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Late Devonian antiarch remains (placoderm fish) from the Gilberton Formation, north Queensland

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ABSTRACT

New Devonian fish remains are described from the lower part of the Gilberton Formation of north Queensland, the first identifiable specimens found since the original specimen was described in 1936. They include the first determinable dermal skull bones from this deposit. Some dermal bones of the trunk armour are closely associated, and of similar size with morphology consistent with coming from the same fish, permitting a provisional reconstruction of the ventral wall of trunk armour. The new morphological evidence indicates a form close to the antiarch *Remigolepis*, and a likely age of late Famennian for the lower fossiliferous strata of the Gilberton Formation.

❑ *Devonian fish; placoderms; antiarchs; Remigolepis; Gilberton Formation; Famennian*

The Devonian-?Carboniferous Gilberton Formation was named by White (1959, 1965) for a fluviatile deposit composed of siltstones, sandstones and conglomerates in the Gilberton Basin of north Queensland (Fig. 1). It covers about 120 km^2 in three separate outcrops (Withnall *et al*. 1980). Some other similar sedimentary rocks that underlie Carboniferous volcanics to the north of the Gilberton type area have been provisionally assigned to the unit (Withnall & Hutton 2013).

The fossiliferous lower part of the formation comprises interbedded quartzose and feldspathic sandstone and siltstone, likely deposited in a proximal braided stream system (Withnall *et al*. 1980). Plant fossils are relatively common, dominated by the lepidodendroid *Leptophloeum australe*, as described by M. White in White (1965). Vertebrate fossils, however, are extremely rare. A single placoderm plate impression was described by Hills (1936) as the posterior median dorsal plate of an antiarch placoderm, and was the first Australian record of this group attributed to the Middle Devonian. This specimen came from the southern outcrop of the Gilberton Formation, south of the Gilbert River (Fig. 1). Withnall *et al.* (1980) reported a further collection of "several plates, scales, a fragment of a spine, and an otolith [sic]" from low in the Gilberton Formation. They did not specify localities, and cited Dr Alex Ritchie (pers. comm., 1976) that the specimens were unidentifiable. The whereabouts of these samples is unknown.

In this paper we describe the first identifiable fish remains from the Gilberton Formation to be found since the original specimen was collected in 1934, including the first bones from the head of the fish. All the fish specimens belong to antiarch placoderms, a major subgroup of the Placodermi (extinct 'armoured fishes'), the most diverse group of fossil fishes from the Devonian Period (Young 2008, 2010a).

The precise age of fossiliferous strata in the Gilberton Formation has been uncertain, as the plant taxa reported show varying ranges. Hills (1936) assigned a Middle Devonian age, but Withnall *et al.* (1980) considered that the balance of evidence supported a Late Devonian (Famennian) age for the lowermost levels, with the higher unfossiliferous strata possibly extending into the Early Carboniferous. However, Wyatt and Jell (1980) considered it more likely that the Gilberton Formation was entirely Late Devonian, because earliest Carboniferous sandstones elsewhere in North Queensland had different lithology, perhaps reflecting climate change across the Devonian-Carboniferous boundary. Our new fossil fish evidence also supports a Late Devonian age (see below).

STRATIGRAPHIC SETTING

No type section was defined for the Gilberton Formation, but two representative sections were described by Withnall *et al.* (1980; also in Wyatt & Jell 1980). The first reference section, in the southeastern part of the main outcrop area north of the Gilbert River (Fig. 1), comprises over 200 m of arkosic sandstones, with flaggy green and purple ferruginous siltstones in the lowermost 8 m producing plant remains including *Leptophloeum australe* (White 1965). The 200 m thickness was considered a local minimum for this area (Withnall *et al.* 1980), but the absence of marker beds makes total thickness for the main outcrop area difficult to estimate. However, Wyatt and Jell (1980) considered it unlikely to be much greater than 200 m.

The smaller outcrop south of the Gilberton River (Fig. 1), which produced the fossil fish described below, is the only outcrop that is not fault-bounded. A second representative section of about 150 m thickness was described by Withnall *et al.* (1980; also Wyatt & Jell 1980). The locality producing the fossil fish is close to the base of this reference section. The base of the Gilberton Formation, exposed at the eastern end of Commissioners Hill, rests unconformably on Proterozoic metavolcanics. The section extends from here to the highest preserved part of the Gilberton Formation about 1 km to the east-southeast. In the southern outcrop area, as in the main area to the north, the lowermost siltstone-bearing part of the Gilberton Formation is no more than about 10 m thick (Withnall *et al.* 1980). Most of this reference section comprises interbedded mid-brown, olive-green and purple lithic sandstones and subordinate siltstones (Withnall *et al.* 1980).

MATERIALS AND METHODS

The specimen (UQF13909) described by Hills (1936) was collected by de V. Gipps during survey work in 1934. The new specimens described here were collected in the same vicinity ('Fossil Gully', CJB19/04) by CJB, Bruce Burrow, John Armstrong and Ian Hutchings in May 2019. The plates are preserved as weathered bones and impressions in sandstone blocks collected as float in the gully. The bone is dark when fresh, and light in colour after weathering. The rock matrix is very hard siliceous sandstone or quartzite. Casts of the bone impressions were made with Pinkysil®, whitened with ammonium chloride, then photographed with a SZ40 Olympus dissecting microscope and DP12 imaging system. However, the best images were obtained by direct photography of the original impressions. Specimens are reposited in the Queensland Museum collection (QM F).

Abbreviations. Institutional abbreviations are as follows: UQF, University of Queensland Geology Department fossil collection [now part of the QM F collection]; QM, Queensland Museum.

We have used standard abbreviations for the dermal bones ('plates') of antiarch placoderms in the text and figures as follows: AMD, anterior median dorsal plate; AVL, anterior ventrolateral plate; MV, median ventral plate; Nu, nuchal plate; PDL, posterior dorsolateral plate; PL, posterior lateral plate; PMD, posterior median dorsal plate; PVL, posterior ventrolateral plate; SM, submarginal plate. Other abbreviations used in the figures are given in figure captions.

