

# A new basal actinopterygian fish from the Middle Devonian Aztec Siltstone of Antarctica

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**Abstract:** A new basal actinopterygian fish, *Donnrosenia schaefferi* gen. et sp. nov., is described from the Middle Devonian (Givetian) Aztec Siltstone of southern Victoria Land, Antarctica. *Donnrosenia* gen. nov. is characterized by the large parietals which are of almost equivalent size to the frontals, very small intertemporals, a small accessory operculum situated dorsally to the prominent anterodorsal process of the suboperculum, a deep dentary with anterior flexure, porous ornamentation on the clavicle, an elongate body form with macromeric squamation, an absence of paired fringing fulcra on the fins, and pectoral lepidotrichia which are unsegmented for much of their length. A phylogenetic analysis based on dermal skeletal features of Devonian actinopterygians indicates that *Donnrosenia* gen. nov. is the sister taxon to *Howqualepis* from the Middle Devonian of Victoria, Australia, and is embedded within a possible clade containing the actinopterygians from the Gogo Formation, Western Australia. This supports the concept of an endemic radiation of East Gondwanan actinopterygians, and reinforces the already strong biogeographical similarities between the Middle Devonian palaeofaunas of Australia and Antarctica.

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## Introduction

Actinopterygians (ray-finned fishes) are today the most diverse group of vertebrates, with over 30 000 extant species (Nelson 2006). After their earliest appearance in the fossil record as isolated scales from the Late Silurian, the group was a sparse component of most Devonian faunal assemblages; only 11 genera were sufficiently complete to be included in a recent phylogenetic analysis by Friedman & Blom (2006). Here we describe a new genus and species of actinopterygian from the Middle Devonian of Antarctica, based on a variety of material including some articulated but incomplete specimens. This is the fourth actinopterygian genus to be documented from the Devonian of East Gondwana.

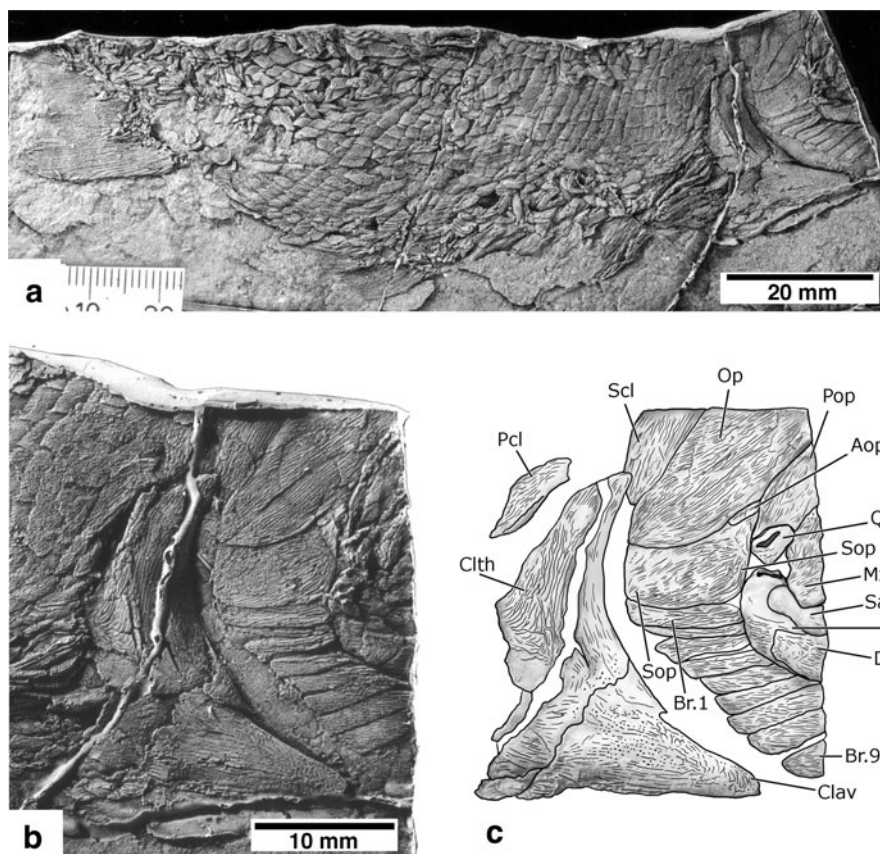
The fossil record of the ray-finned fishes remains patchy for much of the Devonian. The only known Early Devonian forms include some partially articulated specimens of stem osteichthyans that could potentially be basal actinopterygians: *Dialipina salgueiroensis* (Schultze & Cumbaa 2001), a skull roof and some other undescribed specimens of *D. markae* (Schultze 1992), a skull roof with braincase of *Ligulalepis* (Basden *et al.* 2000, Basden & Young 2001) and isolated scales of *Ligulalepis*, *Dialipina*, *Terenolepis* and *Naxilepis* from various localities (e.g. Schultze 1968, Burrow 1995). The few actinopterygian taxa represented by articulated remains from Middle Devonian deposits include *Cheirolepis trailli* (Pearson & Westoll 1979) and *Stegotrachelus finlayi* (Woodward & White 1926, Gardiner 1963), both from the Old Red

Sandstone of Scotland, and *Howqualepis rostridens* Long (1988) from Mount Howitt, Victoria, Australia (age revised by Long 1999, Young 1999).

