.

Remarks. Rade has figured a plate which he determined as part of the median dorsal of *Holonema*, on the evidence of the ornamentation. However, Ritchie (1969) has since reported that all the placoderms from the Mt Jack area are new, and it seems possible that Rade's specimen will prove to belong to the non-holonematid form '*Wuttagoonaspis*'.

Genus Deirosteus Wells, 1942

Definition. 'Holonemid arthrodires of large proportions, distinguished by the surface sculpture of the external shield, which is essentially concentric and consists of stellate tubercles and more or less continuous acute ridges separated by relatively broad and often tuberculated interspaces' (Wells 1942, p. 655).

Type species. *Glyptaspis abbreviata* Eastman 1907.

Remarks. Stevens (1964, p. 173) and Denison (1968, p. 284) have questioned the validity of the genus *Deirosteus* on the grounds that the ornamentation is a poor character in holonematid

classification. However, it seems preferable at present to keep *Deirosteus* separate from *Holonema*, until more complete specimens are available to establish its relationships. It seems possible that *Deirosteus* will prove to be a valid genus.

***Deirosteus abbreviatus* (Eastman, 1907)**

Glyptaspis abbreviata sp.nov. (Eastman 1907, p. 147, Plate 13)

Holonema abbreviatum (Eastman) (Hussakof & Bryant 1918, p. 102, Plate 31)

Dinichthys sp. (Hussakof & Bryant 1918, p. 60, Figure 18, Plate 19, Figure 2)

Deirosteus abbreviatus (Eastman) (Wells 1942, p. 655, Plates 95, 96, 97, Figures 1-3)

D. abbreviatus (Wells 1943, p. 5)

H. abbreviatum (Stevens 1964, pp. 172-174, Figure 1D)

D. abbreviatus (Eastman) (Denison 1968, p. 285)

Definition. This species was not formally defined by Wells (1942). The character of the ornamentation has been used in the generic definition, and the value of the characters available for defining the species is not known. *D. abbreviatus* may be defined provisionally as a species in which the median dorsal plate has a convex anterior margin.

Occurrence. Lower Upper Devonian (Senecan) of western and central New York.

Remarks. The median dorsal plate (figure 124 C) is relatively short and broad for a holonematid, as restored by Wells, but the posterior region is incomplete and it may have been of more normal proportions. Although the anterior margin is convex, the anterior median angle (*ang.a*)

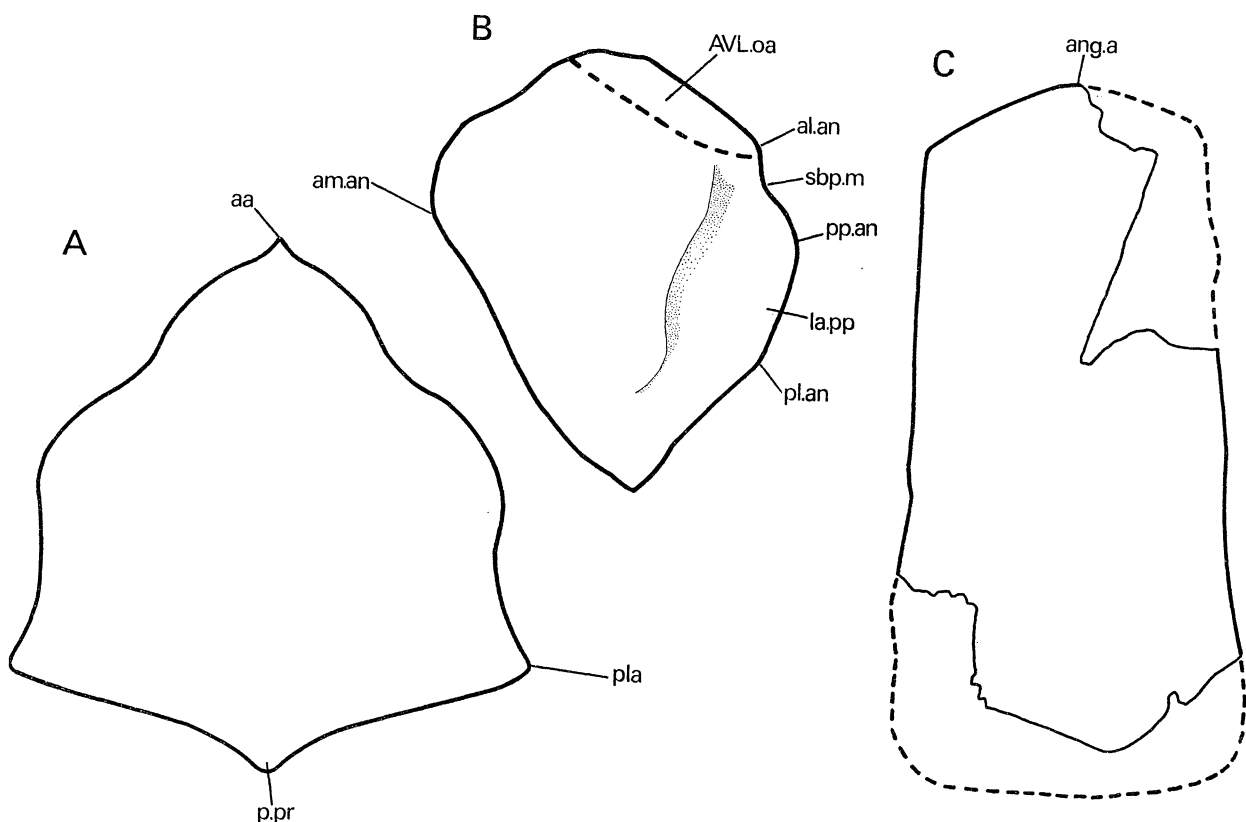


FIGURE 124. *Deirosteus abbreviatus* Eastman. A, nuchal plate; B, left posterior ventrolateral plate; C, median dorsal plate. After Hussakof & Bryant, and Wells.

is not well defined. The ornamentation is divided into five zones on the median dorsal plate, as in some species of *Holonema* (p. 175). The posterior ventrolateral plate (figure 124B) is similar to that of *H. westolli*. It has a short, embayed subpectoral margin (*sbp.m*) and a low postpectoral lamina (*la.pp*). Wells (1942, Plate 96, Figures 1, 2) has figured two fragmentary specimens which he has tentatively determined as a posterior dorsolateral and anterior dorsolateral plate. I agree with these determinations, but the specimens show nothing of special interest. A third fragmentary specimen (Wells 1942, Plate 96, Figure 3) is either the posterior lateral or the submarginal. A nuchal plate (figure 124A) which has been referred to this species by Wells is typically holonematid. It has a distinct anterior angle (*aa*), a bow-shaped posterior margin with a short median process (*p.pr*), and both anterolateral and lateral margins. The median posterior process appears to be monocuspid.

Conclusion. Whatever the correct generic assignment of this species proves to be, there can be no doubt that it is a good holonematid and closely related to *Holonema*.

***Deirosteus omaliusii* (Agassiz, 1884)**

Holoptychius omaliusii Agass. (Agassiz 1844, p. 75, Plate 24, Figure 11)

H. omaliusi, L. Agassiz (Woodward 1891, p. 331)

Deirosteus omaliusii (Agassiz) (Wells 1942, pp. 655–656)

Occurrence. Agassiz gave the occurrence simply as ‘... dans le vieux grès rouge des environs de Namur’. Wells, however, elaborated this to ‘Poudingue de Caffiers, base of Middle Devonian (Givetian)’, but as this is the horizon given by Dutertre (1929) for a specimen of *Holonema* (see p. 217), it seems to have been quoted in error.

Remarks. Agassiz figured part of a median dorsal plate, which Wells interpreted as having the ornamentation characteristic of *Deirosteus*, but tending more to form a network than in *D. abbreviatus*. This plate is about four times as big as the Givetian median dorsal described above (p. 218) as *Holonema* sp. 5. It is possible that there is some affinity between these two Belgian forms, as the ornamentation of the latter exhibits broad interspaces, although it does not form a network. *D. omaliussi* cannot be defined, but it may be left in *Deirosteus* pending the discovery of better material. Denison (1968, p. 285) has remarked that the ornamentation is intermediate between that of typical species of *Holonema* and *Deirosteus*. If Agassiz’s specimen and those described above as *Holonema* sp. 5 belong to the same species, they should probably be referred to *Holonema*. This would more distinctly separate *Deirosteus* from typically ornamented species of *Holonema*.

***Deirosteus angustatus* Obruchev, 1961**

Deirosteus angustatus Obruchev, sp.nov. (Obruchev 1961, p. 562, Plate D-88, Figure 3)

D. angustatus Obruchev (Obruchev 1964, Plate 2, Figure 1)

Occurrence. Middle Devonian (Eifelian) of Salair, Kuznets Basin, U.S.S.R.

Remarks. This species is based on an incomplete posterior dorsolateral plate with the *Deirosteus* type of ornamentation. No comparisons are possible with other holonematids.

Genus *Gyroplacosteus* Obruchev, 1932

Definition. Holonematids with an ornamentation of coarse tubercles which fuse into sinuous ridges and have a concentric arrangement on the median dorsal plate.

Type species. *Gyroplacosteus panderi* Obruchev, 1932.

Remarks. This genus is distinguished by the character of the ornamentation, which is believed to be outside the range of variation in *Holonema*.

***Gyroplacosteus panderi* Obruchev, 1932**

Coccosteus obtusus (partim) (Trautschold 1889, Plate 6, Figures 1 to 6)

Gyroplacosteus panderi sp.nov. (Obruchev 1932, pp. 108–109, Figures 18 to 23, 27b, Plate 5, Figure 1, Plate 6, Figures 3, 4, Plate 8, Figures 2, 6)

G. panderi Obruchev (Obruchev 1964, Plate 2, Figure 3)

Definition. The ornamentation comprises single and fused tubercles; the sides of the median dorsal plate enclose an angle of 150°.

Occurrence. Upper Devonian (Shelon beds), Leningrad district, U.S.S.R.

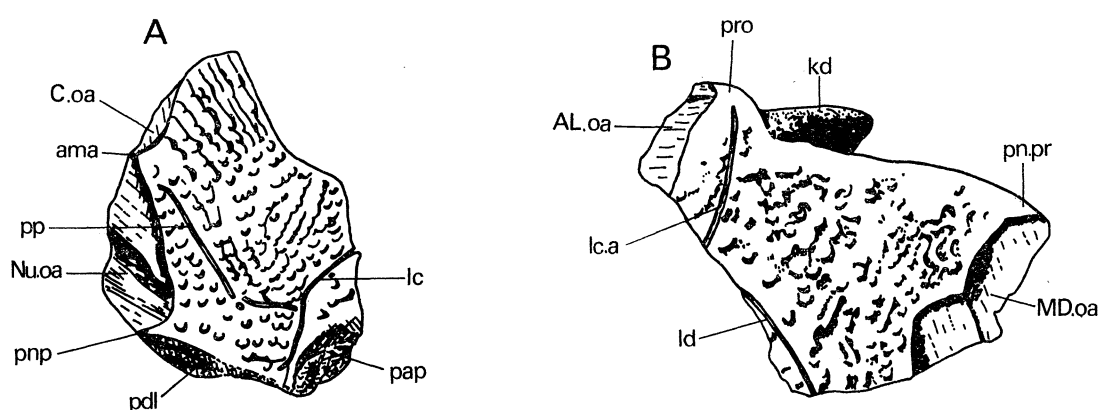


FIGURE 125. *Gyroplacosteus panderi* Obruchev. A, right paranuchal plate; B, left anterior dorsolateral plate. After Obruchev.

Remarks. Plates of this species have been described by Obruchev. The nuchal lacks a median posterior process, has a less acute posterior margin and a less extensive nuchal thickening than in *Holonema*. The median occipital crest is broad and bears a median groove as in some specimens of *H. westolli*. The transverse fossa is divided into distinct paired pits, but these are not bounded posteriorly by a transverse occipital crest. The paranuchal (figures 125A) differs from that of *Holonema* in the higher and shorter form of the lateral articular fossa, which has a breadth/length index of about 50 (taken from Obruchev's figure). The occipital para-articular process (*pap*) is well developed. The posterior pit-line (*pp*) is represented by two separate grooves (cf. *H. westolli*). Other features include the distinct overlap surfaces for the central and nuchal plates (*C.oa*, *Nu.oa*), which meet at the well-formed anterior mesial angle (*ama*), and the posterior descending lamina (*pdl*). In all these features, *G. panderi* resembles *Holonema*. The median dorsal plate has the typical short posterior 'keel' of holonematids (confirmed by R.S.M. 1902.72.29), and a distinctly convex posterior margin with a short median process. The anterior region of the anterior dorsolateral plate is typically holonematid (figure 125B). The articular condyle (*kd*) is, however, relatively shorter than in *Holonema*, as might be expected from the structure of the paranuchal plate. Its long axis encloses an angle of about 45° with the upper surface of the dorsolateral lamina. Obruchev (1932, Figure 27) suggested that *Gyroplacosteus* has a relatively deeper armour than *Holonema*, but this is not borne out by the flat form of the median dorsal plate.

It remains for future work to show whether the features of the posterior region of the nuchal plate and the short form of the cranio-thoracic joint are characteristic of the genus *Gyroplacosteus*, or only of the species *G. panderi*.

Gyroplacosteus butovi Obruchev, 1932

Gyroplacosteus butovi sp.nov. (Obruchev 1932, pp. 109–110, Plate 7, Figures 1, 24)

G. butovi Obruchev, 1932 (Obruchev 1961, p. 562, Plate D-89, Figure 2)

Definition. The ornamentation of the median dorsal plate forms a net-work with a concentric arrangement; the sides of the median dorsal are more steeply inclined than in *H. panderi* and enclose an angle of about 135°.

Occurrence. Upper Devonian of the river Jaja in the Kuznets Basin, U.S.S.R.

Remarks. Only an incomplete median dorsal plate is known. It has the characters given in the definition.

Gyroplacosteus vialowi (Kulczycki, 1957)

Operchallosteus vialowi gen.nov., sp.nov. (Kulczycki 1957, pp. 335–336, Plate 12, Figure 3)

Gyroplacosteus (Obruchev 1964, p. 142)

Definition. A species with the ornamentation comprising 'basally sharply limited meandering ribs, and by less numerous, flattened tubercles in the median part of bones' (Kulczycki 1957, p. 335).

Occurrence. Frasnian of the Wietrznia hills of Kielce, Poland.

Remarks. This species is known by a single plate which was originally described as a posterior ventrolateral. It is, however, more probably the posterior part of a long, slender anterior ventrolateral plate. *G. vialowi* was originally referred to the new genus *Operchallosteus*, which was said to differ from *Gyroplacosteus panderi* in the 'more delicate pattern of ornamentation', and 'less regular arrangement of elevations and their flattened tops'. However, Obruchev transferred this species to *Gyroplacosteus*, and this seemingly reasonable step is followed here.

Gyroplacosteus sp. 1

Occurrence. Frasnian (Upper Plattenkalk) of Bergisch Gladbach, Germany.

Remarks. This record is based on a fragment of bone in the Swedish Museum of Natural History (S.M.N.H. P. 5434) which Dr Ørvig has kindly drawn to my attention. It shows the typical *Gyroplacosteus* ornamentation and is mentioned here to establish the presence of this genus in the Devonian of Germany.

Genus Deveonema Kulczycki, 1957

Type species. *D. obrucevi* Kulczycki, 1957.

Remarks. This genus is based on one incomplete plate, the holotype of the type species.

Deveonema obrucevi Kulczycki, 1957

Deveonema obrucevi gen.nov., sp.nov. (Kulczycki 1957, pp. 331–332, Plate 10, Figure 1)

D. obrucevi Kulcz. (Obruchev 1964, p. 143)

Definition. 'Ornament composed of separate small tubercles, rarely fusing in groups of 2 or 3,

mostly scattered randomly, but arranged in longitudinal rows in middle part of mediodorsal' (Obruchev 1964, p. 143).

Occurrence. Frasnian of Wietrzna hills, Kielce, Poland.

Remarks. The only known specimen is the small part of a median dorsal plate, with the ornamentation given above. The visceral surface bears a broad, shallow median groove, flanked by broad overlap surfaces, and on this evidence the specimen is placed in the Holonematidae. Clearly this evidence is not satisfactory, and this must be regarded as a provisional classification.

Genus **Megaloplax** Obruchev, 1932

Definition. Holonematids in which the median dorsal plate bears scattered tubercles centrally and concentric ridges marginally.

Type species. *Palaeoteuthis marginalis* Eichwald, 1871.

Remarks. This genus is based on fragmentary specimens of the type species, and is insecurely founded.

Megaloplax marginalis (Eichwald, 1871)

Palaeoteuthis marginalis (Eichwald 1871, pp. 6–15, Plate 1, Figures 1, 2)

Palaeoteuthis? marginalis (Schmidt 1873, pp. 135–136, Plate 5, Figures 9, 10)

Megaloplax marginalis (Eichwald) (Obruchev 1932, pp. 110–111, Figure 25, Plate 7, Figure 2)

M. marginalis (Eichwald) (Obruchev 1964, Plate 2, Figure 5)

Definition. This species is defined by the characters of the genus. The median dorsal plate appears to have reached a length of at least 300 mm.

Occurrence. Upper Devonian of the Chut River, Timan, and Asha River, Urals, U.S.S.R.

Genus **Rhenonema** Obruchev, 1964

Definition. Holonematids in which the median dorsal plate has a rounded posterior margin and a high median crest; the ornamentation is coarser than in *Holonema* and forms concentric ridges on the median dorsal plate.

Type species. *Dinichthys eifeliensis* Kayser, 1880.

Remarks. Obruchev (1964) erected this genus for a species formerly named *Holonema eifeliensis*, after Wells, (1943, footnote 4) had stated that it does not belong in *Holonema* (also Denison 1968, p. 284). Although the case for this move has never been fully argued (Wells mentions the high crest), *Rhenonema* is accepted here as a valid genus.

Rhenonema eifeliense (Kayser, 1880)

Dinichthys? eifeliensis (Kayser 1880, p. 818)

Dinichthys eifeliensis Kayser (v. Koenen 1895, pp. 16–18, Plate 4, Figures 4, 5, Plate 5, Figure 1)

Holonema eifeliense Kayser (Gross 1933, pp. 45–48, Figures 12B–D, 13, Plate 5, Figures 4, 5)

H. eifeliense (Kayser) (Gross 1937, pp. 35–38, Figure 18, Plate 5, Figure 5, Plate 7, Figure 3)

H. (?) eifeliense (Gross 1958b, pp. 142–143)

Rhenonema (Obruchev 1964, p. 199)

H. eifeliense (Stevens 1964, p. 170)

Definition. As for the genus; this is the only known species.

Occurrence. Givetian of the Rhineland.

Remarks. This is a large species, with the anterior ventrolateral plate reaching an estimated length of at least 240 mm. Only the paranuchal and suborbital plates are known of the head-shield. The paranuchal (figure 126B; Gross 1933, Figure 12D, Plate 5, Figure 4) shows a number of normal holonematid characters, with, for example, the paranuchal crista (*cr. PNu*), nuchal thickening, occipital para-articular process and lateral articular fossa (*laf*) all well developed. The articular fossa is long and narrow (breadth/length index about 32); its long axis encloses an angle of about 25° with the upper surface of the plate; and the 'upper joint process' is present. On the upper surface of the plate, the posterior pit-line is represented by a single, continuous groove, which does not connect with the main lateral-line. It is similar to the posterior pit-line of *Holonema rugosum*. The posterior half of the suborbital plate is preserved (figure 126C). The specimen ('Unbestimmbar Knochen', Gross 1933) shows the expected sensory line grooves. However, the sinuous trace of the postsuborbital line (*psoc*) cannot yet be matched in *Holonema*.