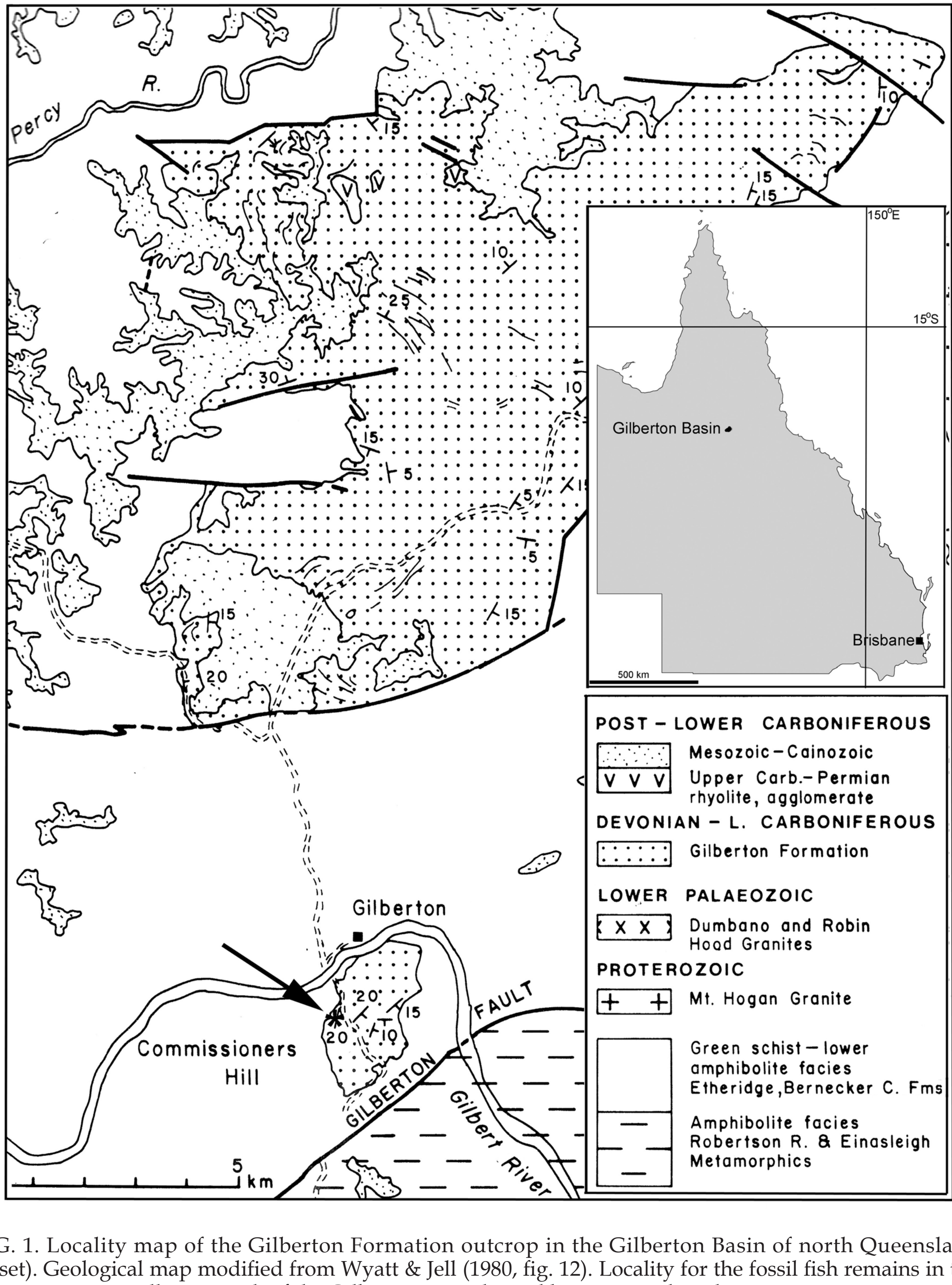

FIG. 1. Locality map of the Gilberton Formation outcrop in the Gilberton Basin of north Queensland (inset). Geological map modified from Wyatt & Jell (1980, fig. 12). Locality for the fossil fish remains in the Commissioners Hill area south of the Gilbert River indicated by an asterisk and arrow.

Proportions of antiarch dermal bones are normally expressed as breadth divided by length or vice-versa multiplied by 100 to give a 'breadth/length' or 'length/breadth' index. This is abbreviated to B/L or L/B index.

SYSTEMATIC PALAEONTOLOGY

Subclass PLACODERMI M'Coy, 1848

Order ANTIARCHI Cope, 1885

Family REMIGOLEPIDAE Stensiö, 1931

cf. *Remigolepis* sp. indet.

(Figs. 2, 3, 4, 5A, 6A-B)

1936 Antiarch: Hills, p. 163, fig. 3.
1958 *Asterolepis:* Hills, p. 89.
1960 antiarchan fish remains: Hill and Denmead, p. 154.
1961 antiarchan: White, p. 14.
1962 *Antiarchan:* White, p. 7.
1965 Antiarchan: White, p. 62, table 5.
1967 antiarchan fish: Hill, p. 615.
1967 *Asterolepis?*: Hill et al., p. d30, pl. DXV, fig. I.
1968 *Asterolepis*: Gilbert-Tomlinson, p. 207.
1973 Antiarchan fish remains: Smart, p. 7.
1978 *Asterolepis* sp.: Denison, p. 113.
1980 Antiarchan (Placoderm): Withnall et al., p. 79
1981 *Bothriolepis?* sp.: Young & Gorter, p. 90.
1982 *Bothriolepis*? sp.: Turner, p. 600.
1983 "antiarch plate … may belong to … *Bothriolepis*": Young, p. 71.
1990 antiarch: Young, p. 35.
1991 "probably a *Bothriolepis* plate": Long, p. 363.
2000 "dorsal plate of a placoderm": Turner, Basden & Burrow, p. 487.
2013 "fish fragments": Withnall & Hutton, p. 103.

Material. One posterior median dorsal plate (UQF13909); one nuchal plate (QM F 60156a,b); one submarginal plate (QM F 60150); two anterior ventrolateral plates (QM F 60151, 60152a,b); two posterior ventrolateral plates QM F 60153, 60154); one indeterminate impression, possibly an incomplete posterior ventrolateral plate (QM F 60155).

Remarks. In the dermal skull roof of *Bothriolepis* and related antiarchs (family Bothriolepidae), the nuchal plate reaches to the orbito-nasal fenestra on either side of a small post-pineal bone. However, the new nuchal plate from the Gilberton Formation lacks orbital facets, demonstrating that it was separated from the orbito-nasal fenestra by a large post-pineal bone (unknown). This is a primitive character seen in asterolepid antiarchs and various other antiarch sub-groups. Of four described antiarchs from the Upper Devonian of Australia, *Grenfellaspis* Ritchie *et al*. (1992) has a different skull shape and ornament with an elongate nuchal (family Sinolepidae). Three other non-bothriolepid antiarchs, two grouped in the family Pambulaspidae, have been named from the Australian Upper Devonian. *Pambulaspis* Young (1983) differs in the broad obtected nuchal area across the skull margin and the configuration of the sensory grooves. *Merimbulaspis* Young (2010b) has a distinctive ornament of anastomosing tuberculate ridges, which is completely different to the ornament in this new material. Two species of the genus *Remigolepis* Stensiö 1931 (family Remigolepidae) have been described from Australia: *R. redcliffensis* Johanson (1997a) and *R. walkeri* Johanson (1997b). Only in *Remigolepis* do we see similar characters for the nuchal plate as described below. In addition, the associated anterior ventrolateral plate from the trunk armour has a large anterior embayment indicating paired rectilinear semilunar plates, as also occur in *Remigolepis*. In *Asterolepis* this bone is paired, but quite different in shape. In bothriolepids the semilunar plate is unpaired.

We have assigned the small number of antiarch placoderm bones described below to cf. *Remigolepis* sp. indet., because there are numerous undescribed 'remigolepid'-like bones documented from many localities in the Upper Devonian of Australia (e.g. Young *et al*. 2010), with a distinct likelihood that new genera will be described in the future.

Age. Late Devonian (Famennian), Gilberton Formation.

Description. Dermal bones of the head.