Most Devonian ray-fins come from middle Frasnian to Famennian deposits. These are mainly known from European and North American sites: *Cheirolepis canadensis* (Arratia & Cloutier 1996), *Cuneognathus gardineri* Friedman & Blom (2006), *Kentuckia hlavini* Dunkle (1964), *Limnomis delaneyi* Daeschler (2000), various species of *Moythomasia* (Gross 1950, Jessen 1968), *Osorioichthys marginis* Casier (1952, 1954, Taverne 1997) and *Tegeolepis clarki* Newberry (1888, Dunkle & Schaeffer 1973). The only articulated taxon from outside this region is *Krasnoyarchthys jesseni* from Siberia (Prokofiev 2002). In the Southern Hemisphere, fossil actinopterygians of exceptional quality are known from the Frasnian Gogo Formation of Western Australia. Of these, *Moythomasia durgaringa* and “*Mimia*” *toombsi* (currently preoccupied and soon to be renamed) have been described (Gardiner & Bartram 1977, Gardiner 1984) with additional forms currently being examined by one of the authors (BC).

## Previous work on the Aztec Devonian fish fauna

The first Devonian fossil fish, indeed the first fossil vertebrates, to be discovered on the Antarctic continent came from glacial moraine at Granite Harbour investigated by T. Griffith Taylor’s party during the British Antarctic ‘*Terra Nova*’ expedition of 1910–13. The material was



**Fig. 1.** *Donnrosenia schaefferi* gen. et sp. nov. Holotype (AM F54363) in right lateral view. Specimen is a latex cast whitened with ammonium chloride. **a.** photograph of entire specimen. **b.** Photograph. and **c.** drawing of the partial skull, opercular-gular series and pectoral girdle. Abbreviations: **An** = angular, **Aop** = accessory operculum, **Br.1** = 1st branchiostegal ray (counting from suboperculum), **Br.9** = 9th branchiostegal ray, **Clav** = clavicle, **Clth**. cleithrum, **Den** = dentary, **Mx** = maxilla, **Op** = operculum, **Pcl** = postcleithrum, **Pop** = preoperculum, **Qj** = quadratojugal, **San** = supra-angular, **Scl** = supracleithrum, **Sop** = suboperculum.

described by Woodward (1921), who identified six major groups of Devonian fishes, one of which ('Order Actinopterygii') was based on isolated 'palaeoniscid' scales.

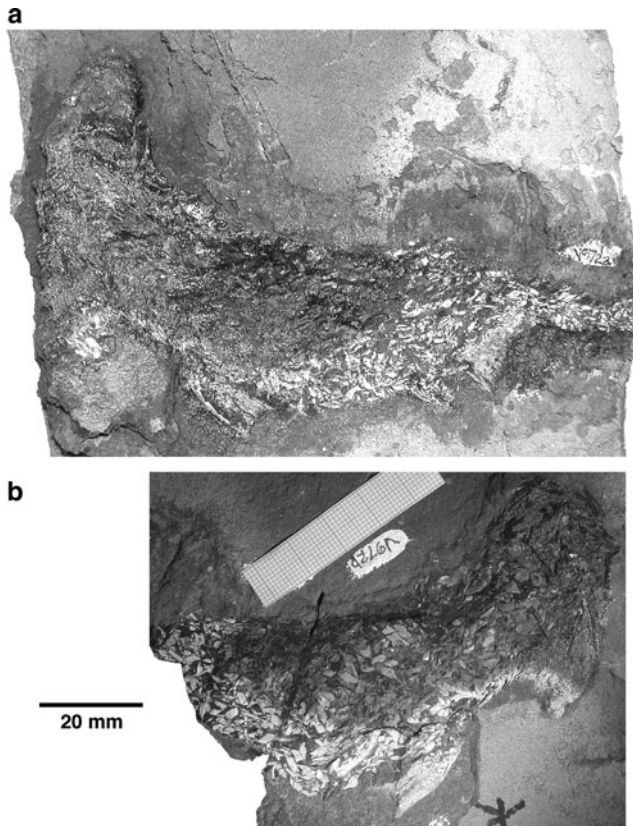
The first *in situ* fossil fish material, described by White (1968), was collected during the Trans-Antarctic Expedition of 1955–58. It came from the Aztec Siltstone (Taylor Group, Beacon Supergroup; McPherson 1978) in the Skelton Névé region of the Transantarctic Mountains, the same area in which abundant fossil localities were discovered during the 1968–69 summer field season of the New Zealand Antarctic Research Program (NZARP). The main fossil fish collection was made by A. Ritchie and G. C. Young in the following summer field season (1970–71), as part of a Victoria University of Wellington Antarctic Expedition (VUWAE 15). Summaries of the fish fauna were given by Young (1989a, 1991). Later expeditions (1976–77, 1988–89, 1991–92) collected material from new localities in the Cook Mountains (Woolfe *et al.* 1990, Long & Young 1995, fig. 1), 100 km to the south of previously known sites (M.A. Bradshaw, NZARP, event 33; J.A. Long, NZARP-ANARE expedition).

The Aztec fossil fish fauna is one of the most diverse known assemblages of Middle–Late Devonian age (at least 45 taxa; Young & Long 2005, table 1). Most of the major Devonian vertebrate groups are represented, including

thelodont agnathans (Turner & Young 1992), placoderms (Ritchie 1975, Young 1988, Long 1995, Young & Long 2005), chondrichthyans (Young 1982, Long & Young 1995, Hampe & Long 1999), sarcopterygians (Campbell & Barwick 1986, Young *et al.* 1992, Johanson & Ahlberg 2001, Johanson 2004), acanthodians (Young 1989b, Young & Burrow 2004), and the actinopterygians dealt with here. Ray-finned fish are relatively rare in the Aztec assemblage, but the material described in this paper is significant because it includes several partly articulated specimens, as well as a range of isolated bones and scales. A preliminary reconstruction of the Antarctic palaeoniscoid was given by Young (1989a, fig. 3C).