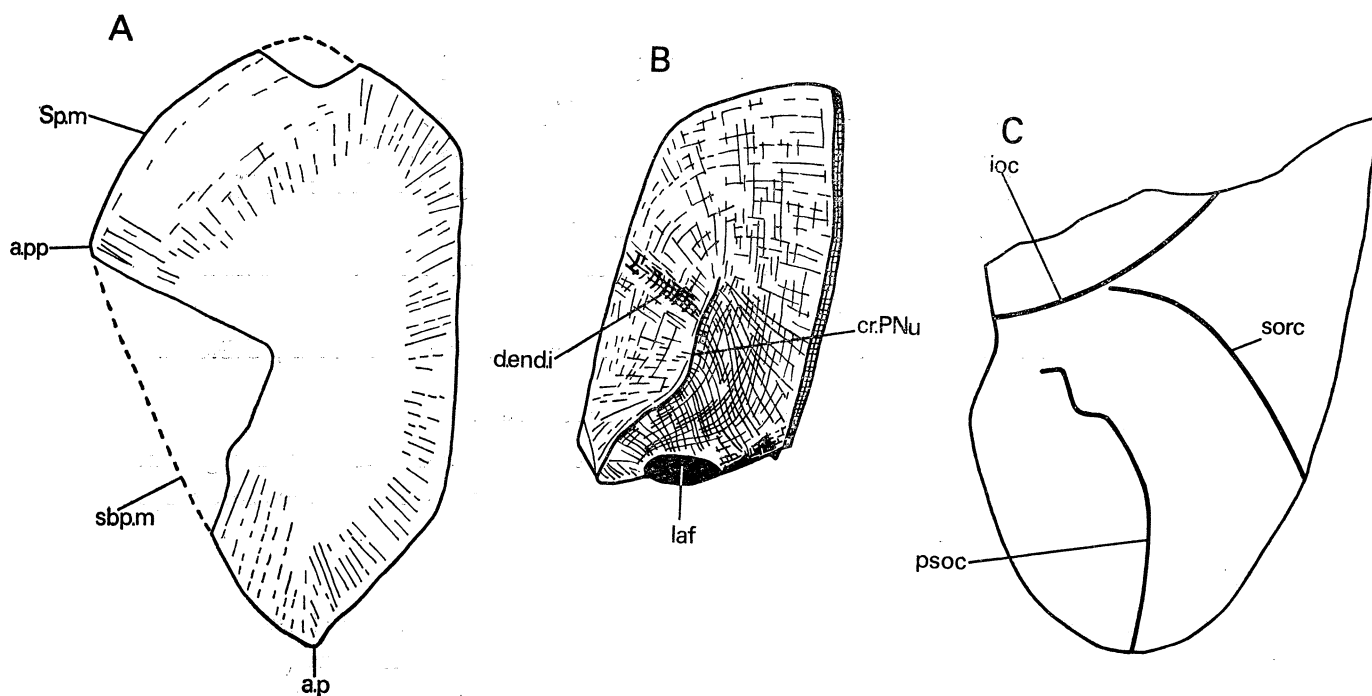


FIGURE 126. *Rhenonema eifeliense* (Kayser). A, anterior ventrolateral plate; B, right paranuchal plate in visceral view; C, right suborbital plate. After Gross.

Gross (1937, p. 36, Plate 5, Figure 5) has described the median dorsal plate as having a rounded anterior margin and a high posterior crest. However, the path of the anterior dorsolateral sensory line and the configuration of the ornamentation (cf. the 'club' of other holonematids) show that Gross has misorientated the specimen (Wells 1942, p. 654; Stevens 1964, p. 170). Thus it is the posterior margin that is rounded, and the median crest is anteriorly situated. R.S.M. 1891. 41. 3 shows that there is a slight posterior 'keel'. The anterior dorsolateral plate (v. Koenen 1895, Plate 4, Figures 4, 5) is incompletely preserved, but it is known to have a long articular condyle. Gross (1937, Figure 18, C, F) has figured the anterior region of the anterior lateral plate, but his interpretation (with posterior dorsolateral and posterior lateral contact edges) is inaccurate because he did not know of the great length of the plate in its complete

state. The configuration of the anterior margin, with the obstatic process and postbranchial notch, and the postbranchial lamina compare well with those of *Holonema westolli*. An incomplete interolateral plate has been figured by v. Koenen (1895, Plate 5, Figure 1). The postbranchial lamina shows the same type of ornamentation as in *H. westolli*, with parallel rows of bead-like tubercles. The anterior ventrolateral plate (figure 126A) is characterized by its considerable breadth across the prepectoral angle (*a.pp*), although this is less than in *H. harmae*, and relatively short spinal margin. The *Lsp/Lt* index is about 28. There is no groove for the ventral sensory line.

Conclusions. The most conspicuous characters of the material brought together as *Rhenonema eifeliense*, apart from the ornamentation, are the high median dorsal crest and the form of the anterior ventrolateral plate. Whether these characters are typical of the genus *Rhenonema*, or of only *R. eifeliense*, is unknown, but they are used here and in other recent works to separate *Rhenonema* from *Holonema*. Although the anterior ventrolateral plate resembles that of *H. harmae* in some features, it is clearly distinct in its short spinal margin. In all other characters *Rhenonema* is typically holonematid.

Genera excluded from the Holonematidae

Obruchev (1964) divided the 'Suborder Holonematoidei' into the Holonematidae and Groenlandaspididae, the former with *Aspidichthys* and ?*Glyptaspis* in addition to the genera considered above, and the latter with *Groenlandaspis*, ?*Grazosteus* and ?*Tropidosteus*. These five genera may be considered briefly here, together with the more recently described *Arctonema* (Ørvig 1969). All of them are poorly known arthrodires, and none is here accepted as closely related to the holonematids. With the exception of *Aspidichthys*, they are monotypic genera.

Aspidichthys. Some of the nomenclatural problems associated with this Upper Devonian genus have been reviewed elsewhere (Miles 1964 *b*). The median dorsal plate is long, ornamented with large tubercles and bears a stout carinal process, but is without a keel. The genus has been referred to the holonematids on the characters of this plate. However, the elongated form and the lack of a well-developed keel are characters of phlyctaenaspid and primitive coccosteomorph-level arthrodires (Miles 1969), which do not signify phyletic relationship, and the presence of a carinal process distinctly separates *Aspidichthys* from the holonematids. It is possible that *Aspidichthys* is a euleptaspid arthrodire; it is not a holonematid.

Glyptaspis. *G. verrucosa* Newberry (1889, p. 158, Plate 13, Figures 1, 2) from the Upper Devonian of Ohio is a large species with a tubercular ornamentation which tends to fuse into concentric ridges. The posterior median ventral plate is, however, typically brachythoracid, resembling in shape those of coccosteomorph arthrodires, and there seems to be no possibility that this species is a holonematid.

Groenlandaspis. *G. mirabilis* Heintz from the Upper Old Red Sandstone of East Greenland has been linked with the holonematids because of the narrow median dorsal plate with a poorly developed keel, and the convex posterior margin of the skull-roof (Heintz 1932 *b*, Figures 10, 11). To these characters may be added the length of the anterior lateral plate (not otherwise *Holonema*-like) and the form of the central plate (misorientated in Stensiö 1939, Figure 12, with the anterior and posterior ends reversed). However, the posterior dorsolateral plate is short and high, with an overlap surface for the anterior lateral as well as the median dorsal, anterior dorsolateral and posterior lateral plates (Stensiö 1939, Figure 13), and the posterior ventrolateral plate is elongated with a long, low postpectoral (postbranchial) lamina (Miles 1964 *a*, Figure 9). The characters of the posterior dorsolateral and posterior ventrolateral plates clearly show that *Groenlandaspis* is a dolichothoracid unrelated to *Holonema*. The similarities between

these fishes in the trunk-shield reside in primitive characters which are widely found in phlyctae-naspid- and primitive coccosteomorph-level arthrodires.

Grazosteus. *G. hoernesii* Gross (1958*b*) from the Devonian of the Rhineland is represented by one specimen, a tuberculated median dorsal plate with a low keel and a high dorsal spine. This plate does not have the great length of the median dorsal of holonematids (Gross 1958*b*, p. 142), and there is no reason to refer it to this group. *Grazosteus* must be regarded as a placoderm of uncertain position.

Tropidosteus. *T. curvatus* Gross (1933) from the Givetian of the Rhineland is also based on a single plate, apparently a median dorsal which is long and narrow with a dorsal crest and no keel. Its affinities are quite uncertain and there is no reason to place it with the holonematids.

Arctonema. *A. crassum* Ørvig (1969) is based on an incomplete anterior dorsolateral plate from the Middle Devonian of Spitsbergen, which Ørvig restores with the short, high form found, for example, in coccosteid arthrodires. This species has been referred to the holonematids because of the configuration of the grooves for the flank canals, but the pattern of these grooves does not differ radically from that of coccosteids, and the evidence for holonematid affinities is poor. Other characters of the plate definitely suggest that *A. crassum* is not a holonematid. They include the ornamentation of large, discrete tubercles, the strong development of the 'dorsolateral edge' as a distinct ridge, and the continuation of the main lateral-line as a groove over the anterior margin. I suggest that *Arctonema* is a non-holonematid arthrodiere of uncertain position, but possibly related to the coccosteids.

5. RELATIONSHIPS AND CLASSIFICATION OF HOLONEMATIDAE

The arthrodires (*sensu* Miles 1969) are commonly divided into the taxa Dolichothoraci and Brachythoraci, although the phyletic analysis and classification of the group is still at an early stage of development. I am at present engaged in a study of the phylogeny of arthrodires, the early publication of which is uncertain. I have, however, found additional support for my earlier conclusion that the Brachythoraci are a valid, monophyletic group (Miles 1969), although it now seems clear that the Dolichothoraci are a paraphyletic group, with some species phylogenetically closer to brachythoracids than they are to other dolichothoracids. Fortunately this last conclusion does not seriously prejudice the following discussion.

A preliminary stage in the analysis of arthrodiere phylogeny has been the description of evolutionary trends within the group. This has facilitated the identification of primitive and advanced characters and has resulted in the recognition of four successive levels of evolution (grades), the actinolepid, phlyctae-naspid, coccosteomorph and pachyosteomorph levels (Miles 1969). The first two levels comprise the dolichothoracids and the last two the brachythoracids. These trends and their functional significance have been considered in a number of papers (Heintz 1934, 1938; Westoll 1945, 1958; Denison 1958; Miles 1966*a*, 1969, also p. 202 above), and it will be sufficient to list them here without further comment, as a guide to the following discussion. They include: the enlargement of the scapulocoracoid and base of the pectoral fin; the reduction of the flank plates from behind; the reduction of the spinal plate and the spinal margins of the anterior lateral and anterior ventrolateral plates, the development of the craniothoracic joint and the consolidation of the posterior region of the skull-roof; the enlargement of the nuchal gap; the development of the median dorsal keel; the enlargement and specialization of the gnathals; the reduction in size and closer incorporation in the head-shield of the

submarginal plate, with at first the correlated increase in size of the postsuborbital plate; and the separation of the palatoquadrate into autopalatine and quadrate structures.

The strength of the orthodox analysis of arthrodiran evolutionary trends, pioneered by Heintz and Westoll, is that the postulated changes are both functionally reasonable and concordant with the occurrence of the fossils in the geological record. The primitive dolichothoracids are predominantly from the Lower Devonian, the intermediate coccosteomorph brachythoracids are mostly from the Middle Devonian and the advanced pachyosteomorphs are over-whelmingly from the Upper Devonian. Stensiö (1959, 1963*b*, 1969*a*), however, has proposed a classification of arthrodires which assumes that some of the quintessential characters of pachyosteomorphs† are primitive, and a logical extrapolation would be for him to interpret the evolutionary changes in the trunk-shield in the opposite direction to Heintz and Westoll. Stensiö's 'purely anatomical approach' has been praised by Nelson (1970*b*), but as Van Valen (1983, p. 261) has remarked: 'A morphological series can give suggestive evidence of relative affinities, but it is only by stratigraphical evidence applied at some point that the relative primitiveness of any of the members of this series can be determined. Without such evidence, either end point or something between them may be equally validly considered most primitive, . . .'

The main problem at the present time is essentially a statistical one, although it has not so far been treated quantitatively. Stensiö's interpretations of the phylogeny of arthrodires demand that our sample of the fossil record is so strongly biased that the true evolutionary sequences are at best muddled and in some cases actually reversed. I am, however, strongly disinclined to believe that this is the case, and find support for this view in the striking operation of Westoll's 'law of diminishing returns in exploration' (see Miles 1969, p. 127) as new faunas are discovered in hitherto unexplored parts (e.g. Gogo): 'new material tends more and more to confirm what has already been known or suspected, though the systematic arrangement of the whole corpus may require revision'.

The holonematids are referred to the new order Holonemida by Stensiö (1969*a*), but *Holonema westolli* fully supports the long standing view that they are arthrodires (Woodward 1891), and Stensiö's proposed change is unjustified. Within the arthrodires, Obruchev (1964) and Romer (1966) have recently classified the holonematids as dolichothoracids (arctolepids), and Miles (1966*a*, 1969) and Ørvig (1969) as brachythoracids. Miles (1969, p. 150) has further suggested that the holonematids diverged from the ancestral stock of the coccosteids, but this now appears to be incorrect and does no merit further discussion. The similarities between these groups in the pattern of the sensory canals on the flank (p. 193) are probably the result of parallel evolution.

The foregoing description of *Holonema westolli* confirms that the holonematids include in their make-up a mosaic of primitive (normally dolichothoracid) and advanced (normally brachythoracid) characters. The most important of these may be listed as follows.

Normally dolichothoracid characters

1. Preorbital plate lacking a preorbital lamina.
2. Paranuchal crista well developed.
3. Skull-roof lacking a 'lateral consolidated region'.
4. Skull-roof with poorly developed orbital lamina (supraorbital vault).
5. Eyes small.

† The terms coccosteomorph and pachyosteomorph are not strictly interchangeable as used by Stensiö and Miles, but they are close enough for present purposes to be used in this way.

6. Sclerotic ring well developed.
7. Submarginal plate large.
8. Postsuborbital plate small, and not fused with the palatoquadrate.
9. Suborbital plate lacking internal laminae.
10. Inferognathal lacking a blade.
11. Trunk-shield long.
12. Flank plates not strongly embayed from behind.
13. Median dorsal plate with small keel and no carinal process.
14. Spinal plate and spinal laminae of anterior lateral and anterior ventrolateral plates long.

Normally brachythoracid characters

15. Nuchal plate relatively short and posteriorly broad.
16. Nuchal plate with paired pits (or single fossa in their place).
17. Paranuchal with postnuchal process.
18. Paranuchal lacking a large cucullaris fossa.
19. Skull-roof with well developed nuchal thickening.
20. Skull-roof with distinct pre-endolymphatic thickening.
21. Postmarginal plate small.
22. Extrascapulars as separate plates carrying the occipital cross-commissure sensory line.
23. Supraorbital sensory line groove extending on to central plate.
24. Large pectoral fenestra.
25. Short postpectoral wall.
26. Well-developed postbranchial laminae of anterior lateral and interolateral plates.
27. Spinal plate lacking a mesial wall ('pseudospinal').
28. Strongly reduced pectoral spine.

Other characters which are possibly primitive for arthrodires may also be noted. They have not been listed above because there is still some doubt about their significance.

Additional primitive (?) characters

29. Presence of a compound postnasalo-rostral plate.
30. Presence of an infrapostsuborbital plate.
31. Anterior extension of the postsuborbital sensory line on to the suborbital plate.
32. Lack of a connexion between the supraorbital and infraorbital sensory lines.
33. Perichondral ossification of the palatoquadrate as a single unit.

Finally there are some specialized characters of holonematids which are not found in exactly the same form in other arthrodires.

Specialized holonematid characters

34. Small size of head-shield relative to the trunk-shield.
35. Snout with (presumed) nasal openings in the fenestra orbitalis.
36. Great length of the preorbital region of the skull-roof.
37. Great depth of the suborbital plate and the lack of a distinct infraorbital lamina.
38. The convex posterior margin of the nuchal plate.
39. Strongly reduced anterior superognathals, perhaps represented by a single median element.
40. Pipe-like ornamentation of the gnathals.
41. Great length of anterior ventrolateral relative to the posterior ventrolateral plates.

The specialized characters that define the Brachythoraci are listed above as numbers 15, 17, 19 and 22. These characters are all concerned with the posterior margin of the skull-roof and the development of the dermal cranio-thoracic joint, which is more completely formed than in phlyctaenaspid-level dolichothoracids. The possession of these characters places the holonematids unequivocally in the Brachythoraci. The presence of numerous primitive characters as a hold over from ancestors at the phlyctaenaspid level of organization has no bearing on this decision. Character number 24 places the holonematids at the coccosteomorph level of organization within the Brachythoraci. At this level they also have a mosaic of primitive and advanced characters. The former include the elongated form of the median dorsal plate; the poor development of the keel and absence of a carinal process; the great length of the spinal region of the trunk-shield; and the moderate nuchal gap. The latter include the greatly enlarged pectoral fenestra; the short postpectoral wall; and the reduced pectoral spine. The 'pseudospinal' structure of the spinal plate is also found in advanced coccosteomorphs (undescribed Gogo species) and in spine-bearing pachyosteomorphs (Heintz 1932, 1968; Mark 1963). It may be concluded on balance that the holonematids are brachythoracids at the primitive coccosteomorph level of organization.

The total array of primitive (dolichothoracid) characters sharply separates holonematids from other brachythoracids. Some of these characters, such as numbers 11, 12, 13 and 14 may be shared by euleptaspids, and 13 and 14 are shared to some degree by *Gemuendenaspis* (Miles 1962, 1969). But these shared primitive characters are not a sign of affinity, and it is not surprising that they should have been retained in several distinct, early branches of the Brachythoraci. Further, if the primitive characters of the head- and trunk-shield are allied with the specialized characters (numbers 34 to 41), we are drawn to the conclusion that the holonematids comprise an early branch of the Brachythoraci, phylogenetically equally distinct from all other families. Thus I recommend that the Brachythoraci should be classified in two collateral taxa, the sections Holonematei and Eubrachythoracei, of which the first would appear to be the most primitive group despite its obvious specializations. The Holonematei include the single family Holonematidae, and the Eubrachythoracei include the remaining families of brachythoracids listed in Miles (1969).

