

STRUCTURE AND FUNCTION OF THE PECTORAL JOINT AND OPERCULUM IN ANTIARCHS, DEVONIAN PLACODERM FISHES

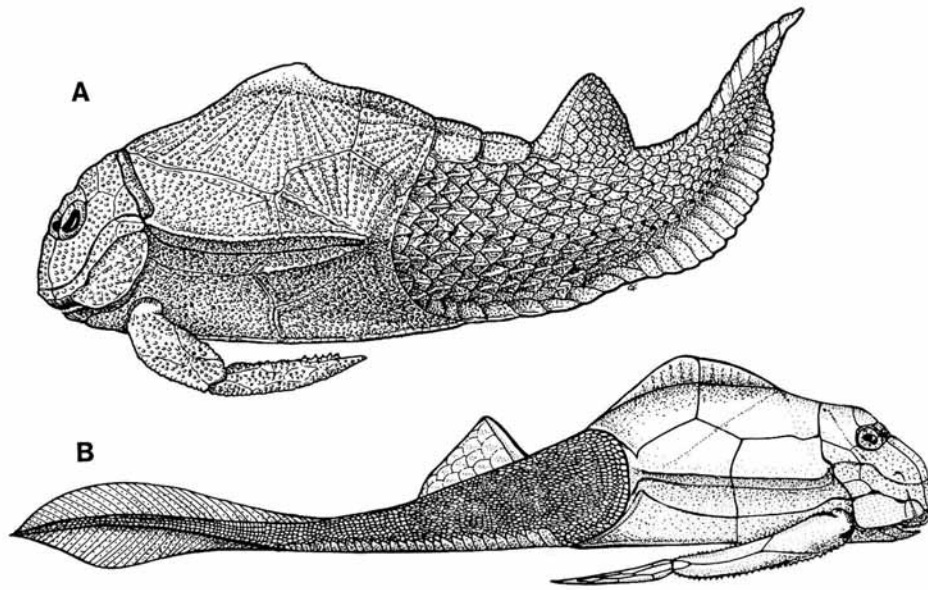
by G. C. YOUNG and ZHANG GUORUI

ABSTRACT. The structure and function of the pectoral fin joint and operculum in antiarchs (Devonian placoderm fishes) are re-examined in the light of new evidence from primitive Early Devonian representatives from South China, and acid-prepared material from the Late Devonian of Western Australia. The characteristic dermal brachial process of advanced antiarchs is absent in *Yunnanolepis*, and rudimentary in *Procondylolepis*. The latter displays a perichondrally ossified articular surface of the scapulocoracoid surrounded by three large foramina, which may be homologized with similar structures in primitive anarthroids. It is proposed that during the evolution of the complex brachial articulation of advanced antiarchs the posterior two foramina fused to form the axillary foramen, which carried nerves and vessels to the fin, but not a muscle. *Procondylolepis* is reinterpreted to have had two proximal dermal articulations on its pectoral fin, which was rotated by an abductor muscle inserting posteroventral and an adductor muscle inserting posterodorsal to the scapulocoracoid articulation. A similar interpretation is applicable to other antiarchs. Manipulation of the fin in acid-prepared *Bothriolepis* indicates that an oar-like swimming function was most unlikely. The same specimen reveals a small groove and opening adjacent to the anterior articulation of the submarginal plate (dermal operculum), which probably contained the spiracular tube.

THIRTY years ago D. M. S. Watson wrote a short morphological paper for *Palaeontology* on one of the most widely known groups of Devonian placoderm fishes, entitled 'Some additions to our knowledge of antiarchs' (Watson 1961). The two most striking morphological characteristics of the antiarchan fishes (Text-fig. 1) are their box-like thoracic dermal armour, and their highly modified pectoral fins, which are enclosed in dermal bone to form arthropod-like appendages, sometimes with a distal 'elbow' joint. One of the best-known representatives is the so-called '*Pterichthys*' or winged fish of Hugh Miller (1841) from the Middle Old Red Sandstone of Scotland (genus *Pterichthyodes*, comprehensively revised by Hemmings 1978). The unusual form of the carapace led some early workers to the conclusion that they were dealing with fossilized remains of turtles or beetles (e.g. Anderson 1840), while Romer (1966, p. 24) referred to the antiarchs as 'grotesque little creatures which look like a cross between a turtle and a crustacean'.

Their unusual appearance attracted a number of investigations into their structure and interrelationships, with the revision by Traquair (1894–1914) of Scottish antiarchs resolving most of the questions concerning the general morphology of their dermal skeleton. More detailed monographs on the group were published by Stensiö (e.g. 1931, 1948), and Gross (e.g. 1931, 1941a, 1941b), and by the time of Watson's (1961) paper the antiarchs were regarded as well known morphologically. Only some special details of functional morphology were apparently outstanding, and two such topics – respiration, and function of the peculiar arm-like appendages – were the subject of Watson's short paper.

In this paper we reconsider the two aspects of functional morphology discussed by Watson (1961) in the context of the increase in knowledge of antiarch systematics and morphology which has ensued over the last three decades. The taxonomic database for antiarchs has increased dramatically in recent years. Gross (1932) listed only seven antiarch genera, but Denison's (1978) handbook included seventeen named genera. A survey of papers recently published or in press shows now there



TEXT-FIG. 1. Reconstructions of two antiarchs. A, *Sherbonaspis hillsi* Young and Gorter, 1981; Middle Devonian; southeastern Australia; left lateral view; actual length c. 200 mm; based partly on restorations in Hemmings (1978). B, *Bothriolepis gippslandiensis* Hills, 1929; Late Devonian; southeastern Australia; right lateral view; actual length c. 380 mm; modified from Long (1983).

are thirty-seven named genera. Thus from the seven genera named in the century since Eichwald (1840) erected the genera *Bothriolepis* and *Asterolepis*, the next half century has seen more than a five-fold increase in presumed taxonomic diversity at generic level. This may be because the middle Palaeozoic vertebrate faunas of extra-European areas, which were regions of Devonian endemism (Young 1981), are now being actively investigated palaeontologically.

The classification used here follows Denison (1978) in recognizing the Placodermi as a major gnathostome group (subclass), containing some seven or more subgroups (orders), of which the Antiarchi and Arthrodira are the two of primary concern in this paper. There are four suborders within the antiarchs (Yunnanolepidoidei, Sinolepidoidei, Asterolepidoidei, and Bothriolepidoidei), but the first may be paraphyletic. It should be noted that in Stensiö's (1959) monograph on the pectoral fin, the term 'Arthrodira' was used in a more inclusive sense than current usage, equivalent to 'Placodermi' as used here. Specimen numbers mentioned in the text indicate repositories by the following prefixes: IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; CPC, Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra, Australia.

PECTORAL FIN

The remarkable arthropod-like pectoral fin of antiarchs, with its complex dermal articulation, is unique amongst vertebrates, and has attracted several detailed descriptions and analyses of function (Traquair 1894; Stensiö 1931, 1948, 1959; Gross 1931; Watson, 1961; Wells and Dorr 1985).

Westoll (1945, 1958, pp. 206–7) considered that the pectoral fin evolved by mobilization during phylogeny of the rigid spinal plate of arthrodires (and by implication that therefore the pectoral fin was not homologous to that of other gnathostomes). This view was rejected by Stensiö (1948, 1959), who showed that in *Bothriolepis canadensis* the fin contained a perichondrally ossified endoskeletal core interpreted as retaining a vestigial articulation with the scapulocoracoid. Surprisingly, in spite of this strong morphological evidence, Westoll's opinion was recently reiterated by Denison (1978) and Wells and Dorr (1985).

The structure of the complex dermal articulation between the pectoral appendage and the anterior ventrolateral plate of the trunk armour has been well known for antiarchs of Middle and Late Devonian age, where it shows little variation. The fin fitted closely around a prominent 'helmet' or brachial process (pbr, Text-fig. 2H), and the presence of this structure has been used to define a major antiarch subgroup, the euantiarchs of Janvier and Pan (1982), including the Asterolepidoidei and the Bothriolepidoidei.