#### Localities, stratigraphic occurrence, and age

Full locality and stratigraphic details for 24 fossil fish localities of the 1970–71 and earlier Antarctic expeditions were given by Young (1988, pp. 6–9). Locality maps for these and later collecting sites were figured by Young & Long (2005, fig. 1). Actinopterygian remains are only known from three of these localities: the original site in moraine near Mount Suess at Granite Harbour (locality 2 on the published map), Mount Crean (locality 8), and Portal Mountain (localities 11, 12 on the published map). Possible actinopterygian remains from the Cook Mountains



**Fig. 2.** *Donnrosenia schaefferi* gen. et sp. nov. Photographs of ANU V972. **a.** V972a in left lateral view, **b.** V972b/c in right lateral view. Specimens are bone remains and impressions in the rock.

(Woolfe *et al.* 1990, p. 513) need to be confirmed and were not included in this study.

The scales called ‘Palaeoniscid type II’ by White (1968, p. 24) came from the lower MS6 horizon at Mount Crean in the Lashly Range. Young (1988, p. 12) considered this to approximate to Unit 3 of section L2. Palaeoniscoid remains were noted from collection sites MC2 and MC3 at Mount Crean, the latter yielding an articulated specimen in a darker shale horizon considered to approximate to the 60–70 m level in the interpretation of this outcrop (Young 1988, fig. 4). At Portal Mountain palaeoniscoid remains were reported in units 4 and 14 of section P1.

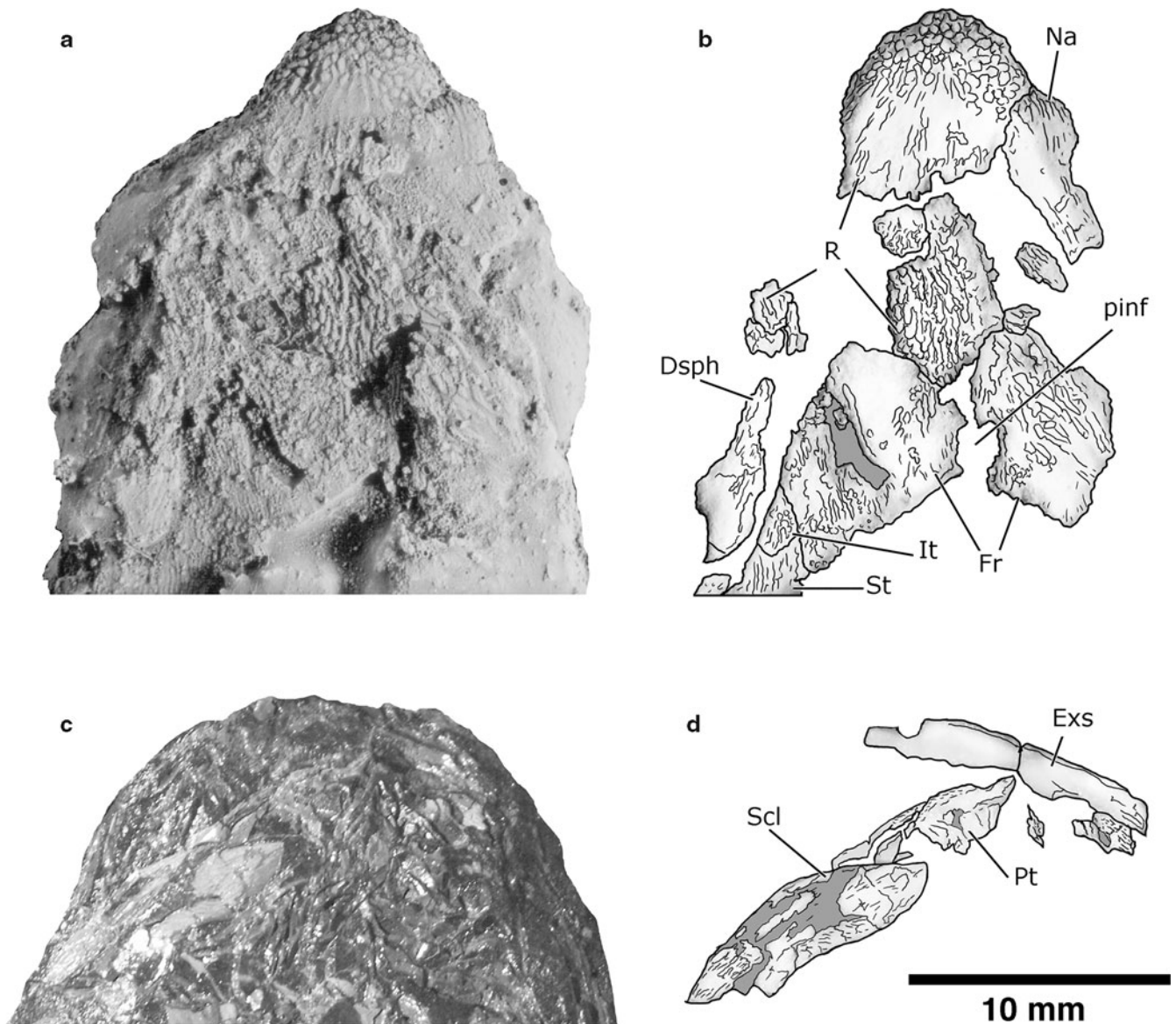
The Aztec fish fauna is now assessed as considerably older than the Upper Devonian age first assigned by Woodward (1921; see discussion in Young 1993). It was placed in the late Middle Devonian (Givetian) in the macrovertebrate biostratigraphic zonation for East Gondwana of Young (1996; MAV6), aligning approximately with the *varcus* conodont zone of the middle Givetian (Young & Turner 2000, fig. 2). Turner (1997) considered the thelodont *Turinina antarctica* to be of early Givetian age; this taxon identifies the lowest two zones (6a, 6b) in the

