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A REVISION OF THE ANATOMY OF THE EARLY DEVONIAN JAWED VERTEBRATE *PTOMACANTHUS ANGLICUS* MILES

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Abstract: The spine-bearing jawed vertebrates (gnathostomes) assigned to the assemblage 'Acanthodii' play a key role in understanding the early evolution of osteichthyans and chondrichthyans. Amongst 'acanthodians', the genus *Ptomacanthus* has played a prominent role owing to its shark-like tooth files. Recently described braincase material from this taxon contrasts strongly with the osteichthyan-like braincase of *Acanthodes*, the only other 'acanthodian' for which this anatomy is well known. This seriously challenges acanthodian monophyly or at least the prevailing interpretation of *Acanthodes*. This study presents a redescription and updated comparison of the anatomy of *Ptomacanthus* based on unfigured material from the type and referred specimens, as well as adding new data on spine and scale histology. *Ptomacanthus* is remarkably heterosquamous compared to some other 'acanthodians'. Further to its resemblances to *Climatius*, *Ptomacanthus* shares some features of the external morphology of its scales with the enigmatic genus *Obtusacanthus*. The scale crowns of *Ptomacanthus* exhibit both superpositional and areal growth. The bases, however, grow separately from the crown. As in *Acanthodes*, scales are here inferred to be added to the body from posterior to anterior. In spite of its chondrichthyan-like form and characters, *Ptomacanthus* remains difficult to place on either the chondrichthyan, osteichthyan or gnathostome stem. Different placements each require invoking considerable character incongruence. Nevertheless, these new data from *Ptomacanthus* provide broader anatomical context for hard tissue characters commonly described on the basis of isolated remains.

Key words: Acanthodii, scale histology, gnathostomes, Palaeozoic, Chondrichthyes, stem groups.

PTOMACANTHUS *anglicus* Miles, 1973*a* is an early gnathostome (jawed vertebrate) with paired and median fin spines from the Early Devonian of the Welsh Border regions. In spite of the limited number of specimens available, all material is extremely well preserved. The taxon has featured prominently in debates on the characters of early gnathostomes and the problem of 'acanthodian' relationships. Jarvik (1977, 1980), in advocating a chondrichthyan status for all 'acanthodians', appealed to the complete upper arcade of shark-like tooth files in *Ptomacanthus* as evidence of a median symphysis of the palatoquadrates, as found in modern elasmobranchs. This contrasted with Miles' (1973*b*) re-description of the endocranium of *Acanthodes* and accompanying cladistic analysis where he established a synapomorphy scheme for the relationships of *Acanthodes* (which proxied for all acanthodians) with osteichthyans. Neither Jarvik nor Miles (1973*b*), who first described *Ptomacanthus*, made much if any mention of the preserved endocranial material—particularly the neurocranium. This was the subject of a recent description by Brazeau (2009), which provided evidence of a braincase differing remarkably from that of *Acanthodes*. These data contribute significantly to the growing body of data suggesting the nonmonophyly of the Acanthodii.

Resolving the relationships of 'acanthodians' to their proper stem placements is critical to understanding the evolutionary assembly of the morphologies of the two principal gnathostome lineages: chondrichthyans and osteichthyans. Now that acanthodian monophyly has come seriously into question, and at least one explicit cladistic solution is available, detailed anatomical data of whole skeletons become of ever-increasing importance. It no longer suffices to paint the problems in broad strokes, making reference to probably paraphyletic groups like 'Acanthodii' and 'climatiiformes'. The relationships of the spine-bearing gnathostomes we know of as 'acanthodians' have to be considered in terms of much more precise taxonomic units and assessed in the context of gnathostome relationships as a whole. Otherwise, we make spurious and unnecessary presuppositions of monophyly leading to groupings that

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are overly coarse for interpreting of available character data.

The present study provides a critical update and reinvestigation of the anatomy of *Ptomacanthus anglicus* Miles, 1973*a*. Miles described much of the anatomy of this taxon, but the present study provides new detail, amends problems and expands on this description by presenting previously unfigured material along with details of scale and spine morphology and histology. Along with this, it is shown that a large patch of flank scales with modified lateral line scales was incorrectly assigned to *Ptomacanthus* in the original description and likely represents *Euthacanthus macnicoli* or a closely related species.

Institutional abbreviation. NHM, Natural History Museum, London.

Terminology. Classical taxonomies still have pervasive use in studies of early vertebrate palaeontology. 'Acanthodian' is frequently used as a convenient shorthand only for fishes with spines preceding their paired and median fins. The symplesiomorphy-based convention 'vent-spined gnathostomes' will be substituted here to refer to the Palaeozoic gnathostomes with a full complement of spines on the median and paired fins, and especially identified by an anal fin spine, regardless of whether they have been referred to as 'acanthodians'.

MATERIALS AND METHODS

Fossil material. The current reinvestigation of *Ptomacanthus* is based on NHM specimens P 19998 and 19999 (holotypes); P 20002 and 20003; P 24919*a*, *b*; P 53285*a*, and P 53880*a*. Fresh silicone peels were made of the holotype and P 20003*a*, *b*. Excluded from this account is specimen P 16615, an articulated portion of flank scales showing specialized, enlarged lateral line scales, assigned to *Ptomacanthus* by Miles. Examination of this specimen reveals that these scales bear little or no resemblance to the rest of the *Ptomacanthus* hypodigm. They consist of a simple monocuspidate rhombic crown with short, regular striations that scallop the leading edge of the crown which sits atop a bulging base. This contrasts with the scale morphology of *Ptomacanthus* described by Miles and expanded upon below. In the light of this, there is nothing to substantiate the attribution of specialized lateral line canal scales to *Ptomacanthus* (Miles 1973*a*, text-fig. 2). In fact, the scale bases can be observed in the region of the lateral line of the posterior part of P 19999. As far as can be seen, they are uniform in shape with neighbouring flank scales and are not noticeably larger. Enlarged, differentiated lateral line scales are seen in *Euthacanthus macnicoli* specimens (Newman *et al.* 2011), suggesting possible alternative affinities for P 16615.

Sectioning and histology. Specimen P 53880*a* is the only *Ptomacanthus* specimen that retains significant portions of the dermal skeleton. A part of it was sectioned to obtain scale histology information. These sections were imaged using regular transmitted light and Nomarski interference microscopy on a Leica DMXRE binocular light microscope. Photographs were taken using a Zeiss Axiophot.

Scanning electron microscopy. Patches of scales from the holotype were cast in silicone, mounted on stubs and gold-coated for scanning electron microscopy (SEM). Silicone was used at the request of the Palaeontology Conservation Unit of the Natural History Museum for conservation purposes, in spite of the superior results typically obtained by using latex for this purpose. Two blocks resulting from thin sectioning were polished down to 1 μm grit and etched for 10 s in 0.1 M hydrochloric acid. These were coated in graphite and imaged under SEM.

SYSTEMATIC PALAEONTOLOGY

Superclass GNATHOSTOMATA Gegenbaur, 1874

Genus PTOMACANTHUS Miles, 1973*a*

Type species. Ptomacanthus anglicus Miles, 1973*a*.

Material. Specimen NHM P 53880 is added to the list of *Ptomacanthus* material, as it is not mentioned by Miles (1973*a*). As mentioned above, P16615 is removed from the list of *Ptomacanthus* material because of lack of any distinguishing traits of *Ptomacanthus* and clear resemblance to *Euthacanthus macnicoli* (Newman *et al.* 2011).