Structure of the brachial articulation in early antiarchs

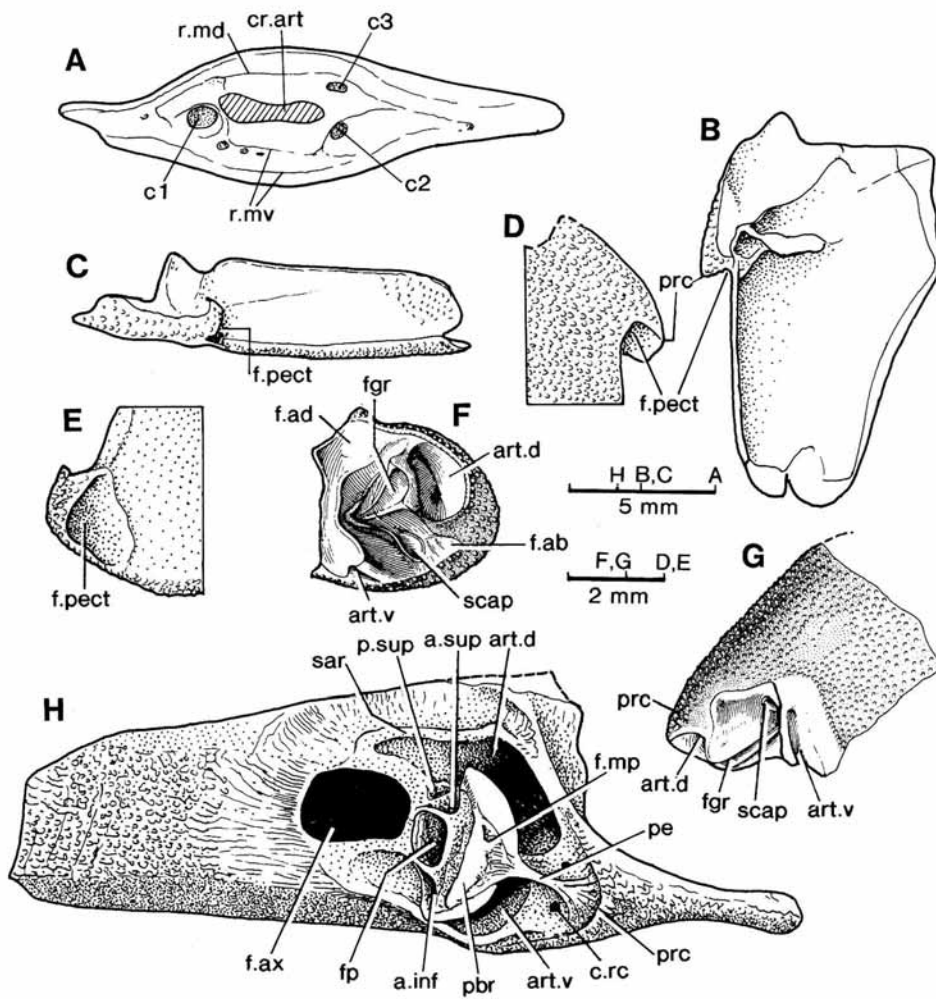
When Watson dealt with this aspect in 1961, the oldest known antiarchs were from the Middle Devonian of Europe. However, in recent years descriptions of older and apparently primitive antiarchs from South China have shown that this structure is not characteristic of the group as a whole. Zhang (1978) and Chang (1980) showed that in the Early Devonian genus *Yunnanolepis* the brachial process of Middle–Late Devonian antiarchs was absent. That this is the primitive condition for antiarchs is indicated by outgroup comparison (the dermal pectoral articulation is not known in any other group of vertebrates), and by the Early Devonian age. Zhang (1984) described another genus, *Procondylolepis*, which had an incompletely developed brachial process (Text-fig. 2F–G), and Ritchie *et al.* (in press) recently suggested that the dermal articulation was rudimentary in another major antiarch subgroup, the sinolepidids. *Yunnanolepis*, *Procondylolepis*, and another apparently primitive genus, *Phymolepis*, occur together in the Cuifengshan Formation near Qujing, Yunnan Province. They are of earliest Devonian (Lochkovian, 'Gedinnian') age, making them the oldest named antiarchs. However, undescribed antiarch remains occur in Upper Silurian sediments in the same sequence (see Pan and Dineley 1988, table 6). The sinolepidids are best known from the Late Devonian of China (Liu and Pan 1958) and Australia, but Early (?Emsian) and Middle Devonian genera also occur in South China (Zhang 1980; Ritchie *et al.* in press).

These groups provide new information on stages in the presumed phylogenetic transformation of an inferred primitive endoskeletal articulation (between basals of the pectoral fin and the scapulocoracoid), to the largely dermal articulation of advanced antiarchs. Here we consider the structure of the brachial articulation in these early antiarchs, to establish homologies between the various antiarch subgroups. The terminology used here is based on the descriptions of Stensiö (1931, 1948) for *Bothriolepis* and *Asterolepis*, as summarized in Text-figure 2H.

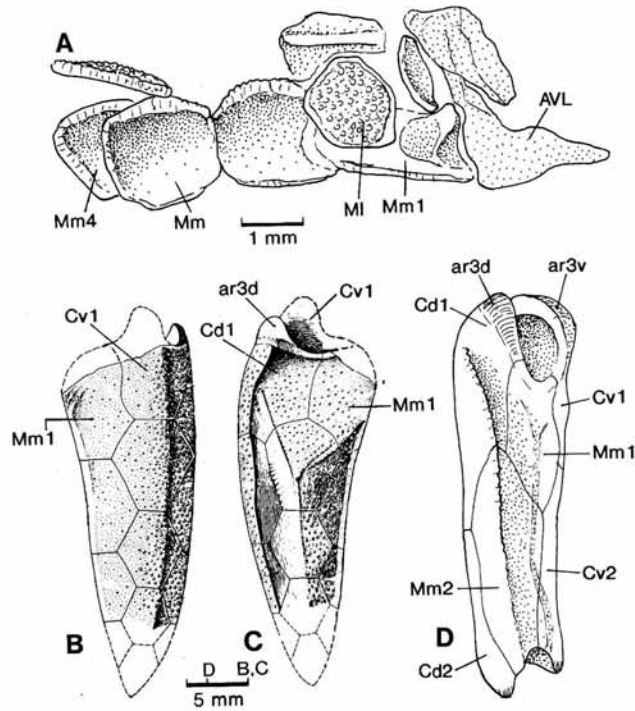
Yunnanolepis. This genus displays what may be considered the primitive condition by outgroup comparison with arthrodires. There is a small pectoral fenestra enclosed by dermal bones of the trunk armour (f.pect, Text-fig. 2B–E). As in arthrodires (Text-fig. 2A) this must have contained the lateral face of the scapulocoracoid and its articular surface for the pectoral fin. It is suggested that the funnel-like vestibule to the pectoral fenestra formed by the surrounding dermal bones could have been a preadaptation to the development of the dermal brachial articulation in other members of the group. The prominent prepectoral corner (prc) has the same morphological position as the prepectoral spines of acanthodians and the prepectoral spinal plate of various other placoderms, and Chang (1980, pl. 3, figs 2–4; pl. 5, figs 2–3) identified an incomplete suture defining a separate spinal element in several specimens of *Yunnanolepis*.

The fin itself is not known in *Yunnanolepis*, but a similar structure may be inferred to that known for the next genus discussed.

Phymolepis. This form is associated with *Yunnanolepis*, and the pectoral fin opening has the same structure (Zhang 1978; see below). In addition a series of small hexagonal plates which covered the



TEXT-FIG. 2. A, external view of the left scapulocoracoid of the arthropod *Dicksonosteus* (after Goujet 1984). B-E, left anterior ventrolateral plate of *Yunnanolepis* in dorsal, left lateral, ventral, and posterolateral views (B-C modified after Zhang 1978; D-E, showing only the region of the pectoral fenestra, modified after Chang 1980). F-G, pectoral articulation on the anterior ventrolateral plate of *Procondylolepis* in right lateral and ventral views, as figured by Zhang (1984). H, right anterior ventrolateral plate of *Bothriolepis macphersoni* in right lateral view (after Young 1988), with structures of the pectoral fin articulation labelled using the terminology of Stensiö (1931, pp. 92-97). For list of abbreviations see p. 464.



TEXT-FIG. 3. A, Dermal plates of the right pectoral fin as preserved in *Phymolepis* (right lateral view, after Chang 1980, pl. 5, fig. 1; see also Zhang 1978, fig. 11). B-C, left pectoral fin of *Procondylolepis* restored in ventral and dorsal views (modified after Zhang 1984, with proximal elements labelled according to evolutionary rather than positional homology). D, left pectoral fin of a euantiarch in mesial view (*Asterolepis*, after Gross 1931). For list of abbreviations see p. 464.

fin are preserved in one specimen (Text-fig. 3A). This specimen indicates that the arm-like appendage enclosed in dermal plates evolved before a dermal articulation.