biostratigraphic scheme for the Aztec sequence first proposed by Young (1988, fig. 5). All actinopterygian material so far identified from the Aztec sequence comes from equivalent horizons at Mount Crean, and also from the slightly higher ‘portalensis’ biozone at Portal Mountain. Young & Long (2005, fig. 12) showed the entire Aztec assemblage (MAV6) confined to the *varcus* conodont zone, and whilst this is reliable for the phyllolepid placoderms which come from the uppermost Aztec zones, it should be noted that a reliable maximum age constraint for the Aztec sequence is not available. Young & Long (2005) provided evidence that the entire sequence is diachronous from the north to the south. On present evidence, all of the actinopterygian material described below is at least as old as Givetian, and may be older (?Emsian–Eifelian), given that there is no convincing evidence placing an older age limit on the Aztec sequence.

### Materials and methods

The fish material from the Aztec Siltstone is generally preserved as light coloured bone in a darker siltstone or fine sandstone matrix. The bone is generally dark when unweathered. Preparation by mechanical removal of matrix is difficult, and removal of bone for latex rubber casting of impressions has proved effective. The holotype of *Donnrosenia schaefferi* (AM F54363) was prepared this way by Dr A. Ritchie (Australian Museum); the counterpart as collected was illustrated in its unprepared state by McPherson (1975, p. 146). The second articulated specimen (ANU V972) is preserved in a dark slightly calcareous shale, and was partly etched in acetic acid (JAL); acetic acid preparation of this lithology has yielded well preserved scales suitable for histological study. Other semi-articulated specimens from Portal Mountain (AM F55938, ANU V769, 770) may yield more information with further preparation. In several Portal Mountain specimens (ANU V769, 771, 815) actinopterygian scales are associated with conchostracans.

Material described or mentioned here is housed in the Research School of Earth Sciences, Australian National University, Canberra (prefix ANU V or V), the Australian Museum, Sydney (prefix AM F), the National Museum of Victoria, Melbourne (prefix NMV P), the Natural History Museum, London (prefix NHM P), and the Institute of Geological and Nuclear Sciences, Wellington, New Zealand (ex-New Zealand Geological Survey; prefix GS). Terminology herein follows that of Gardiner *et al.* (2005, Gardiner & Schaeffer 1989), and for skull roofing bones we use the older (conventional) actinopterygian terminology, following recent work such as Friedman & Blom (2006), rather than employing tetrapod skull roof homologies (as used in Schultze & Cumbaa 2001).



**Fig. 3.** *Donnrosenia schaefferi* gen. et sp. nov. Skull of ANU V972. **a.** Photograph, and **b.** line drawing of V972a showing anterior part of head in dorsal view. **c.** Photograph, and **d.** line drawing of V972b showing posterior part of head in ventral view. Abbreviations: Dsph = dermosphenotic, Exs = extrascapular, Fr = frontal, It = intertemporal, Na = nasal, pinf = pineal foramen, Pt = post-temporal, R = rostral, Scl = supracleithrum, St = supratemporal.