Emended diagnosis. Further to the diagnosis given by Miles, *Ptomacanthus* can be diagnosed in relation to other gnathostome vertebrates based on the following list of characters. Autapomorphy: scapular blade with pronounced sigmoid profile in lateral view, leading and trailing edges almost parallel. Gnathostome symplesiomorphies: tooth-bearing jaws, paired pectoral and pelvic appendages, lateral line canal extending along flank, palatoquadrate with high posterodorsal expansion (otic process). Characters of uncertain polarity: Head composed of tessellate dermal ossifications, body covered in denticle-like squamation, tooth cusps arranged in monoserial whorls with a single base. Shared feature with uncorroborated homology: high-arching dorsal profile, resembling *Brochoadmones* and *Kathemacanthus*. Characters shared with 'acanthodians': Anal fin spine, row of (three) intermediate (prepelvic) spines, set of prepectoral spines on pectoral girdle, banded distributions of scale morphologies in the caudal fin (Miles 1970). It differs from *Climatius*, *Parexus*, *Vernicomacanthus* and *Brachyacanthus* in the lack of ventral pectoral armour and the absence of any distinctly enlarged postorbital tesserae.

Remarks. *Ptomacanthus* is a relatively large vent-spined gnathostome, measuring up to an estimated 30 cm in snout to tip-of-tail length. Both *Ptomacanthus* and *Acanthodes* are amongst the largest vent-spined gnathostomes for which complete body fossils are known. Given that endoskeletal mineralization is a comparatively late ontogenetic feature, the relatively well-mineralized endoskeleton in these taxa may be correlated with their large size.

Occurrence. All fossils described here originate from the fish lens in the Wayne Herbert Quarry in Welsh Border Regions (see Dineley and Metcalf 1999). One specimen of *Ptomacanthus* from the Lower Devonian of Zalerzychi, Ukraine, consists of a pectoral girdle with its diagnostic sigmoid-shaped scapular profile (Miles 1973*a*).

Comparative description

Overall morphology. As described by Miles, *Ptomacanthus* is a moderately deep-bodied fish with a complement of similarly sized fin spines and head covered in ornamented tesserae (Figs 1–4). There is a row of three intermediate (prepelvic) spines, two prepectoral fin spines and a median pectoral spine (Miles 1973*a*). The pelvic and pectoral fin webs are not clearly seen in any specimen. As remarked by other authors (e.g. Gagnier and Wilson 1996; Hanke and Wilson 2006), the deep body of *Ptomacanthus* as seen in P 19999 compares with 'acanthodian'-type taxa such as *Brochoadmones* and *Kathemacanthus* (Figs 2, 4). However, in these latter taxa it is manifest as a nuchal hump, with the dorsal profile sharply rising behind the head. The anterior dorsal incline is more gradual in *Ptomacanthus* and tapers downward to the tail, giving it a more evenly parabolic profile. Miles restored *Ptomacanthus* without much emphasis on this feature, showing a relatively low body profile, similar to other acanthodians. Indeed, the hump is not so well seen in the counterpart slab (P 19998; Fig. 2). As this is unlike any vent-spined gnathostome known at the time, Miles's reconstruction may have been conservative. However, the same high-arching dorsal profile is confirmed in P 20003 (Fig. 4), which was not figured in full by Miles.

Cranial exoskeleton. As described by Miles, the cranial exoskeleton is composed of tesserae showing slight variation in different regions of the head. The top of the skull (tectal tesserae) of *Ptomacanthus* is shown in P 19998 (Fig. 1) and P 24919*b* (Miles 1973*a*). In the posterior part of the skull, these tesserae form flat

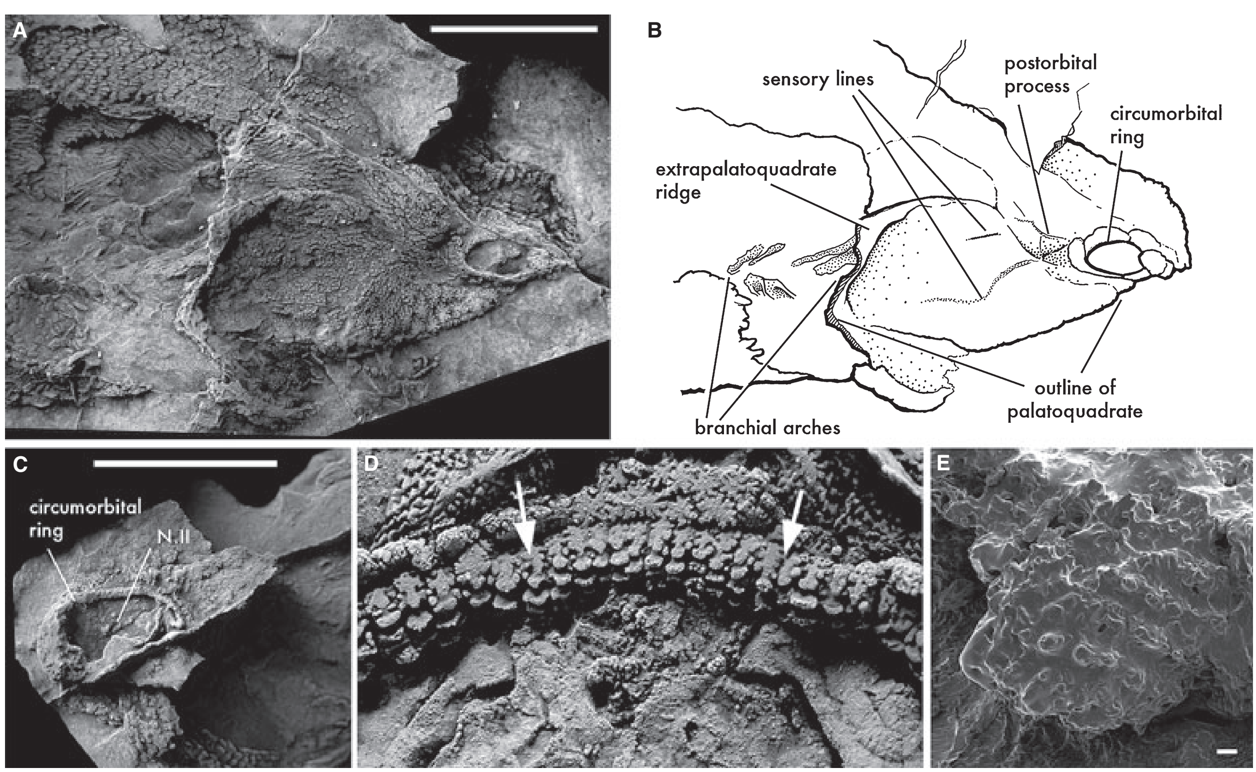

FIG. 1. The head of *Ptomacanthus anglicus* Miles. A, detail of head of head of NHM P 19998, scale bar represents 2 cm; B, interpretive illustration of head; C, detail view of orbit of NHM P 19999 showing presumed opening for optic tract (N.II), scale bar represents 2 cm; D, medial part of upper tooth row in NHM P 24919, showing correspondence of narrower teeth with presumed position of subnasal plate (marked by arrows); E, scanning electron micrograph of pharyngeal denticle whorl from inside pharynx of P 19998, scale bar represents 20 μm.

