# ANATOMY OF THE EARLY DEVONIAN ACANTHODIAN BROCHOADMONES MILESI BASED ON NEARLY COMPLETE BODY FOSSILS, WITH COMMENTS ON THE EVOLUTION AND DEVELOPMENT OF PAIRED FINS

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# ANATOMY OF THE EARLY DEVONIAN ACANTHODIAN *BROCHOADMONES MILESI* BASED ON NEARLY COMPLETE BODY FOSSILS, WITH COMMENTS ON THE EVOLUTION AND DEVELOPMENT OF PAIRED FINS

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ABSTRACT—New anatomical details are described for the acanthodian *Brochoadmones milesi* based on nearly complete body fossils from Lochkovian rocks at MOTH, Mackenzie Mountains, Northwest Territories, Canada. The body and caudal peduncle are deep, and a prominent nuchal hump is present before the dorsal fin origin. The caudal fin is correspondingly deep and ventrally, the caudal fin lies close to and is partly joined to the slender anal fin.

A delicate pectoral fin trails the flattened pectoral-fin spine where previously known specimens showed only a fin spine resembling a bivalve shell. Seen for the first time in any vertebrate, each of the six pairs of prepelvic spines supports a small, scale-covered finlet. Both prepelvic spines and scale-covered finlets increase in size posteriorly. The series of paired prepelvic finlets originates ventral to the branchial chamber and anteroventral to the pectoral fin, and extends posteriorly as far as the pelvic fins.

The scales of the body and fins are thin and flat, without obvious evidence of ossified basal tissue or entry point for vascular tissue. The main lateral-line canal passes dorsal to the branchial chamber and terminates at the trailing edge of the caudal fin web. Lateral-line scales are thicker than body scales and show concentric growth zones. Scales from the dorsal midline of the caudal fin are also thicker, showing few superpositional growth zones in the mesodentine of the crown together with what appears to be cellular basal tissue.

The structure and position of the pectoral spine and fin, the extremely thin body scales, the slender anal fin, and the prepelvic finlets are all unique and appear to be autapomorphic features compared to those of other acanthodians. *Brochoadmones milesi* is derived relative to other fishes traditionally classified in the Climatiiformes. *Kathemacanthus rosulentus* is removed from the Brochoadmonoidei, leaving only *B. milesi* in a monotypic suborder.

## INTRODUCTION

Interpretations of the anatomy of *Brochoadmones milesi* have evolved with discovery of increasingly well-preserved fossils. The species was described by Bernacsek and Dineley (1977) based on two poorly preserved specimens collected from the Devonian fish layer at the MOTH locality, Mackenzie Mountains, N.W.T., Canada. The holotype (NMC 22710) includes a few head scales, body scales, tooth whorls, and fragments of dorsal, prepelvic, pelvic, and anal fin spines, but much of the fish could not be reconstructed accurately (Bernacsek and Dineley, 1977:text-fig. 14; Fig. 1A). The pectoral fin spines were missing from the first two known specimens, so Bernacsek and Dineley reconstructed an elongate pectoral spine with the expectation that it would be similar to that of other acanthodians. Few scales were preserved on the holotype, and therefore, Bernacsek and Dineley (1977) could not provide a detailed account of the squamation.

Bernacsek and Dineley (1977) erected the new family Brochoadmonidae for their new species, although they were unsure whether *Brochoadmones milesi* represented an ischnacanthiform or a climatiiform. Denison (1979) found no reason to assign *Brochoadmones milesi* to a new family, and instead, placed *Brochoadmones* in the family Climatiidae, based on the presence of multiple prepelvic (then called ‘intermediate’) spines, multiple tooth whorls, and ‘cranial tesserae.’ The ‘cranial tesserae’ mentioned by Bernacsek and Dineley (1977) likely were fragments of displaced tooth whorls, because the labial side of the tooth whorls of *B. milesi* have a complex, tuberculated surface (see Gagnier and Wilson, 1996a:figs. 7g–j). Denison thought that the fin spines, which are long, narrow, and have smooth ribs, represented a derived feature relative to other climatiiform taxa.

Gagnier and Wilson (1996a) added to the description of *Brochoadmones milesi* based on 14 new specimens collected between 1983 and 1990. They recognized unique features of *B. milesi* and resurrected the original family assignment provided by Bernacsek and Dineley (1977); they also erected a suborder Brochoadmonoidei to emphasize the distinctiveness of *B. milesi*, and suggested a relationship between *B. milesi* and another taxon from MOTH, *Kathemacanthus rosulentus* Gagnier and Wilson, 1996a. Gagnier and Wilson (1996a) were able to define the shape of the head and trunk, the cranial squamation, dentition, sensory lines of the head and trunk, branchial openings, and details of the external ornament on the prepelvic and dorsal fin spines. In addition, Gagnier and Wilson (1996a) described the unique structure of the pectoral fin spine of *B. milesi*, and showed that dentigerous bones are absent. Unfortunately, the anal and caudal fins were not preserved on any of the specimens available to Gagnier and Wilson (1996a), who suggested that *B. milesi* had an elongate and laterally compressed body (Gagnier and Wilson, 1996a:fig. 2; Fig. 1B).

Until now, *Brochoadmones milesi* has received little attention in phylogenetic analyses of acanthodians, probably because it was imperfectly known. *Brochoadmones* was excluded from cladistic analyses performed by Long (1986), Maisey (1986), and Janvier (1996). In addition, Gagnier and Wilson (1996a, b) did not test their proposed classification of *B. milesi* with a cladistic analysis.

The Climatiiformes as currently defined may be paraphyletic (Gagnier and Wilson, 1996b; Janvier, 1996; Hanke, 2001a; Hanke and Wilson, 2004). Hanke and Wilson (2000, 2004) and Hanke

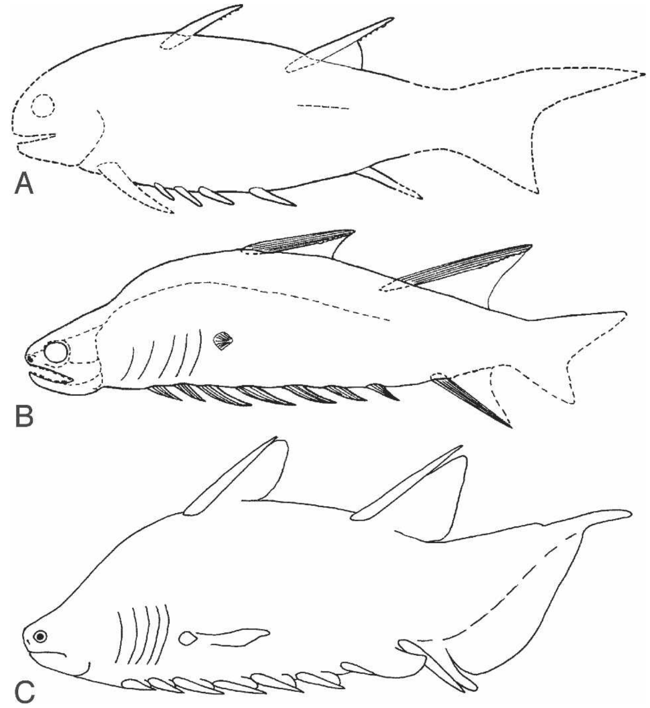

FIGURE 1. The evolution of reconstructions of *Brochoadmones milesi*, **A**, after Bernacsek and Dineley (1977, text-fig. 14); **B**, after Gagnier and Wilson (1996a, fig. 2); and **C**, a new reconstruction based on two new nearly complete body fossils, UALVP 41494 and UALVP 41495.

(2001a) presented results from the first cladistic analysis to include *Brochoadmones*, which was found to be derived relative to *Lupopsyrus pygmaeus* and other typical 'climatiiforms,' and, in a strict consensus analysis, contributed to a polytomy including diplacanthids, ischnacanthiforms, and acanthodiforms. In contrast to the classification proposed by Denison (1979), *Brochoadmones milesi* possesses no synapomorphies to indicate relationship with members of the Climatiidae (e.g., *Brachyacanthus* and *Climatius* spp.); in this respect, the recent cladistic analyses support the family-level distinction proposed by Gagnier and Wilson (1996a). Furthermore, these recent cladistic analyses do not support the monophyly of the Climatiiformes as a whole.

In 1996, an extraordinary fossil slab was collected from the MOTH locality (Fig. 2A). When collected, only a small area of bone was visible, but subsequent preparation revealed well-preserved fossils of eight individual vertebrates representing seven species. Now known informally as the 'Wonder Block,' the slab includes, as its most prominent features, two nearly complete specimens of *Brochoadmones milesi*, one with its right side exposed and the other with its left side exposed (Fig. 2). These two specimens, supplemented by corroborating evidence from other material, provide the basis for the present paper, leading to the third, and, we hope, final reconstruction of the anatomy of this species (Fig. 1C). The new specimens provide data on the pectoral, dorsal, anal, and caudal fins and several other unique features of *Brochoadmones*, and have implications for its phylogenetic position as well as its possible mode of life.