Class Elasmobranchiomorphi
 Subclass Placodermi
 Order Arthrodira
 Suborder Brachythoraci
 Section 1. Holonematei
 Family Holonematidae
 Section 2. Eubrachythoracei

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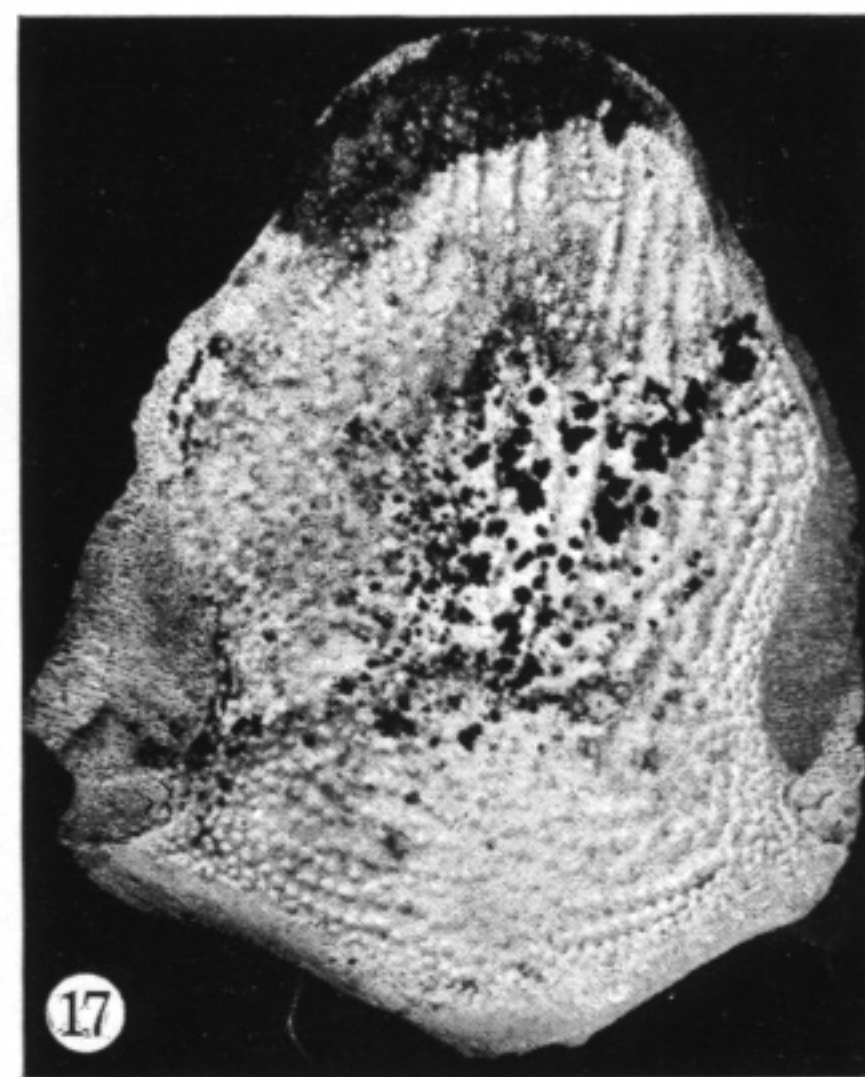
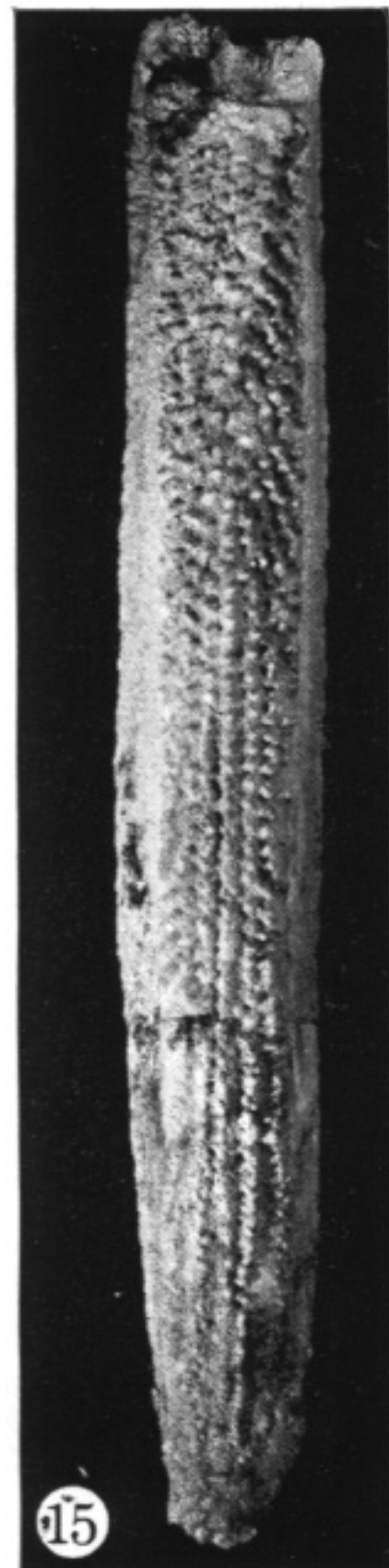
EXPLANATION OF ABBREVIATIONS USED IN FIGURES

ADL	anterior dorsolateral plate	PtO.oa	overlap area for postorbital plate
ADL.cf	contact face for anterior dorsolateral plate	PVL	posterior ventrolateral plate
ADL.oa	overlap area for anterior dorsolateral plate	PVL.cf	contact face for posterior ventrolateral plate
AL	anterior lateral plate	PVL.oa	overlap area for posterior ventrolateral plate
AL.ll.cf	contact face for lateral lamina of anterior lateral plate	R	rostral plate
AL.oa	overlap area for anterior lateral plate	R.cf	contact face for rostral plate
AL.pb.cf	contact face for postbranchial lamina of anterior lateral plate	R.n	rostral notch
AMV	anterior median ventral plate	R.oa	overlap area for rostral plate
AMV.cf	contact face for anterior median ventral plate	RP	rostralo-pineal plate
AMV.oa	overlap area for anterior median ventral plate	R.s	vestigial rostral suture
Ant	antorbital process of neurocranium	Scl ₁	anterior sclerotic plate
APO	anterior postorbital process of neurocranium	Scl ₂	dorsal sclerotic plate
ASG	anterior superognathal	Scl ₃	posterior sclerotic plate
AVL	anterior ventrolateral plate	Scl ₄	ventral sclerotic plate
AVL.oa	overlap area for anterior ventrolateral plate	SM	submarginal plate
C	central plate	SM.cf	contact face for submarginal plate
C.cf	contact face for central plate	SO	suborbital plate
C.oa	overlap area for central plate	SO.cm	contact margin for suborbital plate
Esc	extrascapular plate	SO-PSO.cf	contact face for suborbital and postsuborbital plates
ExL	extralateral plate	Sp	spinal plate
IG	inferognathal	Sp.cf	contact face for spinal plate
IG.dp	depression for inferognathal	Sp.m	spinal margin
IL	interolateral plate	Suo	supraorbital process of neurocranium
IL.cf	contact face for interolateral plate	Sv	supravagal process of neurocranium
IL.oa	overlap area for interolateral plate	aa	anterior angle (of central, nuchal, paranuchal and preorbital plates)
IN	internasal bone	a.ad	anterodorsal lamina
IPSO	infrapostsuborbital plate	a.an	anterior angle (of posterior ventrolateral plate)
IPSO.oa	overlap area for infrapostsuborbital plate	aa.ob	orbital articulation surface
Lsp	length of spinal division of anterior ventrolateral plate	a.av	anteroventral external angle (of anterior dorsolateral plate)
Lt	overall length of anterior ventrolateral plate	ada	anterodorsal angle (of suborbital and submarginal plates)
M	marginal plate	ad.an	anterodorsal angle (of posterior dorsolateral plate)
M.cf	contact face for marginal plate	ad.d	adductor depression
MD	median dorsal plate	ae	embayment over lateral articular fossa
MD.oa	overlap area for median dorsal plate	ae.a	anterior angle (of posterior lateral plate)
M.oac	cavity in overlap area for marginal plate	ae.ad	anterodorsal angle (of posterior lateral plate)
Nu	nuchal plate	ae.av	anteroventral angle (of posterior lateral plate)
Nu.oa	overlap area for nuchal plate	ae.d	dorsal angle (of posterior lateral plate)
Op	opercular plate	ae.pd	posterodorsal angle (of posterior lateral plate)
P	pineal plate	ae.pv	posteroventral external angle (of posterior lateral plate)
P.cf	contact face for pineal plate	ah	articular head of hyomandibula
P.oa	overlap area for pineal plate	ala	anterolateral angle (of central, median dorsal, nuchal, postnasalo-rostral, preorbital and rostror-pineal plates)
PDL	posterior dorsolateral plate	al.a	anterior angle (of spinal plate)
PDL.cf	contact face for posterior dorsolateral plate	al.ale	anterolateral angle (of interolateral plate)
PL	posterior lateral plate	al.an	anterolateral angle (of posterior ventrolateral plate)
PL.cf	contact face for posterior lateral plate	alf	anterolateral surface (of posterior superognathal)
PL.oa	overlap area for posterior lateral plate	all.a	anterolateral angle (of posterior median ventral plate)
PM	postmarginal plate	al.pd	posterodorsal angle (of spinal plate)
PM.oa	overlap area for postmarginal plate	alpr	anterolateral process
PMV	posterior median ventral plate	al.pv	posteroventral angle (of spinal plate)
PMV.cf	contact face for posterior median ventral plate	alth	anterolateral thickening
PN	postnasal plate	ama	anteromesial angle (of central, paranuchal, pre-orbital and postorbital plates)
PN.cf	contact face for postnasal plate	am.an	anteromesial angle (of posterior ventrolateral plate)
PN.m	median rudiment of fused postnasal plates	an	anterior notch
PN.oa	overlap area for postnasal plate	ang.a	anterior angle (of median dorsal plate)
PNR	postnasalo-rostral plate	aat	antorbital cartilage
PNu	paranuchal plate	a.p	posterior angle (of anterior ventrolateral plate)
PNu.cf	contact face for paranuchal plate	a.pd	posterodorsal angle (of anterior dorsolateral plate and posterior superognathal)
PNu.oa	overlap area for paranuchal plate	a.pon	anterior postorbital angle
PPO	posterior postorbital process of neurocranium	a.pp	prepectoral angle
PrO	preorbital plate	a.pqth	autopalatine region of palatoquadrate thickening
PrO.cf	contact face for preorbital plate	a.pr	anterior process
PrO.oa	overlap area for preorbital plate		
PSG	posterior superognathal		
PSO	postsuborbital plate		
PSP	parasphenoid		
PtO	postorbital plate		
PtO.cf	contact face for postorbital plate		

a.pv	posteroventral external angle (of anterior dorsolateral plate)	ioc.ot	otic region of infraorbital sensory canal
a.r	ridge separating mandibularis canal from adductor fossa	ioc.pt	postorbital region of infraorbital sensory canal
a.rd	anterior ridge	ioc.sb	suborbital region of infraorbital sensory canal
art.e	articular surface of quadrate	i.rdg	longitudinal ridge
asba	anterior suborbital angle	iw	internasal wall
ath	'anterior keel'	kd	articular condyle
au	autopalatine	la	lateral angle (of nuchal, postnasalo-rostral and paranuchal plates)
ava	anteroventral angle (of submarginal plate)	la ₁	first lateral angle
av.ae	anteroventral angle (of anterior lateral plate)	la ₂	second lateral angle
av.an	anteroventral external angle (of posterior dorsolateral plate)	lac	'accessory twig' sensory line
bd.e	bevelled edge	laf	lateral articular fossa
ca	central area	la.l	lateral lamina (of interolateral plate)
ca.sv	supravagal cavity	l.ale	lateral angle (of interolateral plate)
cc.dp	cucullaris depression	la.pp	postpectoral lamina (of posterior ventrolateral plate)
cd.art	articular condyle of quadrate	lat.la	lateral lamina (of anterior lateral plate)
cf	contact face	la.v	ridge along transverse groove of preorbital plate
ch ₁	channel in pineal overlap surface	lc	main lateral-line canal on head
ch ₂	channel in postorbital overlap surface	lc.a	anterior division of main lateral-line canal on flank
cpo	postorbital crista	lc.b	middle division of main lateral-line canal on flank
cr.art	articular condyle	lc.c	posterior division of main lateral-line canal on flank
cr.art.p	articular crest for pectoral fin	lc.vl	ventrolateral sensory line
cr.d	dorsal crest of quadrate	ld	anterior dorsolateral sensory line
crib	cribrosal wall	ld.a	anterior division of anterior dorsolateral sensory line
cr.PNu	paranuchal crista	l.gr	longitudinal groove
cr.so	suborbital crista	lig.orb	orbital ligament
csc	central sensory canal	l.io	infraorbital lamina
cso	supraorbital crista	l.iscc	infrascapulocoracoid lamina (of anterior and posterior ventrolateral plates)
da	dorsal angle (of submarginal plate)	ll.a	lateral angle (of posterior median ventral plate)
daa	dorsal anterior angle (of suborbital plate)	ln.th	lateral division of nuchal thickening
daf	articular fossa for orbital connexion	lpa	left pineal area
d.edg	dorsal edge	lpq.p	pit
d.end	endolymphatic duct	l.pr	lateral process
d.end ₁	endolymphatic duct on visceral surface	lrd	longitudinal ridge
d.oa	dorsal overlap area	l.sha	lateral shearing area
df	dorsal vascular foramina	lv.v	hypothetical ventral continuation of ventrolateral sensory line
d.kdr	dorsal root of articular condyle	ma	mesial angle (of marginal plate)
dpa	dorsal posterior angle (of suborbital plate)	mc	mandibularis canal
dp.APO	depression for anterior postorbital process of neurocranium	mdf.th	mandibularis canal region of palatoquadrate thickening
dp.po	postorbital depression	mdr	median dorsal ridge
dp.pr.a	depression for antorbital process of neurocranium	mgl	median longitudinal groove
dp.PSG	depression for posterior superognathal	mk	meckelian cartilage
dp.PSP	depression for parasphenoid	mn.th	mesial division of nuchal thickening
d.pr	dorsal occipital process of neurocranium	moc	median occipital crest
dp.pre	pre-endolymphatic groove	mpl	middle pit-line
em	embayment in sclerotic ring	mpt	metapterygoid
em.PM	postmarginal embayment of submarginal plate	mpt.x	pit in central plates
f	foramen	mr	middle region of palatoquadrate
f.am	m. adductor mandibulae fossa	n.cav	nasal cavity
f.d	foramina for dorsal pterygial nerves and vessels	ncp	nasal capsule
f.dl	dorsal depression	n.Sk	neck of Siebknöchen-like bone
fec	fenestra exonarina communis	nt.i	incurrent nasal tube
fe.i	incurrent nasal opening	nt.x	excurrent nasal tube
fe.x	excurrent nasal opening	nvg	neurovascular groove (see <i>nvsp</i>)
f.lig	fossa for orbital ligament	nvsp	neurovascular space (possibly for n. maxillaris, V n. buccalis lateralis and orbito-nasal artery)
f.ll	foramen for n. buccalis lateralis	oa	overlap area
f.lpq	fossa for m. levator palatoquadrati	o _a	anterior division or orbital fenestra
f.mt	metapterygial foramen	oc	opercular cartilage
f.nv	dorsal and ventral nerve foramina	occ	occipital cross-commissure sensory line
fp	small plate fused to median dorsal plate	ocr	median dorsal occipital crest of neurocranium
f.pb	infraorbital area	od	depression on surface of preorbital plate
f.pq	facet for palatoquadrate	oc _a	anterior division of orbital emargination
g.ll	groove, possibly for n. buccalis lateralis	oc _m	middle division of orbital emargination
gr.end	endolymphatic groove	oc _p	posterior division of orbital emargination
gr.pbl	groove for postbranchial lamina of anterior lateral plate	om	middle division of orbital fenestra
gr.scc	groove for semicircular canal	on	orbital notch
ha	hyoid arch	or	ornament of ascending lamina of interolateral plate
hm	hyomandibula	orb.art	orbital articulation
iar	infra-articular ridge	orb.cf	orbital contact face
ioa	infraorbital angle (of postorbital plate)		

(Continued overleaf)

pa	posterior angle(of central, preorbital and postorbital plates)	rd.a	anterior transverse ridge (of marginal plate)
p.ae	posterior angle (of anterior lateral plate)	rd.p	posterior transverse ridge (of marginal and sub-marginal plate)
paf	para-articular face	rdg	ridges on facet for palatoquadrate
p.ale	posterior external angle (of interolateral plate)	rg	ridge on preorbital overlap area
paoa	paraobstantic area	r.pm	posteromesial ridge
pap	occipital para-articular process	rpr	posterior ridge on paranuchal overlap area
pbla	postbranchial lamina	r.PSG	ridge for posterior superognathal
pbn	postbranchial notch	sar	supra-articular ridge
pbp	pit in postbranchial lamina	sbp.m	subpectoral margin (of anterior ventrolateral and posterior ventrolateral plates)
pd	depression above articular condyle of quadrate	scl.p	mesial process of sclerotic ring
pda	posterodorsal angle (of submarginal and suborbital plates)	shf	shelf of bone under palatoquadrate fossa of posterior superognathal
pd.ae	posterodorsal angle (of anterior lateral plate)	sh.s	shearing area of posterior superognathal and inferognathal
pd.an	posterodorsal angle (of posterior dorsolateral plate)	sk	area with Siebknocken-like texture
pdl	posterior descending lamina	sm.r	smooth area on ascending lamina of interolateral plate
pdp	depression (on visceral surface of posterior dorsolateral and posterior lateral plates)	sn.f	subnuchal fossa
pd.pr	posterodorsal process of autopalatine	snl	subnasal lamina
p.ect	ectethmoid process	soa	subobstantic area
pf	posterior face of posterior superognathal	soan	supraorbital angle
p.fen	pectoral fenestra	soc	supraorbital sensory line canal
pi.p	pineal process	sol	suborbital lamina of suborbital plate
pk	anterior cusp	sorc	supraoral sensory line canal
pla	posterolateral angle (of central, median dorsal, nuchal, pineal, postnasalo-rostral and preorbital plates)	sp	pectoral spine
plaa	posterolateral angle (of skull-roof)	sp.f	possible spiracular fenestra
pl.ale	posterolateral angle (of interolateral plate)	sp.fl	posterior flange of spinal plate
pl.an	posterolateral angle (of posterior ventrolateral plate)	sp.m	spinal margin (of interolateral plate)
pma	posteromesial angle (of central, pineal, preorbital and postorbital plates)	sp.m	pit on visceral surface of spinal plate
pmaa	posteromesial angle (of skull-roof)	snf	subnuchal levator fossa
pm.an	posteromesial angle (of posterior ventrolateral plate)	ssc.la	suprascapuloacoracoid lamina
pmc	postmarginal sensory line canal	s.sh	shearing surface of inferognathal
pmd	posteromesial depression	td	triangular depression on suborbital plate
pnp	postnuchal process of paranuchal plate	tdp	depression of visceral surface of postorbital plate
pnpr	postnuchal process of anterior dorsolateral plate	tf	transverse fossa
pnw	prenasal wall	tfc	terminal face of posterior superognathal
po	pineal opening	tg	transverse groove, possibly a depression for the antorbital and supraorbital processes of the neurocranium
poa	postorbital angle (of preorbital, postorbital and suborbital plates)	th.pre	pre-endolymphatic thickening
pon	postobstantic notch	toc	transverse occipital crest
popr	postocular process	tr.am	trunkated anterior margin
pp	posterior pit-line	tr.itb	path of incurrent nasal tube
pp.an	postpectoral angle	tr.xtb	path of excurrent nasal tube
ppan	posterior postorbital angle	ts.w	transverse wall
p.pr	posterior process (of central, marginal, nuchal and postnasalo-rostral plates)	uc.cf	undercut contact face
ppt	pineal pit	uc.oa	undercut overlap area
pq	palatoquadrate	ujf	upper joint fossa
pr.a	posterior angle (of posterior ventrolateral plate)	va	ventral angle (of submarginal plate)
pr.c	'posterior keel'	vaa	ventral anterior angle (of suborbital plate)
pr.det	detent process	va.f	ventral angle of palatoquadrate fossa of posterior superognathal
pr.dl	dorsal process of anterior superognathal	v.f	ventral vascular foramina of palatoquadrate
pr.dp	prerostral depression	vfa	ventral foramina of opercular cartilage
pr.if	interfenestral process	vg	groove for subcutaneous vascular plexus
pr.MD	dorsal process of median dorsal plate	v.kdr	ventral root of articular condyle
pro	obstantic process (of anterior dorsolateral and anterior lateral plates)	v.oa	ventral overlap area
pr.oa	preorbital angle (of suborbital plate)	vap	ventral posterior angle (of suborbital plate)
pr.orb	orbital process	vsl	ventral sensory line canal
pr.pvl	posteroventral palatine process	y	excavation for process of pineal plate
pr.sp	suprapectoral process	x	excavation for process of postorbital plate
psba	postsuborbital angle	x.oa	overlap-like area
p.sha	oral shearing area	x.PM.cf	limit of postmarginal contact face
psoc	postsuborbital sensory line canal	VII.hm	foramen for r. hyoideomandibularis facialis.
pt.p	posteroventral process of inferognathal		
pva	posteroventral angle (of submarginal plate)		
pv.ae	posteroventral angle (of anterior lateral plate)		
pv.an	posteroventral external angle (of posterior dorsolateral plate)		
qu	quadrate		
qu.thpq	quadrate region of palatoquadrate thickening		



Holonema westolli sp.nov.