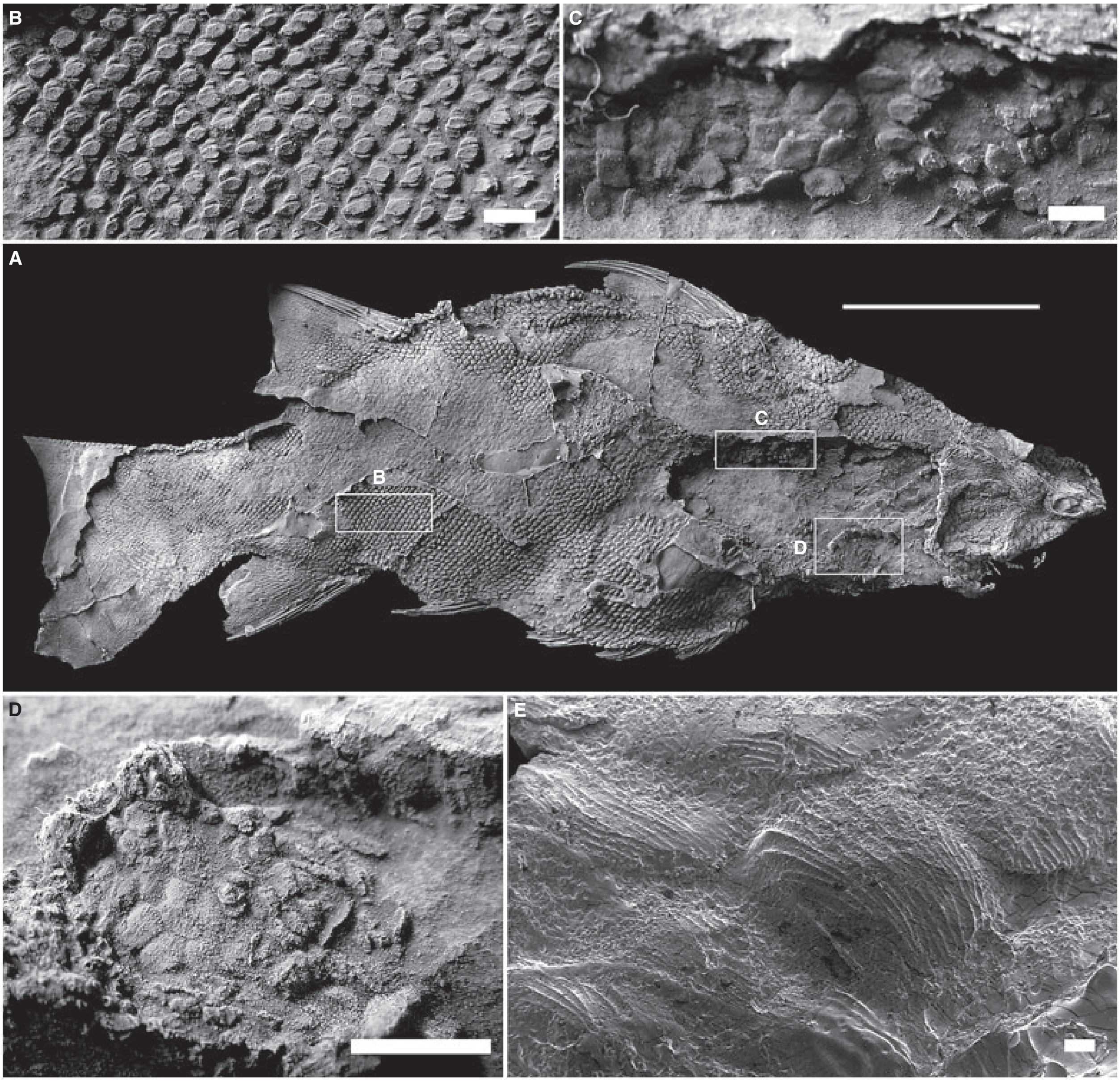

FIG. 2. *Ptomacanthus anglicus* Miles specimen NHM P 19998. A, right lateral view of specimen with boxes showing corresponding location of subsequent photographic figure panels, scale bar represents 5 cm. B, body squamation on flank above anal fin. C, scale bases of left side of body showing central depression. D, scales in pectoral girdle region, scale bar represents 5 mm. E, scanning electron micrograph of flattened scales on pectoral girdle, scale bar represents 100 μm.

and quite regular hexagonal plates, very tightly spaced, with a lobate ornamentation similar to *Gladiobranchus* (Hanke and Davis 2008). Anteriorly, the tectal tesserae have more rounded margins and radiating stellate tubercles. In the rostral part of the head, the ornamentation becomes quite coarse as in the circumorbital and rostral plates of *Climatius*-like taxa and *Cassidiceps* (Gagnier and Wilson 1996) and *Gladiobranchus* (see Hanke and Davis 2008). Note that this is not a uniquely shared comparison between these taxa, but they are among the best preserved examples. This type of ornamentation characterizes also the cheek and jaw covering of *Ptomacanthus* where the plates take on a more rhombic form. Enlarged, heavily ornamented tesserae cover the snout between the circumorbital ring and the nares, as seen in specimens P 19998 and P 24919. Unlike *Brachyacanthus*, *Climatius* and *Parexus* (Watson 1937; Miles 1973*a*), there is no evidence of relatively enlarged postorbital tesserae that would have covered the postorbital process. Instead, this region is covered in tesserae similar in shape, size and ornamentation to the rest of the skull.

The squamation of the cheek (jugal tesserae) can be better seen in *Ptomacanthus* than in most specimens of *Climatius*. The regularly spaced, similar-sized tesserae of *Ptomacanthus* can be seen on the right side of P 19999 and in P 24919. Along the