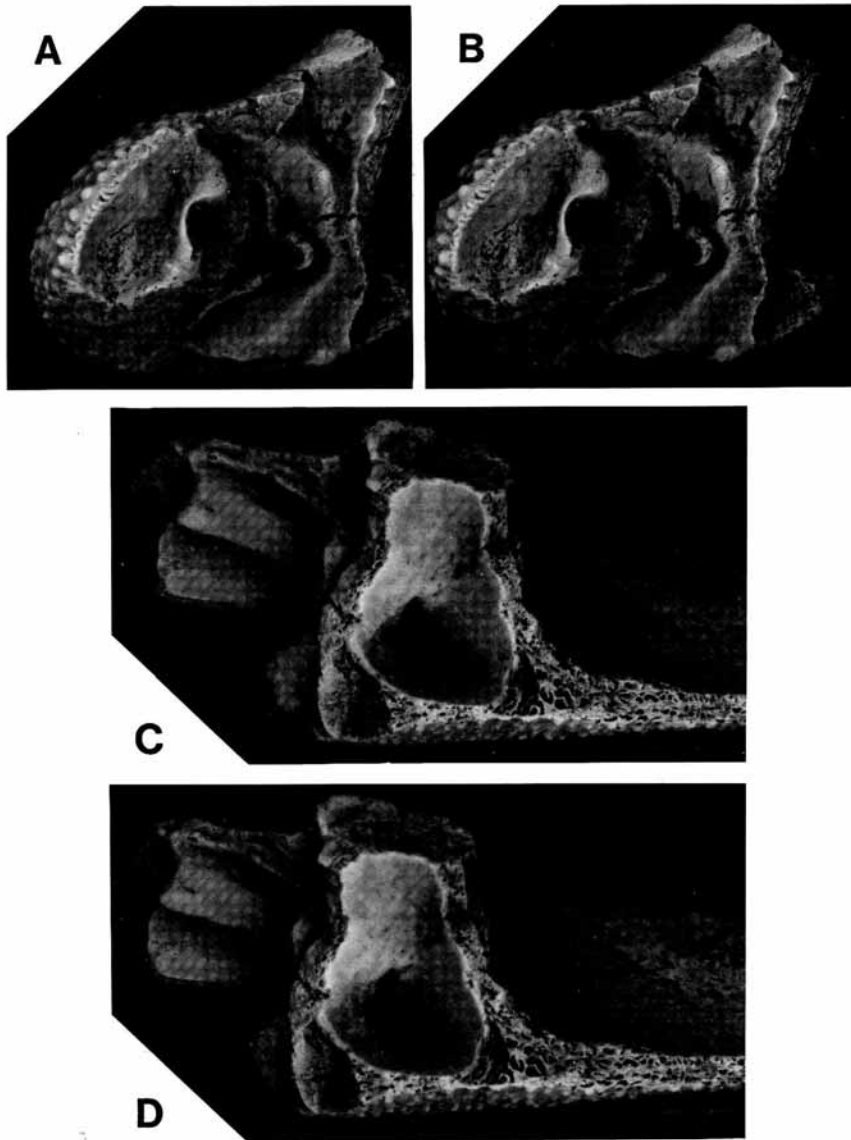
Procondylolepis. The oldest and apparently most rudimentary dermal articulation known occurs in the Early Devonian (Lochkovian) genus *Procondylolepis* Zhang 1984. Several examples of the pectoral fin have been discovered (Text-fig. 3B-C), and the brachial articulation for the fin is commonly preserved on incomplete isolated examples of the anterior ventrolateral plate (Text-figs 4-6), but apart from these the morphology of *Procondylolepis* is completely unknown. As just noted, there is good evidence that the associated genus *Phymolepis* had a similar pectoral fin, but these isolated fragmentary anterior ventrolaterals cannot be referred to *Phymolepis*, because at least one specimen of the latter (Zhang 1978, pl. 6, fig. 5), on which the reconstruction of Zhang (1978, fig. 12) is based, shows a simple pectoral fenestra developed as in *Yunnanolepis*. In other specimens of *Phymolepis* and *Yunnanolepis* this projecting part of the trunk armour is often broken off. In contrast, in *Procondylolepis* it is the only region preserved in otherwise very incomplete anterior ventrolateral plates, because of its much more robust development resulting from the evolution of the rudimentary dermal brachial articulation.

Zhang (1984) analysed the morphological relationship between the pectoral fin elements and the brachial articulation. He identified three distinct pits or grooves on the dermal surface of the pectoral fin attachment of the anterior ventrolateral, which he interpreted as dermal articulations (f.ad, art.d, art.v, Text-fig. 2F). However, on the pectoral fin only one corresponding articular process is known (ar3d, Text-fig. 3B–C), although a second may be inferred on the ventral plate (Cv1). The posterodorsal pit on the anterior ventrolateral (f.ad, Text-fig. 2F) lacks the *siebknocken* texture typical of the dermal pectoral fin articulation in antiarchs, and we now suggest that this may be reinterpreted as a muscle attachment. The remaining two articular surfaces (art.d, art.v, Text-fig. 2F) are assumed to have received two dermal articular processes of the proximal pectoral fin bones, corresponding to the dorsal and ventral articulations of more advanced antiarchs (ar3d, ar3v, Text-fig. 3D). Reinterpretation of the pectoral appendage of *Procondylolepis* as having only two rather than three dermal attachments (Text-fig. 3B–C) permits a more realistic functional interpretation, since, as previously recognized (Zhang 1984), three points of contact would severely restrict the possible movements of the fin. The functional aspect of these articulations is further considered below.

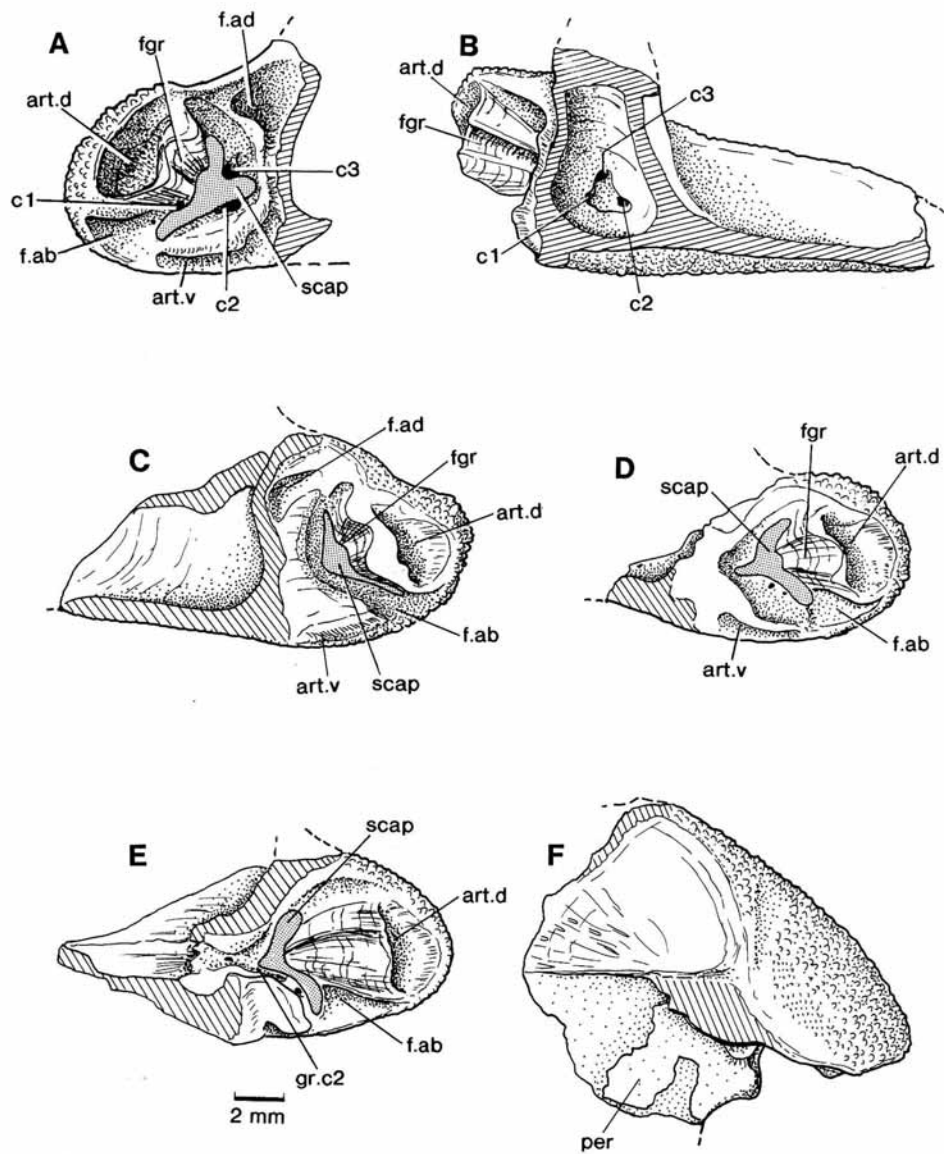
The dorsal articulation on the anterior ventrolateral (art.d, Text-fig. 2F) is developed as a distinct fossa, whilst the ventral is normally a shallow articular groove (art.v, Text-fig. 2F–G). However in some examples referred to *Procondylolepis* (e.g. IVPP.V6941.2) the ventral articulation may also form a small fossa. These structures were fully described by Zhang (1984); we summarize that work here, and illustrate four new specimens of the anterior ventrolateral of *Procondylolepis* showing the joint (IVPP.V6941.10–13). We pay particular attention to the structure in the centre of the fossa articularis formed by a thin lamina of bone, and previously identified as the 'primitive brachial process' by Zhang (1984, fig. 1B: cf. Text-fig. 2F–G). This we now regard as perichondral tissue enclosing the articular surface of the scapulocoracoid (scap, Text-fig. 5).

This bony lamina is normally incompletely preserved with its most distal part broken. It sits in a deep L-shaped cavity behind the strongly projecting prepectoral process (prc). The lamina is best preserved in IVPP.V6941.11, in which the perichondral bone is largely clear of matrix and in articular view is seen to comprise three main lobes (Text-fig. 4A–B; scap, Text-fig. 5A). The small posterior lobe has been lost in other specimens except IVPP.V6941.13 (Text-fig. 5D). Specimen IVPP.V6941.12 has the posterior part broken away to expose the inner extension of the perichondral lamina, constricted mesially and continuous with the laminar bone attached to the inside of the ventral lamina of the anterior ventrolateral plate (per, Text-fig. 5F). The anterior portion of the perichondral lamina is closely attached across the face of the pronounced groove running up the posterior face of the prepectoral process, here termed the 'funnel groove' (fgr, Text-figs 2F–G, 5). However, the perichondral layer is clearly distinguished from the dermal bone by the row of fine pores opening next to its outer surface. These pores go all around the scapulocoracoid, except where enlarged to form three big foramina (Text-fig. 4A–B; labelled c1–c3 in Text-fig. 5A). These have been traced through the bone as follows. The anterior one (c1) opens above the anteroventral lobe, and forms a short external groove running up the prepectoral process beneath the funnel groove (Text-fig. 4A–B). The second (c2) opens beneath the posterior lobe, and the third (c3) above it. The last is the largest foramen. On the inside in IVPP6941.11 is a large opening which also subdivides into three canals (Text-figs 4C–D, 5B). The posterior one is seen on IVPP.V6941.12 to lead to opening c2 (gr.c2, Text-fig. 5E). The dorsal opening leads to c3, and the anterior one, although filled with matrix, can be assumed to lead to opening c1, as labelled in Text-figure 5B.