Nuchal (Nu). An almost complete Nu plate, QM F 60156a,b (Fig. 2), is the first antiarch skull bone recorded from the Gilberton Formation. It is preserved in part and counterpart split within the dark bone, the part of the specimen with most of the bone still intact (Fig. 2A), and the counterpart (Fig. 2B) effectively an external impression with a film of black bone. On the left side, the middle pit line sensory groove (mp) runs from a notch on the lateral margin, and the endolymphatic duct openings are visible centrally (d.end), these structures best shown on the counterpart. Plate margins are complete except for the right side, where the posterolateral corner was sliced off by the rock saw. This shows an oblique section through the right side (Fig. 2C), revealing the transverse nuchal crest that delineated the inside of the posterior skull margin in antiarchs. This seems unusually deep (~4.5 mm), but the crest is normally deepest at the lateral edges of the Nu, where this bone sutures with the paranuchal plate, and is less prominent mesially (e.g. Stensiö 1931, fig. 15; Downs *et al*. 2019, fig. 3C).

The part of the specimen shows that the plate is strongly arched anteroposteriorly. The bone exposed on the surface cut by the rock saw is well preserved, showing the cancellous inner and compact outer layers (Fig. 2C). The cut has not sliced through any tubercles, but low widely spaced coarse tubercles, c. 1 mm diameter, are visible on the external impression. The cut section shows the middle pit sensory groove is

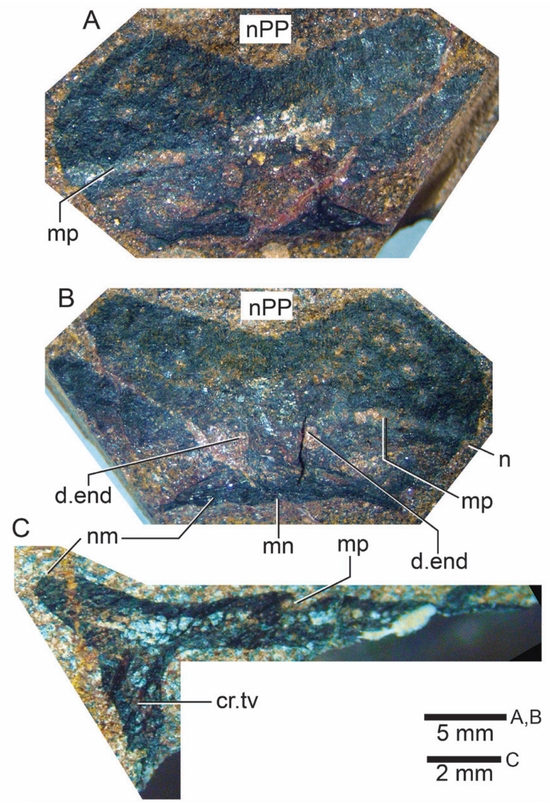

FIG. 2. cf. *Remigolepis* sp. indet., nuchal plate from the dermal skull roof (QM F 60156 a,b). **A**, dorsal view of the part; **B**, counterpart (rock impression with thin cover of bone); **C**, sawn section through the right posterolateral corner. Abbreviations: **cr.tv**, transverse nuchal crest; **d.end**, paired openings for endolymphatic ducts; **mn**, median notch; **mp**, middle pitline groove; **n**, notch; **nm**, obtected nuchal area; **nPP**, post-pineal notch.

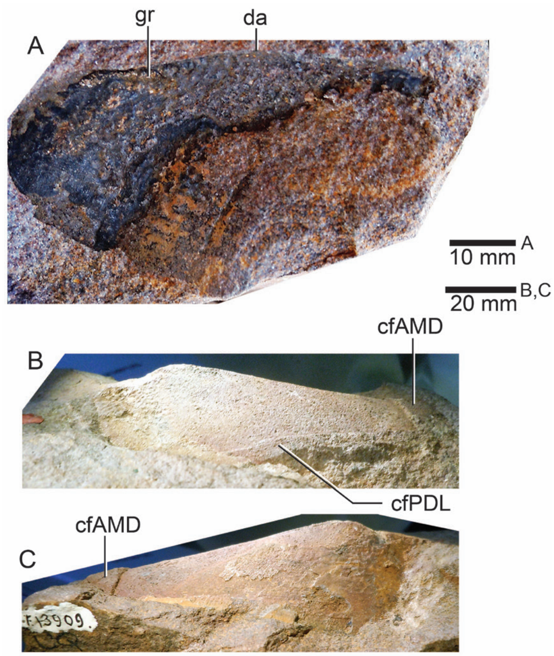

FIG. 3. cf. *Remigolepis* sp. indet. **A**, left submarginal plate from the head (QM F 60150); **B-C**, UQF13909, a posterior median dorsal plate from the trunk armour first described by Hills (1936) in right (**B**) and left (**C**) lateral views. Abbreviations: **cfAMD**, contact face for overlap of the anterior median dorsal plate; **cfPDL**, contact face for overlap of the posterior dorsolateral plate; **da**, dorsal angle; **gr**, groove.

undercut posteriorly, as is normal in *Asterolepis* and *Remigolepis* (but not in *Pambulaspis*; Young 1983). The obtected nuchal area (nm) is slightly inflected upwards to the posterior margin of the bone. The posterior face of the Nu is slightly concave, and about 6 mm deep to the ventral edge of the transverse nuchal crest. Externally the obtected nuchal area forms a narrow depressed strip along the posterior margin (nm, Fig. 2B). There seems to be a posterior indentation or notch at the midline, rather than a posterior process as in some other forms. All angles of the perimeter of the margin are slightly rounded. The endolymphatic duct openings are c. 4 mm apart. Maximum length is ~13 mm and maximum width estimated at 27 mm, giving a breadth/length (B/L) index of ~208. Midline length is c. 9 mm, and the posterior margin is c. 18 mm across.

As restored (Fig. 6A) the plate is short and broad with a shallow post-pineal notch. The B/L is within the range for most other antiarch species, as summarised by Young (1987, table 2). The broadest Nu listed was for *Asterolepis scabra* (B/L index 210), and in *Asterolepis alticristata* (Downs *et al.* 2019) it varies below and above twice as wide as long, but never exceeds a B/L of 210. Comparing various *Remigolepis* species, *R. kochi* is the broadest of the three named Greenland species (Stensiö 1931), but these are known by very few examples, so intraspecific variation is unclear. Similarly, the Australian species *R. redcliffensis* (Famennian from near Grenfell, NSW) is known by a single Nu plate (Johanson 1997a, fig. 9F-G). This is even broader (B/L index ~219), with a shallower postpineal notch than described here. However, this material is tectonically distorted so the bone could have been stretched laterally. Apart from slightly broader proportions, this specimen resembles QM F 60156 in that the middle pitline does not extend to the midline. Finer posterior pitlines are associated with the endolymphatic openings, but given the nature of preservation for QM F 60156 these would not be seen. The pitline configuration around the endolymphatic openings is again quite variable in other species (e.g. for *Asterolepis* see Stensiö 1931, fig. 13; 1948, fig. 64; Downs *et al*. 2019, figs. 3, 7).

Remigolepis walkeri Johanson (1997b) from the Frasnian at Canowindra NSW, is represented by many more specimens. As for *R. redcliffensis*, the middle pitline does not reach the midline, in contrast to some other species (*R. kochi* and *R. cristata* from Greenland, *R. zhongweiensis* and *R. microcephala* from China; Stensiö 1931, Pan *et al*. 1987). Nu proportions for *R. walkeri* are variable (B/L index 168, 188, 191 for three figured examples with the Nu well exposed). Another example is much more elongate (B/L index ~125; Johanson 1997b, fig. 6c), but again tectonic distortion (see Ritchie 2006) may have affected this. An isolated Nu plate from the Upper Devonian Hervey Group of NSW (Hills 1932, pl. 57, fig. 6) was first referred by Hills to 'Antiarchi indet.', but is clearly a *Remigolepis* as indicated by the associated trunk armour bones he described. This Nu plate also resembles QM F 60156 in being relatively broad (but the lateral corners are probably incomplete). It differs in that the post-pineal notch is deeper, and the middle pitlines extend close to the midline, where they are inflected posteriorly. However, the posterior margin seems relatively narrow, in that feature resembling the Gilberton nuchal.