## METHODS

The new specimens of *Brochoadmones milesi* occur on the 'Wonder Block' (Fig. 2A) along with remains of one osteostracan (as yet undescribed), two fork-tailed thelodonts (*Drepanolepis maerssae* Wilson and Caldwell, 1998, and *Furcacauda heintzae* Wilson and Caldwell, 1998), two acanthodians (*Lupopsyrus pygmaeus* Bernacsek and Dineley, 1977, and *Ischnacanthus* sp., similar to material identified as *Ischnacanthus* cf. *I. gracilis* by Bernacsek and Dineley, 1977), and the holotype of a problematic, putatively chondrichthyan taxon, *Obtusacanthus corroconis* Hanke and Wilson, 2004. Only a small area of the first dorsal spine of one of the specimens (UALVP 41495) of *B. milesi* was visible in the field and consequently shows some weathering (Fig. 2A, C); the remainder of the slab was covered by matrix. A thin layer of bone visible on the edges of the slab suggested the presence of additional fossils, as subsequent preparation confirmed. The slab was prepared by repeatedly immersing it in dilute acetic acid followed by rinsing in fresh water; silt-sized siliciclastic residues remaining after each acetic-acid treatment were removed while wet using soft paint brushes. After preparation, the slab was dried slowly and stabilized using a 5% solution of Glyptal™ cement. For most of the photographic illustrations (except Fig. 2), ammonium-chloride sublimate was used to whiten specimens.

For histological study, small groups of scales were removed from other, imperfect specimens of *B. milesi*, embedded in Luminate 83 HA-4 epoxy, polished to expose histological structure using 600- and 1000-grit wet-dry sandpaper, and given a final polish using moistened alumina powder on a glass plate. High-magnification images were taken using a Nikon coolpix 990 digital camera attached to a Nikon SMZ 1500 dissecting microscope. Line drawings were made with the same dissecting microscope and its camera lucida attachment.

**Institutional Abbreviations**—**GSC**, Geological Survey of Canada, Calgary, Alberta, Canada (locality number of type material); **NMC**, Canadian Museum of Nature, Ottawa, Ontario (holotype and paratype specimens); **UALVP**, Laboratory for Vertebrate Palaeontology, Departments of Biological Sciences and Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta, Canada (all other specimens).

**Anatomical Abbreviations**—**af.**, anal fin web; **afs.**, anal fin spine; **asc.**, ascending canal of scale odontode; **br.o.**, branchial opening; **circ.orb.**, circumorbital plates; **dfa.**, anterior dorsal fin web; **dfa.sp.**, anterior dorsal fin spine; **dfp.**, posterior dorsal fin web; **dfp.sp.**, posterior dorsal fin spine; **eno.**, external nasal opening; **epi.ch.l.**, caudal fin epichordal lobe; **gz.**, growth zone of scale; **hl.**, hypochordal lobe of caudal fin; **ins.a.**, insertion area of spines; **ioc.ot.**, otic part of infraorbital sensory canal; **ioc.pt.**, postorbital part of infraorbital sensory canal; **ioc.sb.**, suborbital part of infraorbital sensory canal; **lc.**, main lateral sensory canal; **lt.**, left side; **mdc.**, mandibular sensory canal; **orc.**, oral sensory canal; **ot.**, otic material; **pcf.**, pectoral fin web; **pfc.**, profundus sensory canal; **pfs.**, pectoral fin spine; **pls.**, pelvic fin spine; **poc.**, preopercular sensory canal; **p.pw.**, prepelvic fin web; **prim**., scale primordium; **prp.**, prepelvic spine; **pv.f.**, pelvic fin web; **rt.**, right side; **smc.**, supramaxillary sensory canal; **tw.**, tooth whorls.

## SYSTEMATIC PALEONTOLOGY

Class ACANTHODII Owen, 1846
Order incertae sedis
Suborder BROCHOADMONOIDEI
Gagnier and Wilson, 1996a

**Revised Diagnosis**—As for the only known family, genus, and species.

**Remarks**—*Brochoadmones milesi* has no derived features to indicate close relationship with any of the established acanthodian orders (Hanke and Wilson, 2000, 2004; Hanke, 2001a), and therefore, the position of the suborder Brochoadmonoidei Gagnier and Wilson, 1996a, is left incertae sedis.

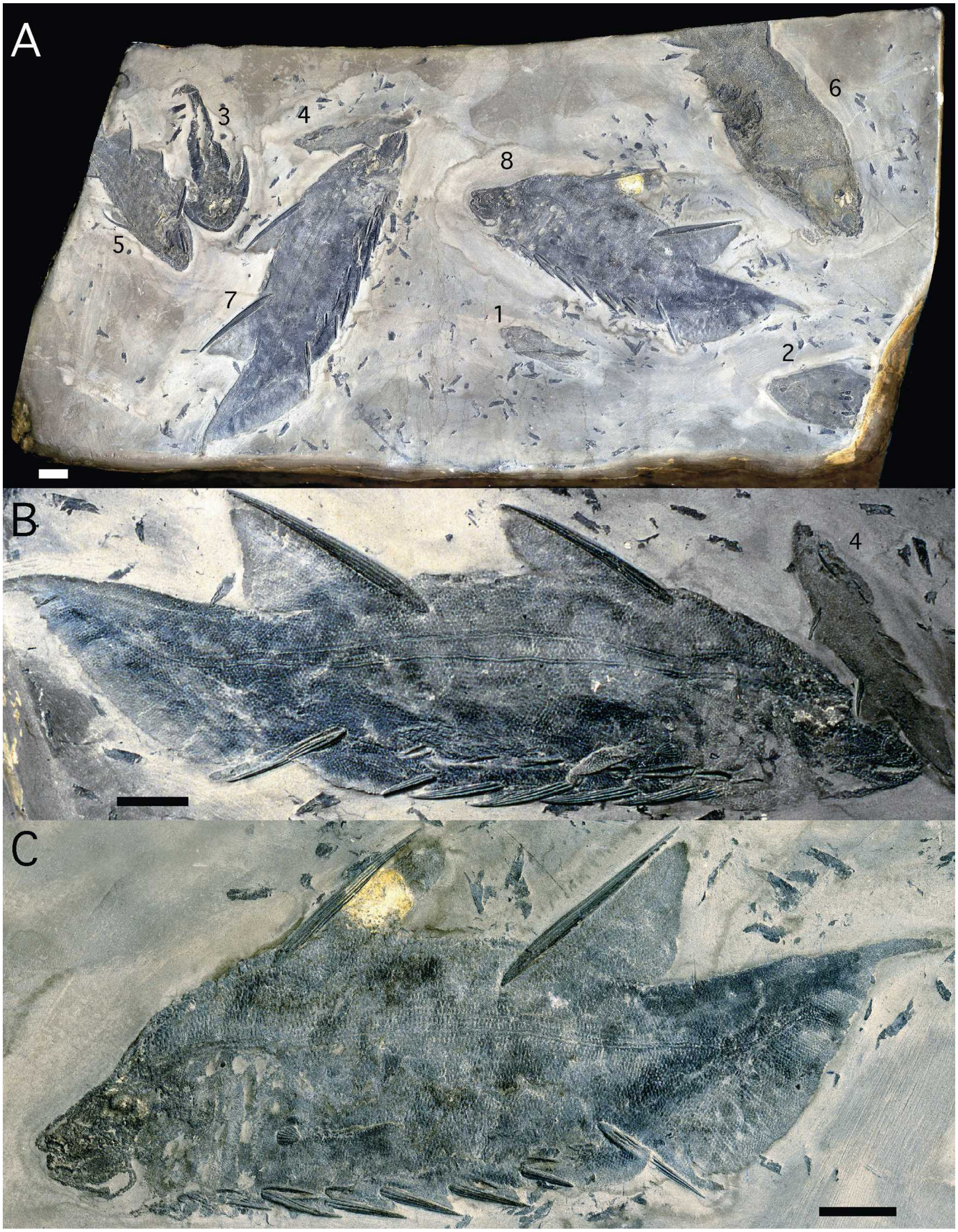

FIGURE 2. **A**, The 'Wonder Block' slab of Lochkovian (Early Devonian) vertebrates from the MOTH locality, containing eight individuals representing seven species. **B**, *Brochoadmones milesi*, UALVP 41494, with its right side exposed; **C**, *Brochoadmones milesi*, UALVP 41495, with its left side exposed. Scale bars equal 1 cm. **Abbreviations**: **1**, the furcacaudid thelodont *Drepanolepis maerssae*, anterior to left, ventral to top; **2**, the furcacaudid thelodont *Furcacauda heintzae*, anterior to left, dorsal to top; **3**, unidentified osteostracan, ventral side exposed; **4**, the primitive 'climatiiform' acanthodian *Lupopsyrus pygmaeus*, ventral to top; **5**, the ischnacanthid acanthodian *Ischnacanthus* cf. *I. gracilis*, ventral to top right; **6**, the holotype of *Obtusacanthus corroconis*, dorsal to upper right; **7**, *Brochoadmones milesi*, UALVP 41494, enlarged in B; **8**, *Brochoadmones milesi*, UALVP 41495, enlarged in C.