Sinolepids. Within this group, the pectoral fin articulation is best known in a new Australian genus (Text-fig. 7C), in which it was also apparently of primitive structure (Ritchie *et al.* in press). It comprised a triangular dorsal and a small ventral articular area respectively for the first dorsal and ventral central plates of the pectoral appendage, which pivoted around a single axis passing through these articulations. This is very different from the brachial articulation of more advanced antiarchs (bothriolepidoids, asterolepidoids), because the brachial process was incompletely formed, and lacked a differentiated pars pedalis. The anterior edge of the brachial process was apparently



TEXT-FIG. 4. *Procondylolepis*; IVPP.V6941.11; incomplete left anterior ventrolateral, whitened with ammonium chloride. A-B, left lateral (articular) view, stereo pair. C-D, mesial view, stereo pair, left on top. All $\times 6$.



TEXT-FIG. 5. *Procondylolepis*; incomplete anterior ventrolateral plates. A-B, IVPP.V6941.11; a left plate, in left lateral and mesial views. C, IVPP.V6941.10; a right plate, in right lateral view. D, IVPP.V6941.13; a right plate, in right lateral view. E-F, IVPP.V6941.12; a right plate, in right lateral and dorsal views. Broken surfaces cross-hatched. For list of abbreviations see p. 464.

continuous with the prepectoral corner of the anterior ventrolateral plate, as in *Procondylolepis*. On the assumption that this was not a degenerate condition, the sinolepids also show that the complete brachial process appeared later in phylogeny than the distal joint in the pectoral fin (Ritchie *et al.* in press).

Homology of structural components in early antiarchs

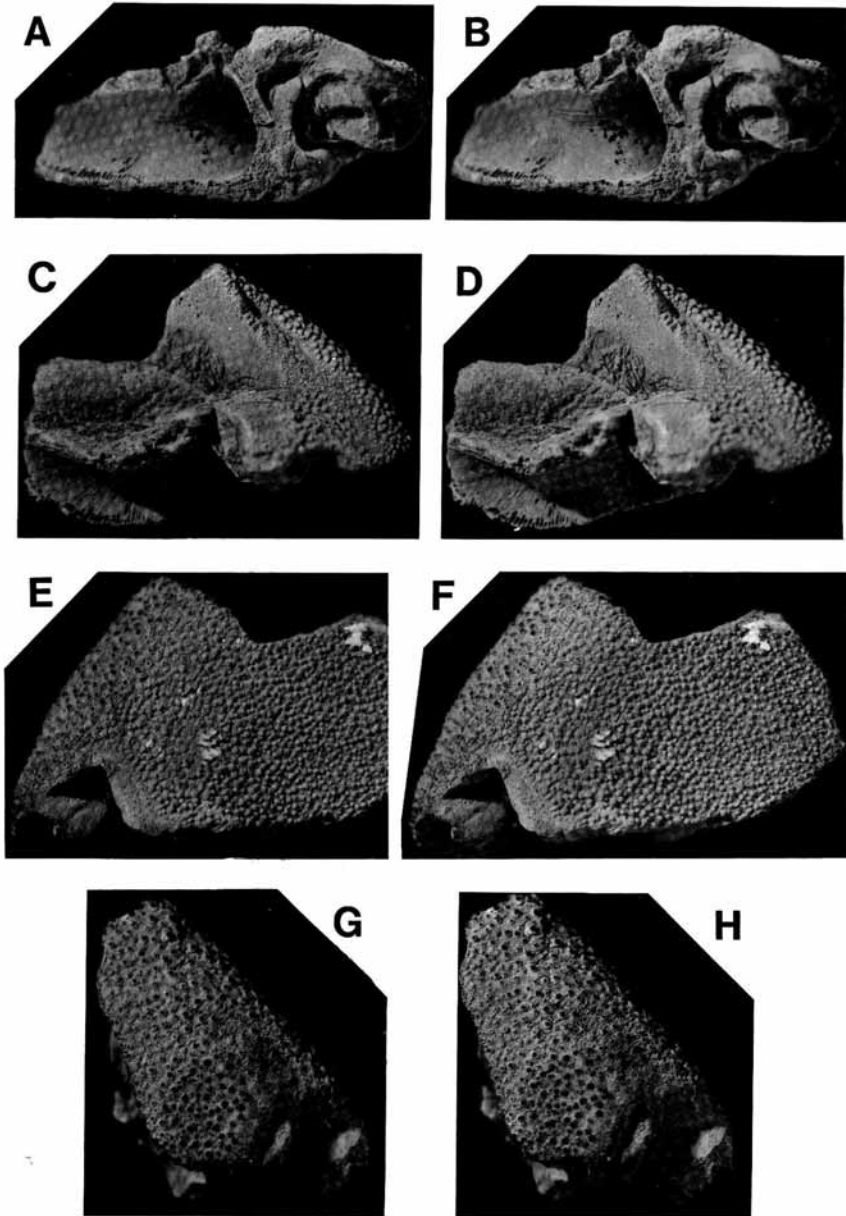
The interpretation of the skeletal features of the pectoral fin articulation of antiarchs is facilitated by comparing the presumed most primitive antiarch condition with that of better-known placoderm groups, such as primitive arthrodires.

Stensiö (1959) identified three types of pectoral fin in placoderms: (i) 'holosomactidial', the type seen in one group of arthrodires (pachyosteorhynchids), which is broad-based, with little concentration of radials, suggestive of the embryonic fin structure of sharks, and considered to be the primitive type; (ii) 'merosomactidial', considered to be derived from the previous type by fusion of anterior radials with the endoskeletal shoulder girdle to form the endoskeletal prepectoral process, and modification of covering scales to form the exoskeletal spinal plate of various placoderm groups; and (iii) 'monomesorhynchid', the most specialized pectoral fin of any fish, and restricted to the Antiarchi. He considered that this evolved by concentration of the endoskeleton into a single rod encased in a much modified exoskeleton of numerous plates, and with a unique double articulation comprising both exoskeletal and endoskeletal components.

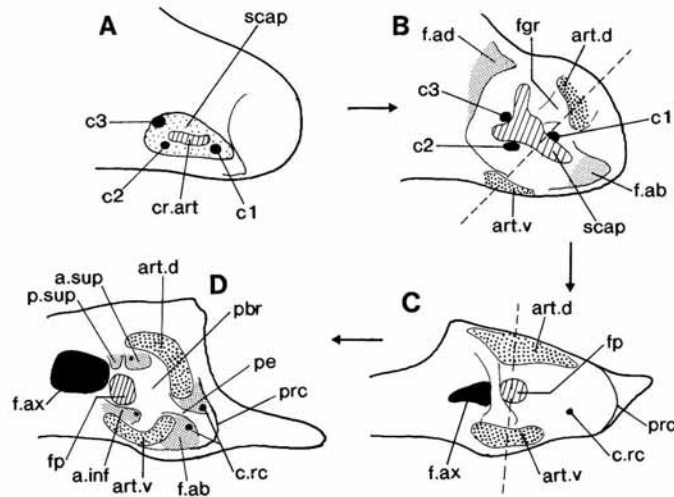
Stensiö (1959, p. 64) could not decide whether the 'monomesorhynchid' fin of antiarchs was derived from the 'holosomactidial' or 'merosomactidial' condition, but these cumbersome terms have not been adopted by other authors, and the first two types have neither the significance nor phylogenetic connotation which Stensiö believed. A narrow-based fin is now considered the primitive condition for placoderms generally (for discussion see Young 1986, pp. 12, 47), and within arthrodires Goujet (1984) suggests that three basal elements articulating with the scapulocoracoid was probably the primitive condition, as in chondrichthyans and actinopterygians.

However, other aspects of Stensiö's (1959) interpretation of the antiarch pectoral fin, derived primarily from comparative anatomy rather than observation of fossils, are now supported by new fossil evidence. Stensiö suggested that the endoskeletal component of the pectoral fin articulation was between the proximal end of the endoskeletal bar within the fin (presumably fused basal elements, as identified in *Bothriolepis* by Stensiö 1931, fig. 55), and a special glenoid cartilage which filled the funnel pit, this glenoid cartilage being derived embryologically as a lateral process of the scapulocoracoid, and corresponding to the articular crest of other placoderms. In contrast Watson (1961, fig. 3B) considered the funnel pit to have received the axial skeleton of the fin, but this would have severely restricted its movements. Basing his views on observations of *Bothriolepis canadensis*, Stensiö hypothesized that in adults this glenoid cartilage became completely separated from the rest of the scapulocoracoid, which was situated inside the dermal pectoral girdle.