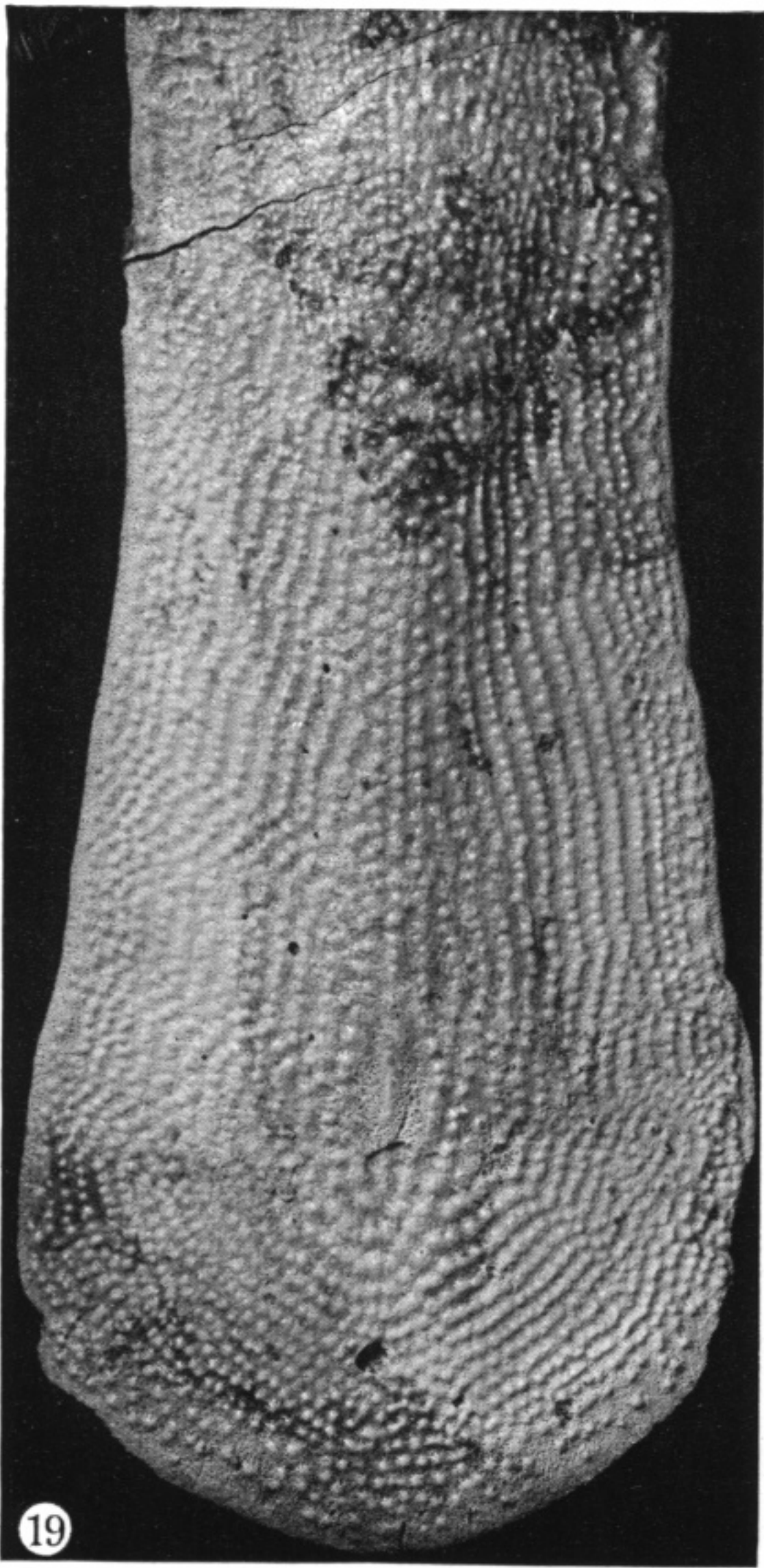
FIGURE 14. Right anterior dorsolateral and posterior dorsolateral plates. P. 51014 ($\times \frac{2}{3}$).

FIGURE 15. Left spinal plate. P. 50988 ($\times 1$).

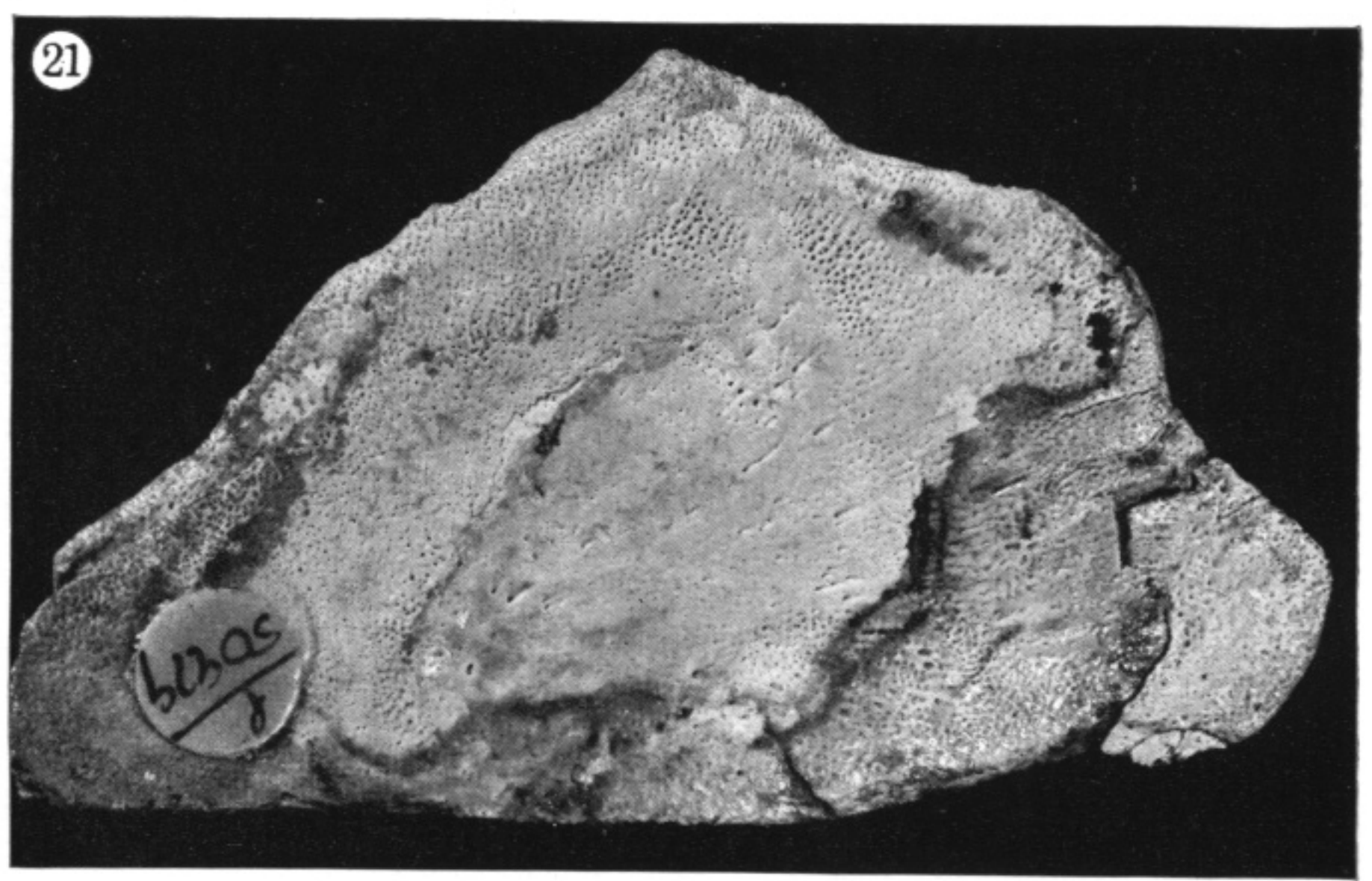
FIGURE 16. Skull-roof. P. 50982 ($\times 1$).

FIGURE 17. Nuchal plate. P. 50995 ($\times \frac{4}{3}$).

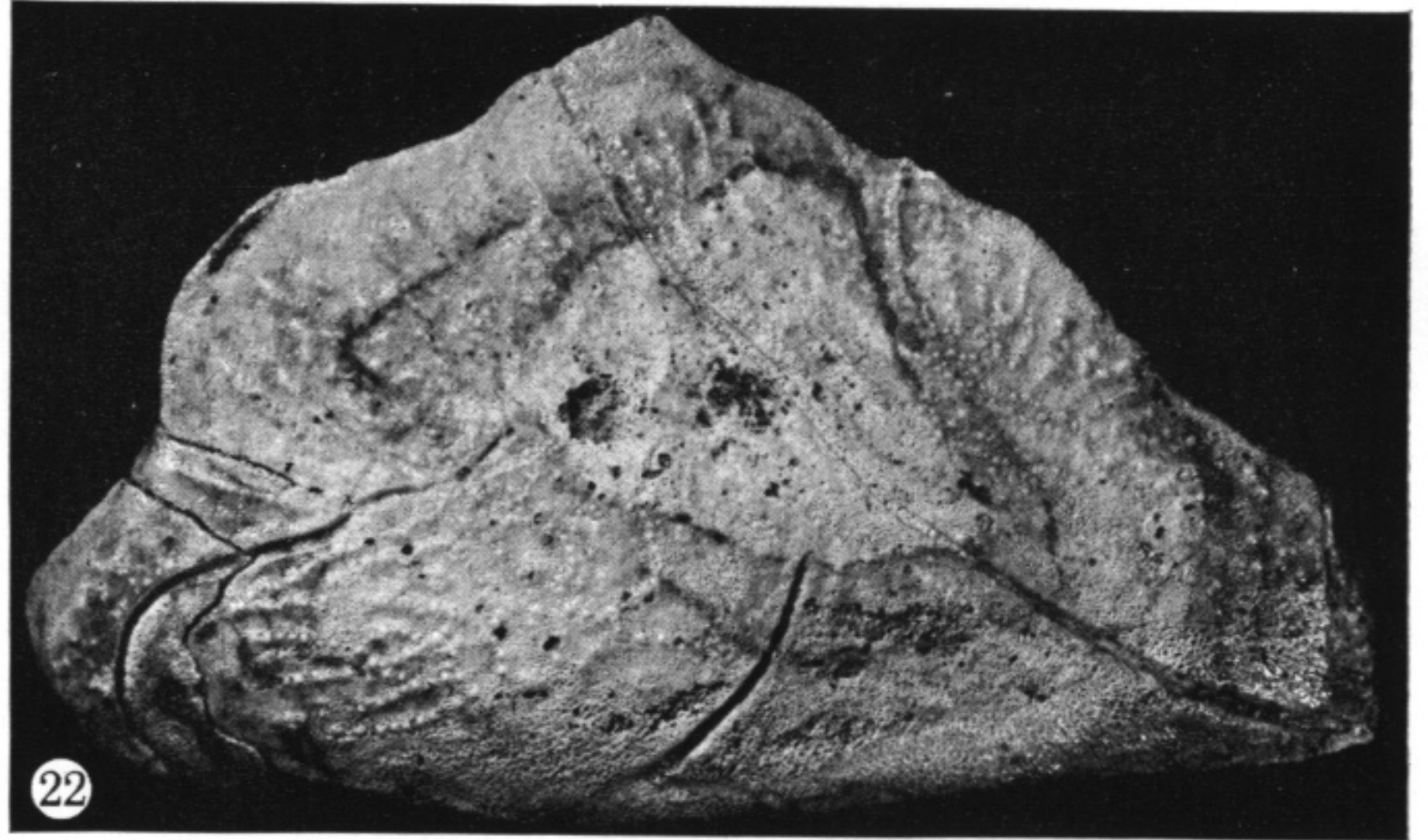
FIGURE 18. Left anterior dorsolateral plate; anterior region of visceral surface. P. 50995 ($\times \frac{4}{3}$).



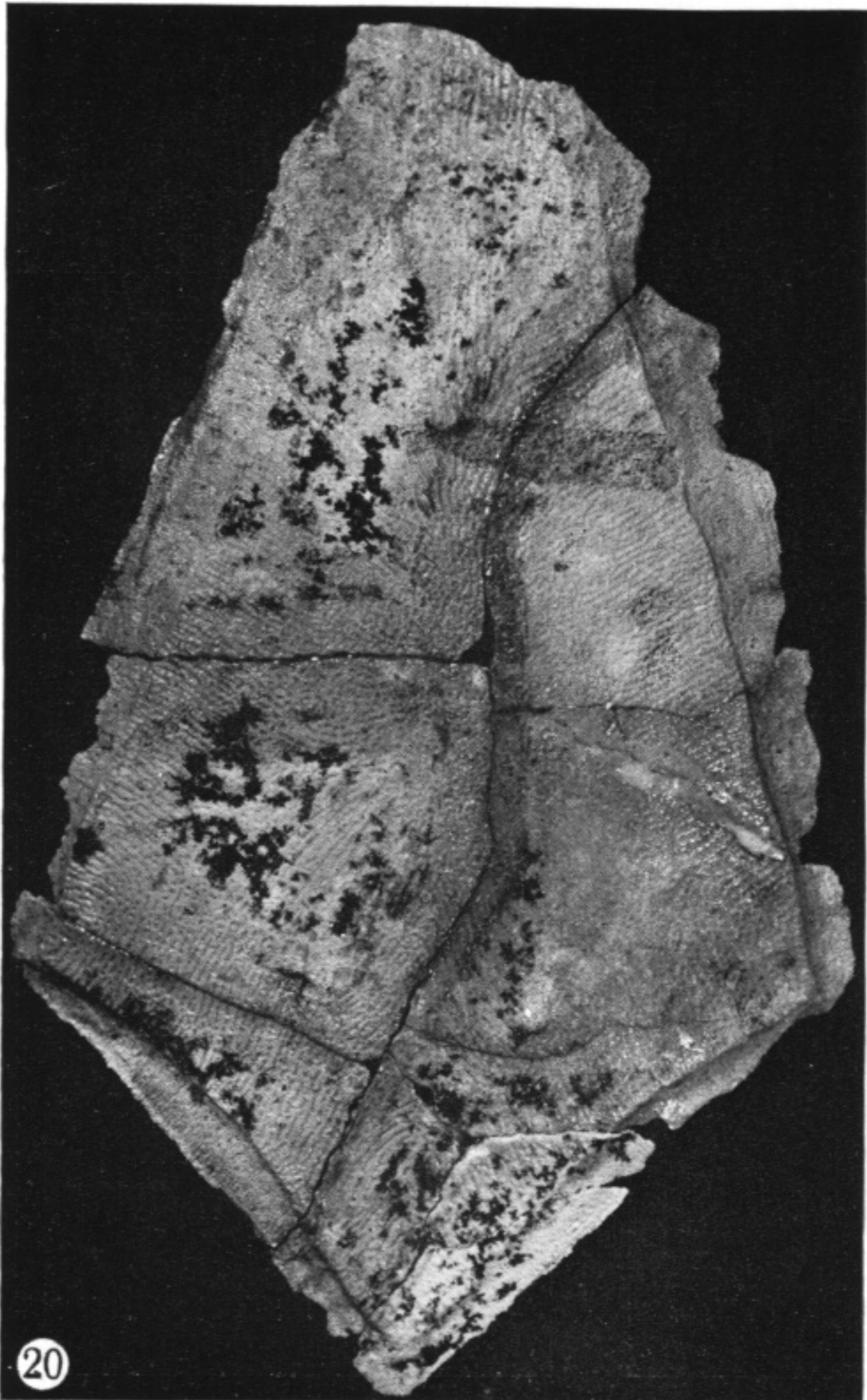
19



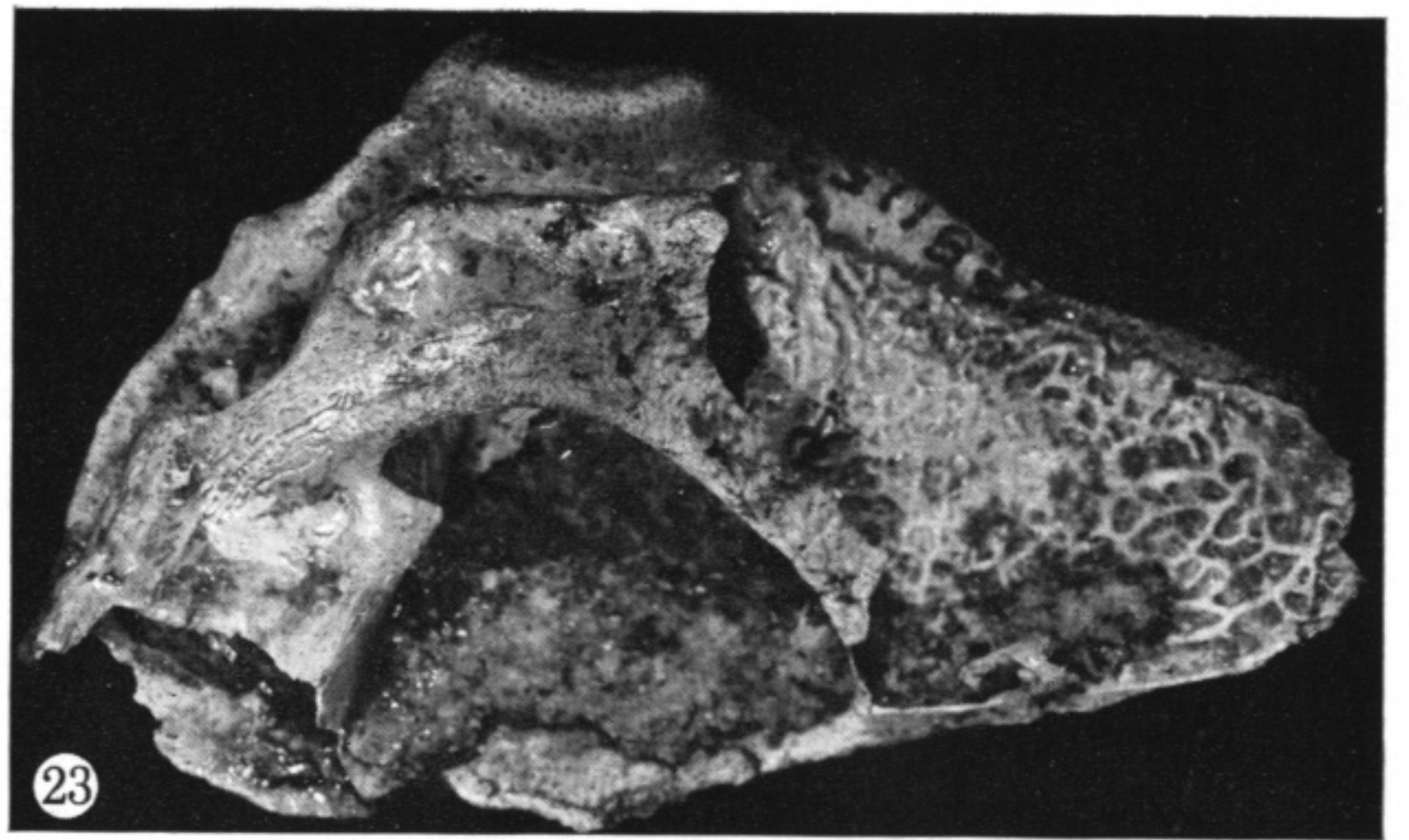
21



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FIGURE 19. Median dorsal plate. P. 50987 ($\times \frac{4}{3}$).