The posterior margin being markedly narrower than across the lateral corners, and the stepped lateral margin at the level of the middle pitline, are distinctive features of QM F 60156, possibly indicating a new species.

Submarginal (SM). The second bone from the head (QM F 60150; Fig. 3A) is evidently a left SM plate ('extralateral plate' of earlier authors). This bone formed the operculum in antiarchs (Young 1984; Young & Zhang 1992), and other placoderms (Young 2010a). It is preserved mainly as an external impression, with faint ornament visible anterodorsally and a sheet of thin bone elsewhere. It has an ovoid shape, and is c. 41 mm long and 21 mm maximum height at about halfway along its length, where there is a slight angle (da) on the straightest edge. We interpret the straightest edge as dorsal, and the curved opposite margin as ventral, by comparison with other forms (e.g. *Remigolepis*;

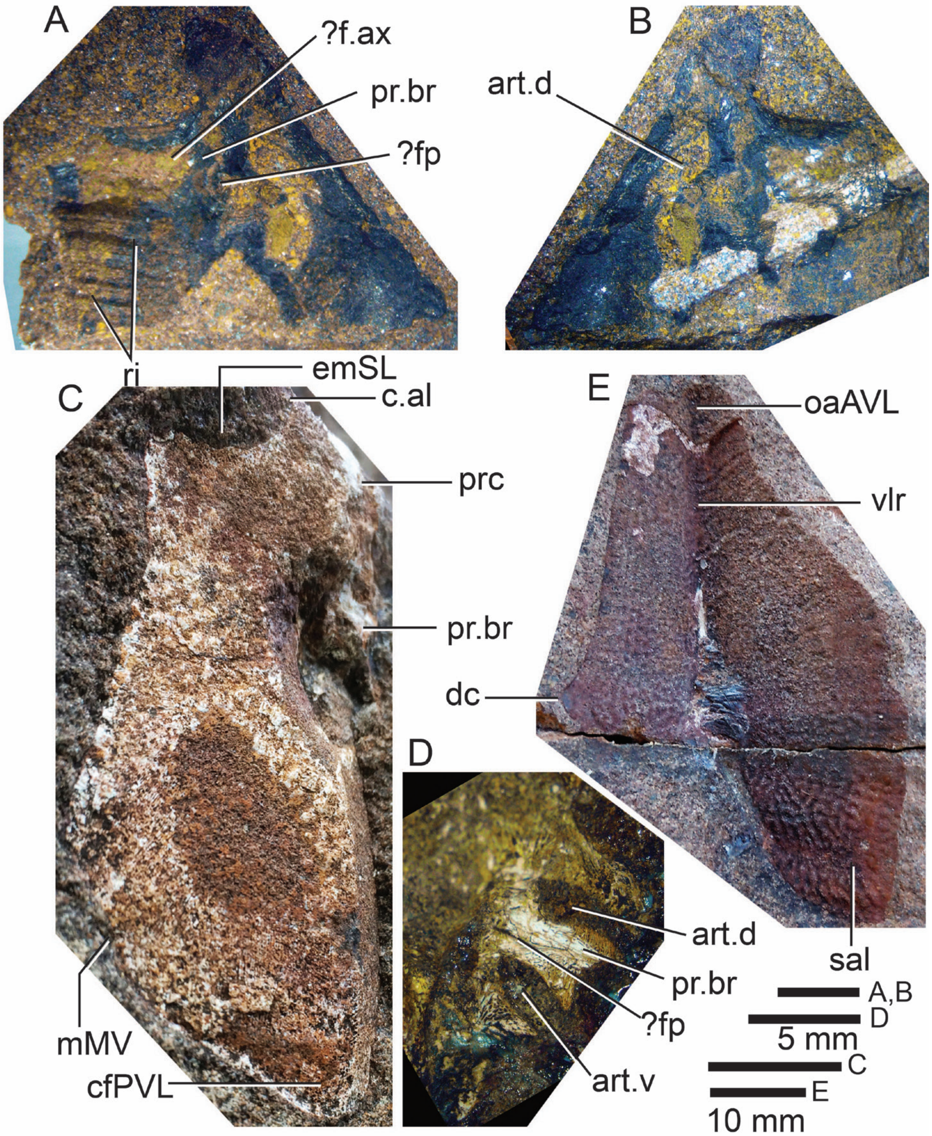

FIG. 4. cf. *Remigolepis* sp. indet. **A-B**, incomplete anterior part of an anterior ventrolateral plate in part and counterpart (QM F 60151). **C**, ventral view of a nearly complete left anterior ventrolateral plate (QM F 60152). **D**, enlarged ventrolateral view of the articular area for the pectoral appendage in QM F 60152. **E**, external impression of a left posterior ventrolateral plate (QM F 60153). Abbreviations: **art.d, art.v**, dorsal and ventral articular depressions to receive the proximal end of the pectoral appendage; **c.al**, anterolateral corner of AVL plate; **cfPVL**, contact face for overlap of the posterior ventrolateral plate; **dc**, dorsal corner of PVL lateral lamina; **emSL**, embayment that contained the semilunar plate; **f.ax**, axillary foramen of pectoral fin articulation; **fp**, funnel pit of brachial process; **mMV**, margin in contact with median ventral plate; **oaAVL**, overlap area for anterior ventrolateral plate; **pr.br**, brachial process for pectoral fin articulation; **prc**, prepectoral corner of AVL plate; **ri**, ridges; **sal**, subanal lamina of PVL plate; **vlr**, ventrolateral ridge of trunk armour.

Stensiö 1948, fig. 16). The slight angle presumably represents the articulation with the skull, as in the SM plates of *Asterolepis* (e.g. Karatajūtė-Talimaa 1963, fig. 32) and *Remigolepis* (Stensiö 1948, fig. 16). There is no evidence for a deep dorsal (spiracular) notch that occurs just in front of the articulation in *Pterichthyodes* and *Sherbonaspis* (Hemmings 1978; Young & Gorter 1981). Some *Asterolepis* spp. have the notch between a double articulation, and the notch may be much smaller or obscure in other forms (e.g. *Remigolepis*; Stensiö 1948, fig. 16; *Merimbulaspis*; Young, 2010b, fig. 4C, D).

The Gilberton SM is dorsoventrally convex. A thin low ridge delineating a shallow groove runs inside and parallel to the dorsal margin. An external ridge is developed behind the shallow dorsal notch in *Merimbulaspis*, and *Remigolepis walkeri* shows a stronger external ridge (e.g. Johanson, 1997b, fig. 3F). Internal ridges and grooves occur inside the dorsal margin of the SM in both *Asterolepis* and *Remigolepis*.

The anteroventral margin is not quite complete, but QM F 60150 is estimated at about twice as long as high. In other taxa, proportions of the SM vary; *Remigolepis walkeri* (Johanson, 1997b) has similar proportions to our new specimen. In the Greenland *Remigolepis* figured by Stensiö (1948, fig. 16) the SM has a more pointed anterior end, and a L/B index of about 210.