In *Procondylolepis* the trilobate form of the articular surface to the scapulocoracoid (glenoid cartilage) as just described, and the three major foramina opening around it, may be compared with the structure of the scapulocoracoid in primitive representatives of two major subgroups of arthrodires (phlyctaenioids and actinolepids). Goujet (1984, pp. 68–71) illustrated the articular portion of the scapulocoracoid in *Dicksonosteus* and *Kujdanowiapsis*, both of which have a short horizontal articular crest (cr.art., Text-fig. 2A) surrounded by three major canals, anteroventral, posteroventral, and posterodorsal to the crest (cl-3, Text-fig. 2A). The last may form a notch between the edge of the scapulocoracoid and the dermal border of the pectoral fenestra (Goujet 1984, fig. 71C–D). As pointed out by Goujet (1984, p. 146), the interpretation of the neurovascular supply to the fin in arthrodires is aided by the fact that the pectoral fenestra completely enclosed the fin articulation in dermal bone. Thus all nerves and vessels for the pectoral fin must have traversed the three observed canals. By comparison with modern representatives of other groups (e.g. Marples 1936; Jessen 1972) each canal probably carried both nerves and vessels. Goujet suggested that the anterior canal probably supplied the propterygium, and possibly also the mesopterygium, and may be the homologue of the ventral brachial canal in the acanthothoracids



TEST-FIG. 6. For legend see opposite.



TEXT-FIG. 7. Hypothesized stages in the evolution of the pectoral fin articulation of antiarchs (right articulation illustrated, with anterior end to the right). Arrows indicate suggested direction of transformation series. Heavy stipple, dermal articular surfaces for the pectoral appendage; light stipple, muscle insertion areas. Dashed lines in C-D show suggested axes of rotation of pectoral appendage around dorsal and ventral dermal articulations. A, hypothesized primitive condition, with the scapulo-coracoid enclosed in a small pectoral fenestra, and bearing a short horizontal articular crest, with three neurovascular canals as in primitive arthrodires, and no dermal articular contact. B, *Procondylolepis*, showing development of anteroventral and dorsal lobes to the articular crest, and muscle attachments to surrounding dermal bone. C, sinolepid (after Ritchie *et al.* in press, fig. 11c), showing posterior migration of dorsal and ventral articular areas to lie above and below circular glenoid cartilage within funnel pit, and coalescence of posterior two canals to form axillary foramen (external opening of rostrocaudal canal not yet identified in this form). D, *Bothriolepis* (a euantiarch), showing enlargement of dorsal and ventral articular fossae as deep subcircular grooves which excavate out the brachial process, associated with differentiation of muscle insertions (cf. Text-fig. 2H). For list of abbreviations see p. 464.

Palaecanthaspis and *Romundina* (Stensiö 1969, fig. 233; Ørving, 1975, pl. 5, fig. 8), because of its similar position anteroventral to the articular crest. The posterior canals probably carried the neurovascular supply to the metapterygium. The previously unrecognized posterodorsal canal may have carried a metapterygial vein, because of its large size.

In the light of Goujet's work we suggest a direct correspondence with the three large canals surrounding the scapulo-coracoid of *Procondylolepis* described above. The three lobes may indicate persistence of three pectoral fin basals (possibly partly coalesced), with three corresponding neurovascular canals. However, because the distal part of the perichondral lining of the glenoid cartilage is not preserved, the actual shape of the articular area is uncertain. Since the anteroventral lobe passes beneath the anterior canal, whereas in arthrodires the anterior end of the crest is situated

TEXT-FIG. 6. *Procondylolepis*; incomplete anterior ventrolateral plates, all whitened with ammonium chloride. A-B, IVPP.V6941.10; a left plate, in posterolateral view, stereo pair, $\times 3.2$. C-D, IVPP.V6941.10; dorsal view, stereo pair, $\times 3$. E-F, IVPP.V6941.10; ventral view, stereo pair, $\times 3.5$. G-H, IVPP.V6941.11; a left plate, in ventral view, stereo pair, $\times 3$.

posterodorsal to the anterior canal, this anteroventral lobe may be interpreted, together with the dorsal lobe, as a new formation. The central region, extending from the funnel groove to include the posterior lobe, may be suggested as the homologue of the short horizontal articular crest of primitive arthrodires, and thus represents the primitive condition in a hypothetical common ancestor of known antiarchs (Text-fig. 7A).

There are two major morphological differences between the arrangement in *Procondylolepis* and that of primitive arthrodires, but both can be explained in terms of the much constricted dermal pectoral fenestra in these primitive antiarchs. All three neurovascular canals in *Procondylolepis* lie between the surrounding dermal bone and the perichondral lamina enclosing the scapulocoracoid. As noted above, the posterodorsal canal in some arthrodires also lies between the scapulocoracoid and the dermal margin of the pectoral fenestra, although in others it is enclosed within the cartilage like the other two canals. Secondly, the attachment surfaces for the fin muscles are situated on the surrounding dermal bone, whereas in *Dicksonosteus* various ridges and depressions on the scapulocoracoid are interpreted by Goujet as muscle attachment surfaces (r.md, r.mv, Text-fig. 2A). With the constriction of the dermal pectoral fenestra these muscles in primitive antiarchs were presumably displaced to attach on the contiguous dermal bone.

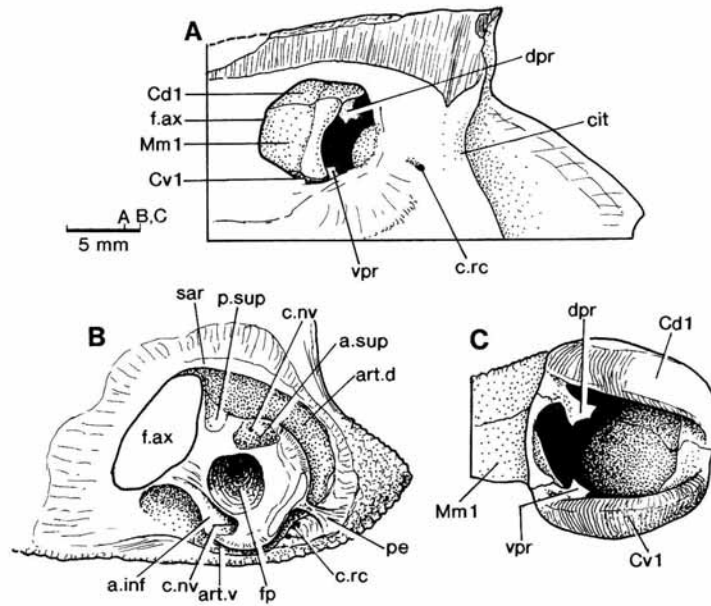
Homology of structural components of the brachial articulation in euantiarchs

The homologies just proposed between the pectoral articulation of a primitive arthrodire (entirely on the scapulocoracoid as in other fishes), and the presumed rudimentary pectoral articulation of *Procondylolepis* (involving a dermal articulation with the pectoral appendage, as in more advanced antiarchs), provide the basis for determining the homology of structural components in the much more complex dermal articulation of euantiarchs, as listed below. It is this fully developed pectoral articulation which defines the Euantiarchi in the sense of Janvier and Pan (1982). In view of the rudimentary nature of the brachial articulation in *Procondylolepis* we cannot agree with the opinion of Pan *et al.* (1987, fig. 51), who include *Procondylolepis* also within the Euantiarchi. The morphological transformations implied by the homologies set out below are summarized in Text-figure 7.

Prepectoral corner (prc, Text-figs 2H, 7C–D). This ornamented lateral projection at the anterior edge of the brachial articulation of euantiarchs is clearly homologous to the ornamented lateral edge of the prepectoral process of *Procondylolepis* (prc, Text-fig. 2G).

Funnel pit (fp, Text-fig. 2H). This unique structure of euantiarchs is a clearly defined conical pit passing through the centre of the brachial process (pbr). It may be of compound origin, with both perichondral and dermal components. In well-preserved acid prepared *Bothriolepis* from Gogo, Western Australia (Young 1984, fig. 7; cf. Text-fig. 8B) it is lined with laminar bone showing concentric striations, which are somewhat reminiscent of the striations across the 'funnel groove' running out from the scapulocoracoid in *Procondylolepis* (fgr, Text-fig. 5). We interpret this groove to be the homologue of the anterior wall of the funnel pit, although in *Procondylolepis* the groove is clearly a dermal structure. We accept the interpretation of Stensiö (1959) that the pit in euantiarchs contained a glenoid cartilage forming the endoskeletal articulation with the pectoral fin. This implies that the walls of the pit may be partly of perichondral origin. In euantiarchs the posterior wall has a distinct lamina lining the pit, which may even be recognized in latex casts of specimens preserved as moulds in sandstone (e.g. Young 1988, pl. 14, fig. 1). We suggest therefore that this is homologous to the posterior perichondral wall of the glenoid cartilage (i.e. external surface of the scapulocoracoid) in *Procondylolepis*. This implies that the trilobed perichondrally-lined space of *Procondylolepis* was contracted and modified during phylogeny into the subcircular or quadrilateral space of the funnel pit seen in euantiarchs. The distinction between the clearly differentiated dermal and perichondral bone layers described above in the funnel groove of *Procondylolepis* is no longer apparent in euantiarchs.