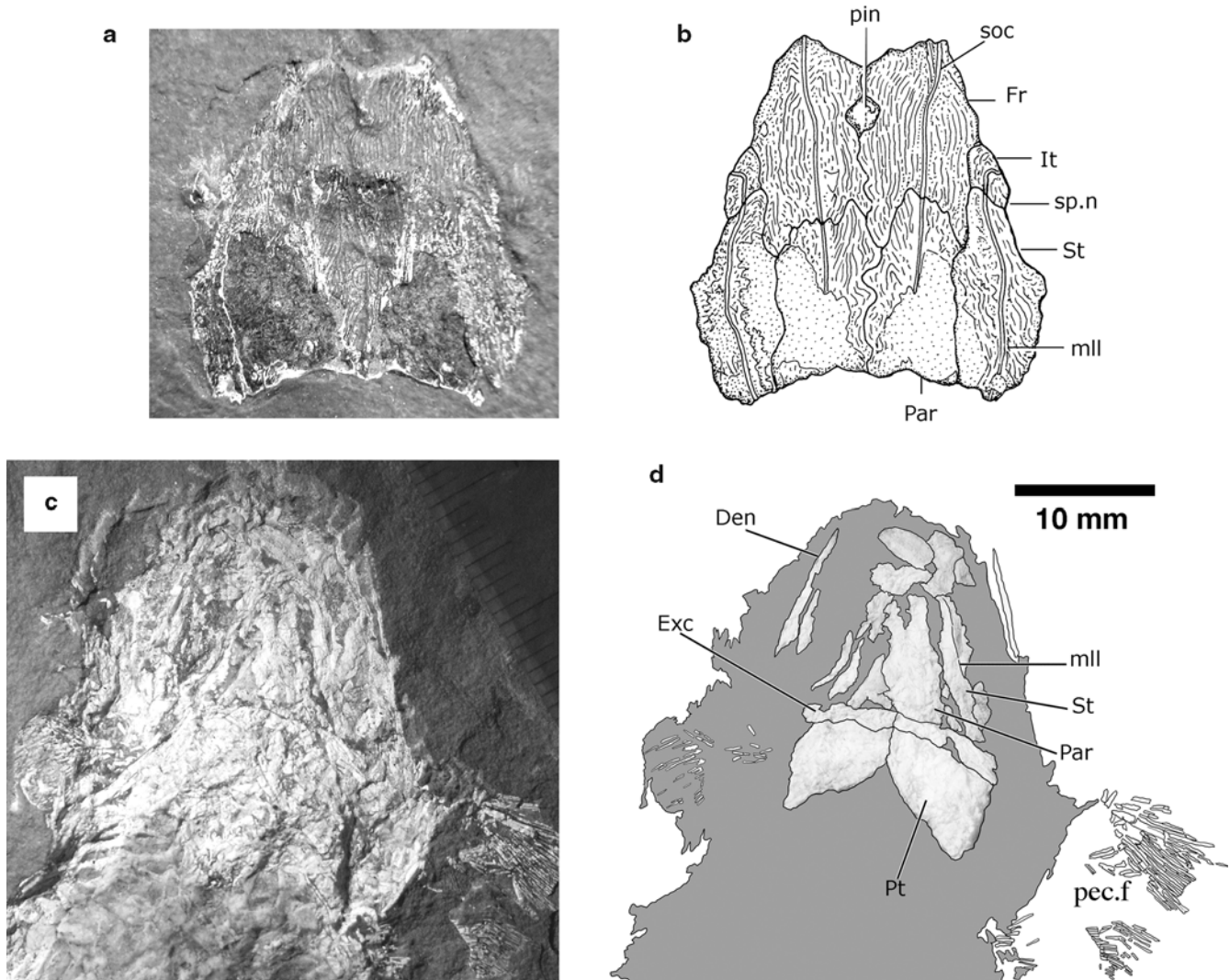
### Systematic palaeontology

Class OSTEICHTHYES Huxley, 1880  
 Subclass ACTINOPTERYGII Woodward, 1891  
 Family HOWQUALEPIDIDAE fam. nov.

*Diagnosis.* Basal actinopterygian fishes with an open spiracular slit bordered by a very small intertemporal, a median rostral that narrows anteriorly, an elongate tripartite dermosphenotic, a narrow, steeply inclined opercular and a suboperculum with a prominent anterodorsal process. The body form is elongate and fusiform with macromeric squamation, each scale being rhombic with parallel ganoine ridges. Pelvic fins are long based. True fringing

fulcra are absent and are functionally replaced by short spine-like lepidotrichia. Lepidotrichia of the pectoral fin are proximally unsegmented for most of their length. Ventral series of scutes does not extend anteriorly past the cloacal region. Dorsal series of scutes does not extend to the occipit.

*Remarks.* Gardiner (1993, p. 611–12) united “*Mimia*” from Gogo and *Howqualepis* Long, 1988 from Victoria within a new family Mimiidae, but did not provide a diagnosis. Subsequent phylogenetic analyses have consistently failed to recover an exclusive sister-group relationship between these two genera (Taverne 1997, Schultze & Cumbaa 2001, Friedman & Blom 2006). Our new phylogenetic



**Fig. 4.** *Donnrosenia schaefferi* gen. et sp. nov. Skulls in dorsal view. **a.** Photograph, and **b.** line drawing of ANU V2246. **c.** Photograph, and **d.** line drawing of AM F55938. Both specimens presented at the same scale. Abbreviations: Den = dentary, Exc = extrascapular, Fr = frontal, It = intertemporal, mll = median lateral line, Par = parietal, pec.f = pectoral fin, pin = pineal foramen, Pt = post-temporal, soc = supraorbital sensory canal, sp.n = spiracular notch, St = supratemporal.

analysis (see Discussion) suggests that *Howqualepis* is more closely related to *Donnrosenia* gen. nov., whereas an exclusive sister-group relationship between “*Mimia*” and the slender-bodied Givetian forms was not recovered.

