Partial articulated specimen of the Early Devonian putative chondrichthyan *Polymerolepis whitei* Karatajūtė-Talimaa, 1968, with an anal fin spine

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ABSTRACT

Polymerolepis whitei Karatajūtė-Talimaa, 1968 was described based on isolated polyodontode scales recovered from the Ukraine, and originally was thought to be heterostracan (Agnatha). Additional scales with neck canals were described years later, and as a result, *P. whitei* was reclassified as a bradyodont holocephalan because it had scales similar to those of *Listracanthus* Newberry & Worthen, 1870. Until now, no articulated body fossils were known, and so the classification of this taxon has remained uncertain and based only on the original author's opinion. New specimens of *P. whitei* from the Mackenzie Mountains, Northwest Territories, Canada, show articulated scale patches from the head, with the best specimen showing part of an anal fin, caudal peduncle, and caudal fin. This new material confirms that the original account of scale variation was accurate, but also that *P. whitei* possesses an anal fin spine, a feature that, until recently, was thought to be a synapomorphy of acanthodian fishes among Palaeozoic fishes. Several primitive chondrichthyans (*Obtusacanthus* Hanke & Wilson, 2004; *Lupopsyroides* Hanke & Wilson, 2004; *Kathemacanthus* Gagnier & Wilson, 1996; *Seretolepis* Karatajūtė-Talimaa, 1968; *Doliodus* Traquair, 1893; *Antarctilamna* Young, 1982, and also problematic taxa such as *Gyracanthides* Woodward, 1902, and now *Polymerolepis* Karatajūtė-Talimaa, 1968), are known from articulated remains and show a fin-spine complement like that of acanthodian fishes. They also have placoid scales or polyodontode scales that grew by areal rather than superpositional accretion. These taxa blur the distinction that exists in historic literature between acanthodians and early chondrichthyans.

KEY WORDS
Lower Devonian,
Lochkovian,
chondrichthyan,
Bradyodonti.

RÉSUMÉ

Un nouveau spécimen, partiellement articulé avec présence d'une épine anale, de Polymerolepis whitei *Karatajūtė-Talimaa, 1968, un supposé chondrichthyen du Dévonien inférieur.*

La description de *Polymerolepis whitei* Karatajūtė-Talimaa, 1968 a été réalisée à partir d'écailles isolées trouvées en Ukraine, et alors rapportées à un hétérostracé (Agnatha). Plus tard, d'autres écailles ont été décrites, et la présence de canaux dans le collet a induit le rattachement de *P. whitei* aux bradyodontes holocéphales, ses écailles étant semblables à celles de *Listracanthus* Newberry & Worthen, 1870. Jusqu'à maintenant, aucun fossile articulé n'était connu et, pour cette raison, la classification de ce taxon demeurait incertaine et n'était appuyée que par l'opinion de l'auteur original. De nouveaux spécimens de *P. whitei*, provenant des montagnes Mackenzie, aux Territoires du Nord-Ouest, Canada, possèdent des écailles articulées dans la région céphalique ; le spécimen le mieux conservé présente une partie de la nageoire anale, le pédoncule caudal et la nageoire caudale. Ce nouveau matériel confirme la description originale quant à la variation des écailles, et démontre également que *P. whitei* possède une épine sur la nageoire anale, caractère habituellement considéré comme une synapormorphie des acanthodiens parmi les vertébrés paléozoïques. Plusieurs des premiers chondrichthyens (*Obtusacanthus* Hanke & Wilson, 2004 ; *Lupopsyroides* Hanke & Wilson, 2004 ; *Kathemacanthus* Gagnier & Wilson, 1996 ; *Seretolepis* Karatajūtė-Talimaa, 1968 ; *Doliodus* Traquair, 1893 ; *Antarctilamna* Young, 1982, ainsi que certains taxons problématiques tels que *Gyracanthides* Woodward, 1902 et maintenant *Polymerolepis* Karatajūtė-Talimaa, 1968) sont identifiés à partir de restes articulés et présentent un appariement épine-nageoire similaire à celui connu chez les acanthodiens. Ils ont aussi des écailles placoïdes, ou écailles polyodontodes, qui ont une croissance par accrétion linéaire plutôt que superposée. Ces quelques taxons rendent floue la distinction historique entre les acanthodiens et les premiers chondrichthyens.

MOTS CLÉS
Dévonien inférieur,
Lochkovien,
chondrichthyen,
Bradyodonti.

INTRODUCTION

Renewed study of the anatomy of early chondrichthyans (e.g., Maisey 1984, 1989a, b; Maisey & de Carvalho 1997; Coates & Sequeira 1998; Coates *et al.* 1998; Stahl 1999; Miller *et al.* 2003), has demonstrated great anatomical diversity in the Palaeozoic. Early chondrichthyan taxa known to date had a wide variety of specialized denticles, cephalic spines, cephalic and pelvic claspers, and fin spines. The diversity of Palaeozoic chondrichthyans provides a large pool of data for phylogenetic analyses, and we now know that some taxa, known from well-preserved body-fossils (e.g., *Doliodus* Traquair, 1893, *Kathemacanthus* Gagnier & Wilson, 1996, *Seretolepis* Karatajūtė-Talimaa, 1968, *Obtusacanthus* Hanke & Wilson, 2004, *Lupopsyroides* Hanke & Wilson, 2004, and *Gyracanthides* Woodward, 1902), had a fin-spine complement historically thought to be diagnostic of acanthodians, and body scales like those of early chondrichthyans. Despite all the new data, Brazeau (2009) and Davis *et al.* (2012) show there is little consensus on relationships among early acanthodians and chondrichthyans, and their cladograms mirror the "odd cladogram" produced by Janvier (1996: 331, fig. 9.1). Thus the discovery of spiny chondrichthyans has tended to complicate rather than simplify the classification and definition of primitive chondrichthyans and acanthodians (Gagnier & Wilson 1996; Warren *et al.* 2000; Miller *et al.* 2003; Hanke & Wilson 2004, 2010; Brazeau 2009; Davis *et al.* 2012).