Dermal bones of the trunk armour.

Posterior median dorsal (PMD). The original specimen (UQF13909) is a PMD plate, preserved mainly as an internal impression. It was described by Hills (1936, p. 163) as follows: "The plate is 8 cm. long and approximately 5.6 cm. wide at the widest part, where it is probably incomplete. Anteriorly and laterally, the areas of overlap on to the anterior median dorsal and posterior dorso-laterals are clearly shown, the posterior edge being free."

Hills noted the absence of diagnostic characters (still the case), but accepting the geological age provided to him by F.W. Waterhouse, called this the first record of an antiarch from the Middle Devonian of Australia. Later, Hills (1958, p. 89) ascribed the generic name *Asterolepis* to the specimen, presumably by comparison with European sequences, and this entered the international literature (e.g. Denison 1978, p. 113). Hills noted however that the Gilberton example was younger than the marine Middle Devonian fishes of eastern Australia (now known to be Early Devonian), and could even be Upper Devonian (*Asterolepis* in Europe has a stratigraphic range of Middle-Upper Devonian).

As restored by Hills (1936, fig. 3) this plate is relatively elongate, with a B/L index of 82, comparable to the PMD plates in restorations of *Remigolepis* (82 for Greenland; Stensiö 1931 fig. 80; 88 for *R. walkeri*; Johanson 1997b, fig. 20a). Similar variation (76-100) occurs in *Asterolepis* (e.g. Karatajūtė-Talimaa 1963, p. 163). There is little to add to Hills' description, the PMD plate being generally similar in different antiarch taxa. For the first time here we illustrate lateral views of the specimen, to show the convex inner surface (Fig. 3B-C).

The new examples of trunk armour bones described below all come from the ventral wall of the trunk armour, and represent at least two individual fish. There are two anterior and two posterior ventrolateral plates, all from the left side.

Anterior ventrolateral (AVL). QM F 60151a,b, is a very incomplete anterior portion of the lateral lamina of an AVL from the left side. It is preserved in part and counterpart broken through the articular region for the pectoral fin (Fig. 4A-B). The bone has a steeply inclined anterior margin, presumably the anterior edge of the lateral lamina of the AVL. If not fractured, then this appears more steeply inclined than in *Bothriolepis macphersoni* (Young 1988, fig. 56), or *Remigolepis* AVLs from Greenland (e.g. Stensiö 1931, pl. 24, figs 2,4). Part of the ventral surface and the brachial process are visible; the distal end of the latter is possibly preserved inside the rock. A rounded space may represent the funnel pit (fp) inside the brachial process. According to Johanson (1997a) the funnel pit is much larger in *Remigolepis redcliffensis* than in the Greenland *Remigolepis*, but the latter are preserved as eroded AVLs, so this difference is not clearly demonstrated.

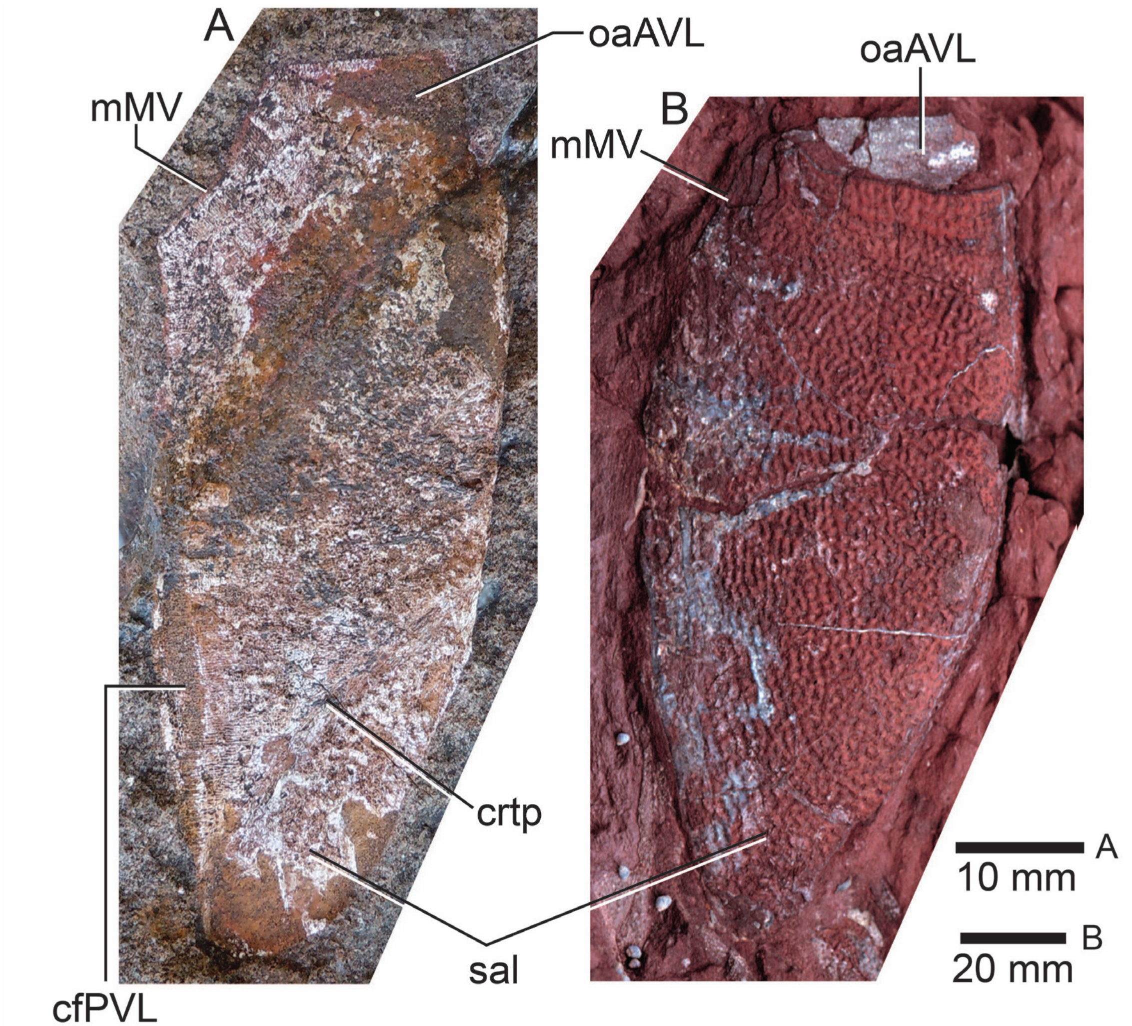

FIG. 5. Remigolepid left posterior ventrolateral plates in ventral view. **A**, cf. *Remigolepis* sp. indet. (QM F 60154) from the Gilberton Formation, showing the impression of the internal surface in ventral view. **B**, *Remigolepis* sp. nov. from the Worange Point Formation at Boyds Tower south of Eden, NSW far south coast (uncollected specimen in outcrop, showing the ornamented external surface in ventral view). Abbreviations: **cfPVL**, contact face for overlap with opposite posterior ventrolateral plate; **crtp**, posterior internal transverse crest of trunk armour; **mMV**, margin in contact with median ventral plate; **oaAVL**, overlap area for anterior ventrolateral plate; **sal**, subanal lamina of PVL plate.