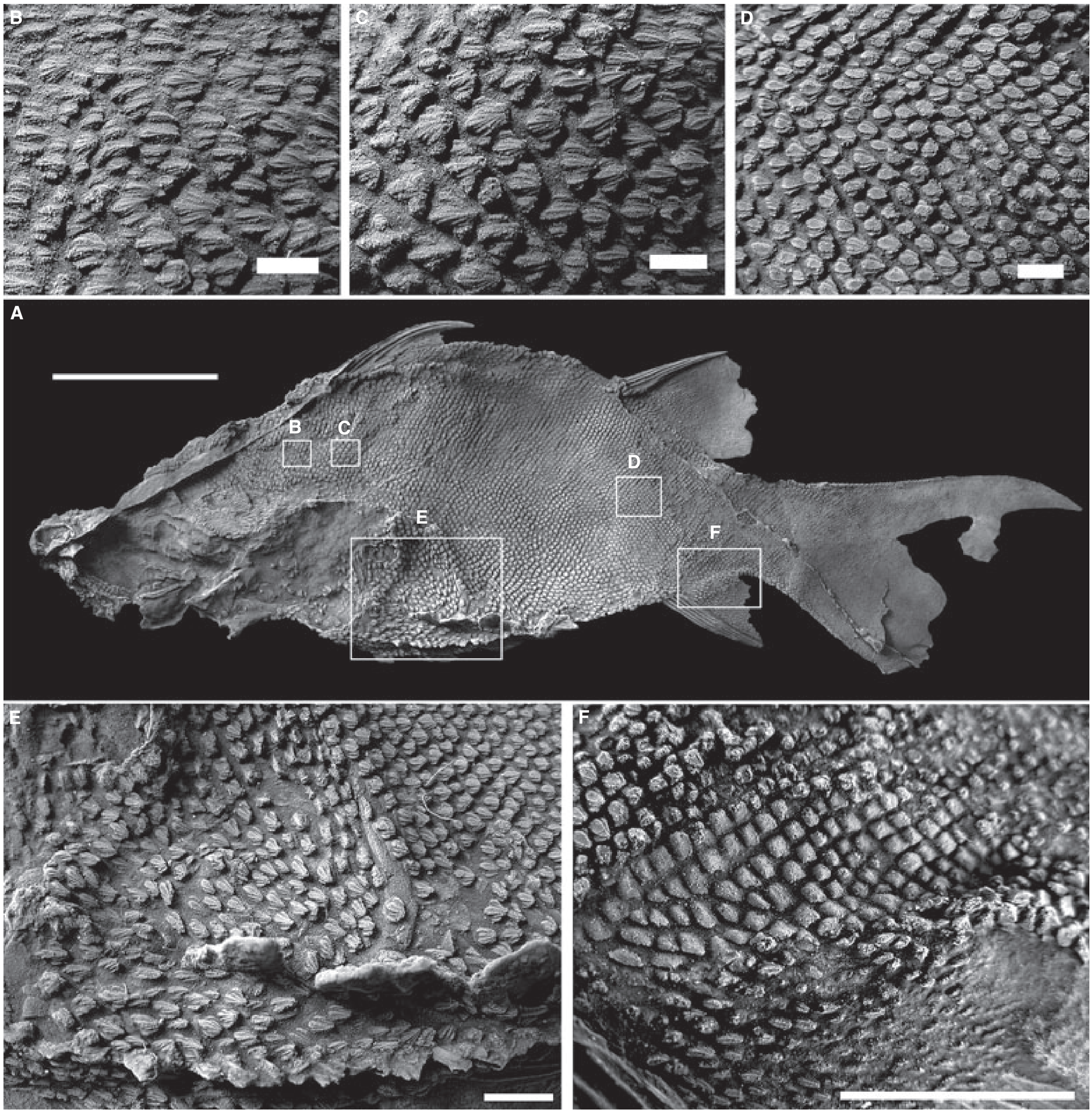

FIG. 3. *Ptomacanthus anglicus* Miles specimen NHM P 19999. A, specimen in left lateral view, scale bar represents 5 cm. B, anterior body scales with three cusps and numerous fine cristae. C, intermediate flank scales with central depressed navicular area. D, posterior body scales with flat central principle crown and lacking ornamentation. E, body scales in anteroventral portion of the trunk, behind the position of the pectoral girdle. F, scale bases above anal fin showing bulging scale bases, scale bars represent 1 cm.

lateral margins of the mouth, the most ventral tesserae are distinctly enlarged and adjoin in a vertical interfingering pattern. Evidence of the supramaxillary and preopercular sensory line canals can be seen as short, open grooves on the cheek of P 19998 (Fig. 1). Only the former is visible in P 24919*b*.

As described by Miles, a row of distinct, flat tesserae are aligned with the labial margin of the tooth whorls (Fig. 1). These tesserae are smooth with deeply scalloped margins, similar to scales found in *Obtusacanthus* (Hanke and Wilson 2004) and those attributed to the nominal chondrichthyan scale-based taxon *Polymerolepis* (Karatajute-Talimaa 1992, 1998).

Cranial endoskeleton and visceral arches. Ptomacanthus represents one of a very small number of 'acanthodians' with a mineralized endocranium (Brazeau 2009). Evidence of a postorbital process can be seen in P 19998 (Fig. 1) where the tesserae are in articulation over a pronounced lateral projection of the head. It appears to have been stout and anteroposteriorly broad, similar to that of

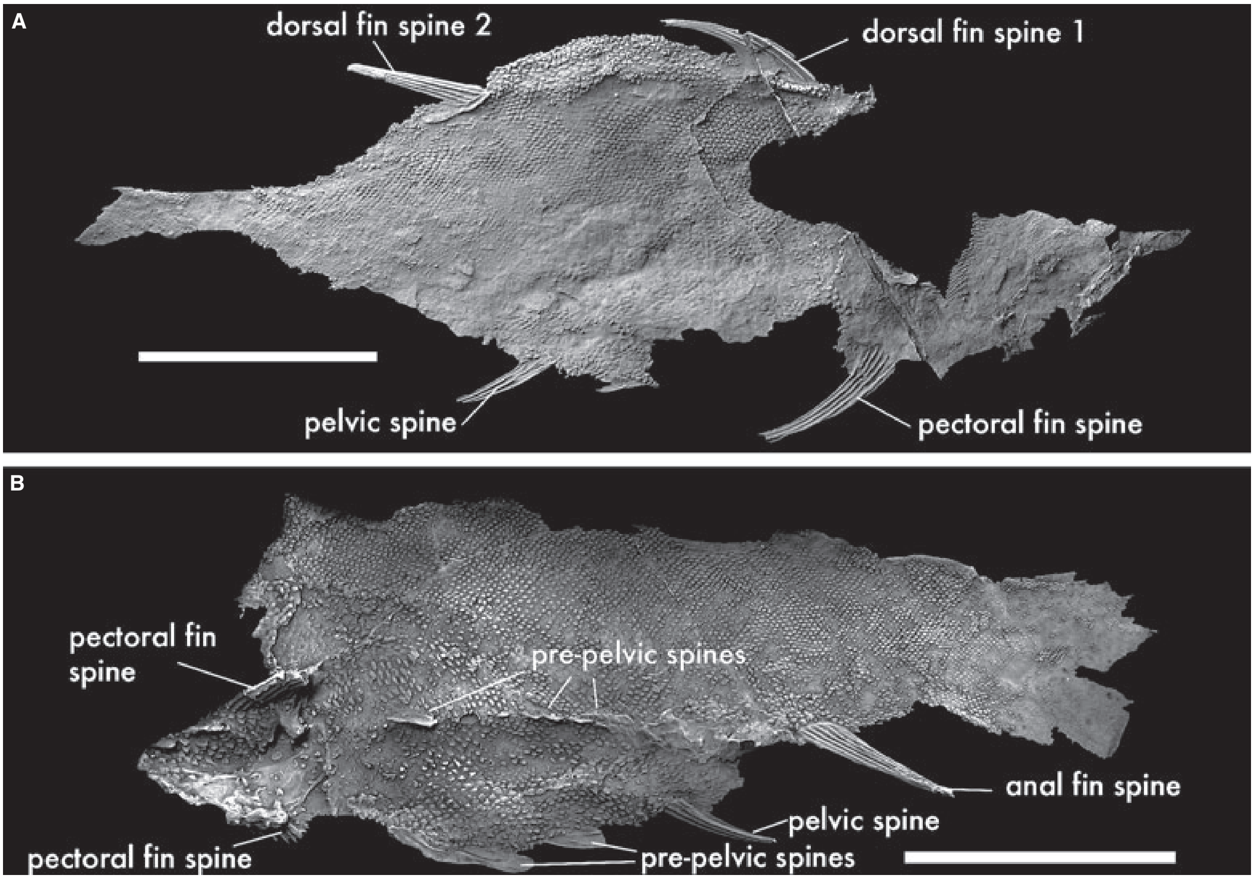

FIG. 4. *Ptomacanthus anglicus* Miles specimens NHM P 20002 and 20003 (part and counterpart of the same specimen). A, P 20002, right lateral side showing high-arching profile or dorsal margin. B, P 20003, left lateral side, also showing ventral surface between rows of prepelvic spines. Scale bars represent 5 cm.