Polymerolepis whitei Karatajūtė-Talimaa, 1968, was described based on isolated scales (Obruchev & Karatajūtė-Talimaa 1967). In the original description, *P. whitei* was classified as a heterostracan and placed in its own order Polymerolepidiformes and family Polymerolepididae (Karatajūtė-Talimaa 1968). Karatajūtė-Talimaa (1977) included a more detailed account of scale variation and structure, and placed *P. whitei* among the "bradyodonts" (Chondrichthyes: Holocephali) based on scale growth and the presence of scale neck canals – although neck canals are not unique to holocephalan scales. Bradyodonts now are reclassified within the Euchondrocephali (Ginter *et al.* 2010). Some "bradyodonts" have synchronomorially growing scales (Patterson 1965), a condition that Karatajūtė-Talimaa thought characteristic of *Polymerolepis* scales. Other "bradyodonts" have scales like those of *Listracanthus* Newberry & Worthen, 1870 (Stahl 1999), some of which look leaf-like and similar to scales of *Polymerolepis* (see Ivanov 2005: fig. 5L). However, species of *Listracanthus* are far removed in time from Lochkovian records of *Polymerolepis*. Karatajūtė-Talimaa (1977) also compared *Polymerolepis* to petalodonts, and while *Janassa bituminosa* (Schlotheim, 1820), has stellate scales illustrated along with tooth plates (Hancock & Howse 1870: pl. II), other species in the same genus have simple mushroom-like scales (e.g., Brandt 1996: fig. 7); other holocephalans from North America lack scales like those of *Polymerolepis* (Grogan pers. comm.). None of these scales is sufficiently similar to those of *Polymerolepis whitei* to suggest close relationship. More recently, Karatajūtė-Talimaa (1992) proposed a scheme to organise early chondrichthyan taxa based on scale growth (but not indicating phylogenetic relationships), classifiying *P. whitei* among chondrichthyans showing "non-growing" scales. Herein, we tentatively leave both Polymerolepidiformes and its contained family Polymerolepididae as incertae sedis within the Chondrichthyes, and cannot support a more explicit classification until more-complete articulated remains of *Polymerolepis* are found.

Until recently, *P. whitei* was known only from scales from the Ukraine (Karatajūtė-Talimaa 1968, 1977, 1997), Nevada (Turner & Murphy 1988), the Canadian Arctic (Vieth 1980; Langenstrassen & Schultze 1996), and the United Kingdom (Vergoossen 1999, 2000); these scales seem useful for biostratigraphical correlations of Lower to Middle Lochkovian rocks (Vergoossen 1999, 2000). Interestingly, there still are no teeth or paired fin spines attributable to *P. whitei*, and its endoskeleton is unknown. However, the MOTH assemblage contains a diverse array of chondrichthyans represented by tooth whorls, most as yet undescribed. It is possible that one of these tooth types could belong to *P. whitei*.

The Lower Devonian fish-bearing layer at MOTH (southern Mackenzie Mountains, Northwest Territories, Canada) contains a diverse assemblage of Early Devonian fishes (Wilson *et al.* 2000); most of the species present, including *P. whitei*, are represented by articulated body fossils in addition to isolated microremains. In this paper, we present new information on *P. whitei*, based on one fossil showing a portion of the caudal peduncle, anal fin, and caudal fin, and other specimens consisting of skin patches with scales in close association or articulation. These new specimens show that *P. whitei* differs from any undisputed holocephalan or elasmobranch (*sensu* Nelson 2006) in one important feature: it has an anal fin spine. If *Polymerolepis* is eventually found to be holocephalan as suggested by Karatajūtė-Talimaa (1977), it will be the first known to have an anal fin spine. Several other spiny chondrichthyans from MOTH also have anal fin spines, but their taxonomic position is not yet resolved.

MATERIAL AND METHODS

Fossils were prepared with repeated immersion in dilute, buffered acetic acid followed after each immersion by rinsing in fresh water; silt-sized siliciclastic residues remaining after each acetic-acid treatment were removed while wet using very soft paint brushes. After preparation, each slab was dried slowly while wrapped in paper towels and stabilized using a 5% solution of Glyptal™ cement.

For histological study, isolated scales were removed from rocks and embedded in Luminate 83 HA-4 epoxy, polished to expose tissue structure using 600- and 1000-grit wet-dry sandpaper, and given

a final polish using moistened alumina powder on a glass plate. The flat, polished side of the scale then was fixed to a standard microscope slide with the same epoxy and the specimen was then polished from the other side until thin enough to permit light transmission.

Images of individual scales were taken using a JEOL JSM 6301 FXV scanning electron microscope (SEM) in the Earth and Atmospheric Sciences Department, University of Alberta. Specimens were mounted to metal stubs using two-sided tape and then sputter coated with gold for better resolution in the scanning electron microscope. Larger specimens were coated with ammonium-chloride sublimate to whiten specimens before digital photography. All images (except SEM images) were taken using a Nikon Coolpix 990 digital camera; close-up images were taken with the same camera while attached to a Nikon SMZ 1500 dissecting microscope.

All specimens are deposited in the collections of the University of Alberta, Laboratory for Vertebrate Palaeontology (UALVP).

SYSTEMATICS

Class CHONDRICHTHYES
Subclass *incertae sedis*
Order POLYMEROLEPIDIFORMES
Karatajūtė-Talimaa, 1968
Family Polymerolepididae
Karatajūtė-Talimaa, 1968
Genus *Polymerolepis* Karatajūtė-Talimaa, 1968

Polymerolepis whitei Karatajūtė-Talimaa, 1968
(Figs 1-5)

Material examined. — UALVP 23154, 32419, 32442, 32436, 32465, 32578, 41385, 41486, 41551, 41572, 41684, 41685, 41706, 41707, 41793, 41966, 41969, 42057, 42080, 42188, 42543, 42657, 43936, 43937, 43938, 43940, 43946, 43988, 43989, 43990, 43991, 43992, 45015, 45174-45203, 45271-45285.

Locality and age. — All scale patches and articulated remains of *P. whitei* from the MOTH section are 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 Zorn *et al.* 2005: fig. 2), corresponding to UALVP Locality 129. The same fish-bearing interval is at approximately 411 m in section 43 as reported by Gabrielse *et al.* (1973) (GSC locality 69014). 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, a recent detailed sedimentological, ichnological, and taphonomic study suggests that the fish layer was deposited in 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
Body form

Both isolated and articulated specimens of *P. whitei* are found in the MOTH fish layer. The most informative specimen collected to date represents the lower part of the caudal peduncle, most of the epicercal heterocercal tail, and all of the anal fin (Fig. 1A). Unfortunately, there are no specimens showing the shape of the body anterior to the caudal peduncle. Although several specimens consist of patches of scales possibly from the head, there are no teeth, dorsal fin spines, or paired fin spines associated.