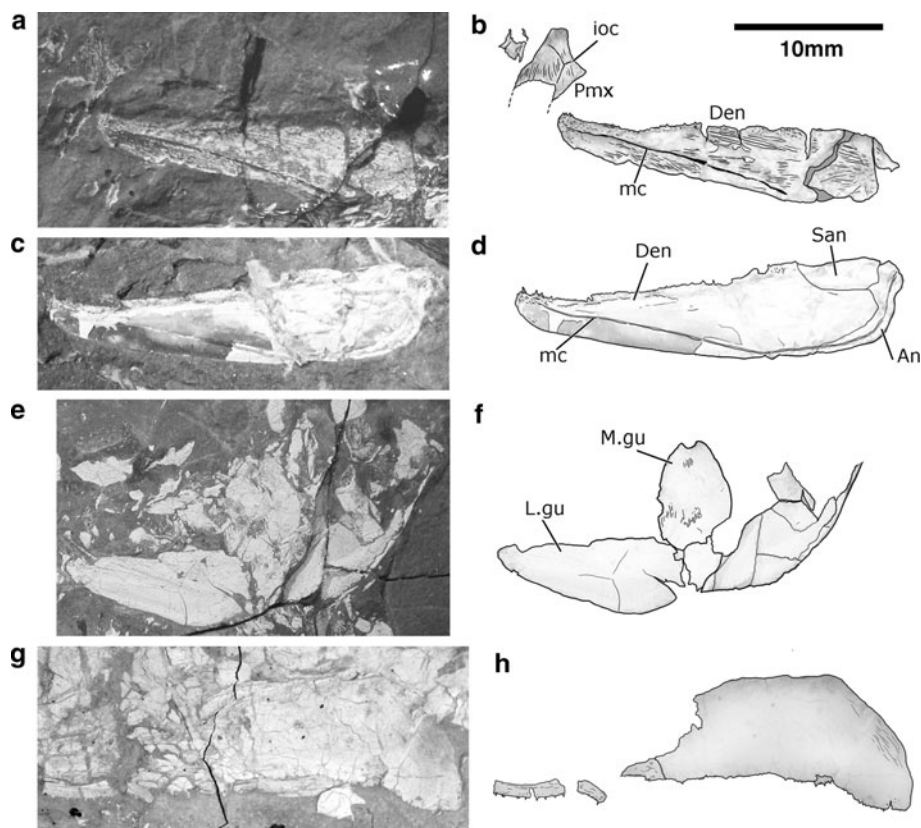
Genus *Donnrosenia* nov.

*Diagnosis.* As for type species (only species in the genus).

*Type Species.* *Donnrosenia schaefferi* sp. nov.

*Etymology.* In honour of the late Donn E. Rosen for his contributions to ichthyology, in particular to our understanding of Gondwanan fish distribution (e.g. Rosen 1974, Nelson & Rosen 1980).

*Remarks.* *Donnrosenia* gen. nov. differs from cheirolepidids by having macromeric squamation and the lack of a lobed base on the pectoral fins; from *Howqualepis* by the presence of an accessory operculum, comparatively larger parietals, taller premaxilla, smaller teeth, a mandibular canal that is deflected upwards in its anterior half, and a shorter postorbital blade on the maxilla; from *Limnomis* and *Cuneognathus* by the presence of well-developed pelvic fins. *Donnrosenia* gen. nov. differs from *Osorioichthys* by its open pineal foramen, single pair of extrascapulars and a lack of a pectoral lobed base. *Donnrosenia* gen. nov. differs from *Krasnoyarichthys* and *Stegotrachelus* in the absence of basal fulcra between and anterior to the pelvic fins, and from *Tegeolepis* by the latter genus having a prominent rostral, large teeth, horizontal preopercular and narrower maxilla.



**Fig. 5.** *Donnrosenia schaefferi* gen. et sp. nov. Elements of the head as photographs and line drawings presented to scale. **a., b.** ANU V781a, partial left premaxilla and dentary in lateral view. **c., d.** ANU V815, left lower jaw in lateral view. **e., f.** ANU V781c, Lateral and median gular plates in visceral view. **g., h.** ANU V769, left maxilla in lateral view. Abbreviations: An = angular, Den = dentary, ioc = infraorbital canal, L.gu = lateral gular, M.gu = median gular, mc = mandibular canal, Pmx = premaxilla.

*Donnrosenia* differs from all post-Devonian actinopterygians principally by the presence of the small supratemporal bone within the skull roof table.

*Donnrosenia schaefferi* sp. nov.

