A NEW ACTINOPTERYGIAN FROM THE LATE DEVONIAN GOGO FORMATION, WESTERN AUSTRALIA.

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Abstract: The study of early actinopterygians (ray-finned fishes) from the Devonian has been hampered by imperfect preservation in the majority of taxa. The Late Devonian (early Frasnian) Gogo Formation of north-western Western Australia is notable in producing complete fossil actinopterygians with exceptional three-dimensional preservation of both the dermal and endoskeletal anatomy. Four taxa have been described and have proved invaluable in understanding the anatomy of early representatives of this clade. Here, we present a fifth Gogo taxon, based on a single exceptionally preserved specimen and representing a new genus and species of early ray-finned fish. The neurocranium was CT scanned, permitting a detailed examination of the endocast. The new taxon possesses unusual features including a greatly enlarged spiracular opening and extensive spinose ornamentation on the dermal skull bones, median ridge scutes and lepidotrichia. The endocast displays a mosaic of characters, some of which are similar to *Mimipiscis* and non-actinopterygian outgroups, while other features are more akin to *Raynerius* from the Late Devonian of France as well as several stratigraphically younger taxa. A phylogenetic analysis resolves the new form as sister taxon to fishes from the Late Devonian of the Northern Hemisphere and all post-Devonian actinopterygians, confirming that the assemblage of fossil ray fins from the Gogo Formation is part of the wider Devonian actinopterygian radiation.

Key words: actinopterygian, Devonian, Gogo, neurocranium, phylogeny

ACTINOPTERYGIANS (ray-finned fishes) are an extremely diverse clade of bony vertebrates with over 30,000 extant species (Eschemeyer *et al.* 2017) combined with a generally rich fossil record (Long 2011). However, the record of these fishes prior to the Late Devonian is comparatively scant. Excluding scale-based taxa, a little over 20 Devonian species have been described, as opposed to well over 200 sarcopterygians from the same period (Cloutier & Arratia 2004; Giles et al. 2015b. The presence of putative early sarcopterygians in the Ludlow-Pridoli of Yunnan (Choo *et al.* 2017; Zhu *et al*. 2011; although see Lu et al. 2017) seemingly necessitates the existence of Silurian ray-finned fishes (Coates 2009), yet the oldest unequivocal fossil actinopterygian based on reasonably complete material is *Cheirolepis trailli* Agassiz, 1835 from the Eifelian Old Red Sandstone of Scotland (Swartz 2009). Stratigraphically earlier taxa proposed as actinopterygians include *Orvikuina* Gross, 1953, *Andreolepis* Gross, 1968 (Janvier 1978), *Naxilepis* Wang and Dong, 1989, *Terenolepis* Burrow, 1995, *Dialipina* Schultze, 1968 (Schultze and Cumbaa 2001) and *Ligulalepis* Schultz, 1968 (Basden and Young 2001). However, the classification of these taxa within Actinopterygii is uncertain or disputed (Gross 1968; Schultze 1977; Friedman and Blom 2006; Zhu *et al*. 2006; Botella *et al*. 2007; Friedman and Brazeau 2010; Zhu *et al*. 2013; Chen et al. 2016; Clements et al. 2018). Most recently, *Meemannia* (Lochkovian, Yunnan, China), a form previously considered to be a stem sarcopterygian, has been proposed as an early-diverging ray-finned fish on the basis of endocranial characters (endoskeletal enclosure of the spiracle, presence of a lateral cranial canal: Lu *et al*. 2016). Additional detailed descriptions of the morphology of early actinopterygians, particularly relating to the character-rich neurocranium and endoskeleton, will better resolve the base of the actinopterygian tree.

The majority of Devonian ray fins are preserved as either articulated two-dimensional skeletons with limited endoskeletal information or otherwise as incomplete specimens preserved in three dimensions. A notable exception to this are the spectacular fossils of the Late Devonian (early Frasnian) Gogo Formation of the Canning Basin, Western Australia, (Long and Trinajstic 2010).

The Gogo Formation, Canning Basin, north-western Western Australia (Fig. 1), represents the deeper inter-reef basinal facies of an extensive Devonian (Givetian–Frasnian *Polygnathus varca* zone – *Mesotaxis asymmetrica* zone) barrier reef complex (Teichert 1949; Playford and Lowry 1966; Druce 1975; Towner and Gibson 1983). Unweathered sections of the Gogo comprise sequences of siltstone and grey-black shales, which contain calcareous nodules interbedded with thin lenses of resistant limestone. Fossils are typically recovered from weathered exposures where the erosion-resistant concretions are concentrated in dense surface aggregates (Playford & Lowry, 1966). The Gogo Formation has a maximum thickness of 430 m with the fossil-bearing nodular horizons dated as lower Frasnian. Fossils recovered within these nodules have revealed a diverse marine fauna world renowned for its outstanding three-dimensional preservation (Long 2006; Long & Trinajstic 2010; Briggs et al. 2011).

The first detailed study of the actinopterygians from the Gogo Formation identified two species (Gardiner and Bartram, 1977): *Moythomasia durgaringa* (Gardiner 1984; Choo 2015) and *Mimipiscis toombsi* (Gardiner 1984; revised Choo 2011). These taxa, especially *M. toombsi*, represent the most thoroughly described Palaeozoic actinopterygians and have featured in numerous studies into early osteichthyan anatomy and phylogeny (Long 1988; Gardiner and Schaeffer 1989; Schultz and Cumbaa 2001; Cloutier and Arratia 2004; Friedman and Blom 2006; Long *et al*. 2008; Swartz 2009). Two additional actinopterygian taxa were subsequently described as *Gogosardina coatesi* (Choo *et al*. 2009) and *Mimipiscis bartrami* (Choo 2011). Choo (2011) mentioned “an additional undescribed form that represents a new genus and species” which is described here as the fifth taxon of ray-finned fish from the Gogo reef fauna.

MATERIALS AND METHODS

During the 1990 Western Australian Museum (WAM) expedition to the Gogo Formation, one of the authors (JL) collected a fossil actinopterygian (WAM 03.6.1) from a nodule aggregation at the Paddys Valley site (Fig. 1). WAM 03.6.1 is the only representative of this taxon that has so far been identified.