No derived features unite *Brochoadmones milesi* with either the suborder Climatioidei or the Diplacanthoidei of the Climatiiformes; accordingly, the suborder Brochoadmonoidei is retained. The suborder as established by Gagnier and Wilson (1996a) was intended to group *B. milesi* with *Kathemacanthus rosulentus*; however, all of the features of the suborder Brochoadmonoidei as originally diagnosed, with the exception of the nuchal hump and the elevated position of the pectoral fin and its fin spine, can now be interpreted as plesiomorphic for all acanthodians. While the elevated pectoral fin origin is a potential synapomorphy, *B. milesi* and *K. rosulentus* differ in many features of their pectoral skeleton (endoskeleton microstructure, prepectoral spine presence, structure of fin web, and size, shape, and ornamentation of pectoral fin spine). *Kathemacanthus rosulentus* further differs from *B. milesi* and resembles the putative chondrichthyan *Seretolepis elegans* in having complex scales showing areal growth, globular calcified(?) endoskeletal microstructure, and prepectoral and prepelvic spines that are similar in number, shape, and position (UALVP collections). Based on these similarities, Hanke (2001b; Hanke and Wilson, 2005) suggested removing *K. rosulentus* from both Brochoadmonoidei and Acanthodii, and grouping it with the putative chondrichthyan *S. elegans*. The details of the morphology of new specimens of *S. elegans* and *K. rosulentus* will be the focus of a separate paper.

The diagnosis of the suborder Brochoadmonoidei now is based solely on the features of the single included species, and it may be argued that any taxa above the level of family or genus are superfluous. The suborder is retained here until such time as there is strong evidence for uniting *Brochoadmones* with one or another of the named suborders or orders of acanthodians.

### Family BROCHOADMONIDAE Bernacsek and Dineley, 1977

**Revised Diagnosis**—As for the only known genus and species.

**Remarks**—As mentioned above, *Brochoadmones milesi* is distinctive in comparison to all other acanthodians, and was classified in the family Brochoadmonidae by Bernacsek and Dineley (1977). This familial rank is retained following the classification presented by Gagnier and Wilson (1996a).

### Genus *BROCHOADMONES* Bernacsek and Dineley, 1977

**Type Species**—*Brochoadmones milesi* Bernacsek and Dineley, 1977.

**Revised Diagnosis**—As for the only known species, *Brochoadmones milesi*.

### *BROCHOADMONES MILESI* Bernacsek and Dineley, 1977
(Figs. 1–8)

**Revised Diagnosis**—Compressed, deep bodied acanthodian with large, terminal mouth, prominent nuchal hump, and short, deep caudal peduncle; multiple adsymphyseal tooth whorls; branchial openings in multiple pairs, separated by septa covered with small, thin scales; pectoral fin spines small, plate-like; prepectoral spines absent; dorsal fin spines with prominent insertion areas and paired rows of tubercles on distal third of posterior face; six pairs of prepelvic spines, each with small, scale-covered finlet; pelvic fin spines shorter than posterior-most prepelvic spines; pelvic fin long-based, web margin overlapping origin of anal fin; anal fin narrow, ribbon-like, with basal portion attached to leading edge of caudal fin; body squamation of thin, smooth-crowned scales; thickened scales along main lateral-line canal and on margin of caudal-fin axis showing concentric growth zones; lateral-line canal of tail following ventral edge of caudal fin axis, bending posteroventrally to end on margin of caudal fin web.

**Holotype**—NMC 22710* (Bernacesk and Dineley, 1977:text-fig. 15, pl. 9, figs. 1–3)

**Referred Material**—Body specimens (*, specimens figured by Gagnier and Wilson, 1996a; §, specimens figured in this paper): NMC 22711, UALVP 19262*, 32472*, 32672§*, 32680*, 39054, 39056*, 39057, 41487, 41490, 41494§, 41495§, 41703, 41803, 41804, 41911, 41936, 41941, 42007, 42154, 42185, 42510, 42511, 42513, 42514, 42535§*, 42536, 42595, 43097, 43099, and 43105.

Isolated elements: UALVP 19269, 32399, 32404, 32406*, 32428, 32471, 32407, 32415, 32416, 32522, 32669, 32690, 32957, 39061, 39077, 41354, 41499, 41532, 41545, 41570, 41654, 41676, 41679, 41708, 41713, 41754, 41819, 41900, 41919, 41926, 41935, 41936, 41949, 41970, 41979, 42005, 42006, 42011, 42019, 42031, 42035, 42093, 42107, 42110, 42116, 42120, 42122, 42125, 42127, 42130, 42133, 42146, 42151, 42162, 42163, 42170, 42175, 42179, 42515, 42527, 42531, 42539, 42540, 42671, and 43098.

Unexamined specimens: UALVP 43027, 43028, 43045, and 44026.

**Locality and Age**—All presently known specimens of *Brochoadmones milesi* are recovered from talus below a Lochkovian (Lower Devonian) fossiliferous interval between 430 and 435 m, as measured in 1996, in the MOTH section, Mackenzie Mountains, N.W.T., Canada (see Gagnier and Wilson, 1996a:fig. 1), corresponding to UALVP Locality 129. The same interval, GSC locality 69014, occurred in section 43 of Gabrielse et al. (1973) at approximately 411 m. The fish layer is composed of calcareous siltstone and/or argillaceous limestone deposited in alternating light and dark laminae. Although previous authors have suggested habitats ranging from intertidal lagoons to deep-water shelf settings, recent sedimentological, ichnological, and taphonomic study suggests an oxygen-poor, intra-shelf topographic low below storm wave base (Zorn et al., 2005) on a shelf that fringed western Laurussia (combined Laurentia and Baltica; Li et al., 1993).

## DESCRIPTION

*Brochoadmones milesi* is a deep-bodied acanthodian with a prominent ‘nuchal’ hump in its dorsal profile immediately posterior to its head (Figs. 2–4). The ratio of body length to depth is 0.28, with the deepest part of the body at the level of the origin of the anterior dorsal-fin spine. The caudal peduncle is short and deep. The axial skeleton is unossified.

The shape of the head is unusual for an acanthodian, tapering to an acutely pointed snout anteriorly, with large orbits (Figs. 2–4). In all well-preserved specimens, the posterior extent of the braincase is indicated by two masses of sandy material interpreted as otic statoconia (Sahney and Wilson, 2001; Figs. 3–5). The structure and shape of the head are indicated only by the arrangement of scales and teeth, because the braincase and visceral arches are unossified.

The orbits are located above the anterior half of the mouth gape, and are ringed by a series of rectangular circumorbital scales (Fig. 4B). These circumorbital scales and other specialized sensory-line scales on the head cradle the cranial branches of the sensory canals in a groove between raised margins of the crown (Figs. 4, 5). There are no sclerotic plates within the orbits of any specimens.

No enlarged cranial tesserae or compound cranial plates are seen in *Brochoadmones milesi*. Scales of the head have a simple, flat crown, and a flat to slightly concave basal surface (Figs. 5B, 7A). The polygonal crowns of head scales fit closely together to form a ‘cobble-stone’ covering. There is no indication of multiple odontodes on any head scales as exist for some climatiid head scales (Denison, 1979:fig. 16). We were unable to prepare informative thin sections of head scales so it has not been possible to determine the extent of basal tissue or the microstructure of the crown tissue.