In QM F 60151 the brachial process (pr.br) shows striations indicating the inner bone tissue is exposed. The axillary foramen is of distinctive size and shape for different genera, but it is unclear on this specimen. An area of rock matrix surrounded by bone (?f.ax) is an opening in about the correct position (cf. Young 2008, fig. 2A), so it may include this structure. Beneath is a series of distinct longitudinal ridges, which can be compared with strong ridging of the ornament in the same position on an AVL plate of *Remigolepis redcliffensis* illustrated by Johanson (1997a, fig. 11G). The axillary foramen in that species is very small.

QM F 60152 (Fig. 4C) is the most complete AVL. It is partly an internal impression, maximum length 55 mm, with most covered by a poorly preserved sheet of bone. Most of the ventral lamina is preserved, except for the anterolateral corner of the subcephalic division, which has broken off at the edge of the block. Thus, the prepectoral (prc) and anterolateral (c.al) corners of the AVL are incomplete. The lateral lamina, mainly an impression, includes a broken brachial process for the pectoral fin articulation (pr.br). The posterior overlap with the PVL is preserved as a very faint contact face on the inner surface, visible because most of the bone has weathered away (cfPVL). The plate margin that contacted the MV is 13 mm long, although the anterior corner is unclear. The margin that was overlapped with the opposite AVL is much longer (c. 30 mm) than the MV margin. In contrast, in *Sherbonaspis hillsi* this margin is relatively shorter (Young & Gorter 1981, fig. 18). The margin for the semilunar plate forms a deep embayment (emSL; not quite complete because the anterolateral corner is missing).

Unusual for an AVL is that the ventral lamina is broadest (22 mm) at the level of the anterior point of the MV, and narrows anteriorly, being only c. 10 mm wide at the level of the pectoral fin joint. Stensiö (1948, p. 134) distinguished the AVL of *Bothriolepis* from *Pterichthyodes*, *Asterolepis* and *Remigolepis* by the ventral lamina being broadest at the level of the prepectoral corner (prc), whereas in the other three genera it is broadest more posteriorly, as in QM F 60152. Even so, for *Pterichthyodes* (Hemmings 1978, pl. 2), and *Sherbonaspis* (Young & Gorter 1981, fig. 18A,C) the ventral lamina of the AVL tends to be of similar width for the whole length. This is also the case for *Remigolepis* from the type locality in East Greenland, and also Canowindra, New South Wales (Stensiö 1931; Johanson 1997b, figs. 19, 20c). The holotype specimen of *R. redcliffensis* (Johanson 1997a, fig. 11A) is broadest at a similar level to QM F 60152, but that material is tectonically distorted, and other proportions of that bone are quite different to the specimen described here. However AVL plates with similar shape are seen in various species of *Asterolepis*, where the lateral edge of the trunk armour is more obtuse and the AVL is more obliquely oriented. Examples are *Asterolepis scabra* (Nilsson 1941, fig. 7) and *A. ornata* (Gross 1931, fig. 19; Karatajūtė-Talimaa 1963, fig. 36). Even in some *Remigolepis* species with an obtuse armour, the AVL has been restored as largely parallel-sided (e.g. *R. zhongningensis*; Pan *et al*. 1987, fig. 30).

Generally in antiarchs the right AVL overlaps the left, so there should be an overlap area on the external surface, but there is no indication of this on this specimen. The overlapped part is much thinner than the main bone, so possibly this has broken off, partly explaining the narrow ventral lamina at this level.

The AVL plate in antiarchs projects forward under the head (the 'subcephalic division' of *E. Stensiö*), forming the floor of the branchial chamber. Towards the front of the AVL, the inner surface always has a distinct ridge or crest (the 'postbranchial lamina') that delineated the posterior wall of the branchial chamber. The numerous examples of *Remigolepis walkeri* from Canowindra NSW (at least 1780 articulated specimens; Ritchie 2006) are mainly preserved as external impressions, so this internal structure is visible in only a few examples (mislabelled as the internal anterior transverse crista by Johanson 1997b, fig. 13a). Better preserved *Remigolepis* (e.g. the holotype of *R. armata*; Lukševics 1991, pl. 1, fig. 8a) show the postbranchial lamina as a strong vertical crest crossing diagonally to the internal corner on the AVL plate within the semilunar notch (also Moloshnikov 2008, pl. 3, fig. 14). Similar