Preserved as part and counterpart within an evenly split nodule, each part was prepared separately via the acid transfer techniques (Toombs and Rixon 1950). The part (WAM 03.6.1a, “A-block”; Fig. 2A) was prepared at the Western Australian Museum (JL) in 2003, revealing a well-preserved braincase, which separated from the acrylic block, along with parts of the snout, cheek and opercular-gular series. The material was loaned to Museums Victoria in 2005; where the counterpart (WAM 03.6.1b, “B-block”) (Fig. 2C) was prepared by David Pickering.

High resolution X-ray tomography was conducted on the braincase by Tim Senden at CTLab (https://ctlab.anu.edu.au/), the Department of Applied Mathematics, Research School of Physical Sciences and Engineering, The Australian National University. The specimen was scanned with a 80kV/200uA reflection-style X-ray source and 1 mm thick aluminium filter at a spatial resolution of 33.6 microns. The specimen was placed 250 mm from the source, and the detector positioned 1000 mm from the source. The specimen was imaged through 360 degrees rotation. Reconstruction was based on 2880 radiographic projections formed on a 2048 × 2048 Perkin Elmer Flat Panel camera. Full details of the process are presented in Sakellariou *et al.* 2004a,b. This represents only the third well-preserved three-dimensional neurocranium of a Devonian actinopterygian to be made available for detailed digital imaging and analysis, along with the *Mimipiscis toombsi* specimen NHMUK PV P.53247 (Giles *et al.* 2014) and the holotype of *Raynerius splendens* (Giles *et al.* 2015c).

Anatomical Abbreviations

Standard actinopterygian bone terminology, as presented by Gardiner *et al.* (2005), and Gardiner and Schaeffer (1989), is used for the description. While the skull roofing bones referred to as the frontal and parietal are homologous with the sarcopterygian parietal and post-parietal respectively, traditional terminology is maintained to facilitate comparisons with the majority of descriptions of early ray-finned fishes (Gardiner and Bartram 1977; Gardiner 1984; Long 1988; Taverne 1997; Daeschler 2000; Prokofiev 2002; Friedman and Blom 2006; Choo *et al*. 2009; Choo 2011; Giles *et al.* 2015c; Choo 2016; Long *et al*. 2008).

An = angular; **ano** = anterior nasal opening; **an.f** = anal fin; **ant.amp** = ampulla of anterior semicircular canal; **art** = articular; **asc** = anterior semicircular canal; **aur** = cerebellar auricle; **Br** = branchiostegal rays; **cao** = aortic canal; **cc** = crus commune; **cla** = canal for lateral aorta; **cau.f** = caudal fin; **Clav** = clavicle; **Clth** = cleithrum; **crsp** = craniospinal process; **Den** = dentary; **dful =** upper basal fulcra of the caudal fin; **Dpl** = dermopalatine series; **drs** = dorsal ridge scute; **Ds** = dermosphenotic; **dor.f** = dorsal fin; **eff =** epibranchial arteries; **esc** = external semicircular canal; **ethc** = ethmoid commissure; **ext.amp** = ampulla of external semicircular canal; **F** = frontal (= sarcopterygian parietal); **fhm** = hyomandibular facet; **foca** = foramen of occipital artery; **focn** = foramen for occipital nerve; **for** = forebrain; **fotc** = otico-occipital fissure; **gstIX** = groove for supratemporal branch of glosspharyngeal nerve; **hpbt** = hole for basipterygoid process; **Hy** = hyomandibular; **ios** = interorbital septum; **inc** = infraorbital sensory canal; **It** = intertemporal; **ivl** = area of insertion of intervertebral ligament; **jc** = jugal canal; **Ju** = jugal; **jug** = jugular groove; **lc** = openings for lateral line sensory canal; **lcc** = lateral cranial canal; **ldv** = canal for longitudinal dorsal vein; **L.gu** = lateral gular; **Mx** = maxilla; **Na** = nasal; **not** = notochordal canal; **oatm** = area of origin of anterior trunk muscles; **oims1** = area of origin of first intermuscular septum; **oims2** = area of origin of second intermuscular septum; **Op** = operculum; **opt.l** = optic lobe; **Pa** = parietal (= sarcopterygian postparietal); **pamp** = parampullary process; **Par** = prearticular; **pdf** = posterior dorsal fontanelle; **pec.f** = pectoral fin; **pel.f** = pelvic fin; **pq** = palatoquadrate; **pinf** = pineal foramen; **pl** = sensory pit lines; **Pm** = premaxilla; **Pop** = preoperculum; **por** = postorbital process; **post.amp** = ampulla of posterior semicircular canal; **psc** = posterior semicircular canal; **Pt** = post-temporal; **Qj** = quadratojugal; **R** = radials; **Ro** = median rostral; **sac** = sacculus; **sda** = suture between dentary and angular; **Scl** = supracleithrum; **Sop** = suboperculum; **spic** = spiracular canal; **spig** = spiracular groove; **spio** = canal for spinooccipital nerve; **spir** = margin of spiracular opening; **St** = supratemporal; **suc** = supraorbital sensory canal; **vfon** = vestibular fontanelle; **vs** = ventral scute; **IV** = canal for trochlear nerve; **V** = canal for trigeminal nerve; **Vprof** = canal for profundus nerve; **VI** = canal for abducens nerve; **VII** = canal for facial nerve; **VIIlat** = canal for lateralis branch of facial nerve; **IX** = canal for glossopharyngeal nerve; **X** = foramen of vagus nerve.

Institutional Abbreviations

NHMUK, The Natural History Museum, London; **MV** Museum Victoria, Melbourne; **WAM**, Western Australian Museum, Perth.

SYSTEMATIC PALAEONTOLOGY

Class OSTEICHTHYES Huxley, 1880

Subclass ACTINOPTERYGII Cope, 1887

Genus *PICKERINGIUS*, gen. nov.