The terminal mouth is large. At least 10–11 multicusped, adsymphyseal tooth whorls per side are positioned in a continu-

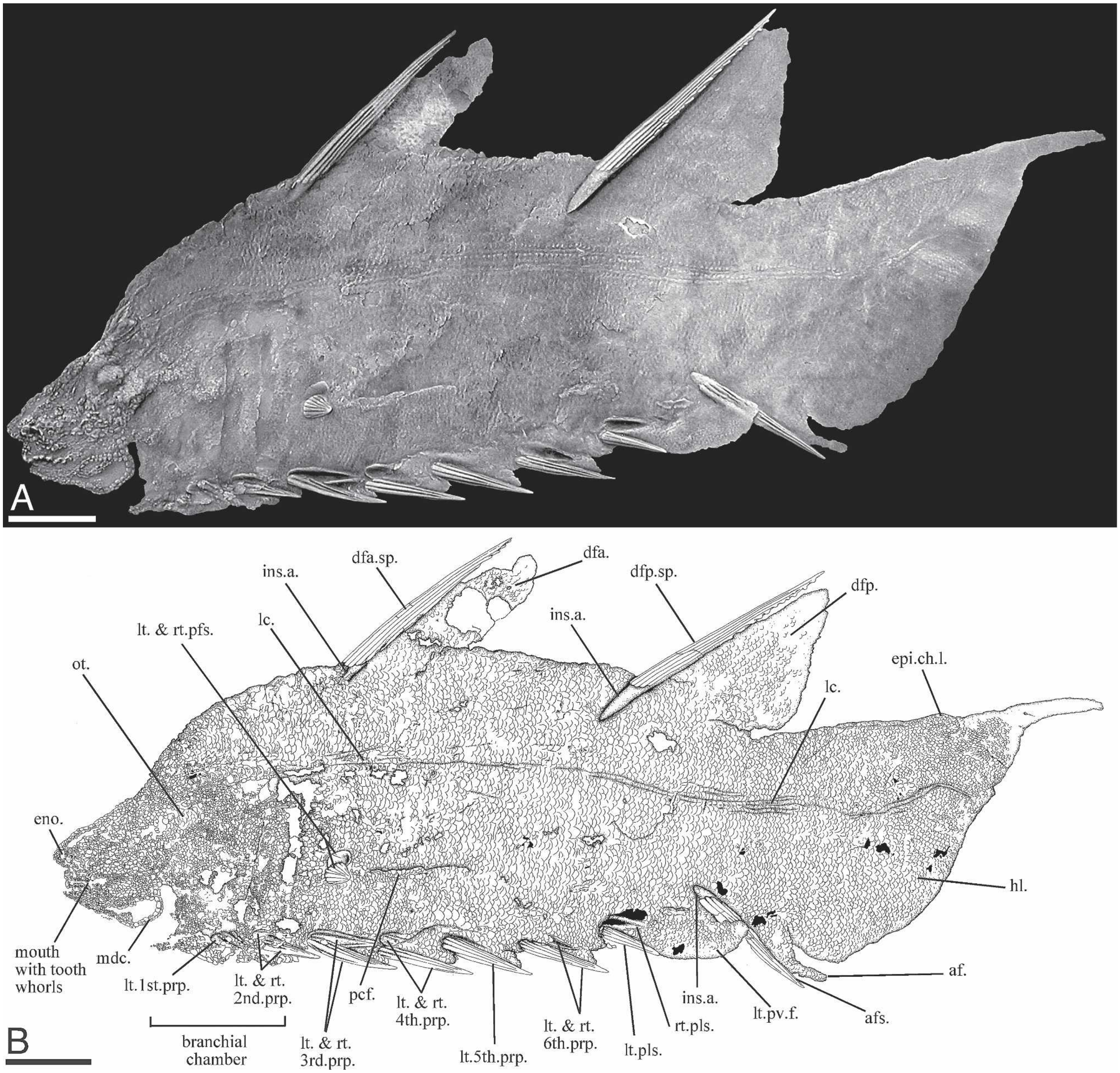

FIGURE 3. *Brochoadmones milesi*. **A**, photograph of UALVP 41495 in left lateral view; **B**, camera-lucida drawing of the same specimen with interpretation of structures; scale bars equal 1 cm. For abbreviations see text.

ous battery along the margins of both the upper and lower jaws (Gagnier and Wilson, 1996a; Figs. 4, 5A). Individual whorls were described in detail by Gagnier and Wilson (1996a). Each whorl is oriented labio-lingually, with the larger cusps of each tooth whorl on its lingual side, suggesting that the whorls rotated labially during the growth of the fish as the fish required larger teeth or as teeth were worn and replaced. The tooth whorls are smallest near the jaw angle and increase in size anteriorly, a pattern reminiscent of the growth of teeth on ischnacanthid dentigerous jaws and constrained by basic jaw mechanics.

Meckel's and palatoquadrate cartilages were unossified, but the posteriorly descending course of the mandibular sensory canal suggests that Meckel's cartilage was deeper posteriorly and more slender and slightly hooked or curved upwardly near the symphysis (Gagnier and Wilson, 1996a; Figs. 4, 5A). A few isolated, tiny, whorl-like denticles are visible in the pharynx of UALVP 41495 (also see Gagnier and Wilson, 1996a:figs. 7g–h), but given the rarity of these denticles, it is possible that they represent small, posteriorly displaced tooth whorls rather than pharyngeal teeth.

The deep branchial chamber is approximately as long as the braincase (Figs. 2, 3, 4A). No branchial ossifications are evident and we could not find any branchial denticles to indicate the position of gill arches. Five external gill slits are present (Gagnier and Wilson, 1996a). The posterior two or three slits are long dorsoventrally, but the anterior two or three slits appear to have been shorter (Figs. 3, 4A, 7E). The best-preserved slits (Figs. 4A, 7E) are separated by an external covering of overlapping scales

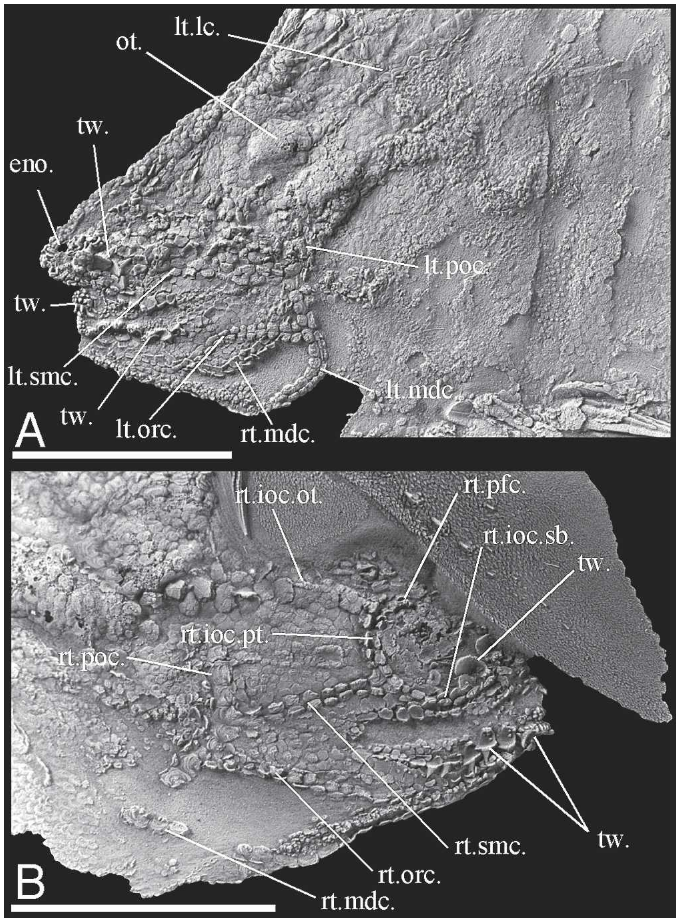

FIGURE 4. *Brochoadmones milesi*. **A**, detail of the head of UALVP 41495, **B**, detail of the head of UALVP 41494, with overlying tail of *Lupopsyrus pygmaeus* (UALVP 41493); scale bars equal 1 cm. For abbreviations see text.

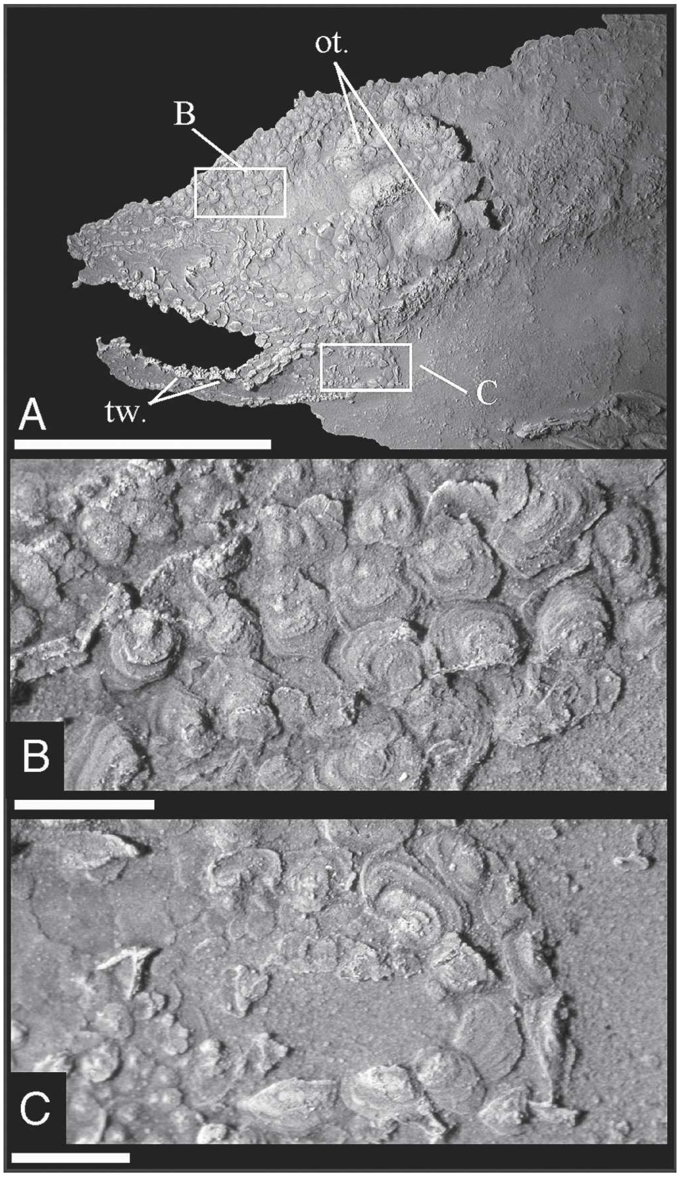

FIGURE 5. *Brochoadmones milesi*. **A**, the preserved parts of the head on UALVP 32672, scale bar equals 1 cm; **B**, detail of scales surrounding the main sensory canal trace; **C**, detail of scales surrounding the mandibular sensory canal trace. Scale bars for B, C equal 1 mm. For abbreviations see text.

similar to, but smaller than, the normal flank scales on the body. Where this covering has been broken away, one can see tiny, well-spaced scales with rose-shaped crowns. These may have lined the anterior face of the inter-branchial septum separating adjacent gill slits (Fig. 7E).