Orthacanthus (Schaeffer, 1981) and *Doliodus* (Miller *et al*., 2003; Maisey *et al.* 2009) or perhaps as in some arthrodires (e.g. *Buchanosteus*, Young 1979). The extrapalatoquadrate crest merges anteriorly with the posterior margin of the postorbital process (Fig. 1). This suggests contact between the otic process of the palatoquadrate and the postorbital process, but there is no direct evidence of an articulation facet as in chondrichthyans.

The orbital wall can be seen in P 19999. It is punctured by a foramen reasonably interpreted as having carried the optic tract (N. II, Fig. 1). It is situated midway between the anterior and posterior boundaries of the orbit, as in many Palaeozoic chondrichthyans (e.g. *Orthacanthus*, *Tamiobatis*, Schaeffer 1981; *Akmonistion*, Coates and Sequeira 1998; *Cladodoides*, Maisey 2005). It is also situated in a dorsoventrally medial position. This contrasts with Palaeozoic chondrichthyans (excepting some symmoriiforms, such as the skull assigned to '*Cobelodus*', Maisey 2007) and *Ligulalepis* where it is ventrally situated (Basden *et al.* 2000; Basden and Young 2001). An eyestalk attachment cannot be identified because of the irregularity of the surface of the orbital wall.

The shape of the palatoquadrate is similar to that of *Orthacanthus* (Hotton 1952; Schaeffer 1981) and *Climatius* (Miles 1973*a*) in that its posterodorsal margin has a high arch with a steep posterior slope. The autopalatine ramus is short as in *Climatius* and *Acanthodes*. In most other early gnathostomes with an expanded otic process of the palatoquadrate (i.e. 'cleaver-shaped', Schaeffer 1975), the posterodorsal margin has a more gradual slope. This is clearly seen in *Acanthodes* (Miles 1973*b*), *Cladodoides* (Gross 1937, 1938) and early osteichthyans (Pearson and Westoll 1979; Jarvik 1980; Gardiner 1984; Long 1988).

Miles reported that the Meckelian element in P 19999 is composed of two separate mineralizations. However, examination of the mould suggests that this conclusion may be based simply on the way the matrix broke away from the specimen after collection or preparation. The mould of the lower jaw may continue under a stump of matrix, which creates the impression of a division in rubber casts. Without potentially destructive preparation of the holotype, it is not possible to determine this and the interpretation of separate mandibular divisions should be regarded with caution.

The branchial arches are preserved on the left sides of P 19999 and P 24919*a*, *b* (Fig. 1). At least four (although likely five) distinct arches can be counted in series behind the head. Unfortunately, the pharyngobranchials are not preserved.

Dentition. The tooth whorls of *Ptomacanthus* have already been described by Miles (1973*a*). Miles noted that, medially, the tooth files become much narrower. Now that the braincase of *Ptomacanthus* has been described (Brazeau 2009), it is possible to see that the narrower teeth would have been situated on the internasal plate (Fig. 1), as they are situated within the margins of the anterior end of the basicranium. The comparative condition has now been directly observed in a fossil chondrichthyan, *Doliodus* (Maisey *et al.* 2009), but it may well be a generalized condition for gnathostomes, in the light of tooth or denticle-bearing plates in the corresponding position in osteichthyans (vomers) and some placoderms (i.e. arthrodires, *Romundina*).

A single whorl-shaped pharyngeal denticle plate was observed in P 19998 under SEM (Fig. 1). It consists of a battery of four or five rows of regularly aligned denticles of increasing size.

Body scale morphology and distribution. Miles described the scales of *Ptomacanthus* as high-crowned with a navicular ('boat-shaped') central portion, flanked by two smaller navicular cusps. The scales are thus tricuspidate and often resemble the scales of *Obtusacanthus*. In the latter taxon, they are reportedly monodontode (Hanke and Wilson 2004), but it is unclear whether the lateral cusps form part of the same odontode or are fused laterally. Miles reported that the scale bases of *Ptomacanthus* exhibit rounded, bulging bases. However, scales of the anterior portion of the body are flat-based (Figs 2, 3), as in *Climatius* and scales frequently attributed to chondrichthyans. These flattened bases are most clearly visible in P 24919 (Brazeau 2009, supplementary information) and P 19998 (Fig. 2). Many of them exhibit a central depressed area, similar to the bases of many presumed chondrichthyan scales that have independently growing bases (Karatajute-Talimaa 1998).

In *Ptomacanthus*, scales with bulging bases occur only in the more posterior part of the body, from about the region above the anal fin back. These are visible in P 19999 where the left side flank scales are missing, revealing the bases of the right side flank scales (Fig. 3). Miles reported concentric striations in the scale bases and concluded that they were the edges of growth zones. SEM imaging shows a series of concentric ridges and grooves as superficial features of the base (Fig. 5). If these ridges are in fact growth lines this would preclude a concentric 'onion-skin' mode of growth, as these edges would not then appear superficially. This separately growing base is confirmed in histological cross-section (Fig. 7), where the addition of basal layers is separate from the addition of generations to the crown.

Ptomacanthus is considerably heterosquamous even though Miles described the squamation as being relatively uniform. Marked anterior-to-posterior variation in scale morphology is seen in *Ptomacanthus*, a feature that compares with *Gladiobranchus* (Hanke and Davis, 2008). This may reflect the relative age of the scales from posterior to anterior (Zidek 1976, 1985). At the anterior of the body, the scales are richly ornamented with numerous fine cristae that converge towards the trailing edge of the scale. Miles described these scales as being localized to the pectoral girdle region, but it is clear that they extend from the ventral to dorsal midline and posterior to the pectoral girdle (Figs 2, 3). In these scales the crown projects backwards at a high angle. As one traces the scales posteriorly along the flank, the fine cristate ornamentation disappears and the crowns become very broad and flat, but remain tricuspidate. The intermediate scales in this transition exhibit the pronounced

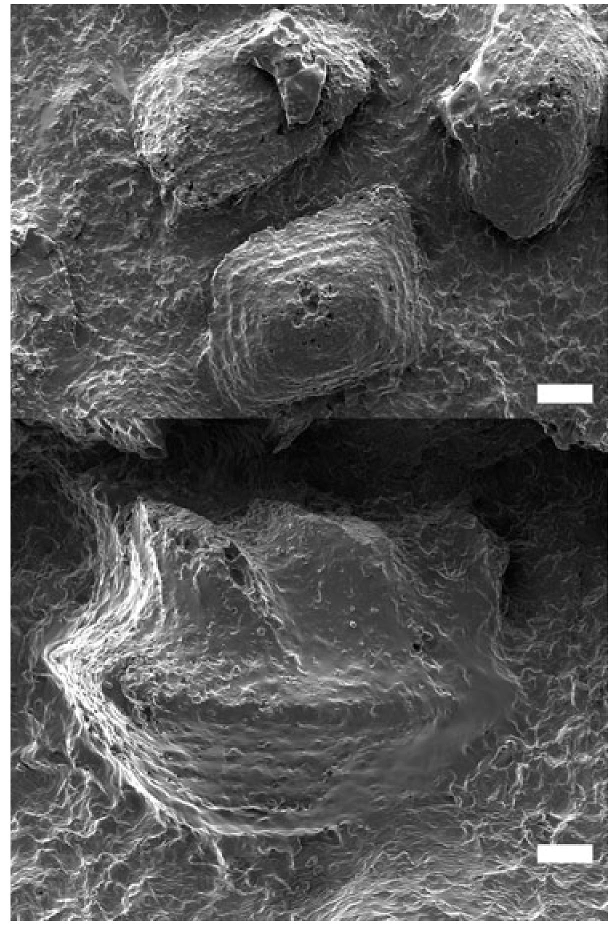

FIG. 5. Scanning electron microscopy images of two scales from the posterior region of NHM P 19999 with bulging bases. A, scales in basal view showing concentric ridges, scale bar represents 200 μm. B, view showing both crown and bulging shape of base typical of the more posterior body scales of *Ptomacanthus*, scale bar represents 100 μm.

boat-shaped central cusp that bears a distinct longitudinal concavity as described by Miles. Posteriorly, these give way to broad, flat-topped central cusps, similar to scales reported for the leading edge of the caudal fin of *Obtusacanthus* (Hanke and Wilson, 2004). As reported by Miles, this type of nonoverlapping flat-topped scale, as well as polygonal tesserae, also characterizes the leading edges of the caudal fin of *Ptomacanthus*, where they are much expanded.