Etymology. After the late Mr. David Pickering, for his irreplaceable contributions to Australian vertebrate palaeontology, as a fossil collector, preparator, curator and science communicator at Museums Victoria.

Diagnosis. As for type species (monotypic genus)

Type species. Pickeringius acanthophorus sp. nov.

Figures 2-13

Locality. Paddys Valley, Gogo Formation, Western Australia, Upper Devonian (lower Frasnian)

Etymology. Latin for "bearer of spines" in reference to the extensive spinose ornamentation on the skull, pectoral girdle, squamation and fins.

Differential Diagnosis. Actinopterygian with rows of sharp barbs on the proximal lepidotrichia of the pectoral, pelvic, anal and caudal fins. Skull roof and pectoral girdle ornamented with raised, pointed denticles bearing small barb-like serrations. Short rostral bone of similar size to premaxillae. Enlarged spiracular opening bordered by the lateral skull roof and the posterior ramus of the dermosphenotic. Deep spiracular groove, dorsally enclosed within a canal. Sharp lateral serrations on median scutes and basal fulcra on the caudal fin.

Holotype and only specimen. WAM 03.6.1. An almost complete articulated fish preserved in counterpart with both halves mounted in resin slabs (Fig. 2). Partial skull roof (Fig. 3, 4), neurocranium (Fig. 3, 4, 5), snout and various dermal bones of the cheek and opercular-gular region (Fig. 7, 8) recovered as separate elements during preparation. Much of the dorsal surface of the postcranium, anterior to the dorsal fin, is not preserved.

DESCRIPTION

Neucrocranium

General features. The neurocranium of *Pickeringius* is well mineralised and undistorted (Fig. 3, 4, 5). It is broken along the interorbital septum (ios, Fig. 3I) and through the ventral otic fissure, a mode of preservation commonly seen in the braincase of *Cheirolepis* (Giles *et al*. 2015b). Consequently, the base of the ethmosphenoid region and the parasphenoid are missing. As is typical for early actinopterygians, the nasal capsules are not mineralised (Gardiner 1984).

Occipital region. The posterior face of the occipital region is dominated by a large notochordal canal. The notochordal canal (not, Fig. 3L) is ovoid in transverse section, as in *Mimipiscis* (Gardiner 1984) and *Cheirolepis* (Giles *et al*. 2015b), rather than the rounded canal seen in *Raynerius* (Giles *et al*. 2015c). Both the roof and floor are incompletely mineralised along the midline. Ridges for the insertion of the first and second intermuscular septa (oims, Fig 3L) are just discernible on the lateral face of the occiput, and the depressions for the origins of the anterior trunk musculature (oatm, Fig. 3L) are shallow. The craniospinal processes (crsp, Fig. 3F,L) are small and postero-laterally directed, unlike the robust, laterally-directed processes of *Raynerius* and Carboniferous actinopterygians (e.g.

Kansasiella, Poplin 1974; *Coccocephalichthys*, Poplin and Véran 1996; *Lawrenciella*, Hamel and Poplin 2008). Dorsally, a small posterior dorsal fontanelle (pdf, Fig. 3I) is present.

As in *Mimipiscis*, the dorsal aorta is fully enclosed in a canal (cao, Fig. 3F,L); the aortic canal has a posterior notch in *Raynerius*, *Moythomasia* (Long and Trinajstic 2010: fig. 5b) and *Gogosardina* (Choo, *et al.*, 2009: fig. 9a). Unusually, the bifurcation point of the lateral dorsal aortae is also enclosed in a canal, whereas it is typically exposed in early actinopterygians (e.g. *Raynerius, Moythomasia, Gogosardina, Kentuckia*: Rayner, 1951). In the Carboniferous taxa *Kansasiella* (Poplin 1974) and *Lawrenciella* (Hamel and Poplin 2008), the enclosed dorsal aorta does not bifurcate until just behind the ventral otic fissure, and a single foramen or paired foramina in the floor of the aortic canal give off the epibranchial arteries. The lateral dorsal aortae are posteriorly enclosed in the Triassic actinopterygians *Pteronisculus*, *Boreosomus* (Nielsen 1942) and *Luederia* (Schaeffer and Dalquest 1978).

It should be noted that a single example of *Mimipiscis* (Gardiner, 1984: fig 15) also displays an enclosed bifurcation point, but it is absent in numerous other congeneric skulls, regardless of relative size to this one individual. Further scrutiny of this specimen (NHMUK P.56483) may be warranted.

In *Pickeringius*, the epibranchial arteries (eff, Fig. 3F) branch off from the lateral dorsal aortae anterior to their bifurcation and extend laterally towards the vestibular fontanelles. Anteriorly, the hyoid artery branches from the lateral dorsal aorta posterolaterally before entering the braincase, and the carotid arteries continue forward into the ventral otic fissure. Although part of their path is enclosed, the length of the dorsal aorta and lateral dorsal aortae is very similar to that of *Mimipiscis*, as opposed to the short dorsal aorta and long lateral dorsal aortae of *Raynerius*, *Gogosardina* and *Moythomasia*.

Large vestibular fontanelles (vfon, Fig. 3F,I) are present in *Pickeringius*. This contrasts sharply with the very small vestibular fontanelles of *Mimipiscis*, and is more similar to the condition seen in *Cheirolepis*, *Raynerius*, *Moythomasia*, Carboniferous taxa (e.g. *Coccocephalichthys*: Poplin & Véran 1996) and sarcopterygians (e.g. *Youngolepis*: Chang 1982; *Gogonasus*: Holland 2014). A bridge of bone lateral to the fontanelle separates it from the jugular groove (jug, Fig. 3F). The vestibular fontanelle is connected to the posterior dorsal fontanelle by the continuous otico-occipital fissure (fotc, Fig. 3F, I, C). The vagus (X, Fig 3 F,I) nerve exits approximately halfway along the length of the fissure, slightly posterior to the small parampullary process (pamp, Fig. 3I).