The pectoral endoskeleton is unossified and neither dermal plates nor prepectoral spines are present (Gagnier and Wilson, 1996a). The pectoral spine (termed the 'flank spine' by Gagnier and Wilson, 1996a, because of uncertainty about its homology) resembles the valve of a brachiopod or bivalve and was at first mistaken for one early in the study of the material eventually described by Gagnier and Wilson (1996a). Finding a similar paired structure on every relevant specimen showed that it was in fact a pair of pectoral spines. Each spine is small, short, and nearly flat, with a wide, shallow basal opening (Figs. 2C, 3, 6A), and presumably did not protrude far from the flank. The spine is ornamented with smooth ribs that converge at the apex of the spine (Gagnier and Wilson, 1996a; Fig. 6A). The pectoral spine is in an elevated position on the flank, immediately posterior to the branchial chamber and well above the level of the prepelvic paired spines (Figs. 2, 3).

The pectoral fins were not preserved on the specimens available to Gagnier and Wilson (1996a) and Bernacsek and Dineley (1977); however, a long, slender pectoral fin is present on one specimen (UALVP 41494; Fig. 6A), and a broken line of attachment for the fin is present on the other (Fig. 3). The detailed shape of the pectoral fin of UALVP 41494 cannot be determined because it appears to have been folded during decay and burial of the carcass.

The pelvic series includes six closely spaced pairs of prepelvic spines (Figs. 1–3, 6B). Gagnier and Wilson (1996a) identified seven spine pairs; however, it is now possible to see that the posterior-most pair in their interpretation corresponds to the pelvic spines, which are very similar. The prepelvic spines are positioned in two diverging rows (Figs. 2B, C, 3, 6A, B), each row beginning anteriorly beneath the anterior half of the branchial chamber, extending posteriorly to end just before the pelvic-fin spines.

Prepelvic spines are ornamented with smooth ribs, which converge on the leading edge of the spine (Figs. 6A, B). Each spine has a large, hollow basal cavity. The lack of a prominent insertion area for each spine is not surprising given their proximity to the coelomic cavity. The prepelvic spines appear to have

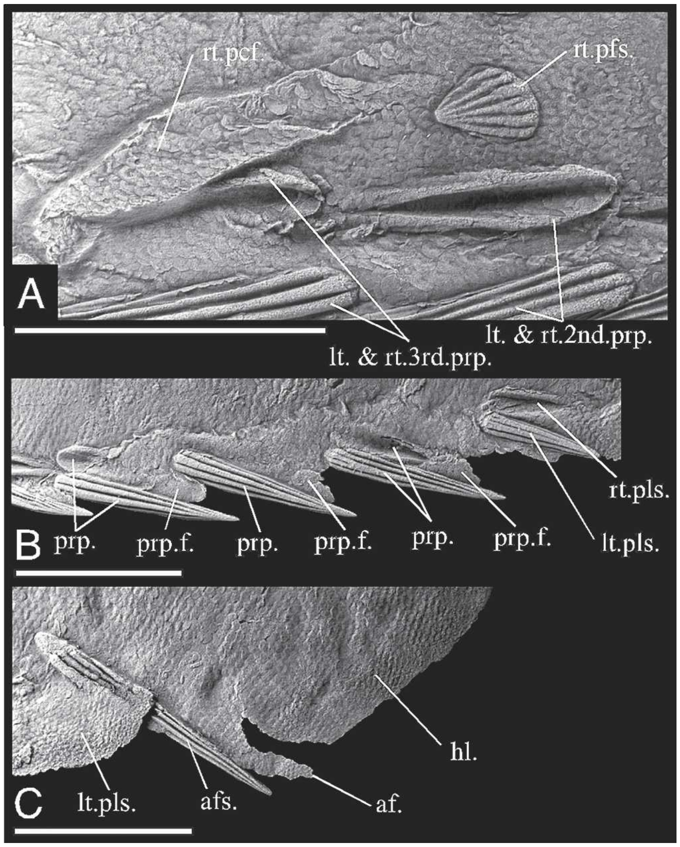

FIGURE 6. *Brochoadmones milesi*. **A**, detail of the pectoral fin spine and pectoral fin (UALVP 41494); **B**, detail of the prepelvic spines and associated prepelvic finlets of UALVP 41495; **C**, detail of the anal spine and associated fin of UALVP 41495; scale bars equal 1 cm. For abbreviations see text.

been held at a low angle to the body margin; their shallow insertion may have allowed some limited mobility. The anteriormost spines are the smallest and the posterior few pairs are the largest in the series (Gagnier and Wilson 1996a; Figs. 2, 3, 6B).

The two specimens of *Brochoadmones milesi* described here provide the first evidence of prepelvic finlets in any vertebrate. Each prepelvic spine forms the leading edge for a small web of scale-covered skin (Figs. 3B, 6B). The paired finlets have scales on both inner and outer faces and were clearly ventrolateral projections from the body wall. The combination of spines plus scale-covered webs resembles theoretical expectations of multiple paired finlets in primitive gnathostomes (e.g., Zug, 1979:fig. 7.2). The prepelvic finlets increase in size posteriorly in concert with their respective spines.

Pelvic spines are slightly shorter than the posterior-most prepelvic spines and approximately half the length of the anal fin spine. The straight pelvic spines have a broad base with an enlarged basal opening (Gagnier and Wilson 1996a; Figs. 2, 3, 6B). Pelvic spines are not deeply inserted in the abdomen. The ribs of the pelvic spines are smooth, of nearly equal thickness, and converge on the leading edge of the spine (Fig. 6B).

Each pelvic spine supports a large, broad-based pelvic fin web. The margin of the pelvic fin web is convex ventrally and posteriorly (Figs. 2, 3, 6C) and slightly overlaps the origin of the anal fin spine, implying that the anus must have been located between the bases of the pelvic fins and the anal spine origin. The scales on the pelvic fin web are aligned in rows and decrease in size towards the fin margin. There is no evidence of endoskeletal support in the pelvic fin base.

The anal-fin spine is long, straight, and has a short base with a prominent insertion area (Figs. 2, 3, 6C). The basal cavity is open along the basal third of the spine. The ribs of the anal spine parallel the leading edge of the spine to within a centimeter of the spine tip. There are no denticles on the posterior face of the anal spine.

The anal fin web is attached to the anal spine for most of the spine's length (Figs. 3B, 6C). In addition, nearly one-third of the trailing edge of the anal fin is continuous with the leading edge of the hypochordal lobe of the caudal fin; in this way the anal spine reinforces the leading edge of the anal + caudal fin complex. The anal fin web has a very short base and is the same length as, or slightly longer than, the anal fin spine (Figs. 3, 6C).

The deep caudal peduncle supports a large, epicercal caudal fin. The large surface area of the caudal fin means that it had a low aspect ratio, the biological significance of which is discussed below. The convex trailing margin of the caudal fin extends about as far posteroventrally as the anal fin and anal spine (Figs. 2, 3, 6C). The transition from typical scales on the caudal peduncle to the scales of the caudal fin web is gradual. Scales on the distal parts of the caudal fin web are aligned in rows (Fig. 6C). The low, lobate, epichordal portion of the caudal fin is covered with small, thickened scales, along the anterior two-thirds of the dorsal midline of the caudal axis (Fig. 7F). The axis of the caudal fin extends about 2 cm posterior to the epichordal part of the fin, and 1 cm beyond the hypochordal portion of the fin (Figs. 2, 3).