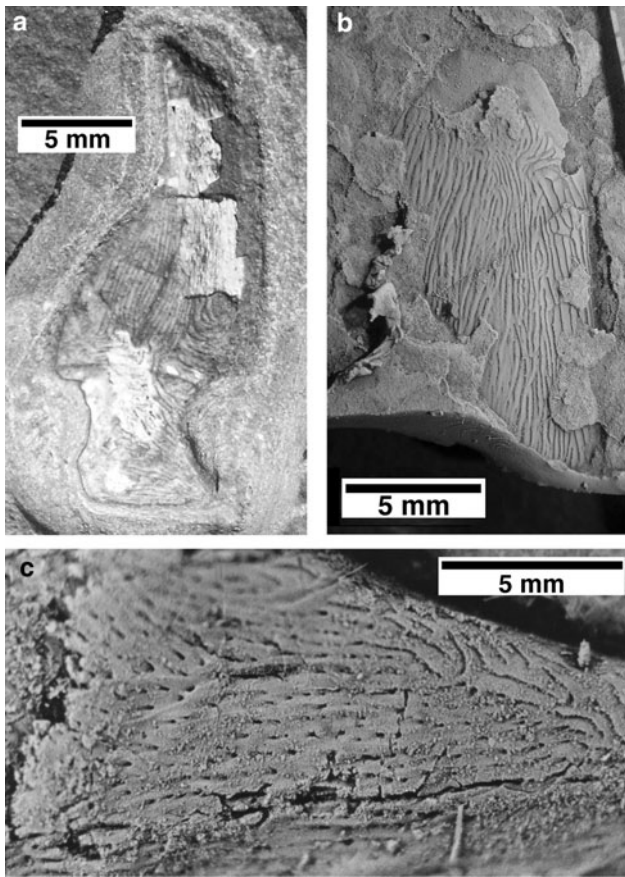
Figs 1–10

- 1921 'Palaeoniscid'; Woodward, p. 60, pl. 1, figs 30–34
- 1968 'Palaeoniscid types I, II'; White, p. 24
- 1975 'palaeoniscid fish'; McPherson, figure on p. 146
- 1986 'Undetermined palaeonisciforms'; Grande & Eastman, p. 116
- 1987 'palaeoniscoids'; Young, p. 46
- 1988 'palaeoniscoids'; Young, pp. 12, 13
- 1989a 'new genus of palaeoniscoid fish'; Young, p. 47, fig. 3C
- 1991 'palaeoniscoid actinopterygian'; Young, p. 545, fig. 15.5(b)
- 1992 'palaeoniscoid osteichthyans'; Turner & Young, p. 90
- 1993 'palaeoniscoid gen. nov.'; Young, p. 248, fig. 9.7
- 1995 'palaeoniscoid gen. nov.'; Long & Young, table 1
- 2005 'palaeoniscoid gen. nov.'; Young & Long, table 1
- 2006 'material from the Aztec Siltstone'; Friedman & Blom, p. 1186
- 2007 'material from the Antarctic Aztec Siltstone'; Young, p. 996

*Diagnosis.* A basal actinopterygian having a fusiform body, skull roof with parietals and supratemporals almost as long as the frontals; spiracular slit well defined on skull; dermosphenotic elongate, tripartite; maxilla with postorbital blade twice as long as deep; anterior suborbital division equal to postorbital blade; opercular elongate; very small accessory opercular present between anterior process of subopercular and anteroventral edge of opercular; subopercular with well-developed anterodorsal process; pectoral and pelvic fins each with approximately 25 fin rays, anal fin with 25–30 fin rays, on each fin the leading fin rays showing terminal branching with only one branch per segment (lacking fringing fulcra). Scales rhombic with well-developed peg and socket articulation. Main trunk scales from zone A almost three times as high as long, with about 12–15 rows of diagonal, slightly sinuous ridges forming the ornamentation.

*Etymology.* In honour of the late Bobb Schaeffer, who not only made numerous contributions to palaeoichthyology, but described the only other fossil actinopterygian from mainland Antarctica (Schaeffer 1972).

*Holotype.* AM F54362-63, an articulated fish preserved in part and counterpart, missing the dorsal margin, anterior portion of the head, and caudal fin.



**Fig. 6.** *Donnrosenia schaefferi* gen. et sp. nov. **a.** ANU V763, left cleithrum in lateral view. **b.** ANU V886, left operculum in lateral view. **c.** AM F54363 (holotype), detail of right clavicle in lateral view showing porous ornamentation.

*Other material.* AM F55938, crushed head and pectoral fins in dorsal view; ANU V972, an almost complete articulated fish preserved in part and counterpart showing the skull in dorsal view. Other isolated material from the 1970–71 collection, some described below, is listed as follows: ANU V762, partial left cleithrum; ANU V763, left cleithrum; ANU V764, disarticulated scales; ANU V765, left lateral gular; ANU V766, isolated flank scale; ANU V769, crushed head in part and counterpart including left maxilla and gular plate; ANU V770, crushed skull; ANU V771, disarticulated fulcra; ANU V772, disarticulated scales; ANU V781, disarticulated skull, anterior left dentary and scales; ANU V782, isolated impression of maxilla; ANU V784, left clavicle; ANU V786–788, isolated scales; ANU V789, isolated fulcral scute, ANU V815, left lower jaw and associated scales; ANU V886, isolated operculum along with placoderm plates; ANU V891, 892, disarticulated scales; ANU V963, isolated fulcral scute; ANU V964, partial cleithrum; ANU V1004, disarticulated scales and fulcra; ANU V2175, isolated flank scale; ANU V2246, articulated skull roof in dorsal view.

The material (mainly isolated scales) described by Woodward (1921; NHM P12563, 576, 589–591) and White (1968; NHMP 49174, 175; GS7399/14) is provisionally included (more detail given below under ‘Discussion’).

*Localities and horizon.* AM F54362/3 (holotype) came from Portal Mountain (locality 12 of Young 1988, fig. 3; lat. 78°7.2'S, long. 159°24'E). Locality information on its label states only ‘E. face Portal Mt ... coll. AR Dec. 1970’, but the lithology is identical to that of ANU V762–64, so it is presumed to come from the same horizon. These and various other palaeoniscoid remains (ANU V765–66, 769–72, 781–789, 815, 2246) were collected from Unit 14, Section P1. One specimen (ANU V2175) came from the adjacent locality 11 of Young (1988, fig. 3; 78°7.2'S, 159°23.5'E), assumed equivalent to Unit 17, Section 10.