The shape of the anal fin and most of the caudal fin of *P. whitei*, can be determined from UALVP 45015 (Fig. 1A). This articulated specimen represents the largest specimen of *P. whitei* collected so far, and compared to body proportions of *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977 (used because of its similar tail shape; see inset in Fig. 1A), this specimen of *P. whitei* could have been 50 cm in total length.

The anal fin of *P. whitei* is lobate, has a convex trailing margin, and overlaps the origin of the hypochordal lobe of the caudal fin (Fig. 1A). The leading edge of the anal fin is reinforced with a short, smooth fin-spine (Fig. 1B). This spine is not deeply inserted into the hypaxial musculature, and has rotated such that the anterior edge is pressed into the underlying rock. The posterior portions of the fin-spine are porous, and there is a large basal opening along the posterior face of the spine. The exposed posterolateral margins of the spine lack ridges or ribs, although there are smooth-topped, widely-spaced, irregularly positioned nodes along
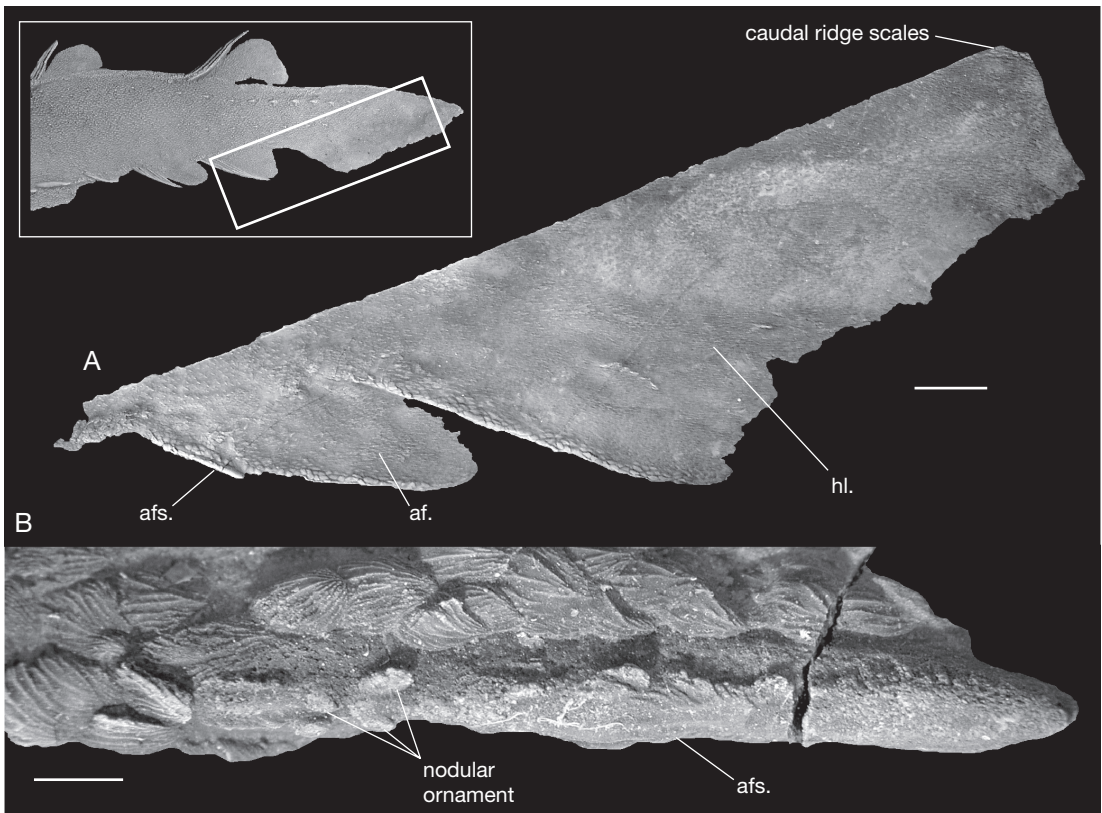
Fig. 1. — *Polymerolepis whitei* Karatajūtė-Talimaa, 1968: **A**, caudal fin, lower parts of the caudal peduncle, anal fin spine, and anal fin web as preserved on UALVP 45015 (the tail of *Lupopsyrus pygmaeus* is inset for orientation and not to scale); **B**, close-up of the anal fin spine of UALVP 45015. Abbreviations: **af.**, anal fin web; **afs.**, anal fin spine; **hl.**, hypochordal lobe of caudal fin. Scale bars : A, 1 cm; B, 2 mm.

the length of the spine (Figs 1B; 4A). The nodes that are on the basal portions of the spine are larger than those positioned towards the tip. The tip of the anal fin-spine is blunt, and the spine is roughly one third the length of the anal fin-web.

The epicercal caudal fin is large, has a well-developed hypochordal lobe, and may be only slightly deflected from the body axis (Fig. 1). Unfortunately, a large portion of the caudal fin axis and the posterior tip of the caudal fin are missing. There is no evidence of the lateral line on the preserved part of the fin or the caudal peduncle. The body scales of the caudal axis grade smoothly into typical scales of the caudal fin-web, and therefore, it is difficult to locate the transition between the caudal fin axis and the fin-web (Fig. 1). The leading edge of the hypochordal lobe of

the caudal fin is nearly straight and the trailing edge appears concave, but ragged in this fossil.

Scale structure

All of the types of scales that Karatajūtė-Talimaa (1968, 1977) assigned to *P. whitei* can be found on the articulated specimens or concentrated scale associations from MOTH. In this species, the limits of scale variation that Karatajūtė-Talimaa (1968, 1977) based on microremains match that now known from articulated material. Most of the patches of scales of *P. whitei* consist of closely packed scales. Some scales are in crown view while others are in basal view, depending on how they were prepared (Fig. 3), giving an indication of the alignment of scales in the skin of the fish.

Typical body scales of *Polymerolepis* are formed by the synchronous fusion of three or more odontodes (Karatajūtė-Talimaa 1992, 1998); the scales that reinforce the leading edges of fins and those scales that are assumed to be head scales (see below) show no partitions and may have developed from a single odontode. Larger body scales have additional trailing flanges that look like accreted odontodes (Karatajūtė-Talimaa 1998: figs 6L, 7C), but are still thought to consist of only three fused odontodes.