Otic and orbitotemporal regions. The dorsal surface of the braincase is tightly sutured to the skull roof except in the region of the posterior dorsal fontanelle (pdf, Fig, 3C) and the pineal foramen (pinf, Fig. 3C). Unlike the condition in Carboniferous and stratigraphically younger actinopterygians (e.g. *Kentuckia*, *Lawrenciella*, *Pteronisculus*), no fossa bridgei is developed.

Posterior to the orbit is a prominent transverse process. This structure, typically referred to as the lateral commissure (Gardiner 1984), is penetrated by the jugular canal (jc, Fig, 3I) and bears the spiracular groove (spig, Fig. 3F, I) and hyomandibular facet (fhm, Fig. 3F, I, L, 4A, B, C). It is in fact a composite structure comprising the postorbital process and the transverse otic process, which are separated by the spiracular groove (Giles *et al*. 2015a). The commissure proper forms the bridge with the sphenoid. As in *Mimipiscis*, the lateral commissure is anteroposteriorly narrow, and the postorbital process sweeps forward to partially enclose the posterolateral corner of the orbit. The hyomandibula articulates on the back of the transverse otic wall in an elongate posterolaterally-directed facet. The spiracular groove is far deeper than in *Raynerius*, *Mimipiscis* or *Moythomasia*, and is enclosed in a canal dorsally (spic, Fig. 3I, Fig. 4A, B, C). While a fully developed spiracular canal is present in *Pickeringius*, the putative Early Devonian stem-actinopterygian *Meemannia* (Lu *et* *al*. 2016) and in most post-Devonian fossil ray fins (including *Kentuckia*, *Lawrenciella*, *Pteronisculus* and *Boreosomus*), such a canal is absent in *Mimipiscis* (Gardiner 1984) and *Raynerius* (Giles *et al*. 2015b). *Moythomasia* possesses a 'spiracular bar' that is variably developed (Gardiner 1984), while lateral processes at the dorsal limit of the spiracular groove in a dorsoventrally-flattened *Cheirolepis* may represent an incipient or broken spiracular bar (Giles et al. 2015b).

The braincase has broken through the interorbital septum, and consequently the exit of the oculomotor (III) and optic nerves (II) cannot be described. As the basisphenoid is missing, only the dorsal portion of the posterior myodome is preserved.

Endocast. The endocast (Fig. 5) can be described up to the region corresponding to the forebrain: the olfactory canals are not preserved. The forebrain (for, Fig, 5B) is narrow, and it is not possible to distinguish between the telencephalic and diencephalic regions. The ventral extension of the diencephalon is not preserved. As in *Mimipiscis* (Giles and Friedman 2014) and *Raynerius*, the area corresponding to the midbrain, comprising the optic lobes (opt.l, Fig. 5B), is narrower than the hindbrain, but as the dorsal surface in this region is incompletely preserved it is not possible to say whether the lobes were differentiated. The trochlear nerve (IV, Fig. 5B,C,D) exits the cranial cavity at the dorsal limit of the optic lobes, as in *Mimipiscis*.

The bulge for the cerebellar auricles (aur, Fig 5B), extending no further posterior than the anterior ampulla, is similar to that seen in *Mimipiscis*; by contrast, the auricles extend much further posteriorly in *Raynerius, Lawrenciella* and stratigraphically younger actinopterygians (Fig. 6). The auricles also project dorsally above the rest of the cranial cavity, a feature seen in *Mimipiscis*. No cerebellar corpus is developed. More posteriorly, the region for the hindbrain rises slightly to the level of the posterior dorsal fontanelle, and drops steeply posterior to the fontanelle.

The exit of the middle cerebral vein from the cranial cavity cannot be identified, but in all other respects the pattern of cranial nerve canals (Fig 5B,C,D) for the trigeminal (V), profundus (Vprof), abducens (VI), facial (VII) and lateralis branch of the facial nerve (VIIlat) are identical to that described for *Mimipiscis*. A large foramen for the lateral cranial canal (lcc, Fig. 5B,D) fills the lateral wall of the cranial cavity between the sinus superior (ssu, Fig. 5D) and the otico-occipital fissure.

Labyrinth. As in *Mimipiscis* and *Raynerius*, as well as sarcopterygians (e.g. *Youngolepis*: Chang 1982; *Eusthenopteron*: Jarvik 1980) and chondrichthyans (e.g. *Orthacanthus*: Schaeffer 1981; *Cobelodus*, Maisey 2007), the crus commune (cc, Fig. 5B,D) of the anterior and posterior semicircular canals projects above the endocranial roof. The sinus superior is well developed in *Pickeringius*, and the underlying sacculus (sac, Fig 5D) is extensive. The lack of a differentiated lagenar pouch lends further evidence to the hypothesis that the lagena of actinopterygians and sarcopterygians are independently derived (Giles and Friedman 2014).

Unlike in *Mimipiscis*, there is very little separation between the lateral extent of the cerebellum and the anterior semicircular canal; this condition is also observed in *Raynerius*, and to an even greater extent in *Kentuckia* and *Lawrenciella*. Although the anterior semicircular canal appears similar, if slightly shorter, to that of *Mimipiscis*, the posterior canal is much shorter, being less than half the length of the anterior canal. The horizontal canal is also short and very tightly curved.

Dermal skull bones

General features. The lateral margins of the skull roof (Fig. 3, 4) are ornamented with a dense field of separate pointed ganoine denticles (Fig. 4d) bearing raised striae. The anterior bones of the opercular-gular series (Fig. 7) have an ornament of separate acutely pointed denticles whereas the ornament on the posterior bones comprises mainly of linear ridges, as does the ornament on the mandible. This differs from the condition in the majority of Devonian actinopterygians where the skull roof is typically ornamented with linear or vermiform ridges (Choo 2011; Gardiner 1984; Long 1988).

Skull roof. The skull roof (Figs 3, 4) has a length of 15.2 mm, from the anterior tips of the frontals to the posterolateral processes of the supratemporals, and is 14.2mm wide. There is extensive fusion between the individual bones and sutures are difficult to discern. The frontals (Fr, Fig. 3C,F) account for over 60% of the skull roof length, tapering anteriorly to apices that were nestled between the nasals and the rostral. About 40% of the median suture between the frontals is interrupted by the large pineal foramen (pinf, Fig. 3C). The rectangular parietals (Pa, Fig. 3C) possess tripartite pit lines (pl, Fig. 3C) that are located well away from the bone margins.