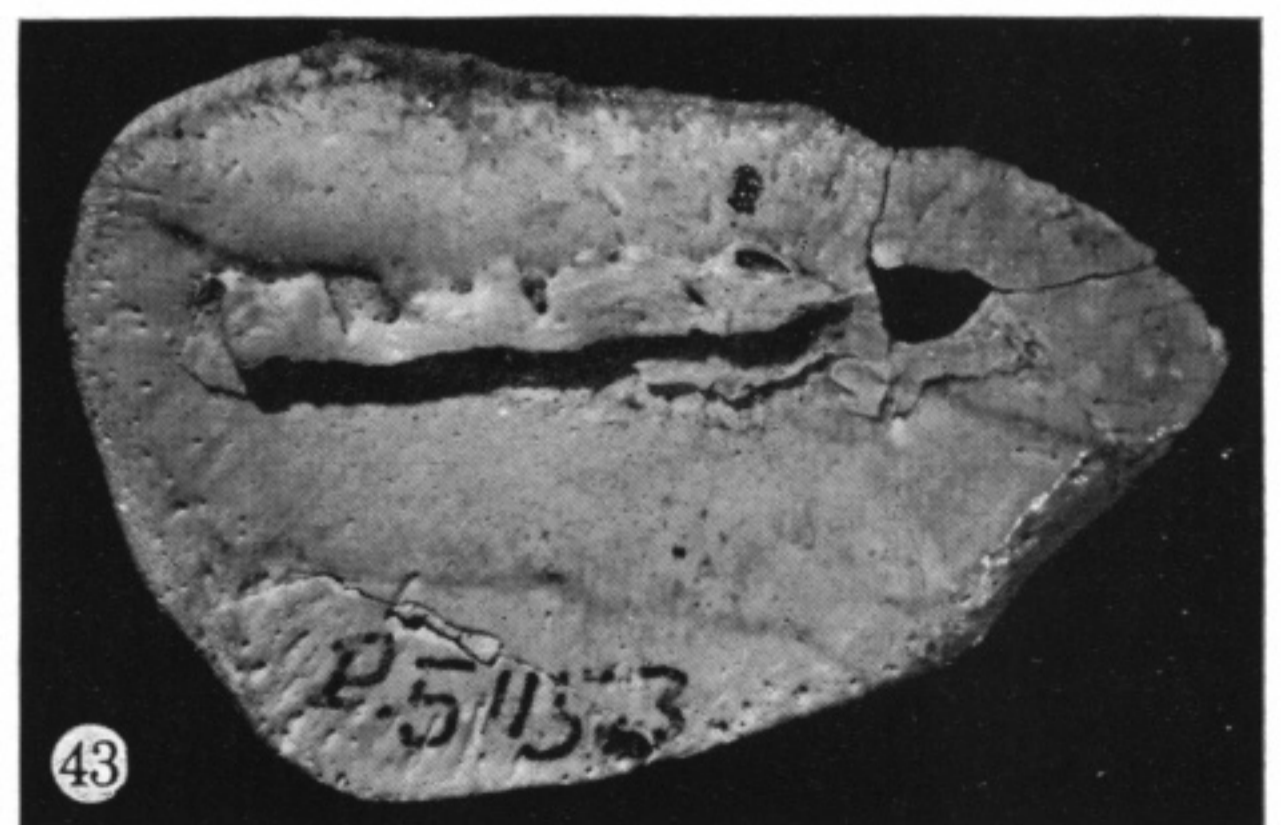
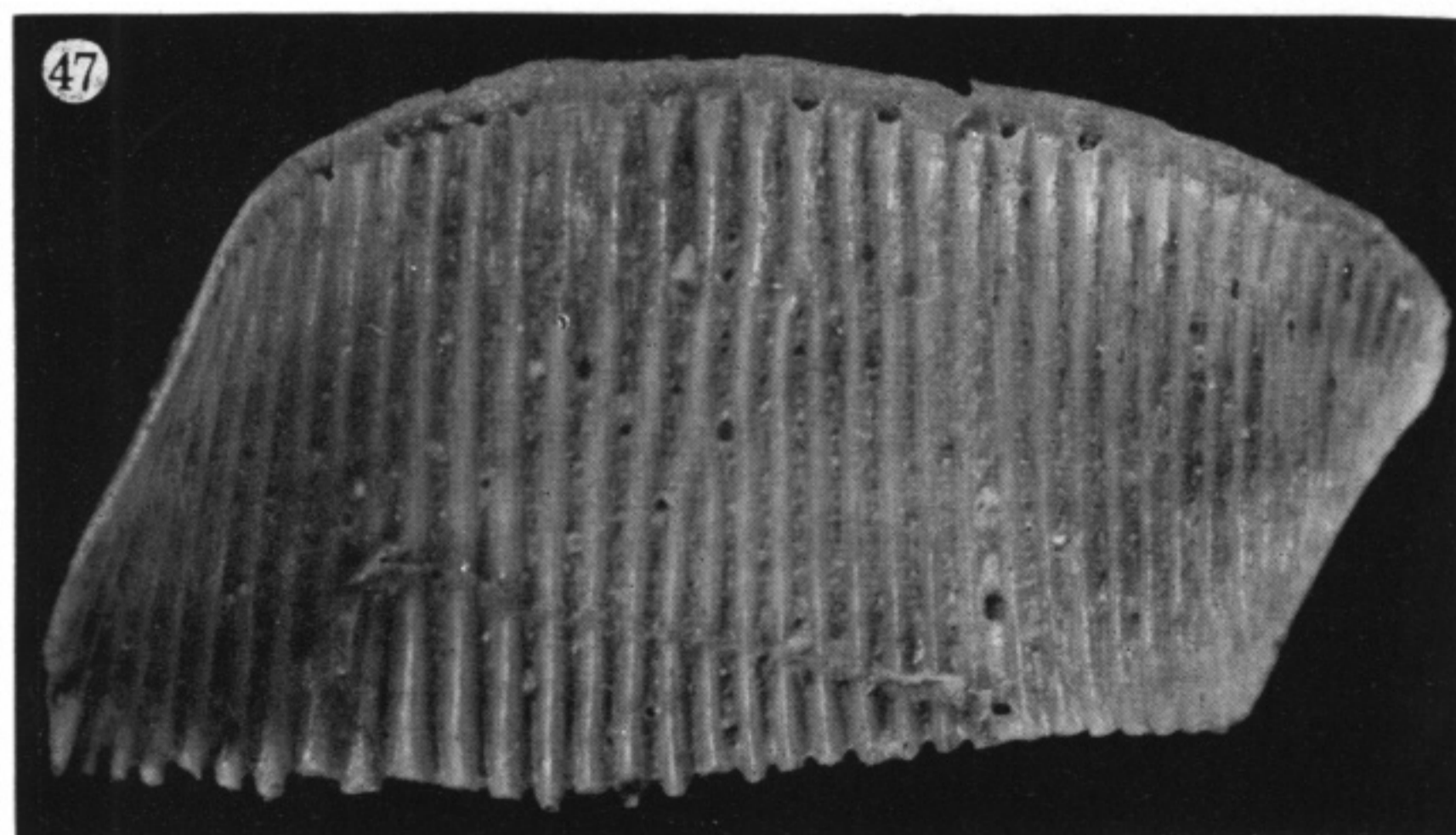
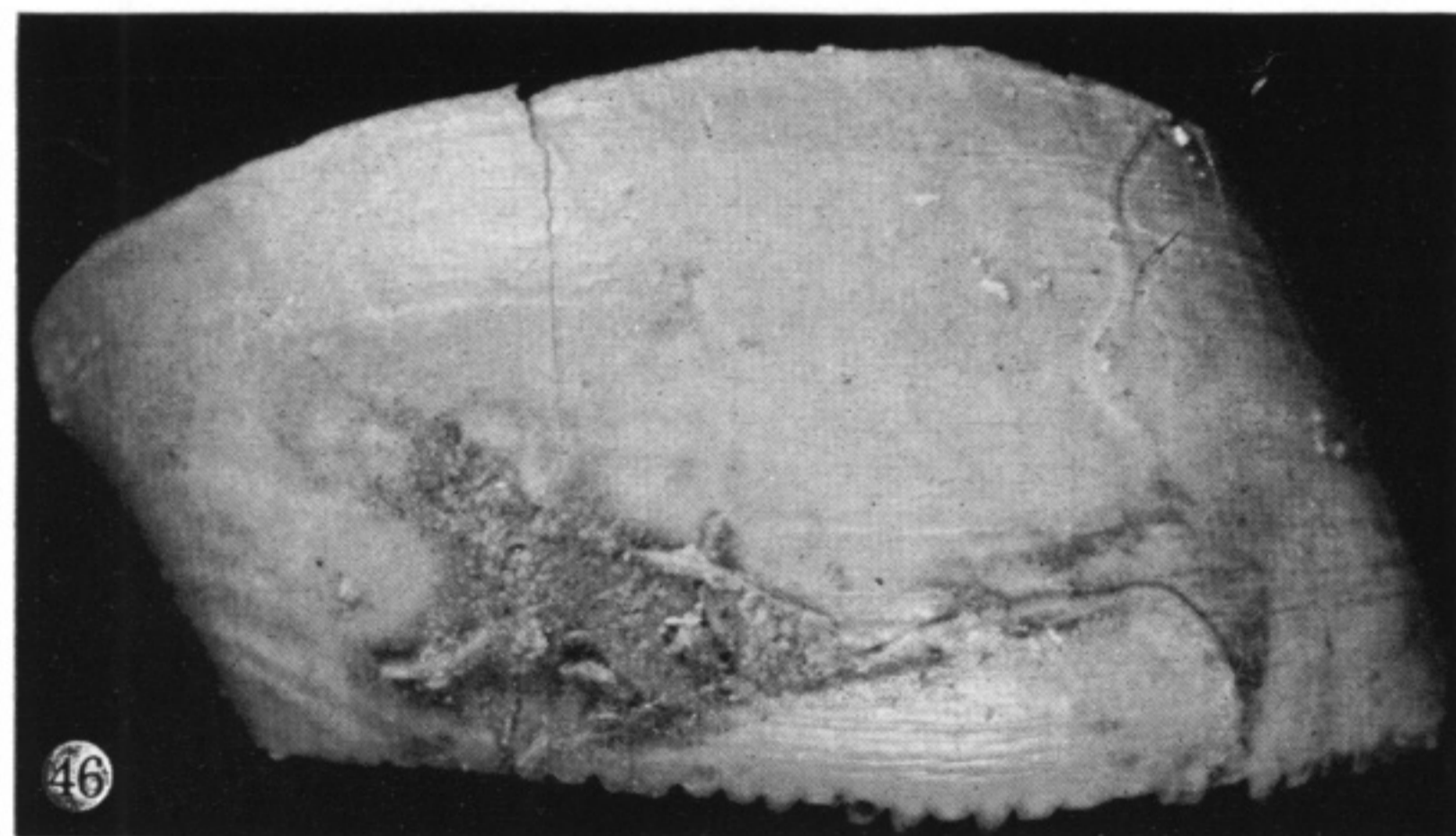
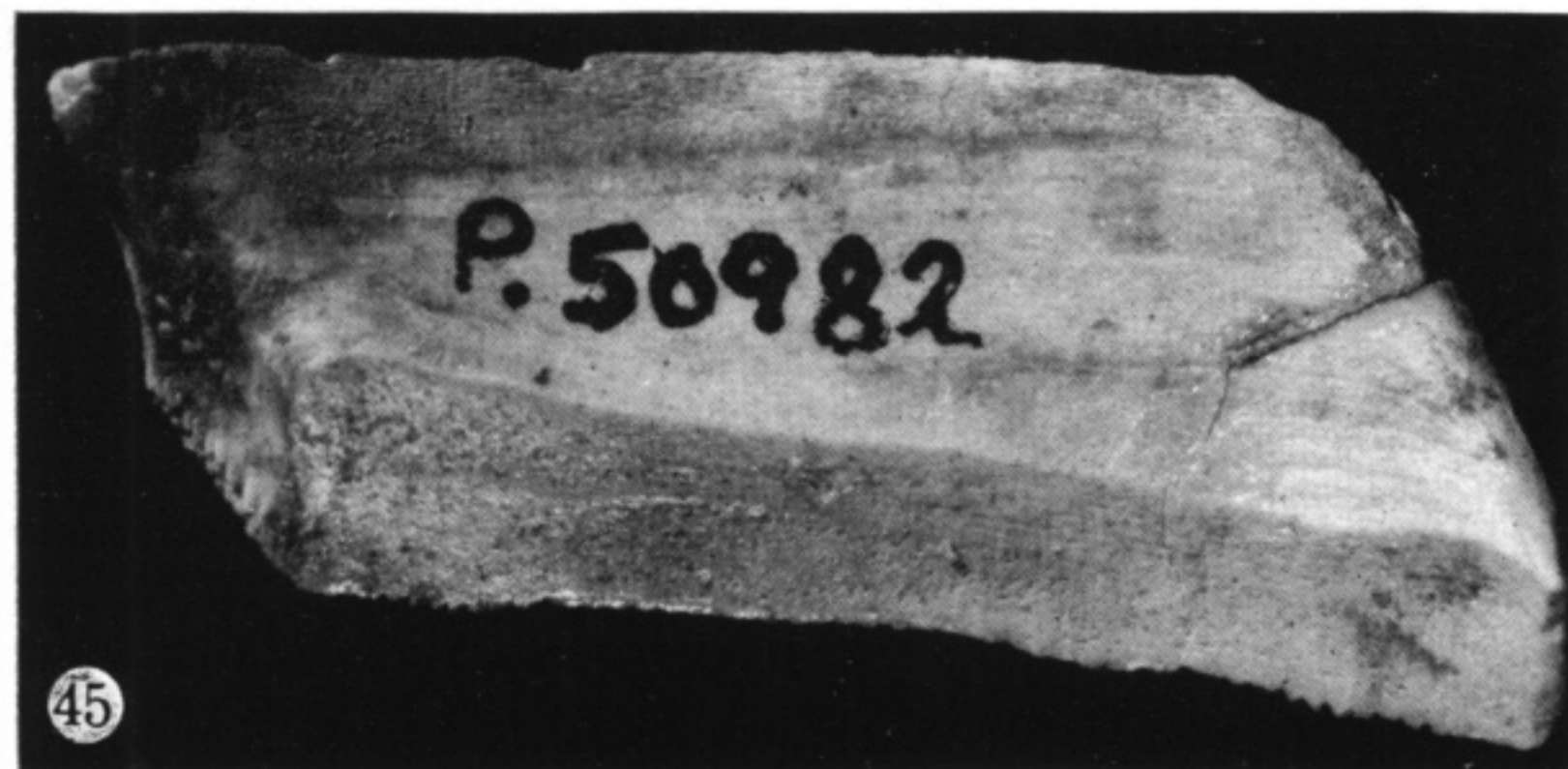
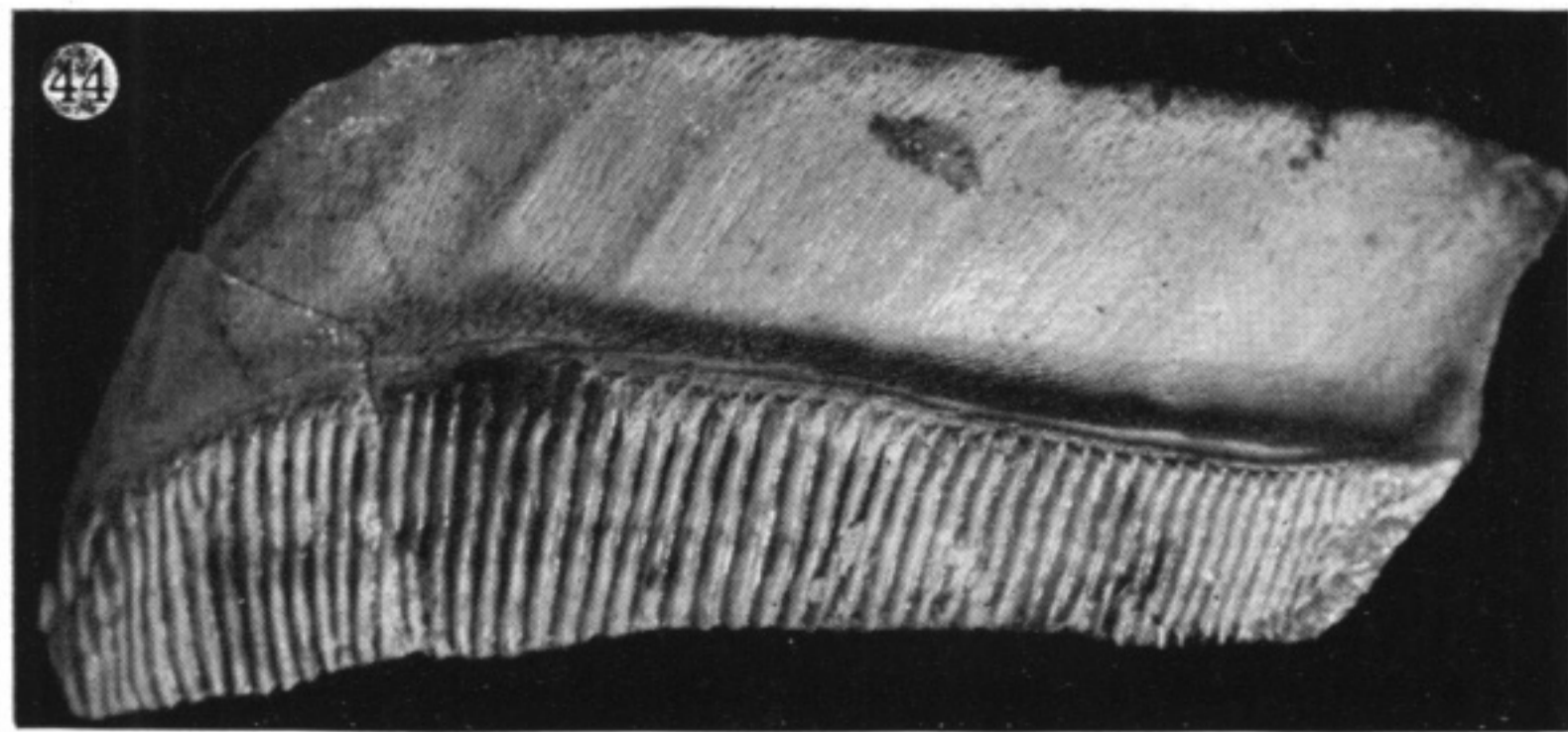
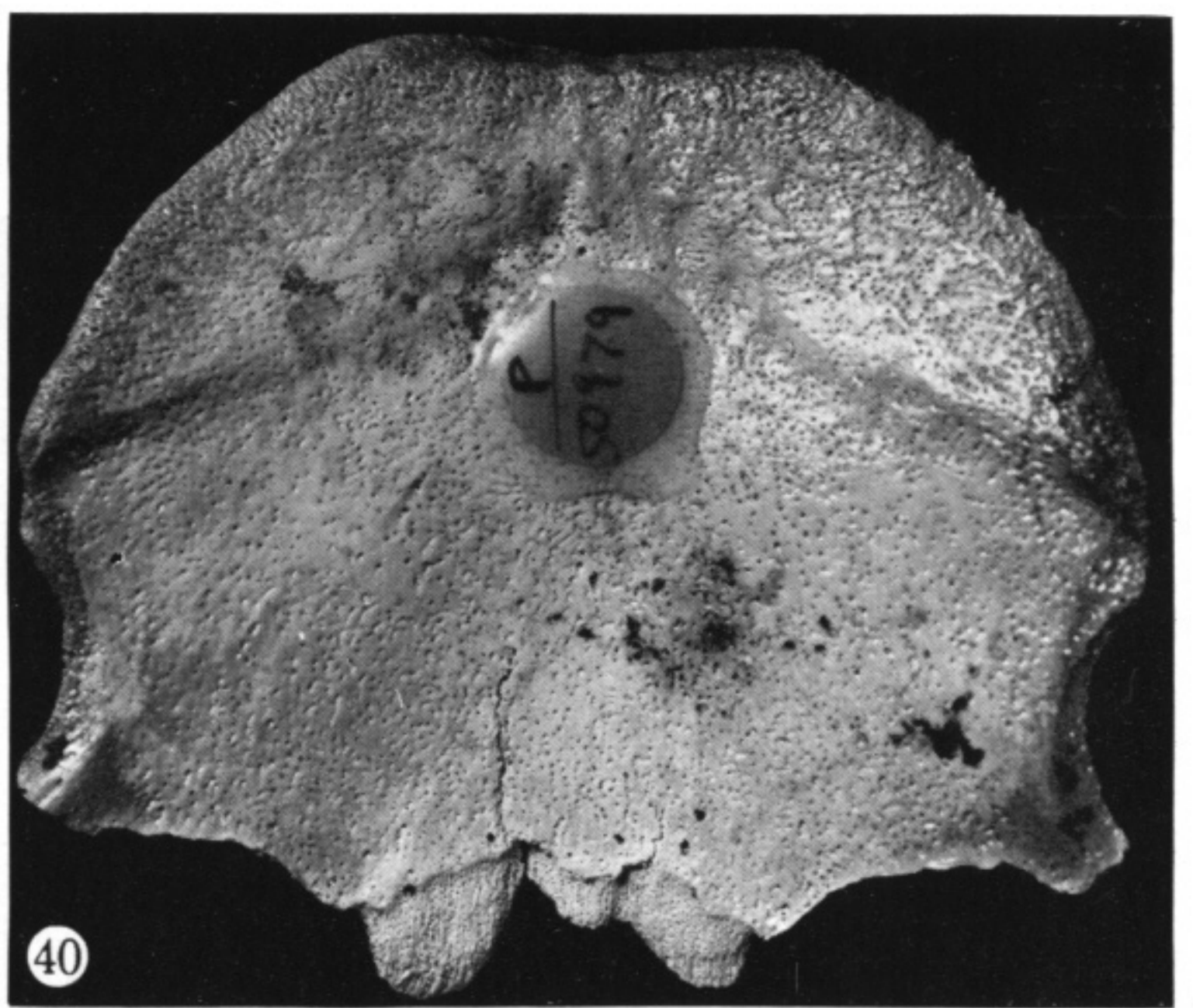
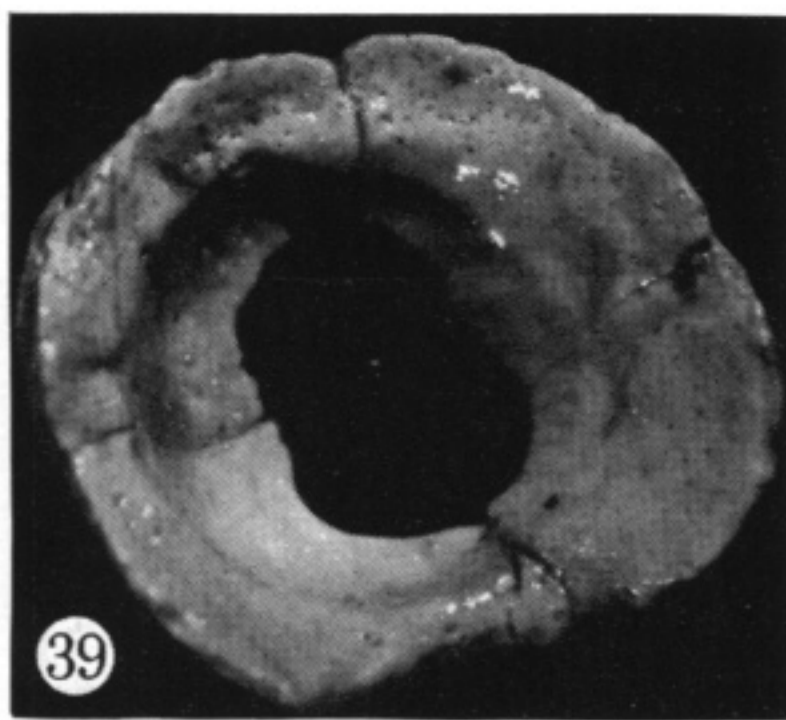
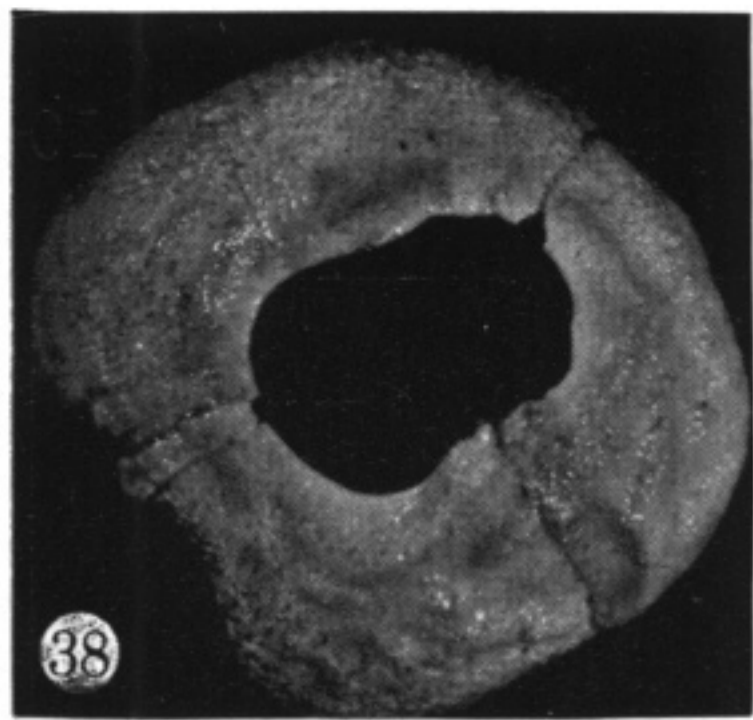
FIGURE 20. Posterior median ventral plate. P. 50984 ($\times \frac{2}{3}$).