UALVP 41706 consists of a scattered mass of scales which, based on the type of scales, could be from the head (Fig. 2) and include rostral(?) scales. The rostral(?) scales of *P. whitei* have a flat to convex crown, with smooth, radiating ridges near the crown margin (Karatajūtė-Talimaa 1977: text-fig. 3, nos 4-6). The marginal ridges may bifurcate toward the edge of the crown. The crowns of these rostral(?) scales may be ovate, asymmetrical, polygonal, or developed into a tear-drop shape (Fig. 2A, B). The striations on the margin of the crown continue onto the scale neck and contribute to the crenulated basal rim. There is no subdivision of the crown, and these rostral(?) scales appear to be formed from a single odontode. The basal rim of each scale is narrower than the scale crown, and is not visible in crown view, resulting in a closely packed scale cover (Fig. 2B). The rostral(?) scales have low necks, and the pulp cavity is filled with the trabecular dentine that forms the core of the pulp cavity (Fig. 2B; also similar to scales in Fig. 2E, F). The rostral(?) scales lack a tumid mass of basal tissue, and the pulp cavity is surrounded by the crenulated rim of neck tissue (Fig. 2B). The histological structure of these rostral(?) scales is identical to that illustrated by Karatajūtė-Talimaa (1977: text-fig. 4, nos 1, 2; text-fig. 5, nos 2, 4). Until more-complete articulated specimens are recovered, we infer that these scales are rostral based on comparison to similar rose-bud-shaped scales on the snout of *Obtusacanthus* Hanke & Wilson, 2004, and polygonal scales on the head of *Kathemacanthus* (see Hanke & Wilson 2010).

Crowns of other head scales (Fig. 2C, D) show a gradational series between the typical smooth-crowned rostral(?) scales (Fig. 2B) and the ridged, polyodontode body scales. The crowns of the head scales are ovate, asymmetrical, polygonal, or are tear-drop shaped. The crown of each head scale is covered with ridges that extend from the margin to a raised tubercle near the centre of the crown (Fig. 2C, D; Karatajūtė-Talimaa 1968: pl. 4, fig. 1; 1977: text-fig. 3, nos 7, 8-10; 1998: fig. 6C, E). The location of the raised "central" tubercle varies; on scales that are closer to the rostral scales, the tubercle is located near the centre of the crown (Fig. 2C, D) and on scales nearer to typical body scales (e.g., the scale in crown view in the centre of Fig. 2F), the tubercle is located nearer the margin of the scale, presumably near the posterior edge. The tubercle elongates and appears to form the median crest along the midline of typical body scales (Fig. 3A). The radiating ridges of head scales are ornamented with fine, raised nodes as on typical body scales, and these nodes increase in size towards the scale margin (Fig. 2C, D). The neck of each scale is low, and forms a crenulated rim around the pulp cavity (Fig. 2E, F). The pulp cavity is shallow in scales that are closer in structure to head scales, whereas those scales closer to body scales have a deep pulp cavity. The basal rim of the head scales is narrower than the scale crown, such that the basal rim is not visible in crown view, resulting in a closely packed scale cover (Fig. 2C, D). The internal microstructure of the anterior-most head scales is identical to that of the rostral scales, but posteriorly grades to that of body scales (see Karatajūtė-Talimaa 1977 for a detailed treatment of histology).