Two dorsal fins are present; each dorsal fin is slightly shorter than, and is attached to the basal half of, its fin spine (Figs. 2, 3). The anterior dorsal fin has a convex trailing margin and is shorter anteroposteriorly than the posterior dorsal fin; the posterior dorsal fin is larger, longer based, and more triangular (Figs. 2, 3). The dorsal fin bases are shorter than their respective fin webs; this condition is especially obvious in the second dorsal fin, the base of which is less than half as long as its fin web, a condition similar to that of many modern sharks and unlike that of bony fishes. The scales on the dorsal fin webs are aligned in rows, and the transition from body to dorsal fin scales is gradual.

The dorsal fin spines are long, slender, tapered, and straight, and each has a narrow base with a well-developed insertion area (Figs. 2, 3). The basal cavity of each dorsal spine is open along the basal one-third of the spine (Gagnier and Wilson 1996a; Figs. 2, 3). The dorsal spines have smooth, closely spaced, longitudinal ribs, which are approximately equal in thickness and parallel the leading edge of the spine to within one centimeter of the spine tip (Gagnier and Wilson, 1996a). The posterolateral ribs on each dorsal spine do not converge on the leading edge of the fin spine; instead, they terminate in a paired series of denticles along the posterior face of each spine (Gagnier and Wilson, 1996a).

The transition from head to body scales occurs anterior to the nuchal hump (Fig. 7A). The scales adjacent to the main lateral-line sensory canal just posterior to the head are somewhat thicker than other body scales and show concentric growth rings (Gagnier and Wilson, 1996a; Figs. 7B, C), but otherwise are shaped like typical body scales. These thickened scales commonly are among the few scales remaining on poorly preserved specimens. Body scales are thin and flat (Fig. 7D), and as a result, usually are poorly preserved (Gagnier and Wilson, 1996a). There is no evidence for the typical inflated mass of basal tissue that would be expected on the underside of a typical acanthodian scale. The crowns of body scales are teardrop shaped in crown view and extend posteriorly to overlap the scales more posteriorly by about half their length, thus forming a shingle-like armor (Gagnier and Wilson, 1996a; Figs. 7B, D). There is little difference in scale size over the entire body, although slightly larger

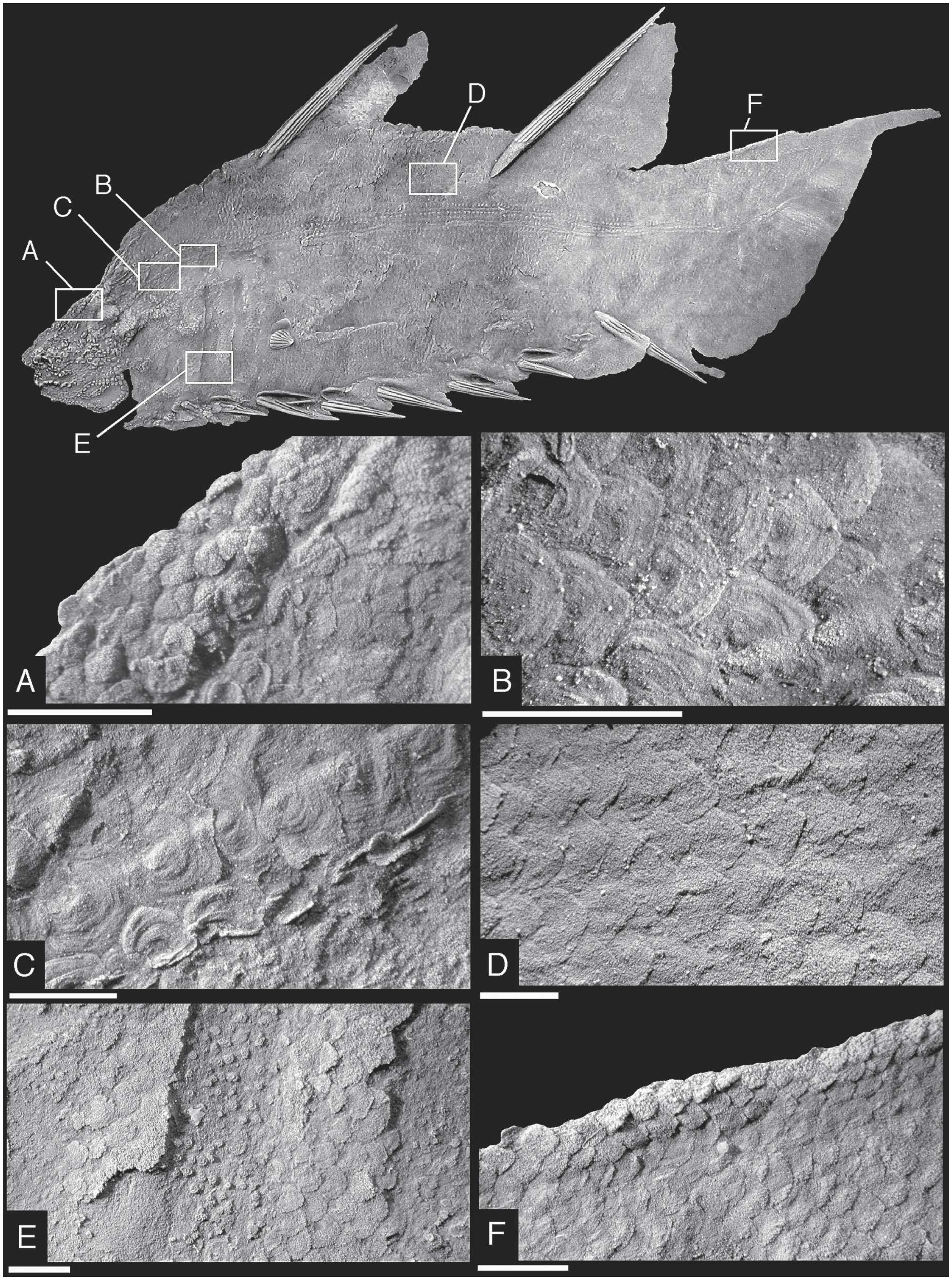

FIGURE 7. *Brochoadmones milesi*, UALVP 41495, overall view of specimen (top) and close-up views of selected scale morphologies. **A**, scales from the nuchal region at the transition from head to body scales; **B**, detail of scales from above the main lateral line trace; **C**, scales surrounding the main lateral line trace; **D**, typical body scales; **E**, minute scales on the opercula; **F**, small, thickened scales along the dorsal midline of the caudal fin axis. Scale bars equal 1 mm.

body scales are found around the base of the posterior dorsal fin. Smaller scales are found posterior to the head and between the gill slits (Fig. 7E). There is a gradual transition from larger body scales to the smaller scales on the fins, and scales decrease in size towards the trailing margins of all fin webs.

Small, bead-like scales reinforce the dorsal midline of the axis of the caudal fin (zone 2 scales of Gagnier and Wilson, 1996a; Fig. 7F), and these scales reveal histological detail that previously was unknown. Microstructure of these scales is generally of the *Nostolepis* type. The basal tissue of each of these scales forms a thin, convex pad containing traces of Sharpey's fibers and cavities that may represent traces of cell lacunae (Fig. 8). Crowns are composed of mesodentine. The scale primordium is large, and relatively few, thick growth zones are present (Fig. 8). The short, large-diameter ascending canals (Fig. 8C) supply each odontode in the scale crown, but in the specific thin-sections prepared, there was no trace of vascular canals running through basal tissue.

The position of the lateral-line canal on the trunk is indicated by parallel rows of modified body scales, the canal presumably lying between the rows in life. Both of the new specimens (UALVP 41494 and 49495) reveal both left and right lateral-line canals, the canal on the exposed side of the fish being more prominent than that on the hidden side (Fig. 3). The canal extends in an arc dorsal to the branchial chamber, then continues, uninterrupted, posteriorly along the trunk and caudal peduncle, at about two-thirds the height of the body, until it reaches the caudal fin web. There, it turns posterodorsally to parallel the ventral edge of the main caudal lobe; about 1 cm from the posterodorsal end of the lobe, it turns posteroventrally and extends across the hypochordal fin web, nearly parallel to the scale rows, to terminate within millimeters of the margin of the fin web (Figs. 2B, C, 3).