While the posterior and mesial boundaries of the intertemporals (It, Fig. 3C, 4A, B) are not clearly visible, the entire lateral margin of each bone forms a concavity that, in conjunction with corresponding embayments on the dermosphenotics, accommodates an enlarged spiracular opening that is over 4 mm in length. The large size of these openings is unlike the minute spiracules typically found in other Devonian actinopterygians (Choo 2011; Choo 2015; Gardiner 1984; Long 2008) and more akin to those of some early tetrapodomorphs, notably *Gogonasus* and elpistostegalians (Long *et al*. 2006).

The supratemporals (St, Fig. 3C, 4A, B) are rectangular, tapering posterolaterally to terminate posterior to the parietals, with the infraorbital sensory canals (inc, Fig. 5A) running close to the mesial margins. The anterior margin contributes to the spiracular opening and contacts the dermosphenotic anterolaterally. The extrascapulae are fragmented and their exact shape and number cannot be determined.

Snout. The snout (Fig. 8A-D) was detached from A-block and comprises nasals, premaxillae and median rostral. Ornamentation consists of a reticulate pattern of short to medium smooth ridges and scattered round tubercles, in contrast to the sharp denticles and striae-bearing ridges on the skull roof. Broadly similar ornamentation is present on the snouts of *Mimipiscis* (Choo, 2011: fig 11,12) and *Gogosardina* (Choo *et al*. 2009: fig 8). The rostral (Ro, Fig. 8B,D) is small, only marginally larger than the premaxillae, and arches into dorsal and anterior laminae of roughly equal size. Although the posterior tip of the dorsal lamina was broken during preparation, the bone originally tapered posteriorly and anteriorly. Lateral notches at the junction of the two laminae contribute to the anterior nares (ano, Fig. 8B). The paired premaxillae (Pm, Fig. 8B,D) are pentagon-shaped and meet in a long median suture, embracing the rostral in a V-shaped recess and excluding that bone from the oral margin. The ethmoidal commissure (ethc, Fig. 8D) is clearly visible as a raised furrow on the medial surface as in *Mimipiscis* and *Gogosardina* (Choo 2011), but unlike *Moythomasia* (Choo 2015). The dentition is typical for Devonian actinopterygians (Gardiner 1984), consisting of conical teeth on the biting margins of the premaxillae, maxilla and dentary which are situated mesial to an outer row of smaller marginal teeth. Only a posterior fragment of the right nasal (Na, Fig. 3C) is preserved, displaying denticulate ornament similar to that on the skull roof, while the left nasal is fragmented. The position of the posterior nasal opening is not known.

Cheek. The jugal (Fig. 8E-F) is crescentic and ornamented with short ridges, with the infraorbital canal (inc, Fig. 8F) running close to the margin of the orbit. There is space for a small lacrimal, but this bone is not preserved. The dermosphenotic (Fig. 8I-L) is exceptionally large at 9mm in length (roughly 60% the length of the skull roof). It is a tripartite unit with elongate posterior ramus. The lateral margin of the spiracular opening forms a prominent excavation on the dorsal margin (spir, Fig. 8J), accounting for about 1/3 of the length of the bone. The infraorbital sensory canal (inc, Fig. 8L) enters from the skull roof via the dorsal margin and exits ventrally into the jugal.

The maxilla (Mx, Fig. 2B, 7B), with a slender suborbital ramus and broad posterior blade, is of similar shape to that of *Gogosardina* (Choo *et al*., 2009) and *Mimipiscis* (Choo 2011), save that the dorsal margin is gently concave rather than straight. Ornament on the post-orbital blade of the maxilla consists of linear ridges near the sutures with the preoperculum, shifting to shorter ridges and tubercles towards the biting margin and on the narrow suborbital ramus.

The palatoquadrate (pg, Fig. 2B) has a raised posterior margin and appears to be ossified as a single unit. The dorsal margin is pierced for articulation with the basipterygoid process (hbpt, Fig. 2B). The dermal covering of the palate is not visible, although the dermopalatines (the number of which is not known) are displaced ventral to the palate (Dpl, Fig. 2B).

An incomplete right preoperculum (Pop, Fig. 2D, 7B), lacking much of the horizontal ramus, is preserved in articulation on the B-block. The preserved section is acutely angled and closely following the contours of the maxilla. It is ornamented with short ridges. A small quadratojugal (Qj, Fig. 6B) is present, although the presence of a pit line cannot be determined due to overlying matrix.

Lower jaw. The right mandible (Den), missing the anterior half, is visible in visceral view on A-block (Fig. 2A-B) while the dermal surfaces are on the B-block (Fig. 2C-D, 7). No suture is visible in the smooth overlap area for the maxilla, indicating that a surangular was present as in *Moythomasia* (Gardiner 1984), but unlike *Mimipiscis* (Choo 2011; Gardiner 1984) and *Gogosardina* (Choo *et al.* 2009) where the angular and dentary meet directly at a prominent suture in the overlap area. Most of the jaw is ornamented with horizontal ridges, with abrupt shifts in form towards the margins. Along the ventral and posterior marginal surfaces are sharp, posteroventrally directed denticles of similar form to those on the neighbouring branchiostegal rays. Towards the occlusal surfaces, adjacent to the marginal teeth, are a mixture of short ridges and bulbous tubercles. A mandibular sensory canal is not visible. The tooth-bearing bones on the medial side of the jaw are imperfectly preserved, with fragmentary denticulated surfaces of the prearticular and coronoid series (Par, Fig. 2B) visible on A-block. Most of the Meckelian ossifications are fragmented, save for the articular (Art, Fig. 2B), which is still in articulation with the quadrate.