The pectoral girdle is covered dorsally and ventrally in flattened, round scales with fine parallel cristae (Figs 2, 6). These scales are quite thin in profile as there is hardly any pronounced neck. The round, flat off-centre base can be seen in a few examples that have been turned over. These are nearly identical in form and similar in position to scales described from the pectoral region of *Obtusacanthus* (Hanke and Wilson 2004). In *Obtusacanthus*, the scale position differs in being placed ventromedial to the pectoral fin. Miles figured an unusual scale of *Ptomacanthus* from the region of the pectoral girdle (Miles 1973*a*, text-fig. 1E), which resembles scales commonly attributed

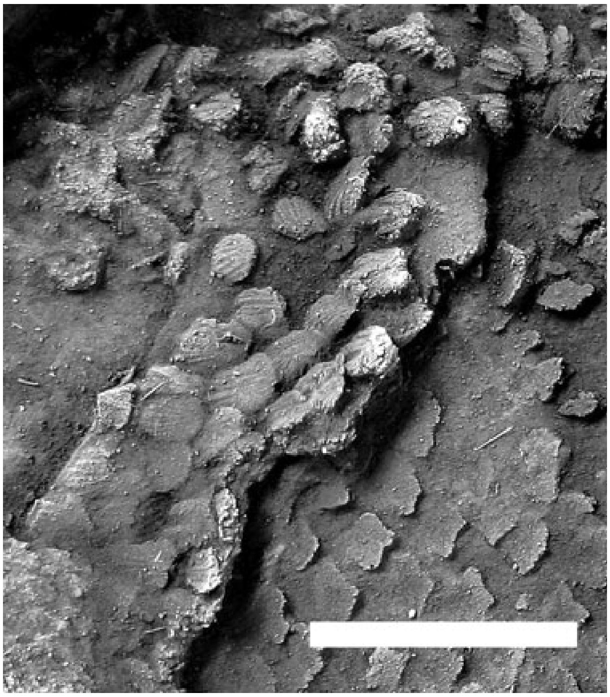

FIG. 6. Flattened scales on the scapular blade of *Ptomacanthus* specimen NHM P 20003. Scale bar represents 5 mm.

to the 'ctenacanth'-type (cf. Karatajute-Talimaa 1992; Williams 1998) in having a narrow, flat base and high crown. However, there is only one example of such a peculiar scale, and this morphology is an illusion caused by the way the scale is oriented with the high-angled leading edge of the scale facing the observer. The rest of the scale appears buried and gives the appearance of being tall, slender and somewhat like 'ctenacanth'-type scales.

Scale histology. The scale histology reported by Miles was based on thin sections taken from the dorsal margin of P 16615. Because this specimen cannot be assigned to *Ptomacanthus*, scale histology data here are based upon P 53880. This is an articulated section of *Ptomacanthus* flank that is identical in all respects to the other articulated specimens. These scales are either recrystallized or lightly altered, but examples do show some limited histological detail. Many fungal hyphae wind and branch through the scales and penetrate the surface of the scale crown. They are easily confused with pulp cavities, cell spaces or canals. However, each of these structures is also genuinely present in the scales.

The scales are polyodontode in the sense that they are composed of more than one generation of odontode deposition. There is evidence of both superpositional and areal growth, as in some species assigned to the scale-type genus *Nostolepis* (Valiukevicius and Burrow 2005). While some specimens show the odontode layers completely covering the previous generation (Fig. 7), some other scales show evidence of the growth zone lines reaching the scale crown (Fig. 7). It is possible that the mode of growth is ontogenetically variable. The lateral cusps were added separately from the central cusp, as evidenced by growth lines that separate them (Fig. 7). However, the laminar base with growth, independent of the crown (Fig. 7), resembles some scales of *Nostolepis striata* described by Gross (1971) and the nominal chondrichthyan *Elegestolepis* (Karatajute-Talimaa, 1998).

The type of dentinous tissue is difficult to determine, but there is abundant *Stranggewebe*, even though this is difficult to see (Fig. 7). One specimen seen in both light microscopy and SEM shows evidence of numerous, fine parallel striations extending towards the crown (Fig. 7), suggestive of orthodentine tubules, but could alternatively be interpreted as fibrous enameloid (Gillis and Donoghue 2007) or are simply a diagenetic artefact. The principal cavities within the scales are quite small and concentrated towards the centre of the scale, and there is also evidence of numerous cell spaces contained within the bony matrix (Fig. 7), indicative of mesodentine. This latter interpretation seems most likely though the possibility for variation of dentine types within the same scale is not to be ruled out.

Both thin sections and SEM of cross-sections of the scales show the basal tissue (Fig. 7), with its distinctive laminated pattern. The bases of the sectioned scales are flat, meaning that they come from the more anterior half of the trunk. Internally, the basal tissue ascends as a conical mass inside the crown. The basal tissue contains numerous cell spaces, but there is no evidence of Sharpey's fibre tubules.

Spine histology. An adequate account of the external morphology of the spines was given by Miles (1973*a*). Here, a partial median fin spine was included in the portion of P 53880 from which sections were taken (Fig. 8). The spines are composed primarily of vascularized bone. The composition of the spine ridges is unclear, as fungal hyphae cross through these structures. However, they do not appear to have been composed of osteodentine. Large vascular canals are present deep within the spine. This region is underlain by a layer of bone laminae within which cell spaces cannot be observed, but also cannot be ruled out as a result of probable recrystallization.