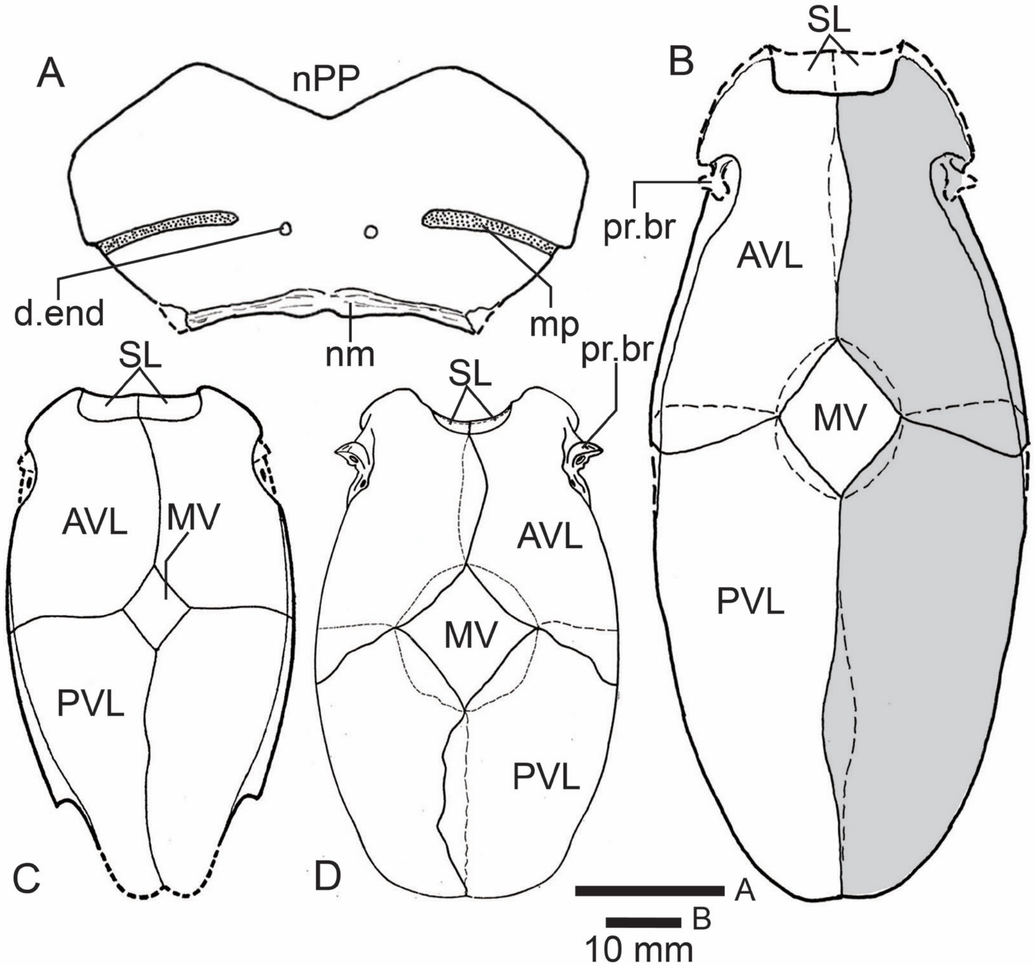

FIG. 6. **A**, cf. *Remigolepis* sp. indet., reconstruction of the nuchal plate from the dermal skull roof (based on QM F 60156 shown in Fig. 2); **B**, cf. *Remigolepis* sp. indet., provisional restoration of the ventral wall of the trunk armour (preserved areas shaded), based on QM F 60152 (Fig. 4C), and QM F 60154 (Fig. 5A). **C**, *Remigolepis* sp., ventral trunk armour restoration (modified from Denison 1978, after Stensiö 1969); **D**, *Asterolepis ornata*, ventral trunk armour restoration (modified from Karatajūtė-Talimaa 1963, fig. 36) (C, D not to scale). Abbreviations: **AVL**, anterior ventrolateral plate; **d.end**, paired openings for endolymphatic ducts; **mp**, middle pitline groove; **MV**, median ventral plate; **nm**, obtected nuchal area; **nPP**, post-pineal notch; **pr.br**, brachial process of pectoral fin articulation; **PVL**, posterior ventrolateral plate; **SL**, semilunar plate.

preservation is seen in undescribed *Remigolepis* from the Famennian of the NSW south coast near Eden. However, there is no sign of this structure in QM F 60152 as preserved. This region is covered with weathered bone, so the inner surface is not exposed, and we assume therefore that the postbranchial lamina is preserved inside the rock.

QM F 60152 retains a partly eroded brachial process which carried the pectoral fin articulation (pr.br, Fig. 4C). A more lateral view (Fig. 4D) shows better detail of the articular area. The eroded brachial process shows a central line, possibly a crack, but more likely the very edge of the funnel pit (fp), and a conical cavity within the brachial process interpreted to have contained the cartilaginous remnant of the scapulocoracoid that articulated with the internal pectoral fin skeleton (Young & Zhang 1992; Young 2008). Deep articular depressions around the brachial process received the rounded proximal end of the dermal pectoral appendage, and as exposed in this section (art.d, art.v) may be compared with similar preservation in an eroded AVL plate from Greenland (Stensiö 1931, pl. 24, fig. 2).

Posterior ventrolateral (PVL). On the same bedding plane and block as QM F 60152 are two PVL plates of different shapes. QM F 60153, which is 160 mm distant from the AVL, is preserved as an external impression, and is also from the left side (Fig. 4E). The lateral lamina is quite complete, highest posteriorly (c. 16 mm) at its dorsal corner (dc), and reducing to c. 7 mm high at the level of the overlap area for the AVL (oa.AVL). The lateral lamina length (excluding the overlap area) is c. 36 mm, but the posterior margin is obscured by a crack through the rock. The ventral lamina is at least 52 mm long (excluding the anterior overlap), with the subanal component c. 20 mm long. Its maximum breadth (c. 20 mm) is at the level of the posterior margin of the lateral lamina. The preserved mesial edge seems complete because the ornament alignment of tubercle rows parallels the edge. More anteriorly the edge is broken off, so there is no evidence of the length of the margin with the MV.

This plate closely resembles PVLs of *Bothriolepis* (e.g. Stensio 1948, figs 170-74; Young 1987, fig. 2C; Young 1988, figs 31A, 43G, 60), but given the associated remains it is assumed to belong to cf. *Remigolepis*. In *Remigolepis* the lateral lamina has a similar configuration to *Bothriolepis*, even though dorsally it is in contact with a different element, the PL plate. *R. kullingi*? from Greenland has similar lateral lamina proportions: ~15 mm high at the dorsal corner, reducing to 7 mm anteriorly (Stensiö 1931, pl. 13, fig. 4). Several other examples from Greenland are similarly developed (Stensiö 1931, fig. 90A; pl. 21, fig. 1; pl. 22, fig. 4). Stensiö (1931, pp. 177-78) noted that in the Greenland *Remigolepis* the PL plate partly overlaps the dorsal edge of the PVL, but that was not the case in QM F 60153, as the ornament goes right to the edge of the impression.

The second PVL impression (QM F 60154) is also from the left side, so represents a different fish to QM F 60153. However, it could have come from the same individual as the most complete AVL just described, being only 75 mm away on the same block. Both examples are similarly preserved with a thin white film of remnants of bone. QM F 60154 has some impressions of ornament but mainly shows the impression of the inner surface of the ventral lamina (Fig. 5A). The lateral lamina is not visible, if preserved being completely buried in the exceptionally hard matrix. Figure 5B compares a similarly preserved PVL of an undescribed *Remigolepis* species from the Famennian Worange Point Formation near Eden on the New South Wales south coast.

In the Gilberton PVL the ventral lamina appears almost complete, with total length of c. 72 mm. An overlap for the AVL is faintly visible (oaAVL). Its ornamented edge is of similar length to the corresponding edge of the nearby AVL (Fig. 4C), i.e. c. 13 mm, consistent with the two bones coming from the same fish. The length of the MV margin (c. 25 mm) is relatively short. In *Remigolepis redcliffensis*, Johanson (1997a) suggested that the MV was somewhat larger than in other *Remigolepis* species. At the level of the posterior corner of the MV, the ventral lamina of the PVL is c. 28 mm wide, and behind this breadth decreases gradually to the posterior margin of the subanal lamina (sal). The posterior half of the mesial margin shows faint overlap, about 5 mm wide, with the opposite PVL along a length of c. 20 mm. Generally in antiarchs the left PVL overlaps the right, so this would be an internal contact face (cfPVL). Maximum width of the contact face is at the level of the anterior end of the subanal lamina. A faint lineation within the texture of the weathered bone is suggestive of the posterior internal crista (crtp), which has a very oblique orientation. This internal crista crosses the subanal part of the ventral lamina, exactly as in *Bothriolepis* (e.g. Stensiö 1948, fig. 172C). The subanal lamina measures about 40 mm along its lateral edge.

On the assumption that this PVL is from the same individual as QM F 60152, a tentative reconstruction of the ventral wall of the trunk shield (Fig. 6B) can be compared with *Remigolepis* from the Famennian of Greenland (Fig. 6C) and *Asterolepis* from the Frasnian of Europe (Fig. 6D). For the Gilberton material, the proportional length of the AVL compared to the PVL (measured from the lateral corner of the MV plate) is about 78%. This is similar to some other restorations for *Remigolepis*, for example 78 from East Greenland (Stensiö 1931, fig. 87), and 77 for *R. walkeri* from Canowindra NSW (Johanson 1997b, fig. 20c). In other restorations the PVL is proportionately less elongate (90, 97 for two examples from East Greenland figured by Johanson 1997b, fig. 19), or 103 (the AVL slightly longer than the PVL) in *Remigolepis zhongningensis* from China (Pan *et al*. 1987, fig. 30). Similar variation is seen in the genus *Asterolepis*. For articulated examples from the Lode Quarry in Latvia, *Asterolepis ornata* varies between 81 and 87 (Lyarskaya 1981, pls. 21-23), and in *Asterolepis radiata* between 96 and 101 (Lyarskaya 1981, pls. 31-32).