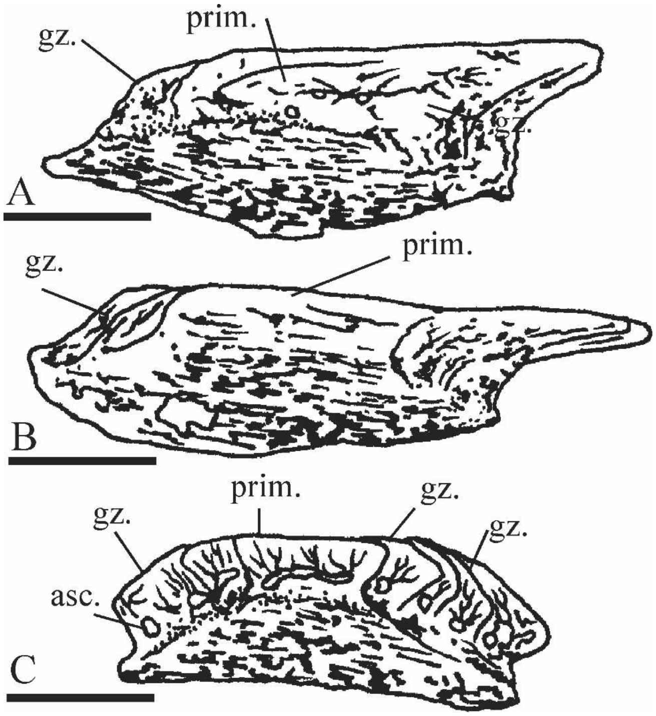

FIGURE 8. *Brochoadmones milesi*, camera lucida drawings of microstructure of scales from UALVP 42535. **A**, **B**, mid-sagittal sections of scales from the dorsal midline of the caudal fin axis; **C**, transverse section through a similar scale. Scale bars equal 100 μm. For abbreviations see text.

## DISCUSSION

### Systematic Position

The systematic position of *Brochoadmones milesi* was uncertain prior to the present study (Gagnier and Wilson, 1996a), and the new specimens of *Brochoadmones* seemingly complicate acanthodian systematics. Despite its unusual features, *Brochoadmones* commonly has been assumed to belong among a group of acanthodians traditionally classified in the order Climatiiformes; however, the relationships of that order to the Ischnacanthiformes and Acanthodiformes have been controversial (e.g., Maisey, 1986; Long, 1995; Janvier, 1996). It now appears that the diagnosis of the Climatiiformes provided by Denison (1979) was based on characters that are primitive for all Acanthodii. Janvier (1996) and Gagnier and Wilson (1996a) suggested that the order Climatiiformes as presently classified is paraphyletic, but no original analyses were presented to support this claim. However, Janvier (1996:331, fig. 9.1) presented what he termed an 'odd phylogeny' suggesting that some acanthodians form a sister group to chondrichthyans while others form a sister group to osteichthyans. Unfortunately, he did not state which acanthodian species he thought were involved in each sister-group relationship. The phylogenetic analyses of Hanke and Wilson (2000, 2004), and Hanke (2001a, b) support the general view that Climatiiformes are basal to other acanthodian groups; however, according to these analyses, the taxa historically classified in the Climatiiformes are paraphyletic relative to the other two acanthodian orders. Thus, it is not surprising that attempts to assign new and divergent taxa to the Climatiiformes have met with difficulty and required restriction of the diagnosis of the order (Gagnier and Wilson, 1996a, b).

Although *Brochoadmones milesi* has many unique characters, several features suggest possible relationships between *B. milesi* and specific climatiiform and ischnacanthiform taxa. For example, the deep, compressed body of *B. milesi* and its enlarged, deeply inserted dorsal and anal fin spines are similar to corresponding features of diplacanthiforms such as *Uraniacanthus spinosus*, *Gladiobranchus probaton*, and *Diplacanthus*, as well as the putative diplacanthiform *Culmacanthus*. However, it is equally or more likely that the deep body shape and fin spine structure were convergently acquired in diplacanthids and *Brochoadmones*, and that the presence of numerous prepelvic spines is a primitive feature (e.g., Denison, 1979) retained in all of these taxa except *Culmacanthus*. The enlarged, so-called circumorbital plates (which in *Gladiobranchus* actually enclose the otic capsule with its sandy infilling; Sahney and Wilson, 2001) and the toothless jaws of all diplacanthids (Watson, 1937; Miles, 1973; Gagnier, 1996; Hanke, et al. 2001) are completely different from the corresponding structures in *Brochoadmones*.

A relationship with Climatiiformes such as *Euthacanthus*, *Climatius*, *Ptomacanthus*, *Vernicomacanthus*, and *Brachyacanthus* is suggested by "enlarged" and plate-like head scales, presence of numerous adsymphyseal tooth whorls, and the well-developed series of prepelvic spines in *Brochoadmones* (see Miles, 1973; Ørvig, 1973; Denison, 1979). Gagnier and Wilson (1996a) used isolated tooth whorls along jaws, number and covering of gill slits, body shape, number of prepelvic spines, and similarities to *Vernicomacanthus waynensis* and *Ptomacanthus angelicus* to assign *B. milesi* to the order Climatiiformes. They specifically compared the hump-backed shape of the climatiiform *P. angelicus* to that of *B. milesi*. However, according to illustrations in Miles (1973:text-fig. 11, pl. 1.2), *Ptomacanthus* does not have a prominent nuchal hump as seen in *Brochoadmones*.

*Ptomacanthus*, *Vernicomacanthus*, and *Climatius* all have multiple adsymphyseal tooth whorls. However, the flattened, spoon-shaped or leaf-like teeth forming each whorl in *P. angelicus* (Miles, 1973:text-fig. 13a, b), *V. waynensis* (Denison, 1979), and

*C. reticulatus* (Miles, 1973:text-fig. 9c, d) differ from the stiletto-shaped primary teeth in the tooth whorls of *Brochoadmones*. Other features that distinguish *B. milesi* from *P. angelicus* include the hyoidean gill plates, head and body scale ornamentation, enlarged 'circumorbital' plates, prepectoral spines, and the number of prepelvic spines of the latter taxon. Hyoidean gill plates were omitted from Miles' (1973:text-fig. 11) reconstruction of *P. angelicus*, giving the impression that the branchial area of *P. angelicus* resembled that of *B. milesi* (Gagnier and Wilson, 1996a). However, Miles (1973:pls. 5, 7) illustrated ornamented hyoidean plates in *P. angelicus*. The dermal branchial coverings in *P. angelicus* and *B. milesi* thus differ in this respect.

Features such as ornamentation of fin spines, ornamentation of head and body scales, and presence of prepectoral spines, ossified scapulocoracoids, and branchial plates distinguish *Vernicomacanthus waynensis* from *Brochoadmones milesi*. Similar features (ornamentation of fin spines and head and body scales, presence of prepectoral spines, ossified scapulocoracoids, hyoidean and branchiostegal plates, and pinnal and lorical plate armor) distinguish *C. reticulatus* from *B. milesi*.

The presence of adsymphyseal tooth whorls might suggest a relationship between *Brochoadmones milesi* and Ischnacanthiformes (e.g., *Ischnacanthus* species); however, Gagnier and Wilson (1996a) stated that the tooth whorls of ischnacanthids are restricted to the anterior part of the mouth and are unlike the multiple whorls in *B. milesi*. Recently discovered, well-preserved ischnacanthids (e.g., UALVP 32520, 42520) from the MOTH locality show multiple tooth whorls posterior to the jaw symphysis (Hermus, 2003:fig. 2.28), a condition more closely resembling that of *Brochoadmones*. The bony tooth whorls of *Ischnacanthus* species are found along with the typical ossified dentigerous jaw bones and simple, needle-like 'tooth' elements along the labial side of the dentigerous element (Watson, 1937; Ørvig, 1967; Miles, 1973; Hanke, 2001b; Hermus, 2003); this complex dental arcade is significantly different from that of *B. milesi*, which has only one type of tooth whorl. *Latviacanthus ventspilsensis* also has tooth whorls along most of the length of its upper jaws (Schultze and Zidek, 1982), resembling *B. milesi* in this respect. However, both Ischnacanthiformes and *Latviacanthus ventspilsensis* have elongate pectoral fin spines, ossified jaws and scapulocoracoids, and a complete set of hyoidean gill covers and/or branchiostegals (Watson, 1937; Miles, 1973; Schultze and Zidek, 1982; Hanke, 2001b; Hermus, 2003), features that distinguish them from *Brochoadmones* and either Ischnacanthiformes or *Latviacanthus*.

Unfortunately, many potentially relevant endoskeletal characteristics cannot be seen in *B. milesi* because its endoskeleton is unossified. This lack of preserved internal features complicates attempts to include this species in phylogenetic analyses. Many other features (see below) represent autapomorphies of *B. milesi*. Therefore, there are relatively few features that indicate relationships of *B. milesi* to the various groups of acanthodians.

The cladograms of Hanke and Wilson (2000, 2004), and Hanke (2001a, b) place *Brochoadmones milesi* either in a polytomy with, or basal to, Diplacanthiformes, Ischnacanthiformes and Acanthodiformes, and all of these taxa are positioned above such primitive acanthodians as *Lupopsyrus pygmaeus* and the climatiiforms *Euthacanthus*, *Climatius*, and *Brachyacanthus*. The few characters supporting this position of *B. milesi* (above typical climatiiforms), are as follows: fin spines with smooth ribs; ribs of fin spines converging on leading edge only near spine tip; 'cobble-stone' pavement of thin, smooth, round to polygonal head scales; lack of dermal plate-like pectoral armor; and lack of prepectoral spines. Using the topologies presented by Hanke (2001a, b) and Hanke and Wilson (2000, 2004), the presence of prepelvic spines, unossified endoskeleton, multiple adsymphyseal tooth whorls, two dorsal fins with spines, mesodentine scale microstructure with few growth zones, and presence of multiple gill openings can be interpreted as primitive features retained from some 'climatiiform' ancestry. Other features, such as shape of anal fin, attachment of anal fin to caudal fin, position of pectoral fin, prominent nuchal hump, prepelvic fins, and structure of body scales are unique to *Brochoadmones* and here are used to define its only known species.