Processus brachialis (pbr, Text-figs 2H, 7D). This most prominent feature of the articulation of



TEXT-FIG. 8. *Bothriolepis* sp; CPC 25205 (same specimen as described by Young 1984); early Upper Devonian Gogo Formation; Canning Basin, Western Australia. A, inner view of the lateral lamina of the left anterior ventrolateral plate, looking out through the axillary foramen with the pectoral fin in fully adducted position. B, right lateral view of the pectoral fin articulation on the right anterior ventrolateral plate. C, articular view of the proximal end of the left pectoral appendage. For list of abbreviations see p. 464.

euantiarchs we also regard as of compound origin, and without a specific homologue in *Procondylolepis*. We suggest a homology between the dorsal and ventral articular fossae of *Procondylolepis* on the one hand, and euantiarchs on the other (art.d, art.v, Text-fig. 2F–H). We consider the dermal part of the brachial process to have resulted from enlargement of these articular fossae, which excavated out deep hemispherical grooves in the dermal bone. The remaining septum of bone separating these two fossae anteroventrally formed the *pars pedalis* of the brachial process in Stensiö's terminology (pe, Text-figs 2H, 7D), and the 'island' of dermal bone enclosed by these excavations is the *pars condyloidea* of the brachial process (pbr).

Axillary foramen (f.ax, Text-figs 2H, 7C–D). This large foramen in euantiarchs lies directly behind the funnel pit, and is separated from it by a partition made up of the laminar lining of the pit just mentioned, and a connection of smooth bone apparently of dermal origin. Stensiö (1931, 1959) and Gross (1931) considered this foramen to have contained the adductor muscle for the fin, or a tendon of that muscle, and Stensiö (1931, p. 96) noted that the smooth anterior wall of the foramen may have been a trochlea for a strong tendon inserted on the pectoral fin. In sinolepids, however, this partition is a less robust upstanding lamina, more comparable to the posterior perichondral lamina of the glenoid cartilage in *Procondylolepis*, and evidently not developed for tendon attachment. Watson (1961), in noting the small size of the axillary foramen in *Pterichthyodes* compared to that of *Bothriolepis*, suggested that it was much too small for a muscle, and must have contained instead the main nerve and artery for the fin. Since in *Procondylolepis* the three observed canals around the

scapulocoracoid correspond to those in primitive arthrodires, we are led to a similar conclusion to Watson. The two canals (c2, c3, Text-figs 5A, 7B) of *Procondylolepis* are separated only by the posterior lobe of the scapulocoracoid, and we suggest that when this articular surface was modified into a subcircular shape these two canals coalesced into a single larger opening (f.ax, Text-fig. 7C-D), bounded posteriorly by dermal bone, and anteriorly by the perichondral lining of the scapulocoracoid. The much more robust anterior margin of this foramen in euanthiarchs, which forms the posterior wall of the funnel pit, may be a thickened perichondral structure, or was perhaps supplemented by a dermal partition.

Rostricaudal canal (c.rc, Text-figs, 2, 7-8). Stensiö (1931) described and named this structure in *Bothriolepis canadensis*. The canal passes through the base of the internal transverse crista of the anterior ventrolateral plate from an opening just in front of the axillary foramen (Text-fig. 8A). The largest of its several branches opens externally adjacent to the base of the pars pedalis of the brachial process, and other small branches include one passing into the base of the funnel pit. This appears to be a relatively constant arrangement amongst antiarchs. The canal has not been described in *Yunnanolepis* or *Pterichthyodes* (Hemmings 1978; Zhang 1978), but in both *Hyrceanaspis* and *Sinolepids* it is known to open internally between the two divisions of the internal transverse crista (Janvier and Pan 1982, fig. 1c; Ritchie *et al.* in press, fig. 11b). A foramen in the same position is seen in *Asterolepis* (Gross 1931, pl. 5, fig. 4; Karatajute-Talimaa 1963, fig. 11), and in *Yunnanolepis* (Chang 1980, fig. 3b; pl. 3, fig. 2). In acid-prepared *Bothriolepis* from Gogo (Text-fig. 8) the rostricaudal canal opens internally through a small but distinct foramen in front of the axillary foramen. On both sides it opens anteriorly through the crista, with small foramina passing externally to the muscle depression anterior to the pars pedalis. Two enlarged foramina open above and below the pars pedalis on the left side, and on the right both lie beneath the pars pedalis (Text-fig. 8b). We therefore consider these foramina to have transmitted nerves or vessels to fin muscles inserting in this area, and thus probably to correspond to the anterior canal (c1) of *Procondylolepis*, which was similarly positioned to innervate the main abductor muscle for the fin inserting in the triangular depression immediately anteroventral to the anterior lobe of the scapulocoracoid (f.ab, Text-fig. 5A).

Evolution of the brachial joint in relation to pectoral fin function

Procondylolepis. In primitive arthrodires (Text-fig. 2A) the fin muscles evidently inserted on the lateral face of the scapulocoracoid above and below the articular crest (Goujet 1984). In *Procondylolepis* (and presumably *Yunnanolepis*), with their very restricted pectoral fenestra filled entirely by the articular area of the scapulocoracoid, the muscles must already have formed an attachment on adjacent dermal bone. In *Procondylolepis* an inclined axis passes through the two dermal articulations (art.d, art.v) for the pectoral appendage and the articular surface (scap) of the scapulocoracoid (dashed line in Text-figure 7B). Disposed in a line approximately normal to this axis are the two depressions considered above to have been for muscle insertion; and anteroventral one (f.ab) which would have rotated the pectoral fin outwards and downwards, and a posterodorsal one (f.ad) for an opposing muscle which would have adducted the fin. The fact that the upper dermal articulation (art.d) is a deep pit (Text-fig. 4A-B), which received the articular process of the first dorsal central plate of the pectoral appendage (ar3d, Text-fig. 3B), suggests a pivoting action about this point. The ventral articulation (art.v, Text-fig. 7B) forms a broad shallow groove, indicating some rotation around the long axis of the fin with the dorsal articulation as fulcrum. (As noted above, the ventral articulation in some specimens referred to *Procondylolepis* is also a deep pit similar to that on the dorsal side, which would preclude such a rotating motion). The muscles controlling this rotation may have been more centrally placed, possibly inserting on the scapulocoracoid. Uncertainty about the shape of the distal surface of the scapulocoracoid, and whether it was entirely an articular surface, renders the interpretation difficult on this point.

Sinolepids. Three main changes from the condition displayed by *Procondylolepis* are considered significant (Text-fig. 7C): (i) the dorsal and ventral dermal articulations (art.d, art.v) have migrated

posteriorly to lie essentially above and below the glenoid cartilage contained within the funnel pit (fp); (ii) the funnel pit and contained cartilage have acquired a subcircular shape; and (iii) a single large posterior opening has developed (f.ax). This we suggested above to have formed by coalescence of the posterior two neurovascular canals of *Procondylolepis* (c2, c3, Text-fig. 7B).

The ventral articulation in sinolepids is a deep pit similar in structure to the dorsal one in *Procondylolepis*: this might indicate independent development (Ritchie *et al.* in press). The larger more diffuse dorsal articulation may indicate that any rotation around the axis of the fin was pivoted in this case ventrally rather than dorsally. Alternatively, the dorsal articulation may be considered as more derived than the small articular pit of *Procondylolepis* because the corresponding articular process on the dorsal central plate of the sinolepid pectoral fin is clearly morphologically closer to that of euantiarchs than the corresponding bone of *Procondylolepis* (cf. Zhang 1984, fig. 2; Ritchie *et al.* in press, fig. 15A). The ventral pit-like articulation may likewise be considered more advanced than the shallow groove in *Procondylolepis*.

Euantriarchs. The asterolepidoids and bothriolepidoids are characterized by enlargement of the dorsal and ventral muscle fossae to form deep hemispherical grooves (art.d, art.v, Text-fig. 7D). Because of the close fit of the articular surfaces of the pectoral appendage these must have permitted controlled rotational movement of the fin. Such more complex movements required further differentiation of the musculature. The abductor muscle insertion (f.ab) was apparently subdivided by the pars pedalis (pe), and the adductor insertion was differentiated on the face of the brachial process into superior (a.sup, p.sup) and inferior (a.inf) attachments surrounding the funnel pit. We suggest that the several openings of the rostrocaudal canal (c.rc) above and below the pars pedalis reflect differentiation of the neurovascular supply to service more complex movements of the fin. At least two of the posterior muscle pits also contain foramina for neurovascular canals (c.nv, Text-fig. 8B). The pattern demonstrated here for two species of *Bothriolepis* (*B. macphersoni*, Text-fig. 2H; *Bothriolepis* sp. nov., Text-fig. 8B) is the same as illustrated by Watson (1961, fig. 2) in Scottish *Bothriolepis* material. It may be a synapomorphy of the genus.

As noted above, and contrary to this interpretation, both Gross (1931, p. 41) and Stensiö (1931, 1948, 1959, pp. 64–65) believed that retractor muscles for the pectoral fin had their proximal insertion on the scapulocoracoid within the trunk armour, and passed through the axial foramen to the fin. Distally the muscle insertion was on the endoskeletal rod within the fin, with the muscle passing through the posteromesial corner of the proximal aperture in the fin exoskeleton. In contrast, Watson (1961, p. 215) maintained that the axial foramen was 'quite unsuitable in both size and character to permit the passage of a muscle', and he concluded that 'the whole musculature of the pectoral fin must be internal, lying within the cavity of the fin and in general distal to the helmet process'.