DISCUSSION

Scale growth and comparison

The presence of both bulging- and flat-based scales may be related to the independent growth of the crown and base and the addition of new scales to the body during growth. Zidek (1976, 1985) showed that scale growth in *Acanthodes* proceeded from posterior to anterior along the body. Such a model of scale growth can be used to explain the axial variation in scale morphology from anterior to posterior in *Ptomacanthus*. If the scale bases grew according to a pattern similar to that described for *Elegestolepis* (Karatajute-Talimaa, 1998), as evidenced by the laminar base histology, then the spatial variation in base shape is explained by the addition of a greater number of basal laminae in the posterior body scales. Therefore, the bulging bases result from the addition of layers, rather than the initial shape of the primordium as seen in scales

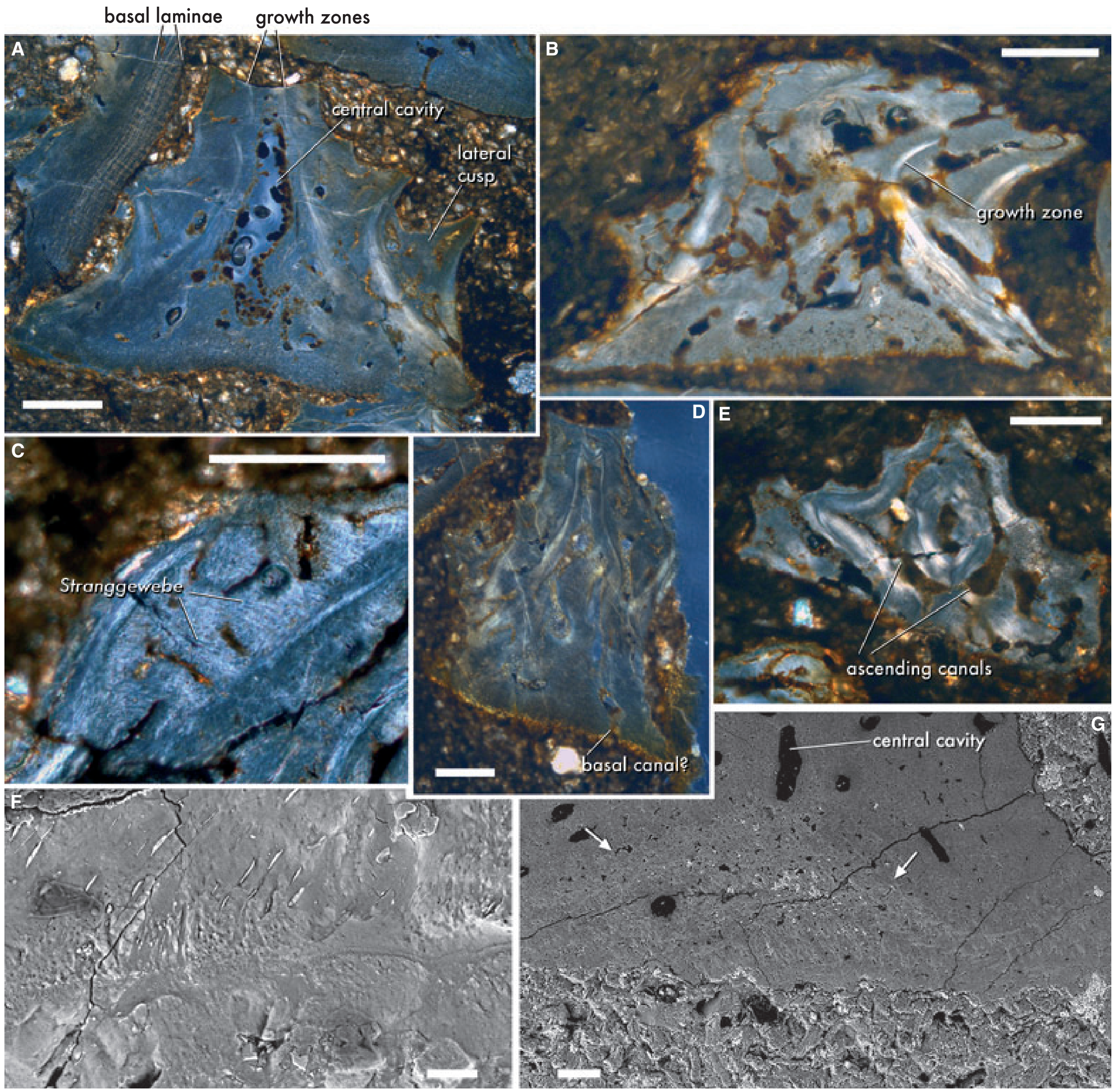

FIG. 7. Light and scanning electron micrographs of sectioned scales of *Ptomacanthus anglicus* Miles specimen NHM P 53880. A, nearly coronal section through flank scale showing partial areal growth. B, nearly sagittal or parasagittal section through scale showing probable superpositional growth. C, closeup of scale showing *Stranggewebe* spaces. D, nearly coronal section from the trailing side of a flank scale. E, coronal section from near the leading part of a flank scale. F and G, scanning electron micrographs of scales. F, the scale crown, showing possible hypermineralized enameloid tissue. G, demarcation of base and crown tissue, numerous osteocyte lacunae visible. Scale bars for A–E represent 200 μm; for F 20 μm and for G 60 μm.

commonly attributed to 'acanthodians'. There is limited evidence of there having been a basal canal connected to a central pulp cavity closed off basally by an ascending cone of basal tissue (Fig. 7); however, no sections show these in confluence.

Crown growth in *Ptomacanthus* scales appears to combine different types of growth patterns. The principal cusps of the scales grow by either superpositional or areal addition of odontodes, with secondary cusps fused on laterally. The base, on the other hand, appears to grow by the addition of independent laminae. They therefore present a unique or very rare combination of characters in any fossil gnathostome known from articulated skeletons. The traits, however, are not unlike some scales attributed to the microremains taxon *Nostolepis* and similar taxa (Valiukevicius 2003, 2004; Valiukevicius and Burrow

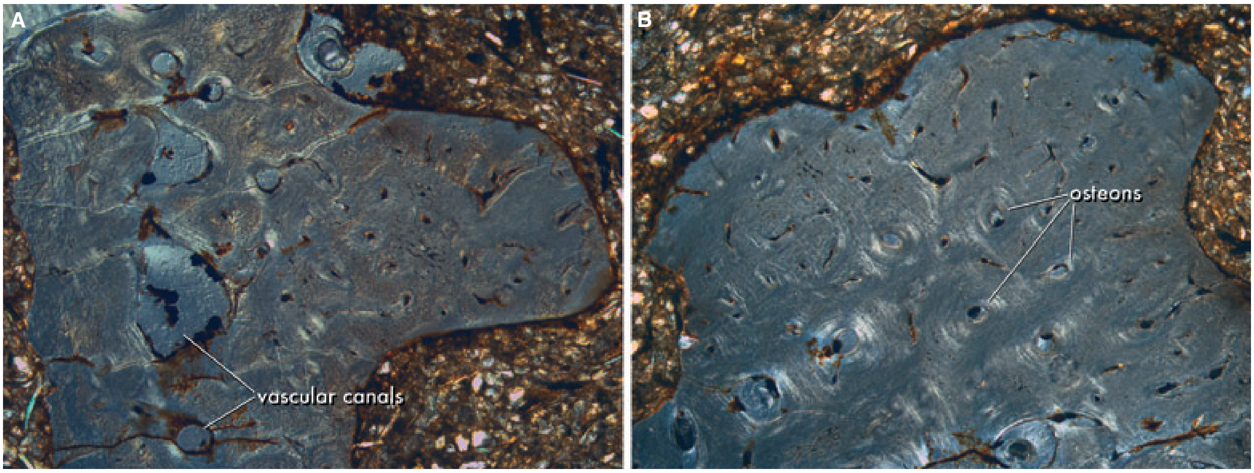

FIG. 8. Light micrographs of fin spine cross-sections of NHM P 53880. A, transverse section through one side of spine, internal side to the left, ridged external surface on the right. B, section of crest of spine's leading edge. Scale bars represent 200 μm.