FIGURE 21. Right suborbital, postsuborbital and infrapostsuborbital plates in visceral view. P. 50979 ($\times \frac{4}{3}$).

FIGURE 22. Same specimen as in figure 21, in lateral view.

FIGURE 23. Left palatoquadrate and suborbital plate. P. 51153 ($\times \frac{4}{3}$).

FIGURE 24. Right palatoquadrate and suborbital plate. P. 51153 ($\times \frac{4}{3}$).



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FIGURE 38. Left sclerotic ring in lateral view. P. 51004 ($\times \frac{8}{3}$).

FIGURE 39. Same specimen as in figure 38 in visceral view.

FIGURE 40. Postnasalo-rostral plate in visceral view. P. 50979 ($\times \frac{4}{3}$).

FIGURE 41. Left submarginal plate. P. 50980 ($\times \frac{4}{3}$).

FIGURE 42. Same specimen as in figure 41, in visceral view.

FIGURE 43. Left submarginal plate with incomplete opercular cartilage; dorsal edge to the bottom of picture.

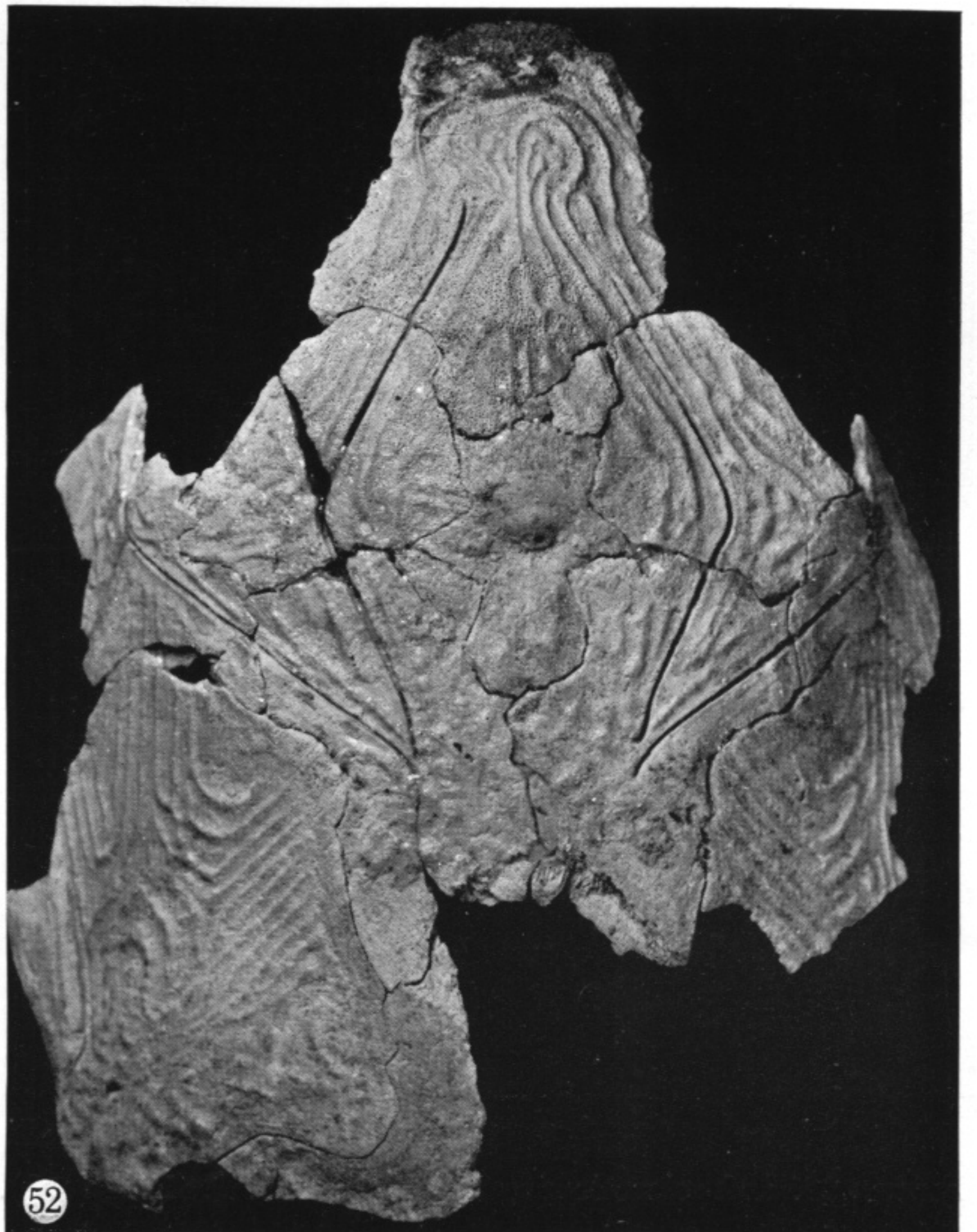
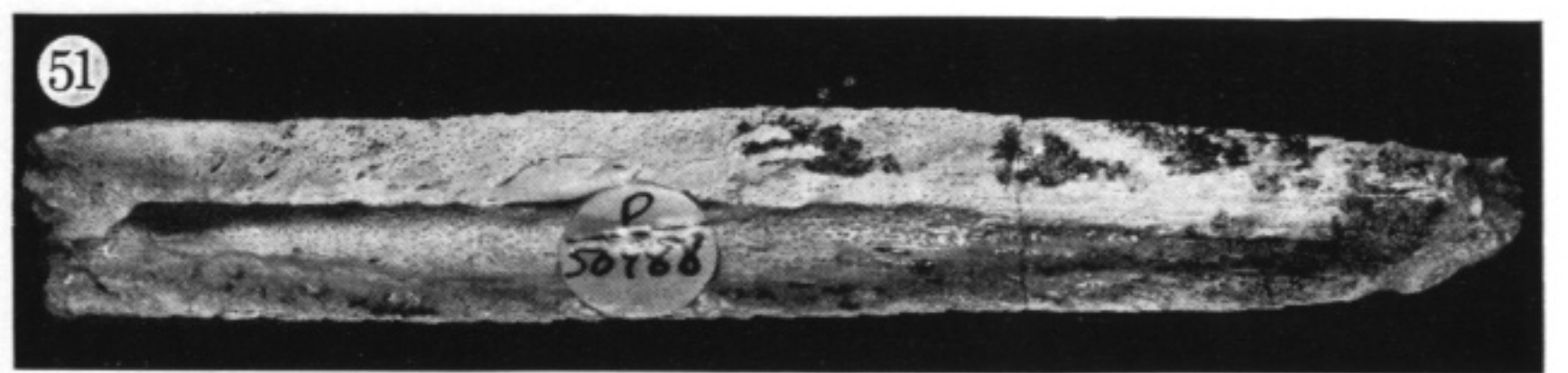
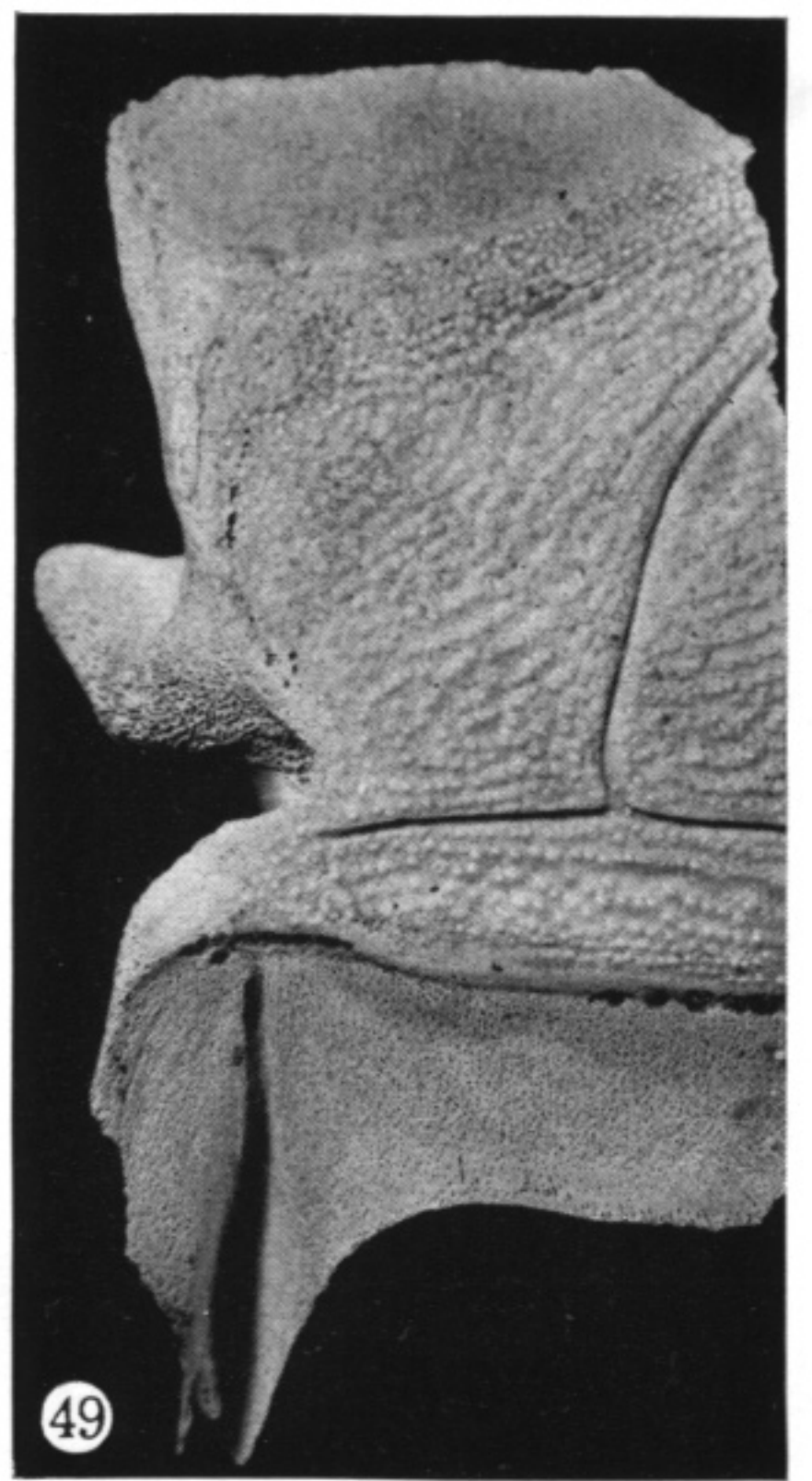
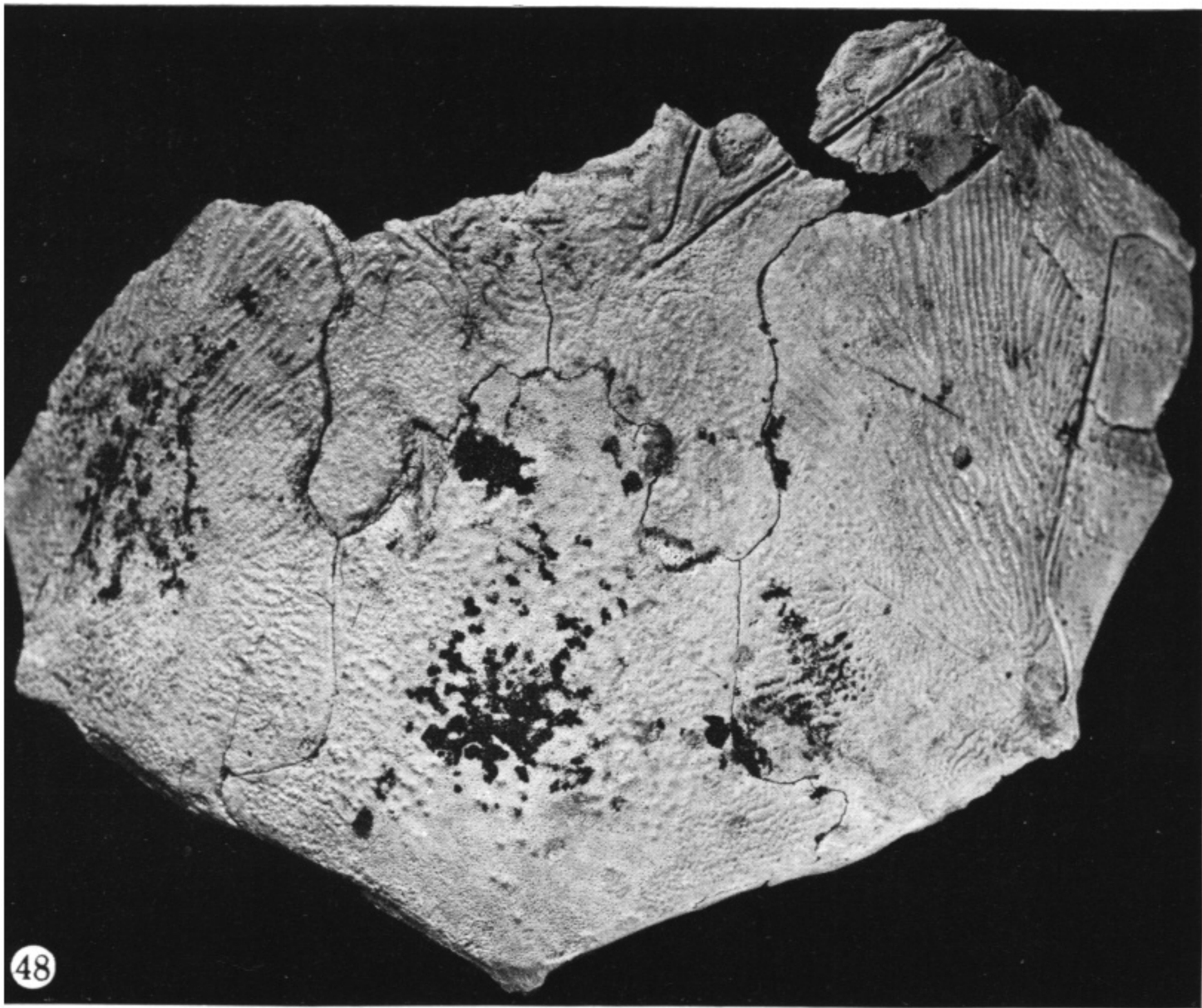
Specimen damaged subsequent to the preparation of figure 36B. P. 51153 ($\times \frac{4}{3}$).