Acid prepared material of *Bothriolepis* from Gogo, Western Australia, in which the complete fin exoskeleton can be manipulated on the brachial process, confirms that the muscle arrangement proposed by Stensiö is most unlikely. In the fully retracted position the fin lies against the trunk armour, and viewed from inside the anterior ventrolateral plate the posterior two thirds of the axillary foramen are obstructed by the proximal end of the first mesial marginal plate of the pectoral fin (Mm1, Text-fig. 8A). This leaves little room for a major muscle to enter the cavity of the fin exoskeleton. This does not preclude insertion of some general adductor musculature on the ridges above and below the axillary foramen (sar, Text-figs 2H, 8B). Like Watson (1961), we regard the axillary foramen as having transmitted the major artery and vein to the fin, consistent with the above suggestion that it was derived in sinolepids by coalescence of the posterior two neurovascular canals of *Procondylolepis*. However, its partial obstruction with the fin fully adducted must mean that, in *Bothriolepis* at least, the space was partly occupied by connective or other soft tissue. As discussed by Zhang and Young (in press), the reason for the large size of the axillary foramen in *Bothriolepis* and *Asterolepis* compared to other forms remains problematic, because it is apparently not correlated with presence of the distal joint, nor length of the proximal segment.

In the same specimen from Gogo two bony projections are preserved on the internal surfaces of

the dorsal and ventral central plates (dpr, vpr, Text-fig. 8), and with the fin adducted these are situated adjacent to the shallow depressions on the posterior face of the brachial process above and below the funnel pit (a.sup, a.inf, Text-fig. 8B). These depressions were considered by Gross (1931, p. 39) and Watson (1961, fig. 2B) to be insertions for retractor muscles, and in the Gogo specimen it is seen that such muscles would have passed across to the processes just described to adduct the fin effectively. The dorsal process has two terminal facets (Text-fig. 8C), perhaps corresponding to the two superior muscle insertion pits on the brachial process.

Watson (1961) interpreted the fin of *Bothriolepis* as capable of twisting about its own axis through an angle of up to 30°. He considered that when the broad dorsal surface of the fin was twisted vertically it would be effective in a swimming stroke, and in the other extreme position (with the narrow outer edge of the fin directed anteriorly) the limb could be brought forward with the least possible resistance from the water. The Gogo specimen shows, however, that in the fully abducted position rotation is not possible due to the triangular section of the pars pedalis, which is much thicker posteriorly than anteriorly. In the fully advanced position of the fin, when its proximal end stands out almost at right angles to the body, the proximal aperture of the fin enclosed the thick end of the pars pedalis, to preclude any rotational or dorsoventral movement (an observation also made by both Gross and Watson). Since it is in the fully abducted position that maximum pull would be obtained in the swimming stroke, it seems most unlikely that the fin was used oar-like to propel the animal through the water. A second point is that oars and oar-like appendages are widest distally, not proximally, and the reverse is the case with antiarch pectoral fins (Wells and Dorr 1985).

Stensiö (1948, p. 154) considered that when fully protracted the fin could not be lowered beneath the horizontal, but in the Gogo specimen it can be lowered to about 25° beneath the horizontal. Rather than some 10° out from the body, as maintained by Wells and Dorr (1985, p. 159), the fully adducted fin fits closely against the lateral wall of the trunk armour, both having the same gentle curvature. Since the greatest mobility of the fin was when it was held back towards the body, it seems more likely that any assistance with swimming involved acting as a hydrofoil by elevating or depressing the narrow leading edge of the fin, causing the fish to rise or fall in the water. The fin may have functioned primarily as a prop or wedge, to fix the animal into crevices or soft sediment on the bottom, either to avoid predators or to provide stability in currents. Secondary functions for the long, primarily protective, pectoral spines in the superficially similar loricariid catfishes include anchoring in strong currents, jostling other fishes for resting places, and crawling and clinging on rocks (Alexander 1965; Wells and Dorr 1985). However the necessity for the fish to prop itself up for breathing (Wells and Dorr 1985, p. 166) seems unlikely if it possessed a spiracle (see below). Another suggestion regarding fin function was that they assisted in pulling the fish through reeds (Gross 1931), but, as noted by Wells and Dorr (1985), modern fishes in this habitat tend to be fusiform, with projections from the body reduced or absent.

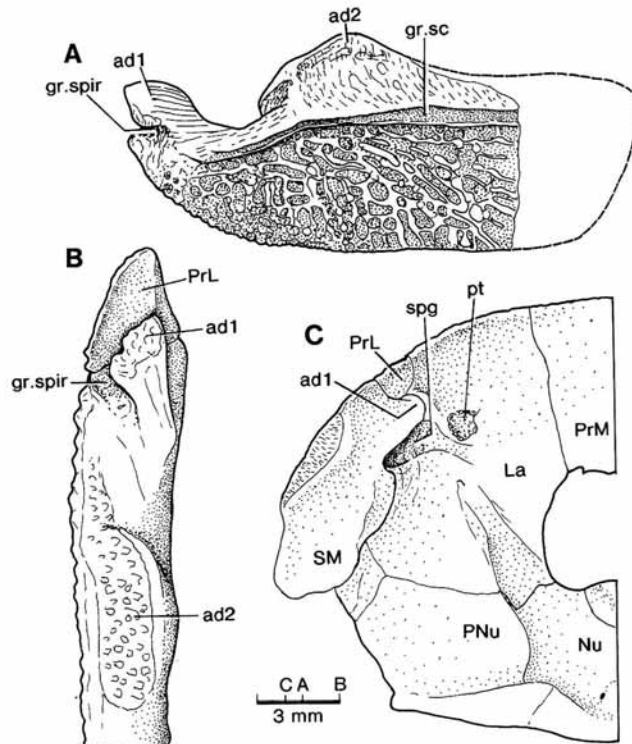
Wells and Dorr (1985) speculated that the appendage may have functioned somewhat like a crutch to enable *Bothriolepis* to walk on the water bottom, in shallows, or even on land. They considered the head and trunk armour to be tightly and rigidly joined, unlike other placoderms, and that this may have had adaptive significance for use on land. However, there was as much movement of the head against the trunk in *Bothriolepis* as in any other placoderm, with the reverse overlap at the postobstantic (postmarginal) corner (Young 1984, fig. 7) corresponding precisely with that in arthrodires (e.g. Young 1980, fig. 18A). The rigidity of the box-like trunk armour on its own could hardly be an adaptation for walking out of water, since many primitive arthrodires (actinolepids, phlyctaeniids) also possessed an elongate box-like armour. Considering the abundance of *Bothriolepis* remains in some deposits (e.g. Escuminac Bay in Canada), some trace fossil evidence of any excursions across mudflats might be expected.

OPERCULUM

In describing an articulated but slightly crushed specimen of *Bothriolepis panderi* which included the cheek plates, Watson (1961, p. 218) noted that the 'opercular' plate ('extralateral' of Traquair 1904, and Stensiö 1948; submarginal of Young 1984) had a distinct anterior process passing upwards and inwards into a matching facet on the lateral plate of the skull. On the left side of the specimen behind this process was a distinct notch (Watson 1961, fig. 1c), which he interpreted as having been completely filled by a rounded process seen on the other side of the specimen projecting from the margin of the right lateral plate. Watson thus rejected the interpretation of Stensiö (1947, 1948) that this notch was in fact the spiracular opening. In accordance with Watson's view, Miles (1968) renamed the 'spiracular groove' on the visceral surface of the head shield the 'transverse lateral groove'. Watson also cast doubt on the existence of a separate small cheek plate (Stensiö's 'prelateral' plate) in front of this opercular articulation, even though both Gross (1941a) and Stensiö (1948) had described in detail and figured this small bone for two species of *Bothriolepis* (*B. cellulosa*, *B. canadensis*). Description of acid-prepared *Bothriolepis* from Gogo, Western Australia (Young 1984) confirmed the accuracy of Stensiö's account regarding these small bones, and further study of the same specimen has now cast doubt on Watson's opinion regarding the spiracle in *Bothriolepis*.

This specimen demonstrates the detailed relationship of the main opercular element (the submarginal) to the two small sensory canal bones just in front of the opercular articulation (Young 1984, fig. 1). It was noted that the dermal articulation between the submarginal and lateral plates in *Bothriolepis* is a unique condition amongst placoderms, and that the articulation is supported by a thickened ridge of bone beneath the lateral plate which may have been an extension of the anterior postorbital process of the braincase. In arthrodires (e.g. Young 1979; Goujet 1984) the submarginal has an equivalent position, but is connected to the braincase by articulation between the endocranial anterior postorbital process and a cartilaginous element fixed to the anterodorsal corner of the dermal operculum (submarginal plate). Outgroup comparison indicates that an articulation between a cartilaginous element and the braincase may have been primitively present in antiarchs, to be replaced in bothriolepids by a dermal articulation. A perichondral ossification in the appropriate position has been tentatively identified in the primitive antiarch *Phymolepis* from the Early Devonian of China (Young and Zhang, in prep). Of interest in this connection is the form of the visceral surface of the submarginal plate in *Bothriolepis cullodenensis* figured by Long and Werdelin (1986, fig. 11A), which in place of a dermal process shows an irregular attachment surface not dissimilar to that in some other placoderms (e.g. Young 1986, fig. 14A). Young (1986) considered further the homology of the submarginal attachment in placoderms. Although the cartilaginous element just mentioned has been interpreted by some workers as the epiphyal, Young (1986) suggested that it was an additional element (the opercular cartilage), probably derived from the hyoid arch, which in placoderms generally formed a unique type of opercular suspension. This is in contrast to the opercular cartilage in living gnathostomes, which never articulates with the braincase.