2005). Although a number of articulated specimens have now been assigned to this genus (e.g. Valiukevicius 2003; Burrow and Turner 2010), the considerable diversity of this typological category (Valiukevicius and Burrow 2005) and its assumed plesiomorphic nature (Ørvig 1967; Denison 1978, Janvier 1996) highlight the possibility that this type of attribution may only give rise to para- or polyphyletic genera.

Clearly, we should be seeking greater context for understanding scale types. What constitutes a 'chondrichthyan' scale is often asserted with great confidence. However, what is known of scale morphologies in articulated or partially articulated Devonian chondrichthyans demonstrates a very wide array of scale types (Woodward and White 1938; Young, 1982; Maisey, 1989; Williams, 1998). Most of these studies offer few clues about scale histology and odontode growth, which can only be inferred by superficial examination. Because they are not observed directly, histological evaluations of growth type cannot be scored in cladistic character matrices for these taxa. Remarkably little is known about the scales of 'placoderms'. The seminal works by Burrow and Turner (1998, 1999) have scarcely been followed up in more than a decade since their publication.

The scales of vent-spined gnathostomes such as *Ptomacanthus*, *Obtusacanthus*, *Lupopsyroides*, *Kathemacanthus*, and according to the account of Burrow and Turner (2010) *Parexus* and *Climatius*, range from superpositional to areal and monodontode. As such, they provide important context for how we attribute areally growing scales to a taxon. The emergent picture of acanthodian paraphyly highlights the incompleteness of the argument underlying taxonomic dichotomies that classify specimens as either chondrichthyan or acanthodian. Such distinctions invite all the problems of paraphyletic groupings: the failure to express more precise overall relationships, imprecise comparison and interpretation, and nonarguments that reflect only semantic rather than empirical distinctions. Several key problems must be addressed before we can begin asserting that certain whole-body fossils belong to the chondrichthyan stem based on attributes of their scales. In particular, histological data from identifiable chondrichthyan and 'placoderm' skeletons are required. More data from chondrichthyans will help establish an array of scale characters that can be positively assigned to other aspects of their anatomies, such as the endoskeleton. Placoderms remain a significant gap in our knowledge of early gnathostome scale anatomy and, as probably stem gnathostomes, would provide critical outgroup comparison data for these characters.

The relationships of Ptomacanthus *and gnathostomes*

Brazeau (2009) examined morphological character distributions relating to the phylogenetic placement of *Ptomacanthus*. Characters such as the absence of an extended trabecular portion of the braincase were consistent with a stem gnathostome placement. While a number of homoplasious features of the postcranium suggested a stem chondrichthyan placement, a placement on the osteichthyan stem would be consistent with the presence of branchiostegal gill coverings, but the radically different braincase morphologies of *Ptomacanthus* and *Acanthodes* would still imply a grade of 'acanthodian'-type stem osteichthyans. The addition of data from the scales of *Ptomacanthus*, such as the partial areal growth pattern, is not unlike scales attributed to chondrichthyans, but the lack of comparative context troubles this interpretation, as well as similar interpretations of other taxa (e.g. *Kathem-*

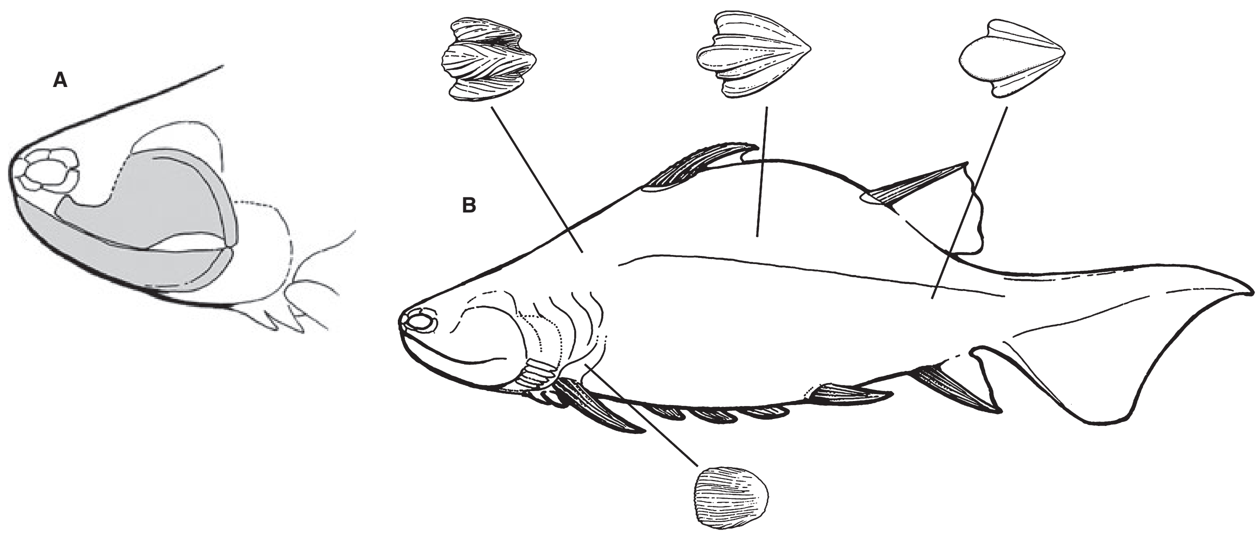

FIG. 9. Revised reconstruction of *Ptomacanthus anglicus* Miles. A, lateral view of the head showing new interpretations of the palatoquadrate and Meckelian element shaded in grey (not meant to indicate divisions of mineralizations). B, lateral view restoration of body showing distribution of different scale crown morphologies.

acanthus, *Seretolepis*, according to Hanke and Wilson 2010).

The stem placement of *Ptomacanthus* within or in relation to the gnathostome crown remains uncertain. What is clear, however, is that resolution of the question of how certain vent-spined gnathostome taxa are related to the principal gnathostome crown lineages (Osteichthyes and Chondrichthyes) will imply significant amounts of reversal or homoplasy. For instance, the trait of having the lateral line canal pass between scales, rather than piercing them or forming a groove in them as in all other outgroups, is uniquely found in vent-spine gnathostomes and chondrichthyans (Janvier 1996). However, osteichthyans and very many (although not all) 'acanthodians' uniquely share branchiostegal gill coverings. As a consequence, it is impossible to place the species exhibiting both these traits on any stem without implying reversal or homoplasy in one of these characters.

CONCLUSION

This reappraisal of *Ptomacanthus anglicus* (Miles, 1973*a*) leads to the new reconstruction presented here (Fig. 9). The new comparative information helps place this taxon into context in the question of basal gnathostome phylogeny. The unusual braincase morphology is accompanied by a peculiar set of dermal characters similar to both 'acanthodians', and some taxa suggested to be stem chondrichthyans. In this way, *Ptomacanthus* adds to the growing list of taxa that erode the formerly clear distinction between 'acanthodians' and other early gnathostome taxa. The uncertain placement of *Ptomacanthus* can be resolved as more work is carried out on the relationships of early gnathostomes in addition to the discovery of more fossils. Greater confidence in how scale and histological characters can be used to place taxa on particular stems depends on greater knowledge of outgroup, or potential outgroup taxa, as well as from chondrichthyans. At present, much of our knowledge is derived from isolated remains attributed to higher taxonomic categories. As a consequence, whole skeletons are now being interpreted in the light of those taxonomies. This inverts the process of discovering phylogenetic (in)congruence of characters. More data from whole or articulated skeletons examined in a cladistic framework will be required to make sense of the compatibility problems of gnathostome characters presented by 'acanthodians'.

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