FIGURE 44. Left posterior superognathal in aboral view. P. 50982 ($\times \frac{8}{3}$).

FIGURE 45. Same specimen as in figure 44, in oral view.

FIGURE 46. Left inferognathal in aboral view; dorsal edge to the bottom of picture. P. 51004 ($\times \frac{8}{3}$).

FIGURE 47. Same specimen as in figure 46, in oral view.



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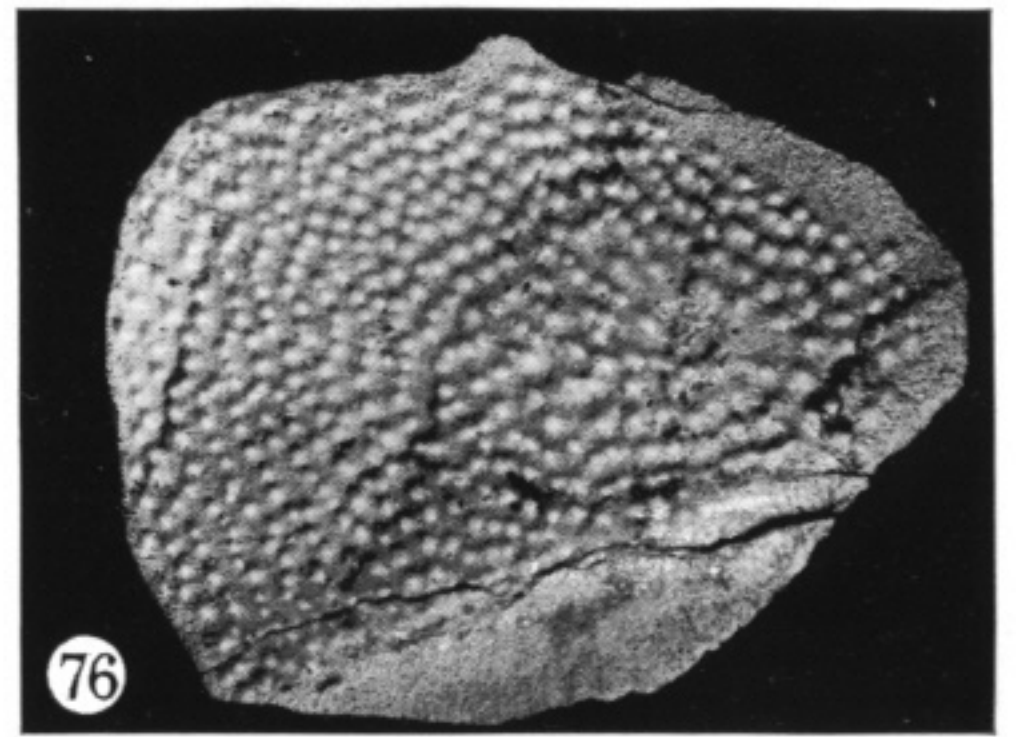
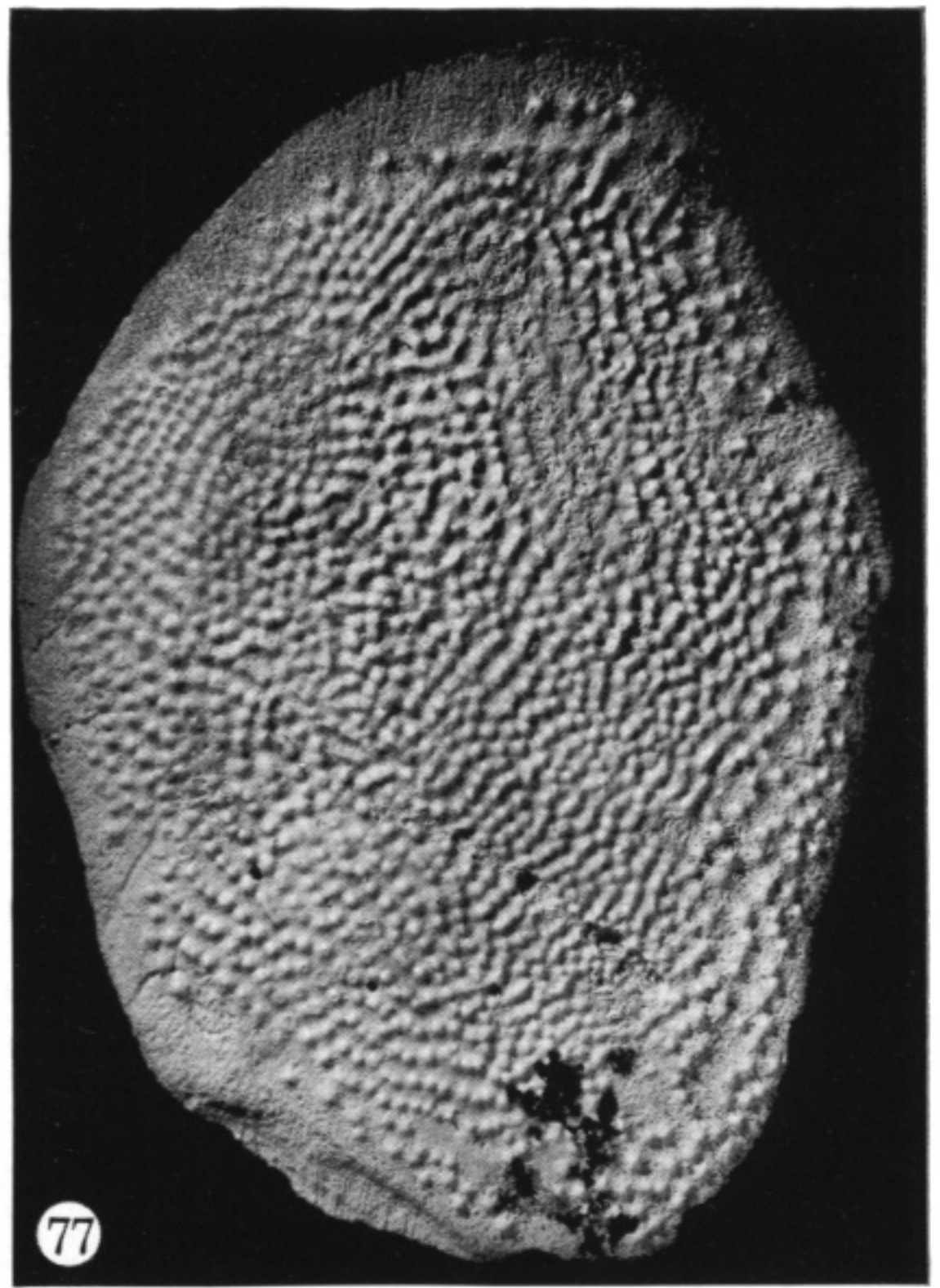
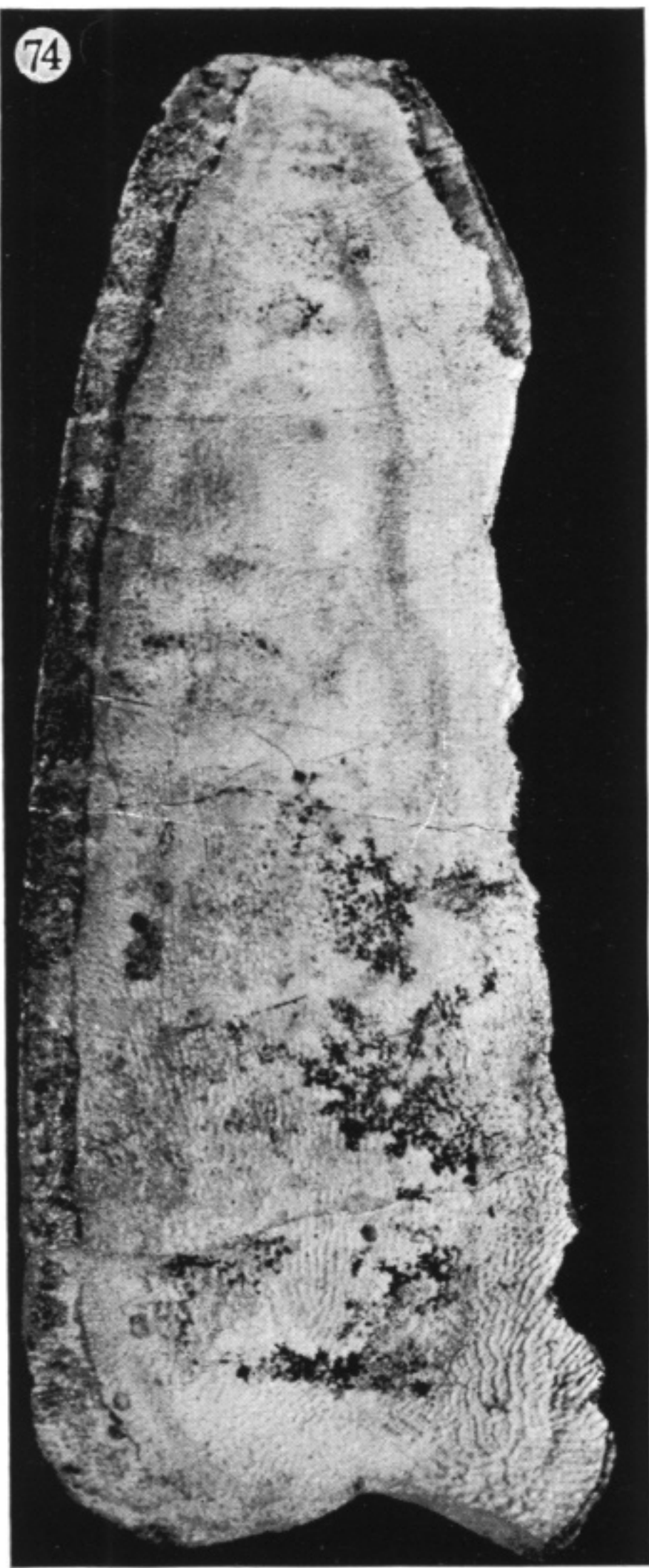
FIGURE 48. Posterior region of skull-roof. P.51152 ($\times 1$).

FIGURE 49. Left anterior dorsolateral plate; anterior region. P.50995 ($\times \frac{4}{3}$).

FIGURE 50. Right anterior ventrolateral plate. P.50986 ($\times \frac{2}{3}$).

FIGURE 51. Left spinal plate, visceral view. P.50988 ($\times 1$).

FIGURE 52. Skull-roof. P.51004 ($\times 1$).



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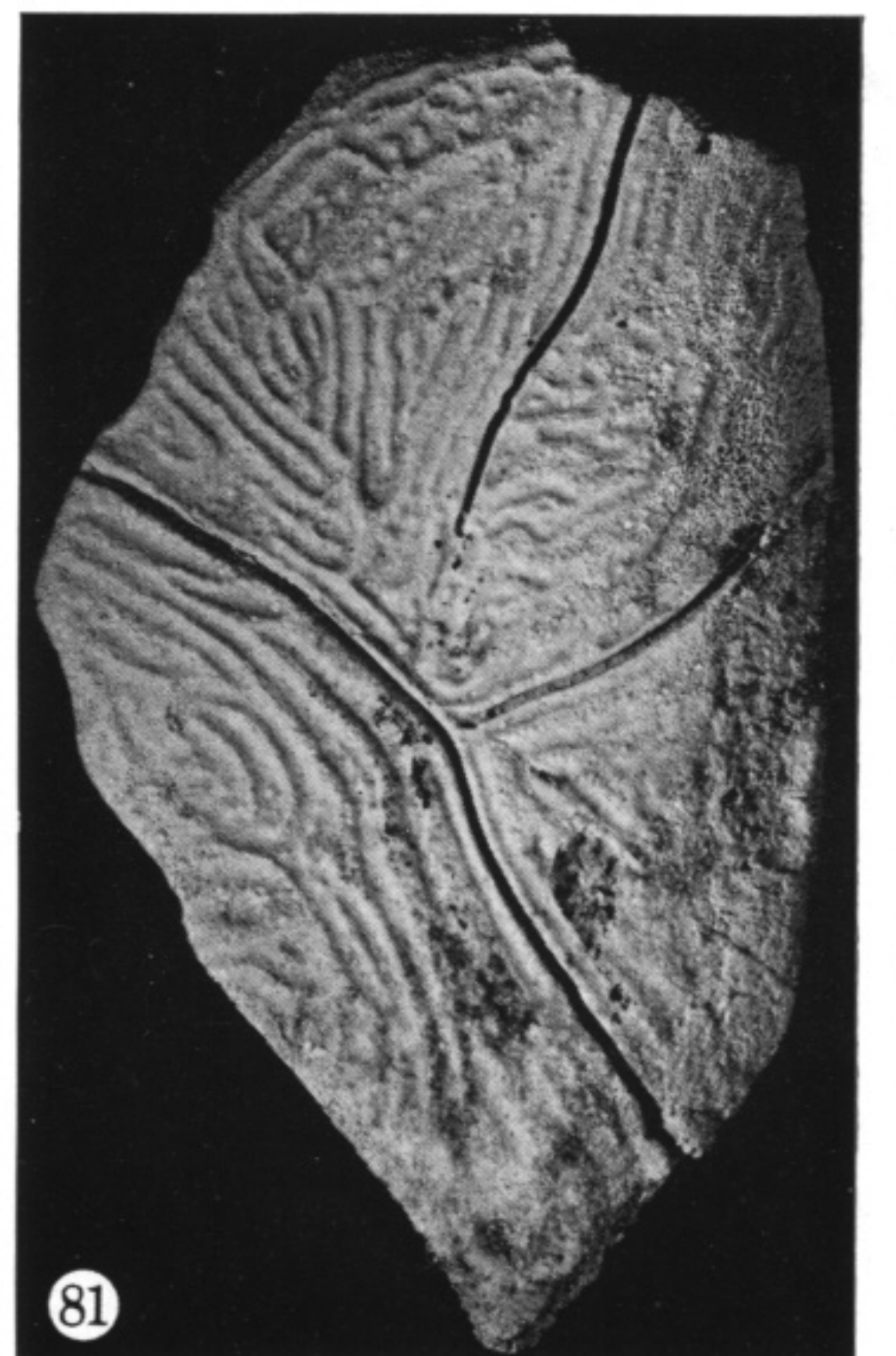
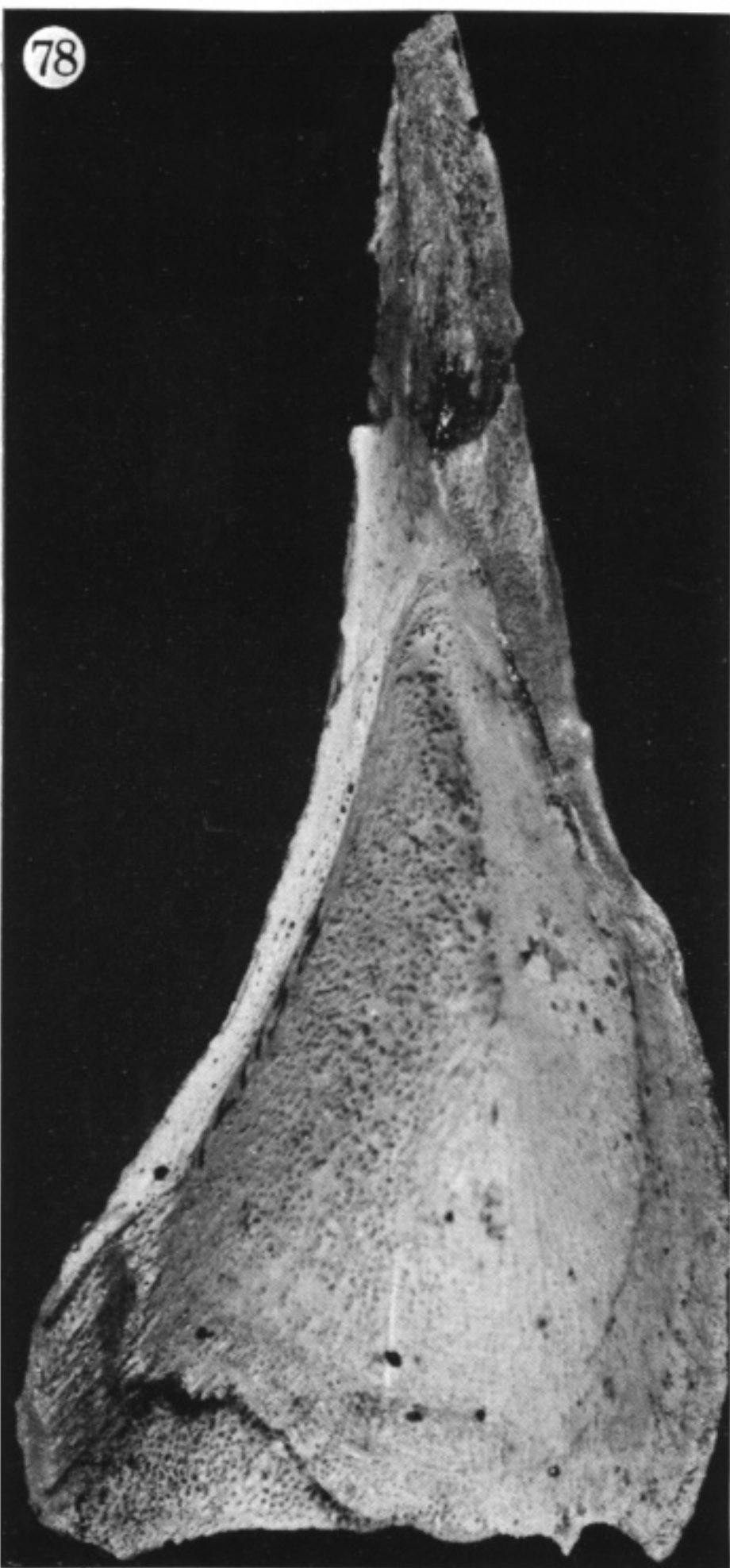
FIGURE 73. Dorsal plates of trunk-shield. Holotype, P. 50984 ($\times \frac{2}{3}$).