The question of a spiracular opening in antiarchs was not addressed by Young (1984), but closer examination of the Gogo material provides new information on this point. The fact that the anterodorsal corner of the submarginal plate in placoderms generally lies adjacent to the exit for the hyomandibular nerve means that a spiracle, if present, would have occupied a similar position. Watson (1961, p. 218) gave as his reason for rejecting Stensiö's interpretation of *Bothriolepis* that 'the spiracle in those fish in which it does occur lies anteriorly and dorsally, and does not form part of the border with which the opercular articulates'. This generalization hardly applies to non-operculate elasmobranchs, and an 'anterior and dorsal' position is not a valid criterion in the case of the highly modified skull morphology of antiarchs. Watson (1961, p. 220) later commented (in contradiction to the quote just given) that any spiracular opening in *Bothriolepis* 'could be expected to come out, either through a special opening in the head shield, or a notch in its border' (that is, in just the position identified by Stensiö). Watson's special pleading led him to the conclusion that



TEXT-FIG. 9. A, *Bothriolepis macphersoni* Young, 1988; incomplete left submarginal plate; Aztex Siltstone; southern Victoria Land, Antarctica. B-C, *Bothriolepis* sp.; CPC 25205 (same specimen as described by Young 1984); early Upper Devonian Gogo Formation; Canning Basin, Western Australia; B, anterior end of left submarginal and attached prelateral plates in dorsal view; C, right half of skull restored in ventral view, with submarginal and prelateral plates attached (cf. Young 1984, pl. 57, fig. 1). For list of abbreviations see p. 464.

because there was no definite evidence for the presence of a spiracle, 'the first gill slit was of full size, and not reduced to its dorsal end alone'. This agreed with the condition which he had earlier (1937) proposed for acanthodians and placoderms, which he grouped together as a major grade of primitive gnathostomes (the 'Aphetohyoidea') characterized by an unmodified hyoid arch. However, there is now much evidence refuting this view for both groups (e.g. Miles 1965, 1973; Miles and Young 1977; Young 1979, 1980, 1986).

The need to re-examine evidence for the presence of a spiracle in *Bothriolepis* arose with the description of a well-preserved submarginal plate of *Bothriolepis macphersoni* from southern Victoria Land, Antarctica (Text-fig. 9A), in which a distinct groove passing laterally around the anterodorsal articular process was identified as possibly containing the spiracular tube (Young 1988, p. 94). A re-examination of the submarginal plate in the acid-prepared Gogo *Bothriolepis* described by Young (1984) revealed a similar groove (gr.spir, Text-fig. 9B), which on reassembly against the skull opens immediately behind the anterior articulation of the submarginal on the lateral plate of the skull. This is exactly the position identified by Stensiö (1948) in *Bothriolepis*

canadensis, but the opening is much smaller than restored by him. It must be recorded that Watson (1961, p. 218) described the same groove in *Bothriolepis panderi* as 'a distinct unornamented groove, clearly recessed below the outer surface of the bone by at least half a millimetre'. Internally this groove is confluent with a deep pocket formed ventrally by the notch between the anterior and posterior dermal attachments between the submarginal plate and the skull, and dorsally by the 'spiracular groove' on the visceral surface of the lateral plate (spg, Text-fig. 9c). Using new evidence of the structure of the jaw cartilages in *Bothriolepis*, Young (1984) concluded that the mandibular joint must have occupied a position just inside the anterior dermal attachment of the submarginal, with the hyoid arch elements immediately behind. In this reconstruction the spiracular groove of Stensiö's (1948) interpretation (spg, Text-fig. 9c) lies in exactly the position expected of the hyoid pseudobranch. We thus consider these various lines of evidence to provide a good indication that there was a spiracle in *Bothriolepis*. In asterolepid antiarchs the submarginal plate has a different morphology from that of *Bothriolepis*, but the dermal attachment to the skull is again subdivided into anterior and posterior areas separated by a shallow notch, which externally is manifested as a small foramen (e.g. Gross 1931, pl. 12, fig. 7). A spiracular opening may thus have been primitively present in antiarchs (or euantiarchs), since it is developed in two major antiarch subgroups.

Finally, some functional aspects of the spiracle may be considered. Stensiö (1948) interpreted the spiracle of *Bothriolepis* as an opening through which water was expelled, this presumably being based on the analogue of modern sharks. But comparison between benthic antiarchs with evidently poor swimming ability and the active predatory habits of most sharks seems inappropriate. We consider it much more likely that the spiracle functioned for the intake of water for respiratory purposes, as is the case in modern batoids. The small ventrally placed mouth and flat ventral surface of the dermal armour in most antiarchs suggest a sluggish benthonic existence, with the weakly developed mouthparts suitable only for soft bottom detritus. In the primitive Early Devonian antiarch *Phymolepis* from South China the normal ornament of fine tubercles on the dermal elements for the upper jaw shows no differentiation at the mouth margin for grasping or biting, and the mouth must have opened in a very restricted space between the suborbital plates forming the dermal upper jaw, and the anterior border of the ventral wall of the trunk armour (Young and Zhang in prep.). The mouth evidently had very limited movement, and opened and closed in a horizontal plane back behind the rostral rim of the skull on the flat ventral surface. In such a position it could hardly have provided an adequate intake for respiratory water during feeding on the bottom. Unlike the suborbital plate, which formed the dermal upper jaw element, the submarginal plate forming the dermal operculum is part of the lateral rather than ventral wall of the armour. Watson (1961, p. 219) commented on the evident mobility of the operculum in *Bothriolepis*, which might be expected in a fish of benthonic habit, where a well-developed opercular pump respiratory mechanism is the norm (e.g. Hughes and Shelton 1962, p. 318). The spiracle would have permitted the intake of clear respiratory water, without interruption to feeding, or the necessity to move from a secure placement on or in the bottom sediment, just as it does in modern batoids.

Acknowledgements. This work was finalized during a visit to Australia by Zhang Guorui in 1989, with the support of an Australian Museum Visiting Fellowship and BMR contract, both of which are gratefully acknowledged. Both institutions are thanked for the provision of working facilities. G. C. Y. acknowledges financial support under the Australian Academy of Science–Academia Sinica Scientific Exchange Agreement for two visits to China in 1981 and 1987, when preliminary work on this project was undertaken, and thanks Chinese hosts for their hospitality, and Dr D. Goujet (Paris) for fruitful discussion on the Chinese specimens. Lu Wenyong, Sun Xiaowen, and Yu Xiaobo assisted with translation from Chinese into English, and Dr A. Ritchie, R. W. Brown, H. M. Doyle and A. Haupt are thanked for assistance with preparation and photography. We thank Drs R. E. Barwick, A. Ritchie and Professor K. S. W. Campbell for useful discussion, and K. S. W. Campbell, B. G. Gardiner and D. Goujet for commenting on the manuscript. G. C. Y. publishes with the permission of the Director, Bureau of Mineral Resources, Canberra.

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G. C. YOUNG
Bureau of Mineral Resources
P.O. Box 378
Canberra, ACT 2601, Australia

ZHANG GUORUI

Institute of Vertebrate Palaeontology
and Palaeoanthropology
Academia Sinica
PO Box 643
Beijing 100044, China

Typescript received 6 October 1990
Revised typescript received 27 February 1991

ABBREVIATIONS USED IN TEXT-FIGURES

ad1, 2, anterior and posterior articular processes on SM; a.inf, ventral muscle insertion on brachial process; ar3d, external articular area of Cd1; ar3v, external articular area of Cv1; art.d, dorsal articular depression for dermal process of pectoral fin; art.v, ventral articular depression for dermal process of pectoral fin; a.sup, anterior dorsal muscle insertion on brachial process; Cd1, dorsal central plate 1; Cd2, dorsal central plate 2; Cv1, ventral central plate 1; Cv2, ventral central plate 2; c1-3, foramina piercing scapulocoracoid; cit, crista transversalis interna anterior on AVL plate; c.nv, canal for nerves and/or vessels; cr.art, articular crest on scapulocoracoid; c.rc, rostrocaudal canal; dpr, dorsal process inside pectoral appendage; f.ab, insertion area for abductor muscle of fin; f.ad, insertion area for adductor muscle of fin; f.ax, foramen axillare of AVL; fgr, funnel groove; f.mp, protractor area of brachial process; fp, funnel pit; f.pect, pectoral fenestra; gr.sc, groove for sensory canal; gr.spir, groove on SM for spiracular tube; gr.c2, groove showing course of canal c2; La, lateral plate of skull; M1, plates probably of the lateral marginal series of pectoral appendage; Mm, plates probably of the mesial marginal series of pectoral appendage; Mm1, mesial marginal plate 1; Mm2, mesial marginal plate 2; Mm4, mesial marginal plate 4; Nu, nuchal plate; PNu, paranuchal plate; PrL, prelateral plate; PrM, premedian plate; pt, lateral pit of head-shield; pbr, brachial process; pe, pars pedalis of brachial process; per, perichondral bone layer; pre, prepectoral corner of AVL; p.sup, posterior dorsal muscle insertion; r.md, ridges for insertion of dorsal fin muscles; r.mv, ridges for insertion of ventral fin muscles; sar, supra-articular ridge; spg, spiracular groove on head shield; SM, submarginal plate; vpr, ventral process inside pectoral appendage.