UALVP 41706 also has two concentrations of simple, upright, monodontode scales (see also Karatajūtė-Talimaa 1977: pl. 3, figs 1-3; 1998, figs 6a, b, 7a) that somewhat resemble the labial scales of *Obtusacanthus corroconis* Hanke & Wilson, 2004 (see also Blais *et al.* 2011: fig. 7). The crown of each of these labial(?) scales is flat to concave and elevated toward the crown apex. The lower side of each crown is ornamented with smooth, straight to sinusoidal, thick ridges (Fig. 2G, H) that converge on the elevated apex of the crown. The neck of each labial(?) scale is elongate, crenulated, and has neck canal pores (Fig. 2H; Karatajūtė-Talimaa 1977: text-fig. 2, nos 1, 2; text-fig. 3, nos 1-3; pl. 7, fig. 3; 1998: figs 6a, b, 7a). The neck is attached to the anterior half of the crown, and forms a crenulated
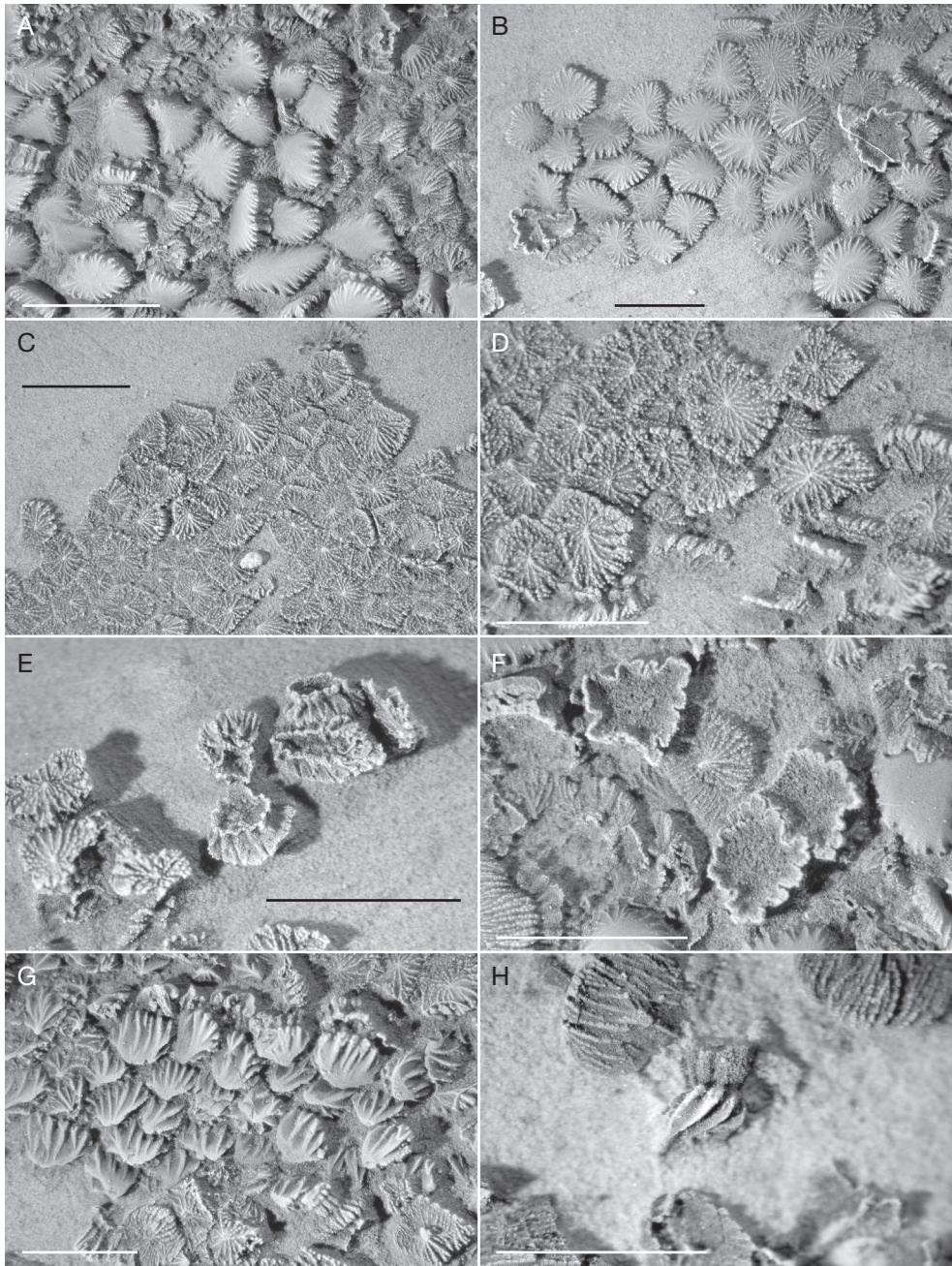
Fɪɢ. 2. — *Polymerolepis whitei* Karatajūtė-Talimaa, 1968, UALVP 41706: **A**, a patch of rostral? scales; **B**, scales that appear transitional between rostral and head scales; **C**, **D**, head scales in crown view; **E**, **F**, basal view of head scales; **G**, a patch of labial? scales; **H**, an isolated labial? scale in side view. Scale bars: 2 mm.
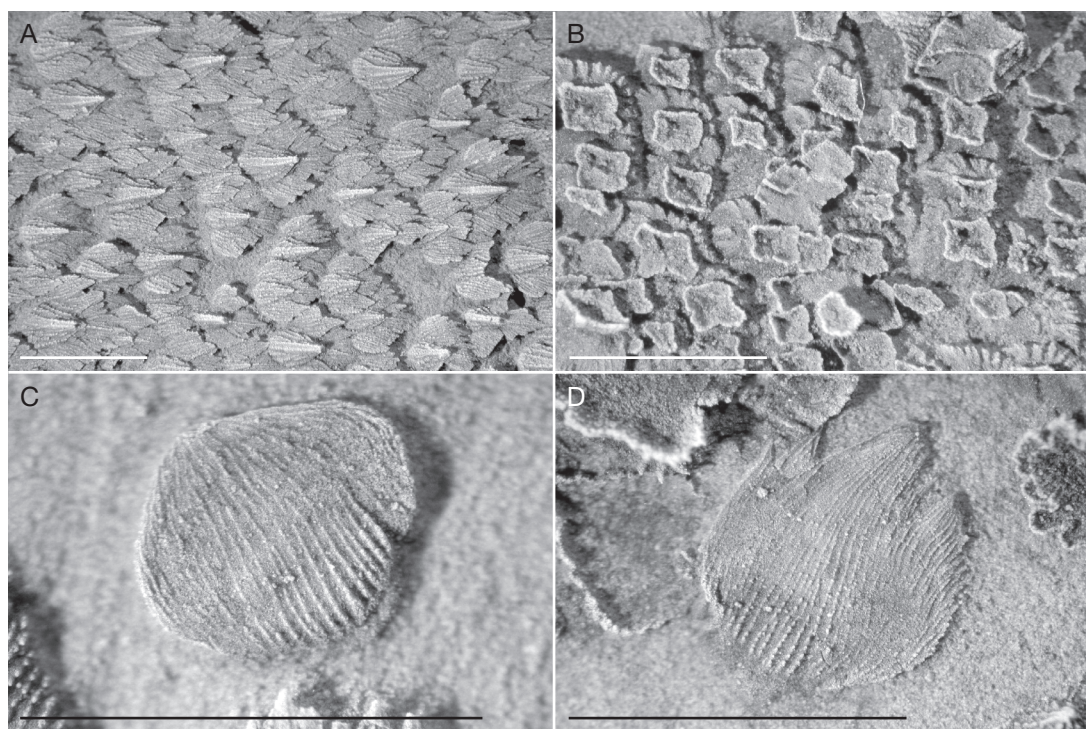
Fig. 3. — *Polymerolepis whitei* Karatajūtė-Talimaa, 1968 scales: **A**, **B**, specimen UALVP 32419; **A**, body scales in crown; **B**, basal views; **C**, **D**, specimen UALVP 41706; **C**, monodontode body scale; **D**, scale that appears to be transitional between monodontode and polyodontode body scales. Scale bars: 2 mm.

cone that may be as wide as or wider than the scale crown. The labial(?) scales are closely spaced, and the elevated apex of one overlaps the lower ridged side of neighbouring scales (Fig. 2G). It is not possible, given the available specimens, to determine whether these scales pointed towards the mouth as in *O. corroconis*, nor whether were from the upper, or lower jaw. Very similar scales are found on the margin of the head of another chondrichthyan from MOTH that has yet to be described.

Most of the scale patches and isolated scales of *P. whitei* recovered from MOTH consist only of body scales (Fig. 3). Body scales are large and set in oblique rows. Although the crowns overlap, the bases of adjacent scales are widely spaced (compare Fig. 3A, B). Most of the scales figured by Karatajūtė-Talimaa (1968: pl. 4, figs 2-5; 1977: pls 2, 3, figs 12-22; 1998: fig. 6g, j-n) are body scales. The external details and microstructure of body scales

was fully described by Karatajūtė-Talimaa (1968, 1977) and will not be repeated here.

Several fairly simple, monodontode scales are associated with the typical polyodontode body scales on UALVP 41706, and could be from the opercular flaps or from the leading edge of a dorsal, pectoral, or pelvic fin. These scales have either simple, tear-drop-shaped crowns (Fig. 3C), or crowns with a trilobate posterior margin and straight to sinusoidal ridges with fine, well-spaced nodes (Fig. 3D). The basal rim of each of these monodontode scales is similar to that of the typical body scales and is attached to the anterior third of the scale crown. Similar scales were figured by Karatajūtė-Talimaa (1977: text-fig. 3, no. 12).