Opercular-gular series

All visible bones of the opercular-gular series (Fig. 7) are ornamented with a mixture of denticles interspaced with short ridges that posteriorly terminate at a sharped apex. The operculum (op, Fig. 2D, 7B) is rhombic, with anteroventral and posterodorsal margins being slightly longer than the dorsal and ventral ones. The square suboperculum (Sop, Fig. 2D, 7B) has a small anterodorsal process and is comparatively large, being over 70% the size of the operculum. There are no accessory operculae. At least nine branchiostegal rays (Br, Fig. 2D, 7B) were present per side; however, due to incomplete preservation the total number cannot be ascertained. Partially preserved lateral gulars (L.gu, Fig. 2D) indicate that they were considerably larger than the adjacent branchiostegal rays.

Pectoral girdle

The dermal ornamentation over most of the pectoral girdle (Fig. 7) consists of short, posteriorly tapering ridges and denticles. The posttemporal (Pt, Fig 2D, 8G,H) is a four-sided bone whose posterior margin tapers inwards towards a narrow median suture. The anterior margin bears a narrow unornamented overlap surface for the extrascapulae. Only the posterior-most section of the left supracleithrum is visible on B-block while the right supracleithrum (scl, Fig. 7B), which separated from A-block, is slender with a straight posterior margin. The ornament of separate conical denticles elongates and anastomoses to form ridges in the central region of the bone. The presupracleithrum and postcleithrum have not been identified.

Both pairs of cleithra and clavicles are preserved in the A- and B-blocks, although their ventromedial margins are obscured. The overall form of the bones displays a similar morphology to that of *Mimipiscis* and *Moythomasia* (Gardiner 1984), although maintaining the unique sharpened ornament of this taxon. The large cleithrum (Clth, Fig. 2A,B, 7B) has a deep posterior embayment for the pectoral fin, a strongly concave anterior margin and a smooth overlap surface for the clavicle. The clavicle (Clav, Fig. 2A,B, 7B) is semiconical, with a triangular vertical face and a broad ventral lamina. No interclavicle is visible.

Fins

The fins of *Pickeringius* (Fig. 2, 7, 9) are unusual in possessing spiny projections on the proximal fin rays. Except for the dorsal fin, the leading edge of which is not preserved, spine-like fringing fulcra are also present on all fins, including the caudal fin. The right pectoral fin is partially preserved on the B-block (pec.f, Fig. 2D, 7, 9B), whereas only a few lepidotrichia of the left fin remain on A-block. Except for some proximal elements adjacent to the radials, the lepidotrichia and fringing fulcra of the right pectoral fin are scattered around adjacent to the gular region. Based on the relative distribution of the disarticulated lepidotrichia, the fin comprised longer proximal lepidotrichia that graded into shorter segments in the distal parts of the fin, as seen in *Mimipiscis* (Choo *et al*. 2009; Gardiner, 1984), *Howqualepis rostridens* (Choo 2009; Long *et al*. 2008) and *Moythomasia durgaringa* (Choo 2011). Each of the proximal fin-rays of *Pickeringius* are unique in bearing a single row of sharp bony projections on dorsal surface, giving the lepidotrichia a saw-toothed appearance. The shortest distal segments are devoid of these barbs, while they are present on several disarticulated elements of intermediate length. Four radials of the right pectoral fin (R, Fig. 7), made of thin perichondral bone, are present on B-block. The anteriormost example ispoorly preserved, while the following three are narrow, hourglass shaped elements. Other pectoral elements, including the propterygium and metapterygium, are not preserved beyond some unidentifiable fragments alongside the radials.

The fin rays of the pelvic fins (pel.f, Fig. 2D, 9A) are scattered on both blocks, roughly 60% down the length of the body. Little can be said about the shape of the fins, but again the lepidotrichia included serrated longer proximal elements and short, unadorned distal segments. The dorsal fin (dor.f, Fig. 2B) is largely missing, with only a few short, barbless lepidotrichia preserved.

The triangular anal fin is well-preserved, particularly on B-block (an.f, Fig. 2B,D, Fig. 9C). 35 fin rays are preserved, although some disruption of elements and lack of preservation of the fin tip indicates the complete fin would have had a greater number of fin rays. All proximal segments and the longer subsequent segments contain sharp, posterolaterally directed barbs, while the posteroventral apex of the fin consists of a fringe of short, barbless segments.

Most of the triangular hypochordal lobe of the caudal fin is present on the holotype (cau.f, Fig. 2B,D, Fig. 9D) while only the base of the upper lobe is preserved. Again, the entire proximal series of lepidotrichial segments are barbed, with the spines extending from one to three segments further down each ray before transitioning into shortened, barbless segments.

Scales

Scales corresponding to eight lateral body zones (Fig. 10A, sensu Esin 1990) are visible on the holotype (Fig.10, 11) in addition to dorsal ridge and ventral fulcral scales (Areas I and II sensu Esin (1990), however most of the dorsal surface anterior of the dorsal fin (Area E) is missing and the scales of this region are poorly preserved. The lateral body scales have a dorsal peg which inserts into the ventral socket on the internal surface of the preceding scale, an ornamented free field with unornamented overlap area of the external surface and a keel that extends from the socket to the peg base on the internal surface of the scale. The scale height and peg height decrease in a rostro-caudal direction, and in a dorso- ventral direction. Area A (Fig 10A) scales have a H/L ratio of 2/1 and Area D scales 1/2 ratio. The keel is well developed on anterior scales and less developed on Area C and D scales. All scales bear an ornament of linear ganoine ridges on the free field, the number of ridges decreasing from 8 to 1 in a rostro-caudal direction. The ridges are teardrop shaped, with a broader anterior section that narrows towards a posterior apex, and are ornamented with fine raised striae. In scales from Area A and B (Fig. 10B) separate ridges extend the full width of the scales, terminating in sharp points posterior to the body of the scale. Scales in Area C (Fig. 10C) and the anterior section of Area D have two columns of ridges. Area C scales in a ventrocaudal position (Fig. 10C) are slightly larger than those on the flanks, with the anterior column of ridges often interfingering and anastomosing into the posterior column. Scales over most of Area D once again possess a single column separate ridges (Fig. 10D).