In general, the restoration (Fig. 6B) based on the new Gilberton AVL and PVL plates has a larger MV, and is more narrow across the AVLs at the level of the pectoral fin articulation than in *Remigolepis* from East Greenland (Stensiö 1931, fig. 87), or *R. walkeri* from Canowindra (Johanson 1997b, fig. 20c). However more examples would be needed to clarify if these are valid species differences. Possibly, the relatively larger MV plate in *Remigolepis redcliffensis* (Johanson 1997a) distinguishes it from the Gilberton taxon, but *R. redcliffensis* resembles the new material in the similar Nu, and ridged area on the AVL plate. The deep rectangular anterior indentation indicates paired semilunar plates of similar shape (SL, Fig. 6B), as seems typical for various *Remigolepis* species. In contrast, these bones are smaller and of more ‘semilunar’ shape in various *Asterolepis* species (e.g. Gross 1931; Karatajūtė-Talimaa 1963; Lyarskaya 1981). Even though *Asterolepis* typically also has a large anterior embayment in the ventral trunk armour (Fig. 6D), of more rounded shape than in *Remigolepis*, the semilunar plates occupy only the posterior part.

The last specimen from Gilberton listed above (QM F 60156) is very incomplete, but is possibly another PVL. It shows an external impression including a 55 mm long external dorsolateral or ventrolateral ridge, with an overlap area which must be at the front of the plate. There is no sign of sensory grooves, so the plate cannot be a mixilateral or dorsolateral plate, and thus may be a PVL.

DISCUSSION

Antiarch classification and biostratigraphy

Asterolepis and *Bothriolepis*, two antiarchs with distinctive skull shapes from the ‘Old Red Sandstone’ facies of Europe, were erected by Eichwald (1840), and subsequently became the genotypes of two higher groupings – families Asterolepidae and Bothriolepidae (sometimes elevated to suborders). They also had different stratigraphic ranges: *Bothriolepis* was first described from the Famennian of Russia, and *Asterolepis* from the Frasnian of the Baltic (Eichwald 1840). *Asterolepis* was later discovered in many Middle Devonian localities (for a recent summary of the history of this genus see Newman *et al*. 2019). The replacement and stratigraphic overlap of *Asterolepis* by *Bothriolepis*, near or just above the Middle-Late Devonian boundary, became recognized as an important biostratigraphic horizon in the fish-bearing non-marine Devonian strata of western Europe (Young 1974). Stensiö (1931) described the new genus *Remigolepis* (placed in its own family) from the ‘*Remigolepis* Series’ of East Greenland, a fossil assemblage made famous (Säve-Söderbergh, 1932; Jarvik, 1952, 1996) by the discovery of *Ichthyostega* and *Acanthostega*, the first Devonian tetrapods (land animals) from the fossil record. *Remigolepis* was unique, among antiarchs then known, in lacking a distal (elbow) joint in the pectoral appendage. Although *Remigolepis* closely resembles *Asterolepis* in the details of skull morphology (e.g. Stensiö 1931; Karatajūtė-Talimaa 1963; Lukševics 2001), the trunk armour differs in having separate

PDL and PL plates (fused into a single mixilateral plate in *Asterolepis* and *Bothriolepis*), and in the configuration of overlap areas on the AMD.

Various later authors (e.g. Denison 1978) rejected a separate family Remigolepidae on two arguments, morphological and stratigraphic: i) absence of the elbow joint was seen in aberrant *Asterolepis*, and ii) the age of the '*Remigolepis* Series' in East Greenland was late Famennian, so the absence of the distal pectoral fin joint was unlikely to have the significance accorded it by Stensiö (1931).

One year after that publication, Hills (1932), based on Stensiö's advice and relying on his unpublished manuscript, recorded the first *Remigolepis* from Australia (Hervey Range in central New South Wales). The Hervey Range material has never been properly collected and described, and there are numerous other undescribed occurrences of '*Remigolepis*' across Australia (e.g. Young 1993; Young *et al*. 2010). It was first assumed that *Remigolepis* in Australia indicated latest Devonian (Famennian), based on its northern hemisphere stratigraphic range, but this caused difficulties with local stratigraphy. Hills (1958) suggested that the placoderm genera *Bothriolepis*, *Phyllolepis* and *Remigolepis* did not have the temporal significance in Australia that they had in Europe. He suggested a 'dispersal centre in Asia', from which older *Bothriolepis* had been recorded. Later, the yunnanolepid antiarchs from China demonstrated an unjointed pectoral appendage in Late Silurian-Early Devonian assemblages, destroying argument (ii) mentioned above for placing *Remigolepis* within the family Asterolepidae. Nevertheless, Pan *et al*. (1987) documented new species of *Remigolepis* from the Upper Devonian of China (Ningxia Province), to which they assigned a Famennian age, again based on East Greenland occurrences. However, an associated spore assemblage may indicate an older age (even late Middle Devonian; see discussion in Ritchie *et al*. 1992, p. 364). For a recent summary comparing Chinese and Australian Devonian antiarch occurrences see Young and Lu (2020).

The most completely described *Remigolepis* preservation (from Australia, and the world), although only casts in sandstone, is *Remigolepis walkeri* Johanson (1997b) from Canowindra in central New South Wales. Canowindra was also first considered of Famennian age, but detailed mapping, and fossil fish and invertebrate collecting from many new sites, showed that it was older, of similar age to the late Frasnian marine transgression documented in Devonian sequences from both eastern and western Australia (Young 1999, 2006, 2007; Young *et al*. 2000). However, other *Remigolepis* occurrences, for example associated with the giant lobe-fin *Edenopteron* on the NSW south coast, are of late Famennian age as in East Greenland (e.g. Young 2007; Young *et al*. 2013, 2019). Subsequent *Remigolepis* discoveries in Europe and Russia (e.g. Lukševics 1991; Panteleyev 1992; Moloshnikov 2008) have all been in Upper Devonian (Famennian) strata.

Meanwhile, older asterolepid antiarchs (family Pterichthyodidae) in eastern Australia were documented from ?Early and Middle Devonian non-marine (Young & Gorter 1981) and marine limestone occurrences (Young 1990). Acid-prepared remains of an unnamed asterolepid antiarch from the Emsian Cravens Peak Beds limestone of the Georgina Basin in western Queensland (Young 1984b) evidently represent the world's oldest occurrence of the family Asterolepidae (see Young & Lu 2020).

Age of the Gilberton Formation fish

Described above is the first remigolepid antiarch documented from Queensland, and in the context of the preceding discussion this would be assigned a Late Devonian age, either Frasnian or Famennian. The lower fossiliferous beds of the Gilberton Formation also have abundant plant remains, mainly *Leptophloeum australe*, which in eastern Australia is most likely confined to the Late Devonian (see discussion in Dunstone & Young 2019), although other macroplants are of Carboniferous aspect (Withnall *et al*. 1980). Palynomorphs of the latest Famennian *Retispora lepidophyta* zone (Young 1996) are also recorded from some percussion drill-holes (Withnall *et al*. 1980). There is no evidence anywhere of antiarch placoderms younger than the Devonian-Carboniferous boundary (e.g. Young 2010a), so the new fish evidence accords with the conclusion of Withnall *et al*. (1980, p. 79) that the lowermost part of the Gilberton Formation is of Late Devonian (Famennian) age. However, although *Remigolepis* in Europe is indicative of latest Devonian (Famennian), in Australia the genus occurs earlier, in the Frasnian at Canowindra, NSW (e.g. Young 1974, 1999), and probably at Genoa River in Victoria (Young 2007). Thus, on the fish evidence alone, a Frasnian age cannot be excluded for the Gilberton Formation.

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