## Implications of Fin Structure

The unusual median and paired fins of *Brochoadmones* have implications for the evolutionary developmental biology of paired fins in primitive teleostomes, even though *Brochoadmones* is the only taxon known to date with these features. Of note are (1) the confluent anal and caudal fins, (2) the physical separation and distinct features of the pectoral and pelvic fin series, and (3) the presence of scale-covered finlets associated with each prepelvic fin spine.

First, in *Brochoadmones* the anal fin is very slender and partly confluent with the hypochordal lobe of the caudal fin. This may be explained by a failure of the two fins to separate during development. In primitive extant bony fishes (e.g., paddlefishes; Bemis and Grande, 1999), the median fins develop from a continuous median fin fold that becomes divided later in development of the embryo. If a similar developmental process occurred in *Brochoadmones*, it is likely that the anal and caudal fins failed to separate completely, leading to the partially confluent fins of the adults as seen in the present specimens (Figs. 2, 3). In the adult form, the anal spine effectively forms the leading edge of a combined anal and caudal fin.

Second, the distinct position and character of the pectoral and pelvic-fin series argues strongly for a decoupling of their developmental processes. The traditional view, expressed very well in the illustration of Zug (1979) and many others, was that pectoral and pelvic fins were separate condensations from a continuous pair of lateral fin folds, i.e., that they were by implication developmentally similar, and that pectoral and pelvic structure was expected to be morphologically similar in primitive gnathostomes. However, doubt has been cast on the paired lateral-fin-fold theory (e.g., Bemis and Grande, 1999), and there is now evidence that pectoral and pelvic fins are distinct anatomically and developed before jaws (Wilson et al., in press). For example, in *Kathemacanthus*, the pectoral fin is situated high on the flank, is large and lobate, and is the posterodorsal end member of a pectoral-spine series with distinct morphology, whereas the pelvic fin is ventral, long-based, and is the end member of its own distinctive pelvic-spine series (Gagnier and Wilson, 1996b; Hanke, 2001b). In many primitive bony fishes, the pectoral and pelvic fins also differ substantially (e.g., *Cheirolepis*; Arratia and Cloutier, 1996), and it is obvious that a similar pectoral-pelvic structural difference is found in modern gnathostomes. *Brochoadmones* strongly supports the distinct nature of the two series of paired-fin structures. Its pectoral fin and spine are elevated above the level of the pelvic series, and their small size as opposed to the large size and length of the pelvic series suggests that they were under separate developmental control in the embryo (a concept called compartmentalization in developmental biology; in this case, one series is fully expressed, while the other is less developed).

Third, the presence of scale-covered flaps of skin behind each of the six pairs of prepelvic spines is a remarkable feature never seen before in any vertebrate. These finlets have scales on both inner and outer faces and regular shape along the fin-spine series, and so are not simply folds of skin resulting from settling of the carcass. We here use the term 'prepelvic finlets' for these structures (each consisting of a spine plus its scale-covered web of skin). They are similar to some theoretical expectations of what an intermediate stage in the evolution of paired fins from ventrolateral fin folds might look like (e.g., Zug, 1979), yet they differ in that they are part of the pelvic series only, and are not serial homologs of a prepectoral-pectoral fin and spine series. The largest prepelvic finlets are the two pairs immediately anterior to the pelvic fins. The spines at the leading edges of these two pairs of prepelvic finlets are larger than the spines of the pelvic fins, but the pelvic fin web is far larger than the posterior-most prepelvic finlet.

Also remarkable is the fact that the anterior-most prepelvic finlets are located far anterior to the pectoral fins, and ventromedial to the middle of the branchial chamber. At the posterior end of the series, the pelvic fins themselves overlap slightly with the anal spine and fin, and flank the probable location of the anal opening. In developing embryos of primitive living gnathostomes, developing paired fins also overlap the median fin fold (e.g., paddlefishes; Bemis and Grande, 1999). This elongate pelvic series suggests strongly that a field of pelvic gene expression extended the entire distance from throat to anus along the lower flank of the animal.

### Predatory Biology

The prominent series of adsymphyseal teeth in the jaws and the deep, compressed, somewhat short body of *Brochoadmones milesi* beg speculation on the predatory biology of this species. Piscivory is indicated by the presence of partly digested acanthodians in the abdominal regions of UALVP 41494 and 32406 (Gagnier and Wilson, 1996a), but the fin shape and body proportions of *Brochoadmones* are unlike those of modern cruising, pelagic predators or ambush predators such as *Esox* spp. (Esocidae) and *Lepisosteus* spp. (Lepisosteidae), which have long, slender bodies with large fins concentrated near the posterior end.

Modern freshwater analogs for a similar body shape can be found among the predatory fishes *Cyrtocara compressiceps* (Cichlidae), *Altolamprologus calvus* (Cichlidae), *Chitala chitala* (Notopteridae), and *Cromileptes altivelis* (Serranidae). All of these extant fishes are ambush predators with deep, compressed bodies, a prominent nuchal hump, posterior fins of low aspect ratio (dorsal fin, caudal fin, and/or anal fin in various examples; posterior dorsal fin and caudal fin in *Brochoadmones*), and large, terminal mouths lined with villiform teeth. These modern fishes rely on stealth and approach their prey head-on, with a head-down posture; prey capture is completed with a short lunge. Obviously the technique that *Brochoadmones milesi* used cannot be observed, but *B. milesi* is not nearly as streamlined as many other acanthodians (including its likely prey) and was evidently not built for sustained, high-speed locomotion. We cannot tell whether the prepelvic finlets were capable of movement, but it is tempting to speculate that subtle motions of these finlets might have aided the predator in its stealthy approach. The large, caudal fin of low aspect ratio also may be used as indirect evidence of ambush techniques, in that such large, broad fins are typically used for rapid acceleration over short distances rather than for sustained cruising.

## CONCLUSIONS

The original and previous descriptions of *Brochoadmones milesi* were limited by the preservation of the available specimens. Two new, nearly complete specimens allow description of previously unknown anatomical details. Specimens of *Brochoadmones milesi* are deep bodied and compressed, have a small, tapered head anterior to a prominent nuchal hump, long median fin spines, large dorsal fins, a short-based, ribbon-like anal fin that is partly attached to the caudal fin, and small, plate-like pectoral fin spines. Ventrally, the body carries a paired series of prepelvic finlets, each consisting of a spine and a scale-covered web of skin. The confluent anal and caudal fins, the presence of fin webs associated with each prepelvic spine, and the reduced pectoral fin spine are unique features for an acanthodian. The upper and lower jaws of *B. milesi* are covered with a series of adsymphyseal tooth whorls that increase in size anteriorly. Scale microstructure is of the *Nostolepis* type, with few, thick growth zones, crown tissue of mesodentine, and cellular basal tissue with abundant traces of Sharpey's fibers.

The body scale microstructure, fin-spine complement, multiple adsymphyseal tooth whorls and gill slits, and the lack of endoskeletal ossifications are retained primitive features of *Brochoadmones milesi*, but the structure of the anal fin, the small pectoral fin spine elevated on the flank, the lack of gill plates, the prepelvic finlet series, and the thin body scales are autapomorphies of the species. The lack of plate-like pectoral armor, lack of prepectoral spines, the ornamentation of the median fin spines, and the structure of the head scales are features that suggest *B. milesi* is more closely related to Ischnacanthiformes or Acanthodiformes than to typical climatiiform fishes. *Kathemacanthus rosulentus* Gagnier and Wilson, 1996b, is removed from the Brochoadmonidoidei, which is left with the single genus and species *Brochoadmones milesi* Bernacsek and Dineley, 1977.

The confluent anal and caudal fins are consistent with the development of median fins from a single, continuous fin fold as seen in embryos of bony fishes. The reduced, dorsally situated pectoral fin and the long pelvic series (prepelvic finlets plus pelvic fin) that extends far anterior to the pectoral fin are evidence for a decoupling of the development of the two fin series, with the pelvic series maximally expressed and the pectoral series minimally expressed in *Brochoadmones*. The prepelvic finlets themselves are evidence of a long field of pelvic gene expression extending from beneath the branchial chamber to a point lateral to the anal opening.

The anatomy of *Brochoadmones milesi* resembles that of several ambush predators from Recent freshwater and marine habitats. While discussion of feeding behavior is largely speculative, the piscivorous nature of *B. milesi* is corroborated by the presence of fish (acanthodian) remains in some well-preserved specimens.

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