Area F scales (Fig. 11A) adjacent to the pectoral fins are oblong in shape with a very narrow overlap area. The free field is covered in three-to-four columns of denticles or extremely short pointed ridges, giving the ventral scales a spinose appearance. Posterior to the pectoral fins, the Area F scales become rhombic in shape and the ornament changes to short anastomosing ridges.

Specialised scales occur around the fins (Areas H and G) are ovoid in shaped (Fig. 11A), becoming elongate towards the fin margins. The largest of these scales occur leading up to the caudal fin (Fig. 11B) and these have extended in length to have a narrow diamond shape with ornament covering the free field and a very narrow overlap area.

Compared with other Gogo actinopterygians, the scales of *Pickeringius* resemble those of *Mimipiscis toombsi* in having linear ridges with a micro-ornament of striae on the scales across all body regions. They can be differentiated from *Mimipiscis toombsi* and *M. bartrami* by the ridges being tear-shaped rather than uniformly narrow, the larger fulcral scales, the more distinct striae micro-ornament that occurs the length of the ridge and the scale H/L ratio; *Mimipiscis* scales being higher and narrower (Area A: H/L 3/1) (Trinajstic 1999b) than scales from *Pickeringius* . Scales from *Gogosardina* also have an ornament of horizontal ridges on the free field, however the ridges are spaced closely together and Area A scales have 10 ridges decreasing to 2 in Area D scales (Choo *et al*. 2009). The micro-ornament is less extensive with only a few fine striae at the anterior margin of the ganoine ridge. Scales from *Moythomasia durgaringa* have anastomosing ridges on the anterior scales (areas A-B and E) with scales from areas C-F having a smooth punctated ganoine surface (Trinajstic 1999a).

Bilaterally symmetrical ridge scutes (Fig. 2, 10E, 11C), considerably larger than the adjacent body scales, are preserved on the dorsal surface, including leading edge of the body mass of the caudal fin and on the ventral surface between the caudal and anal fins. At least two fragmented scutes are preserved immediately behind the original position of the neurocranium, indicating a complete series was originally present from the occipit to the dorsal fin as in *Mimipiscis* and *Moythomasia*. Immediately behind the dorsal fin, the scutes are oval with a shallow anterior cleft. As the series progresses towards the tail, the individual scutes becoming increasingly elongate, culminating in slender basal fulcra on the tail base, each with a deep anterior cleft to accommodate the posterior apex of scute in front. Each element in the series is ornamented with anastomosing ridges with sharp posterior apices. The basal fulcra bear single rows of laterally-directed spines (Fig. 10E). Two pairs of asymmetrical ventral scutes (ventral fulcra) (Fig. 11D) occur anterior to the anal fin. The rear pair are semi-circular with a straight anterior margin; the forward pair are longer with a corresponding straight posterior margin.

PHYLOGENETIC ANALYSIS

To test the phylogenetic position of *Pickeringius*, an analysis was conducted by coding the new taxon into the matrix of Giles *et al.* 2015c that accompanied the description of *Raynerius*. Several codings were updated regarding *Entelognathus* (Characters 3, 5, 64, 117–124, 151, 152, 154-157) and *Onychodus* (Characters 152, 154). PAUP v4.0b10 was used to conduct an equally weighted parsimony analysis with *Entelognathus* as the outgroup. The analysis yielded 145 most parsimonious trees of 531 steps. (Consistency index = 0.3672; Homoplasy index = 0.6328; Retention index = 0.6699; Rescaled consistency index = 0.2460), a strict consensus of which is presented (Fig. 14). This tree was optimised in MacClade 4.08, illustrating unambiguous character changes, and is presented as Supplemental file 1. The recently described *Avonichthys manskii* (Wilson *et al*. 2018) was excluded due to its status as a wildcard taxon. As with the previous analysis, Bremer support for the different actinopterygian clades remains low. The analysis did however attain a higher level of resolution than the parent study, with the reduction of several actinopterygian polytomies within the ray-finned fishes.

Meemannia and *Dialipina* are again resolved as the deepest-diverging actinopterygians (Node A, Fig 14), a position supported by one unambiguous (c.135, lateral cranial canal present) and two homoplastic characters. *Tegeolepis* is positioned as the sister to all remaining actinopterygians (Node C, Fig 14), supported by one unambiguous (c.181, one dorsal fin) and five homoplastic characters. This position was recovered in the reweighted analysis of Giles *et al.* (2015c), although the placement of this enigmatic Famennian taxon has proven variable in previous analyses (Friedman and Blom 2006; Swartz 2009; Taverne 1997). Above this is a polytomy (Node D) comprising *Osorioichthys*, Cheirolepididae and the remainder of Actinopterygii, united by one unambiguous (c.159, fringing fulcra) and three homoplastic characters.

Howqualepididae (*Donnrosenia* and *Howqualepis*, Long *et al.* 2008), a group not recovered by Giles *et al.* (2015a) or Swartz (2009) but reaffirmed here (Node F, Fig 14; supported by three homoplastic characters), falls as sister to all remaining actinopterygians (Node E, Fig. 12; supported by a single unambiguous character c.12, posterior nostril in complete communication with orbital fenestra).

Mimiidae (*Gogosardina*, *Mimipiscis bartrami*, *Mimipiscis toombsi*) is also resolved as monophyletic (Node F, Fig. 14), albeit with the support of just two homoplastic characters. Mimiidae is united with remaining actinopterygians (Node H, Fig. 14) by four homoplastic characters, with the position of *Raynerius* branching a node above (Node I, Fig. 14) supported by one unambiguous (c.94, pituitary vein enlarged) and one homoplastic character.

Contra Giles *et al*. (2015c), *Moythomasia* is recovered as monophyletic; supported by two homoplastic characters. *Moythomasia* and all remaining actinopterygians (Node J, Fig. 14) are united by three homoplastic characters. *Pickeringius* is resolved a node above *Moythomasia* (Node K, Fig. 14), a position supported by two homoplastic characters.

All remaining actinopterygians (Node L, Fig. 14) are united by three unambiguous (c.104, fossa bridgei; c.129, optic lobes same width as cerebellum; c.134, crus commune ventral to roof of cranial cavity) and two homoplastic characters.