FIGURE 74. Left anterior lateral plate in lateral view. P. 51152 ($\times \frac{2}{3}$).

FIGURE 75. Same specimen as in figure 74, but in visceral view.

FIGURE 76. Left posterior lateral plate. P. 50987 ($\times \frac{4}{3}$).

FIGURE 77. Left posterior ventrolateral plate. P. 50987 ($\times \frac{4}{3}$).



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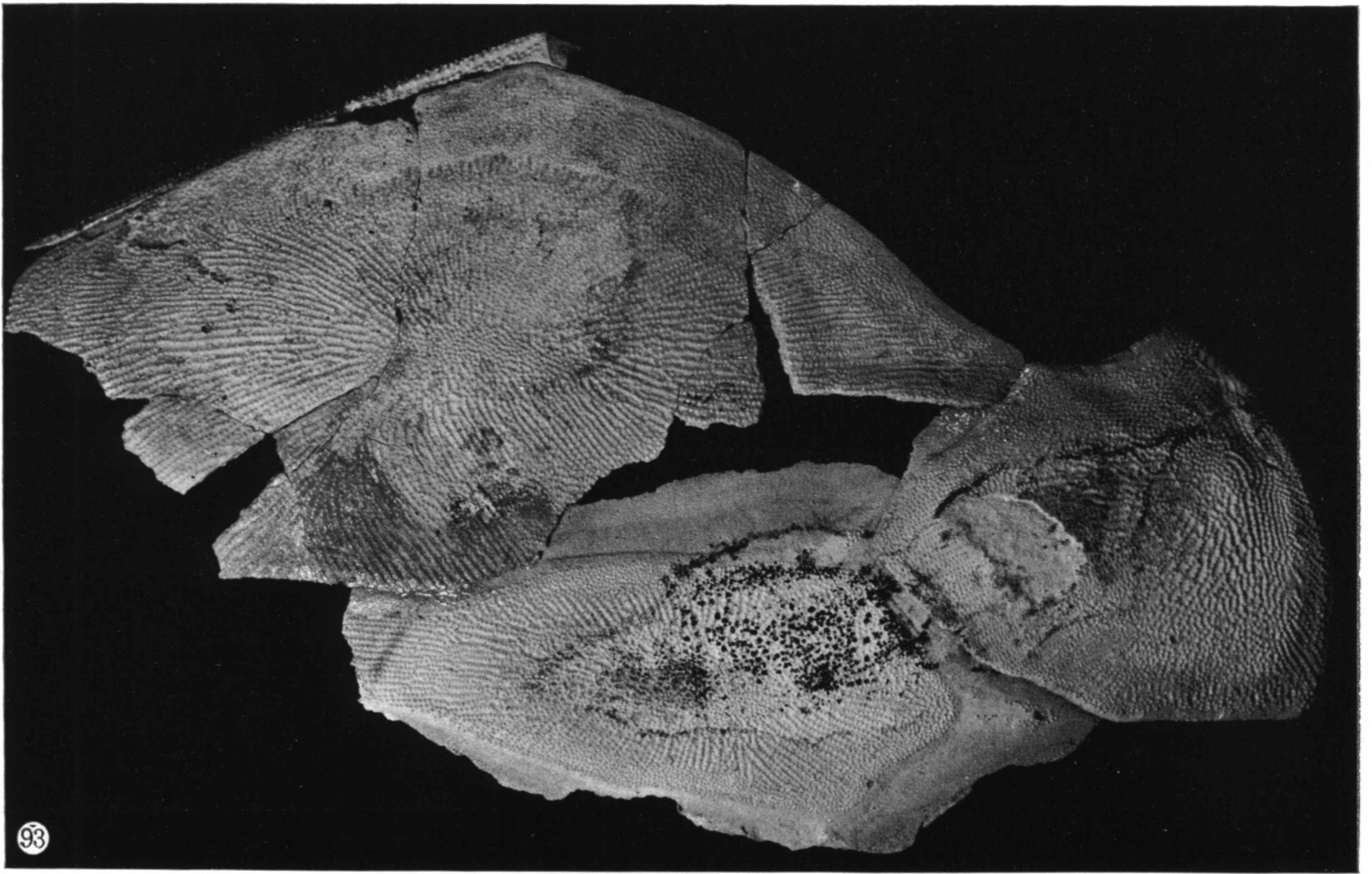
FIGURE 78. Interolateral plate in posterior view. P.51171 ($\times \frac{4}{3}$).

FIGURE 79. Same specimen as in figure 78, but in anterior view.

FIGURE 80. Anterior median ventral plate. P.51152 ($\times \frac{4}{3}$).

FIGURE 81. Left suborbital plate. P.51154 ($\times \frac{4}{3}$).

FIGURE 82. Flank plates with injected gravel *in situ*. Specimen subsequently prepared with acetic acid. P.50893 ($\times \frac{2}{3}$).



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FIGURE 92. Left spinal, anterior ventrolateral, posterior ventrolateral and posterior median ventral plates in visceral view. P. 50995 ($\times 1$).

FIGURE 93. As figure 92, in ventral view.

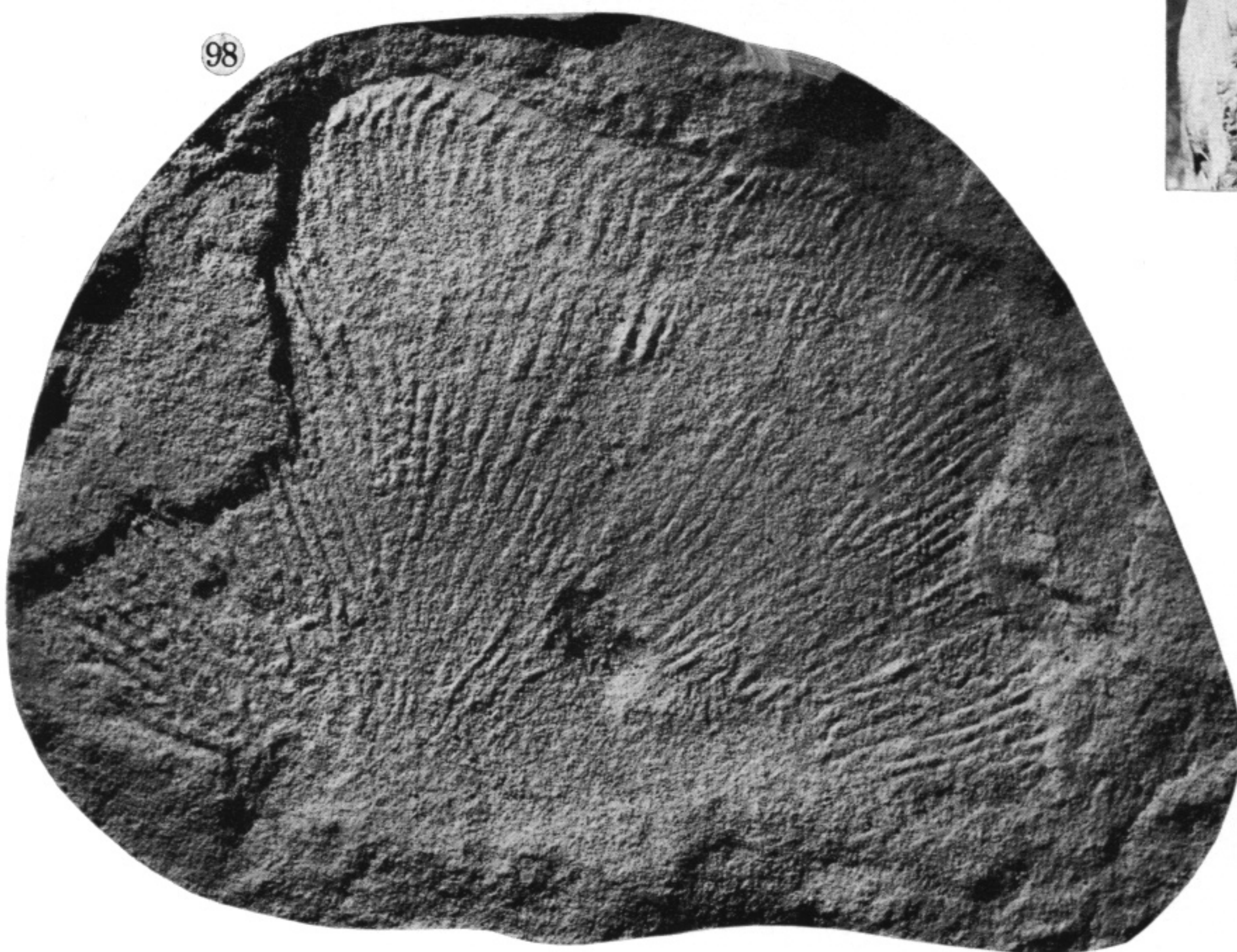
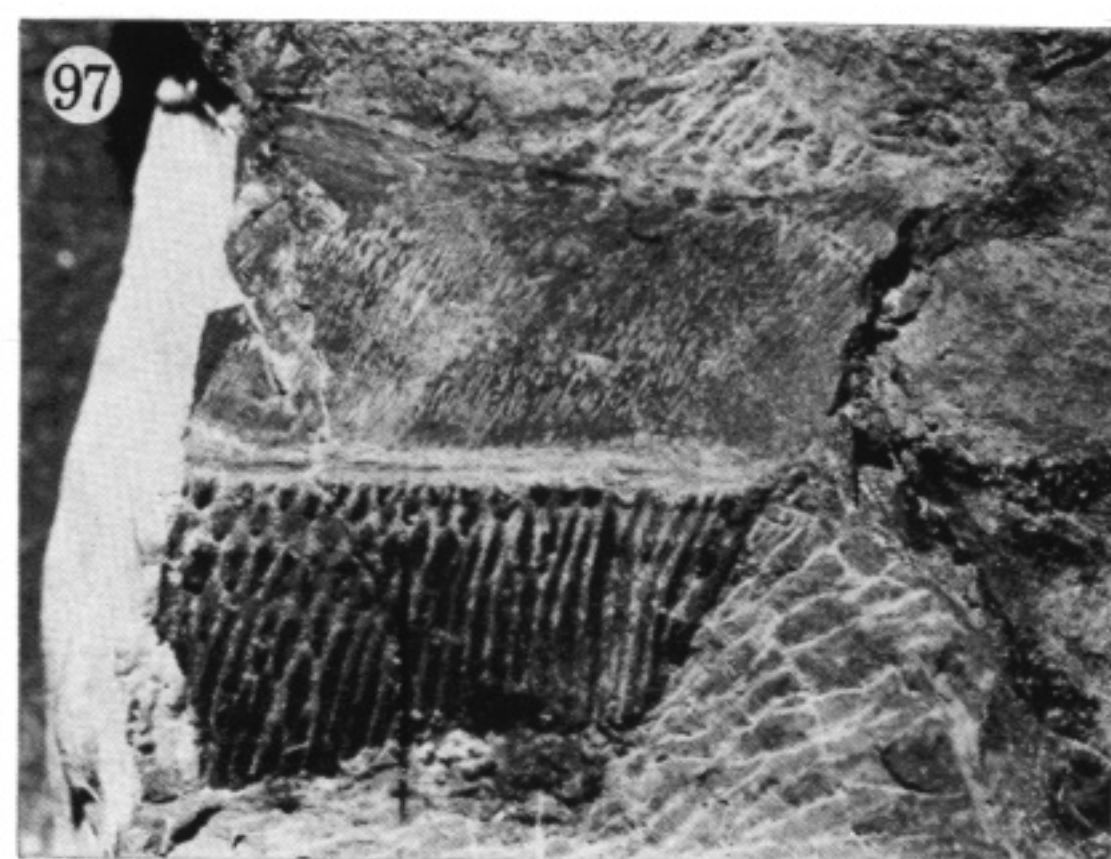
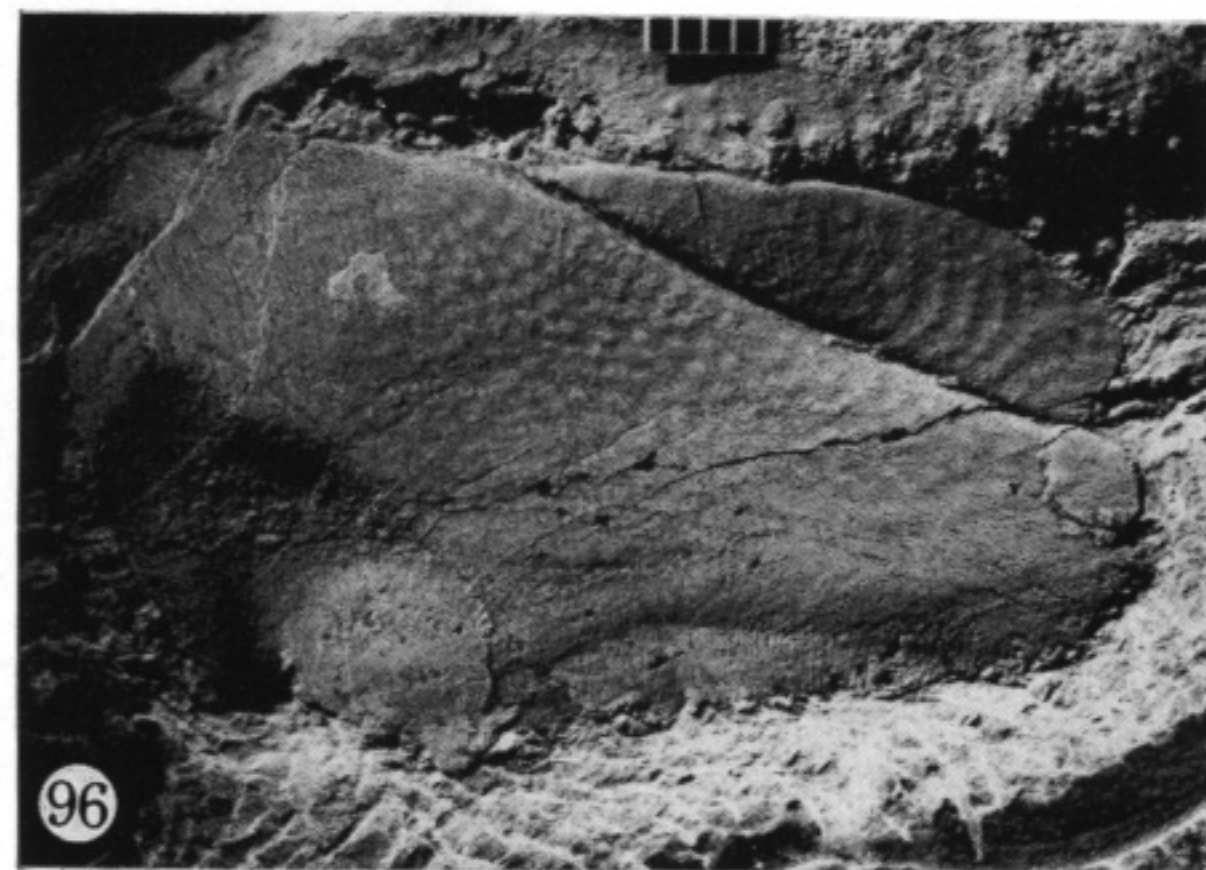
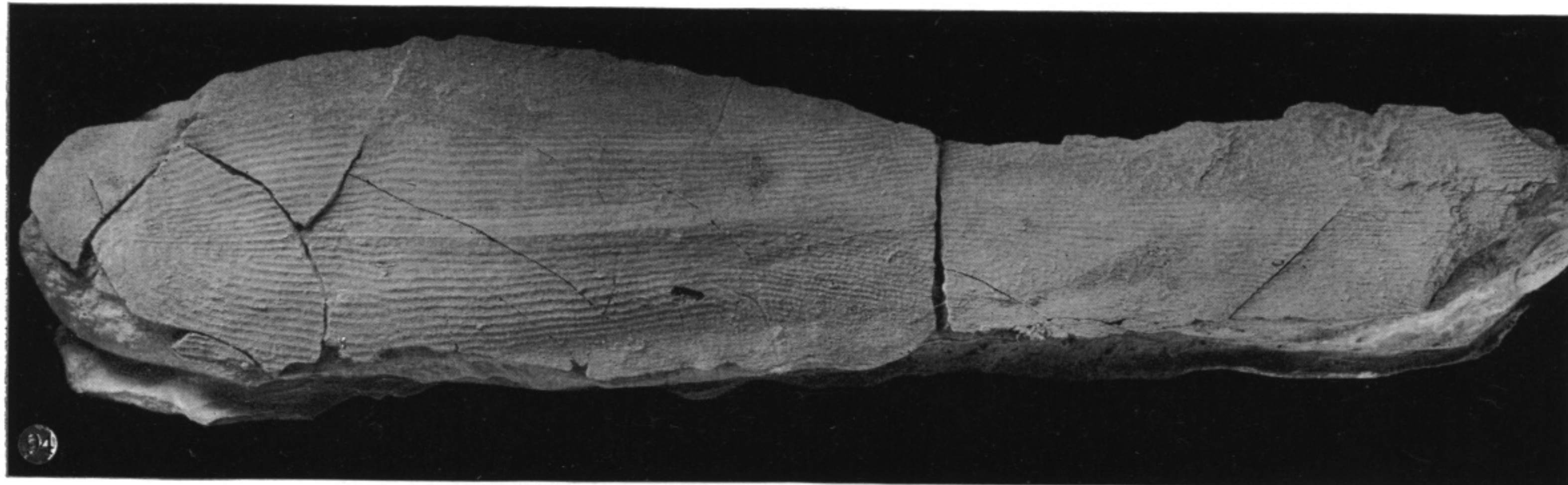


FIGURE 94. *Holonema* sp. Middle Devonian, near Thuin, Hainaut, Belgium. Median dorsal plate. Cast P.43505.

FIGURE 95. *Holonema* sp. Middle Devonian, near Thuin, Hainaut, Belgium. Right posterior dorsolateral plate. Cast P.43504.

FIGURE 96. *Holonema* sp.? Upper Devonian, Upper Plattenkalk, Bergisch-Gladbach, Germany. Right posterior lateral plate. S.M.N.H. P.5421.

FIGURE 97. *Holonema* sp. Upper Devonian, Upper Plattenkalk, Bergisch-Gladbach, Germany. Left posterior superognathal. S.M.N.H. P.5420.

FIGURE 98. *Holonema* sp. Upper Old Red Sandstone, Redheugh, Berwickshire, Scotland. Impression of undetermined plate. Cast P.52915.

FIGURE 99. *Holonema* sp. Upper Devonian, Pickwell Down Sandstone, Woolacombe Bay, Devon, England. Undetermined fragment. P.12397.