The thickened scales on the dorsal ridge of the caudal fin, and those on the basal portions of the leading edge of the anal fin and the hypochordal lobe of the caudal fin, are approximately the same
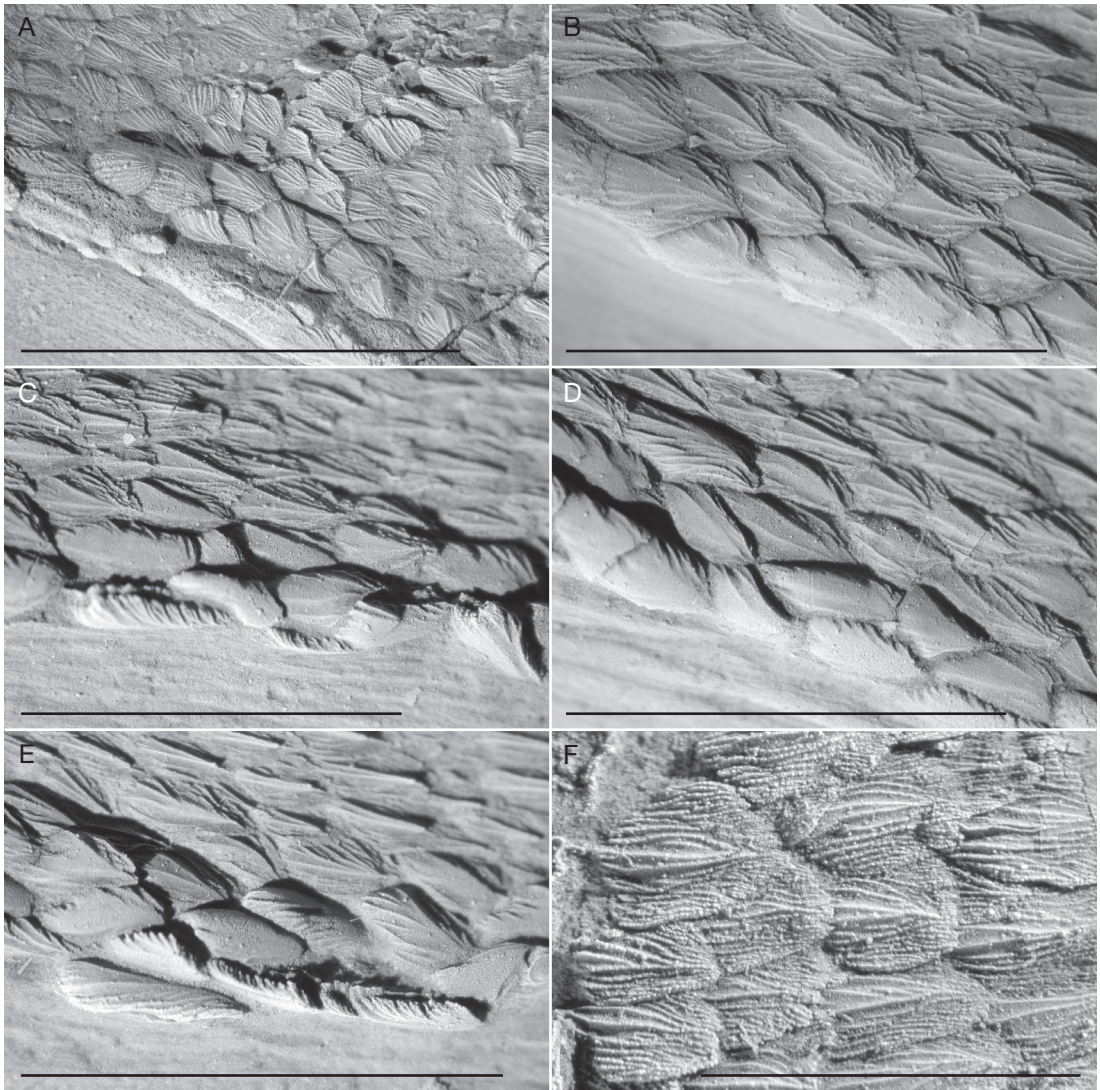
FIG. 4. — *Polymerolepis whitei* Karatajūtė-Talimaa, 1968 (all from UALVP 45015): **A**, scales at the base of the anal fin spine; **B**, scales mid-way along the leading edge of the anal fin web; **C**, scales in side view from near the distal tip of the anal fin web; **D**, scales mid-way along the leading edge of the hypochordal lobe of the caudal fin; **E**, scales from the tip of the hypochordal lobe of the caudal fin; **F**, scales from the base of the hypochordal lobe of the caudal fin. Scale bars: 4 mm.

size as the body scales on the ventral surface of the caudal peduncle (Fig. 4A-E). These fin scales differ from body scales in that they appear to be composed of a single odontode and the crowns are convexly curved, robust, and thick. In addition, the median crests of these thickened fin scales are wide and low, have a shallow median trough, and are flanked by many heavy ridges, which converge towards the posterior apex of each scale (Fig. 4A-E). The median crests of these thick scales may extend anterior to the rest of the crown, forming a weak, anteromedian lobe.

The flat, monodontode scales that appear transitional between typical body scales and these robust

fin scales have crowns with thin, low, median crests, and lateral ridges that are more like those of body scales (Fig. 4F). These transitional scales also may have a serrated posterior margin, and in this respect, better resemble typical body scales than scales from the leading edges of fins. The scales along the leading edges of the caudal and anal fins become smaller and more slender towards the fin tip, and have a low basal rim, a broad, open pulp cavity, and lack a tumid mass of basal tissue. Karatajūtė-Talimaa (1977: text-fig. 3, nos 21, 22, pl. 7, fig. 8; 1998: fig. 6m, n) recovered several of these transitional scales and correctly assumed that they were associated with the fins of *P. whitei*.

The scales that cover the remaining parts of the fin web appear to be formed from a single odontode each, and their crown ornamentation resembles that of the median odontode of typical body scales. These fin scales are slender and have a high, narrow median crest with a thin, shallow, axial trough (Fig. 5A, B). The median crest of the fin scales extends for most of the length of the scale crown and is flanked on both sides by thin lateral flanges. The lateral flanges of each scale have low, fine ridges in the anterior half, but are smooth posteriorly. The posterior margin of fin-web scales can be serrated and can extend posterior to the apex of the median crest. Each fin scale has a broad pulp cavity, and lacks a basal rim or neck tissue (Fig. 5B, C). The underside of the lateral flanges of each scale is smooth and overlaps the anterior margin of adjacent scales. These fin scales were not illustrated by Karatajūtė-Talimaa (1968, 1977).