DISCUSSION

Phylogenetic relationships among early actinopterygians.

Phylogenetic studies of early actinopterygian relationships have traditionally failed to reach a consensus beyond a stem group position for *Cheirolepis* (Cloutier and Arratia 2004; Friedman and Blom 2006; Long *et al*. 2008; Schultze and Cumbaa 2001; Swartz 2009; Taverne 1997). Until recently, *Mimipiscis toombsi* and *Moythomasia durgaringa* represented the only Devonian actinopterygian taxa in which both the dermal and endochondral anatomy was thoroughly described (Choo 2015; Gardiner 1984; Giles *et al*. 2014), with the majority of contemporary forms being primarily known from flattened dermal remains. As a consequence, several earlier studies either omitted many fossil taxa (Gardiner and Masserie 2005) or alternatively omitted braincase characters (Friedman and Blom 2006). More recently, a combination of additional anatomical data for Devonian ray-finned fishes (e.g. *Cheirolepis*: Giles et al. 2015b; *Raynerius*: Giles et al. 2015a; *Pickeringius*: this study) and increased taxon sampling (Giles *et al*. 2015c, 2017) has begun to lay the groundwork for a more robust understanding of early actinopterygian relationships.

Our results support the monophyly of a number of Devonian clades, including Cheirolepididae, Howqualepididae, Mimiidae and *Moythomasia*, although we note that in all cases these clades are supported by homoplastic characters rather than apomorphies (Supplementary PDF). Indeed, few actinopterygian nodes in the analysis are supported by non-homoplastic characters, and only one (a clade comprising Northern Hemisphere Devonian taxa plus a clade of all post-Devonian actinopterygians) is supported by two or more non-homoplastic characters. This is despite recent intensive effort in redescribing both the dermal and endoskeletal anatomy of Devonian ray-finned fishes (Giles et al 2015c), and appears to reflect a paucity of neurocranial data (which are described for well under half of all known Devonian taxa).

A motif repeated from previous analyses is that of Devonian taxa forming a succession of short-lived clades, to be replaced by a radiation of Carboniferous taxa following the end-Devonian mass extinction (e.g. Gardiner et al. 2005, Coates et al. 1999, Giles et al. 2015b, Giles et al. 2017 etc), with the implication that a minimal number of lineages crossed the boundary. Recently, the description of *Avonichthys manskyi* from the Tournasian of Nova Scotia has led to suggestion of greater overlap between Devonian and Carboniferous actinopterygian faunas (Wilson et al. 2018). While *Avonichthys* was excluded from our analysis, we note that it lacks synapomorphies of *Moythomasia* (Choo et al. 2015) and is anatomically compatible with a position nested among other post-Devonian taxa. However, poor preservation of the only known specimen makes determining a more definite position for *Avonichthys* difficult.

Late Devonian actinopterygian diversity in Western Australian marine faunas.

The discovery of *Pickeringius* adds to the already diverse vertebrate fauna of the Gogo reef Lagerstätte, which comprises nearly 50 described vertebrate species, with a particularly high diversity of arthrodire placoderms and dipnoans (Long and Trinajstic 2010). Five actinopterygian species, *Mimipiscis toombsi, Mimipiscis. bartrami, Moythomasia durgaringa, Gogosardina coatesi,* (Gardiner 1984, Choo *et al.* 2009, Choo 2011) and *Pickeringius acanthophorus* are known. Of these species, *Mimipiscis toombsi, Moythomasia durgaringa* (Trinajstic 1999) and *Gogosardina coatesi* (Trinajstic *et al.* 2015) are also known from the contemporaneous Gneudna Formation, Carnarvon Basin, Western Australia. *Moythomasia durgaringa* is recorded from the younger Frasnian-Famennian Virgin Hills Formation, also in the Canning Basin (Trinajstic *et al.* 2015). At least two actinopterygian taxa present at Gogo appear to have persisted into Famennian aged strata in the Dalmeh area of central Iran, including *Moythomasia durgaringa* (Long and Hairapetian, 2000, fig 6 h,j,k) and scales which were considered indeterminate by Long and Hairapetian (2000, fig 6 l,m), but which are here recognised to belong to *Gogosardina* cf.*coatesi*., extending both the geographic and stratigraphic range of these taxa beyond the Frasnian of Australia.

Elsewhere in the world, local vertebrate faunas appear to display a lesser degree of actinopterygian diversity (notwithstanding records of isolated scales, which cannot be identified to a recognisable taxonomic level, e.g. Turner and Blieck, 2000). Marine or marginal-marine Middle-Late Devonian deposits, namely the Miguasha fauna of Quebec and the Denay Limestone of Nevada, each contain a single species of *Cheirolepis* (Arratia & Cloutier 1996, Arratia & Cloutier 2004). Famennian fossil-bearing localities from Belgium (*Osorioichthys marginis*: Taverne 1997) and Western Siberia (*Krasnoyarichthys jesseni*:

Prokofiev 2002) also contain single actinopterygian species. One species of *Moythomasia* is represented in the Snetnaya Group of Latvia, while two are present in the Oberer Plattenkalk, Bergisch Gladbach, Germany (Choo 2015). The Famennian Cleveland Member of Ohio has produced *Tegeolepis clarki* along with one or two species of *Kentuckia* (Carr and Jackson 2008).

However, it is unclear to what extent these records represent true diversity rather than a reflection of preservation bias or worker effort. The Gogo Formation has been the subject of intense study, with a greater focus on ray-finned fishes than is common. The exceptional preservation of the material, where the articulated three-dimensional anatomy can be studied in isolation from the host rock, lends itself to a painfully detailed description of the anatomy. It is therefore likely that these factors have permitted description of the fossil assemblage to a finer taxonomic level than is possible at other, contemporaneous localities.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/XXXXXXXXX

Data for this study are available in the Dryad Digital Repository: http://datadryad.org/review?doi=doi:10.5061/dryad.XXXX [please note that the data for this paper are not yet published and this temporary link should not be shared without the express permission of the author]

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