Scales of *Polymerolepis* are very abundant in the rocks of the MOTH fish layer, and many isolated scales have been recovered during the preparation of other fishes. Histological sections were prepared from isolated head and body scales, but the sampled body scales had poorly preserved internal structure, as did those mentioned in the original description of *P. whitei* (Karatajūtė-Talimaa 1968: fig. 3), and do not reveal any fine histological details. The thicker head and labial scales show histological structure that is identical to what was described by Karatajūtė-Talimaa (1977: text-fig. 4; 1998: fig. 8) for isolated scales recovered from Ukraine. The trabecular layer in the core of the head scales from MOTH does not preserve fine details, but the crown of each scale is composed of weakly branching orthodentine tubules. There is no lamellar basal tissue in any examined scale of *Polymerolepis*.

DISCUSSION

Since *Polymerolepis whitei* was described based on isolated scales, it was placed among the "bradyodonts" (Chondrichthyes: Holocephali) based on synchronomorial scale growth, the presence of scale neck canals, and that Karatajūtė-Talimaa thought some *Polymerolepis* scales resembled leaf-like scales of *Listracanthus* species (Stahl 1999). No other hard parts had been found until recently, and even now there is little available to suggest *P. whitei* is a chondrichthyan, with the exception of the laterally expanded basal opening of body scales (see: Märss *et al.* 2002, 2006). None of the features known to date are strong evidence to assign *P. whitei* to any chondrichthyan group. Therefore, we tentatively leave both Polymerolepidiformes and its contained family Polymerolepididae as incertae sedis within the Chondrichthyes, and cannot support a more explicit classification until more-complete articulated remains of *Polymerolepis* are found.

The earliest chondrichthyans, represented by isolated scales from the Upper Ordovician (Sansom *et al.* 1996; Young 1997), are identified as chondrichthyans based on combinations of the following characteristics: 1) monodontode scales that are non-growing and placoid-like; 2) polyodontode scales that grow by areal accretion of odontodes (which may have basal tissue but are not attached to a dermal plate); 3) presence of neck canals for vascular supply to a scale; and/or 4) retention of open basal vascular cavities or canals in each body scale (Reif 1978, 1982; Karatajūtė-Talimaa 1992, 1997, 1998; Karatajūtė-Talimaa & Mertiniene 1998). Unfortunately, none of these scale characteristics is unique to chondrichthyans as compared with other early jawed and jawless vertebrates (Hanke & Wilson 2004). Perhaps only the laterally expanded basal opening remains as a single feature separating scales of chondrichthyans from those of thelodonts (Märss *et al.* 2002, 2006) or acanthodians such as *Lupopsyrus pygmaeus* (Hanke & Davis 2012).
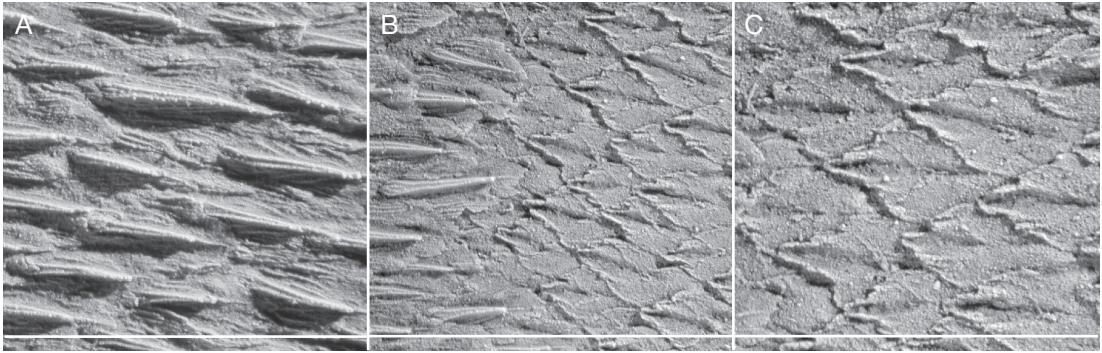
FIG. 5. — *Polymerolepis whitei* Karatajūtė-Talimaa, 1968 (all from UALVP 45015): **A**, articulated series of fin web scales in crown view; **B**, articulated fin web scales in both crown and basal view; **C**, close-up of fin web scales in basal view. Scale bars: 4 mm.

The new material of *P. whitei* does however provide important new information about the extent of variation in the structure of scales in this fish, including variation in the presence or absence of neck canals within the same species and individual. It is now clear that the simple presence or absence of neck canals cannot be used as an unequivocal feature defining chondrichthyan scales. Body scales of *P. whitei* that have a laterally expanded rim surrounding the pulp cavity and have elongate necks also have neck canals. Labial scales also have elongate, developed necks, and therefore, also have neck canals (Karatajūtė-Talimaa 1977: pl. 2, fig. 2). The caudal fin-web scales of *P. whitei* lack necks, and the scales from the leading edges of fins and from the head have low necks and lack neck canals. This variability in scale structure within a single species and individual, means that presence or absence of neck canals cannot be used as a defining character of isolated chondrichthyan scales. Similarly, neck canals have not been identified in all scales of *Seretolepis* (Karatajūtė-Talimaa 1997; Hanke & Wilson 2010), and are not known in any of the scales of *Skamolepis fragilis* Karatajūtė-Talimaa, 1978 (Turner 1991), *Frigorilepis caldwelli* Märss, Wilson & Thorsteinson, 2002, *Wellingtonella gagnieri* Märss, Wilson & Thorsteinson, 2002 (Märss *et al.* 2002, 2006), *Kathemacanthus* (Gagnier & Wilson 1996; Hanke & Wilson 2010), and *Areyongalepis oervigi* Young, 1997, even though these fishes have been considered to be chondrichthyans based on overall

structure of the scale crown and the structure of the basal rim surrounding the pulp cavity of their scales.

Previous discussions of scale variation in *Altholepis* Karatajūtė-Talimaa, 1997, *Seretolepis*, *Polymerolepis whitei*, and other Palaeozoic chondrichthyans, were limited to what could be determined from samples of microremains (e.g., Wells 1944; Karatajūtė-Talimaa 1968, 1973, 1977, 1997; Vieth 1980; Mader 1986; Derycke 1992). In these cases, the limits of scale variation defined for a given species were governed by the experience and intuition of the researcher(s). Fortunately, the discovery of articulated remains of *P. whitei*, *Seretolepis*, and three species of *Altholepis* (the species of *Altholepis* to be presented in a forthcoming paper) help validate the original species descriptions, showing that in many cases, it is possible to provide a fairly detailed and accurate account of scale variation from microremains. However, the ability to understand intraspecific scale variation applies more to complex, ornamented scales that are easier to assign to respective taxa. Simple, smooth-crowned scales are less likely to show enough external features to facilitate species-level identification, and thus the intraspecific variation within these species may go unrecognised.

There are no undoubted chondrichthyan body fossils known from prior to the Devonian (the chondrichthyan affinities of *Frigorilepis caldwelli* and *Wellingtonella gagnieri* are not confirmed; see Märss *et al.* 2002, 2006). Therefore, the anatomy

and phylogeny of the earliest chondrichthyans are unresolved (Anderson *et al.* 1999). The lack of body fossils can be attributed to the poor preservation potential of cartilaginous skeletons. In most cases, the hard parts of the earliest jawed fishes are dermal in origin (scales or scale patches, teeth, pharyngeal denticles, and fin spines), and very little is known about endoskeletal anatomy. What we do know about Palaeozoic chondrichthyan endoskeletons is based mostly on few, sometimes spectacular specimens preserved as articulated body fossils from Devonian or more recent rocks (see for examples: Lund 1977a, b, 1982, 1989; Zangerl 1981; Janvier 1996; Grogan & Lund 1997; Coates & Sequeira 1998; Coates *et al.* 1998; Stahl 1999; Sequeira & Coates 2000; Hanke & Wilson 2010).

Until recently, the presence of an anal fin spine had been used to support acanthodian monophyly (Denison 1979; Maisey 1986), and no chondrichthyans were known to have anal fin spines. Now, an anal spine must be considered characteristic of a larger group of early jawed fishes. A similar conclusion applies to paired fin spines. Discovery of paired fin spines in chondrichthyans is a fairly recent event, before which, the lack of paired and anal fin spines in Middle Devonian or more recent chondrichthyans led researchers to assume that chondrichthyans never possessed these structures. We now know that the chondrichthyan *Doliodus problematicus* (Woodward, 1892) has pectoral fin spines (Miller *et al.* 2003); iniopterygians also have a spine-like leading edge to their pectoral fins. It is possible that the fin spines in *Antarctilamna prisca* Young, 1982 lacking a prominent insertion area, also are pectoral spines given their position behind the gill chamber (Maisey pers. comm.; Wilson *et al.* 2007; Maisey 2009; Hanke & Wilson 2010; and see Young 1982: text-fig. 2). The new material of *Polymerolepis* described here, and *Doliodus problematicus* with its pectoral fin spines (Miller *et al.* 2003), demonstrate that the earliest chondrichthyans may be quite different from their Mesozoic and Cenozoic relatives.

Karatajūtė-Talimaa (1977) classified *Polymerolepis* as a bradyodont holocephalan based on scale growth and that its scales were similar to those of *Listracanthus* species (see Stahl 1999), but all other known holocephalans lack anal fin spines. Perhaps some early holocephalans had anal fin spines, or as we suggest here, *P. whitei* represents a more basal lineage of chondrichthyans. *Lupopsyroides*, *Obtusacanthus*, *Kathemacanthus*, *Seretolepis*, *Gyracanthides*, and *Polymerolepis* all have an acanthodian-like fin spine complement as far as known, yet they have scales of one of two chondrichthyan types: either monodontode (resembling simple placoid scales) or polyodontode and showing areal growth. There are features that separate *Lupopsyroides*, *Obtusacanthus*, *Kathemacanthus*, *Seretolepis*, and *Polymerolepis* from acanthodians (e.g., they lack the superpositional scale growth and perichondral ossifications of acanthodians; Hanke & Wilson 2004), but we also cannot simply classify all taxa showing areal growth of body scales in the Chondrichthyes. Presently, we cannot resolve whether spines and areal scale growth patterns evolved convergently in several lineages, or whether a larger, diverse group of spiny chondrichthyans existed early in the vertebrate fossil record, with acanthodians, elasmobranchs, and holocephalans as the descendant clades. Two putative chondrichthyans from the Silurian, *Frigorilepis caldwelli* and *Wellingtonella gagnieri*, described by Märss *et al.* (2002, 2006), not only lack fin-spines, but the specimens also do not preserve jaws, and what can be seen of their body form rather resembles that of conventional thelodonts. They thus reveal nothing about the order or timing of fin-spine evolution.

The new spiny chondrichthyans from MOTH with their diverse assortment of fin-spine combinations, along with early chondrichthyans such as *Doliodus problematicus*, suggest that that the phylogeny of early jawed fishes is far more complex than the presently-accepted taxonomy suggests. For *Polymerolepis whitei*, the few patches of articulated scales and the articulated tail (UALVP 45015) show little about the body, but confirm that this species has an anal fin spine. We look forward to finding more complete specimens with information about the anterior part of the body in this species so that we can include *P. whitei* in a cladistic analysis of early jawed fishes.

CONCLUSIONS

Volumes have been published on Devonian and more recent cartilaginous fishes, however, Palaeo-

zoic taxa such as *Gyracanthides*, *Kathemacanthus*, *Seretolepis*, *Obtusacanthus*, and *Lupopsyroides* cannot be conveniently placed in the current chondrichthyan classification, nor to they fit neatly in the Acanthodii without revision. The earliest chondrichthyans (as presently classified), including *Polymerolepis whitei*, originally were described from isolated remains, and in many cases, articulated body fossils still are not available for study.

The new specimens of *P. whitei* detailed in this paper have served two important functions. Firstly, the associated and articulated scales have helped verify the accuracy of the original account of scale variation which was based on microremains, and secondly, they illustrate that *P. whitei* possesses an anal fin spine. Until recently, anal fin spines were considered to be a feature of acanthodians among Palaeozoic fishes.

If *Polymerolepis whitei* is correctly classified as a bradyodont, then it is the first one known to possess an anal fin spine. We suggest rather that it represents a more basal lineage of chondrichthyan. It joins *Doliodus problematicus* and problematic taxa such as *Gyracanthides*, *Kathemacanthus*, *Seretolepis*, *Obtusacanthus*, and *Lupopsyroides* to add complexity to the phylogeny of early jawed fishes.

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