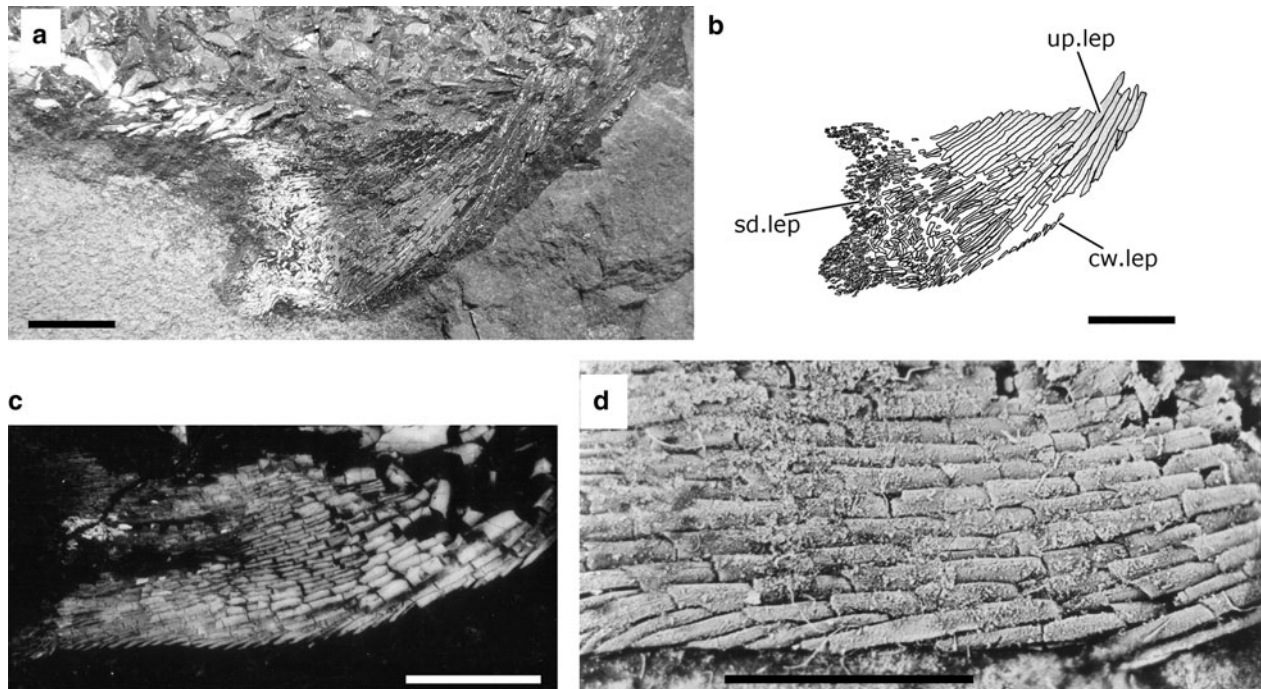
Material from Mount Crean, Lashly Range (locality 8 of Young 1988, fig. 3; 77°53'S, 159°33'E) came from two collecting sites assumed to approximate to the 60–90 m level of the Aztec Siltstone in Section L2 (Young 1988, fig. 4); specimen numbers as follows: MC2 (ANU V886, 891–892), MC3 (ANU V921–22, 963–66, 972, 980, 982, 1004).

### Description

#### Skull roof

The skull table (Figs. 3 & 4) is typical for most Devonian actinopterygians, displaying a similar morphological pattern to that of *Howqualepis* (Long 1988), *Moythomasia* (Jessen 1968, Gardiner 1984) and “*Mimia*” (Gardiner 1984), with subrectangular parietals, elongated supratemporals, and small, wedge-shaped intertemporals. The overall shape of the skull roof tapers towards the snout from a broad posterior region, unlike the blunt-shaped heads seen in cheirolepidids (Pearson & Westoll 1979, Arratia & Cloutier 1996, 2004), *Dialipina* (Schultze & Cumbaa 2001) and *Ligulalepis* sp. (Basden & Young 2001). The supraorbital and main lateral line sensory-line canals are clearly seen in V2246, largely conforming to the typical pattern seen in other Devonian actinopterygians such as *Howqualepis* and “*Mimia*”, except the pit-line organs which are not defined due to missing areas of bone on the parietals. There are no additional clusters of sensory-line pits visible on the skull-roof bones as is seen on the parietals and supratemporals of *Howqualepis*.

The frontals are the largest elements on the skull roof and are well preserved on V2246 (Fig. 3a & b). They are asymmetrical bones that taper towards anterior points, together creating a shallow, V-shaped recess for the rostral. The supraorbital canal traverses the bone lengthwise from the posterior margin to the anterior point. It is deflected outwards from its straight course at the approximate



**Fig. 7.** *Donnrosenia schaefferi* gen. et sp. nov. Photographs of fins. **a.–c.** ANU V972b, **a.** right pectoral fin, **b.** right partial pelvic fin, **c.** anal fin. **d.** Holotype AM F54363, anal fin. (AM F54363), anal fin. Scale bar on each image = 5 mm. Abbreviations: cw.lep = cutwater lepidotrichia, sd.lep = small distal lepidotrichia, up.lep = primary lepidotrichia.

middle of the bone. The pineal foramen interrupts the median suture in the anterior third of the frontals. Ornament consists of fine linear ridges that are rostrocaudally directed in the posterior two thirds of the bone, becoming interspaced with shorter radial ridges towards the anterior.

The comparatively large parietals are only marginally smaller than the frontals. They are subrectangular in shape, being slightly longer than broad. The only near complete examples (Fig. 4b) only preserve the full dermal ornament along the anterior and medial margins. The bones suture with their counterpart in a wavy margin and anteriorly with the frontals; a v-shaped median recess formed by the two is filled by a posterior lappet of the right frontal. The supraorbital canal exits the bone anteriorly. The visible ornamentation consists of short to medium length rostrocaudal linear ridges that become deflected near the edges to conform to the adjacent margin of the bone.

The intertemporal bone is very small, with an anteroposterior length less than one fifth of the total skull roof length. It is a triangular element that sutures with the supratemporal posteriorly and the frontal medially. The main lateral line canal bends from its straight course to exit the bone on the posterior margin and into the dermosphenotic. Ornament consists of short longitudinal ridges.

As with *Howqualepis* (Long 1988), the posterolateral margin of the intertemporal and anterolateral margin of the supratemporal together form the dorsal margin of the

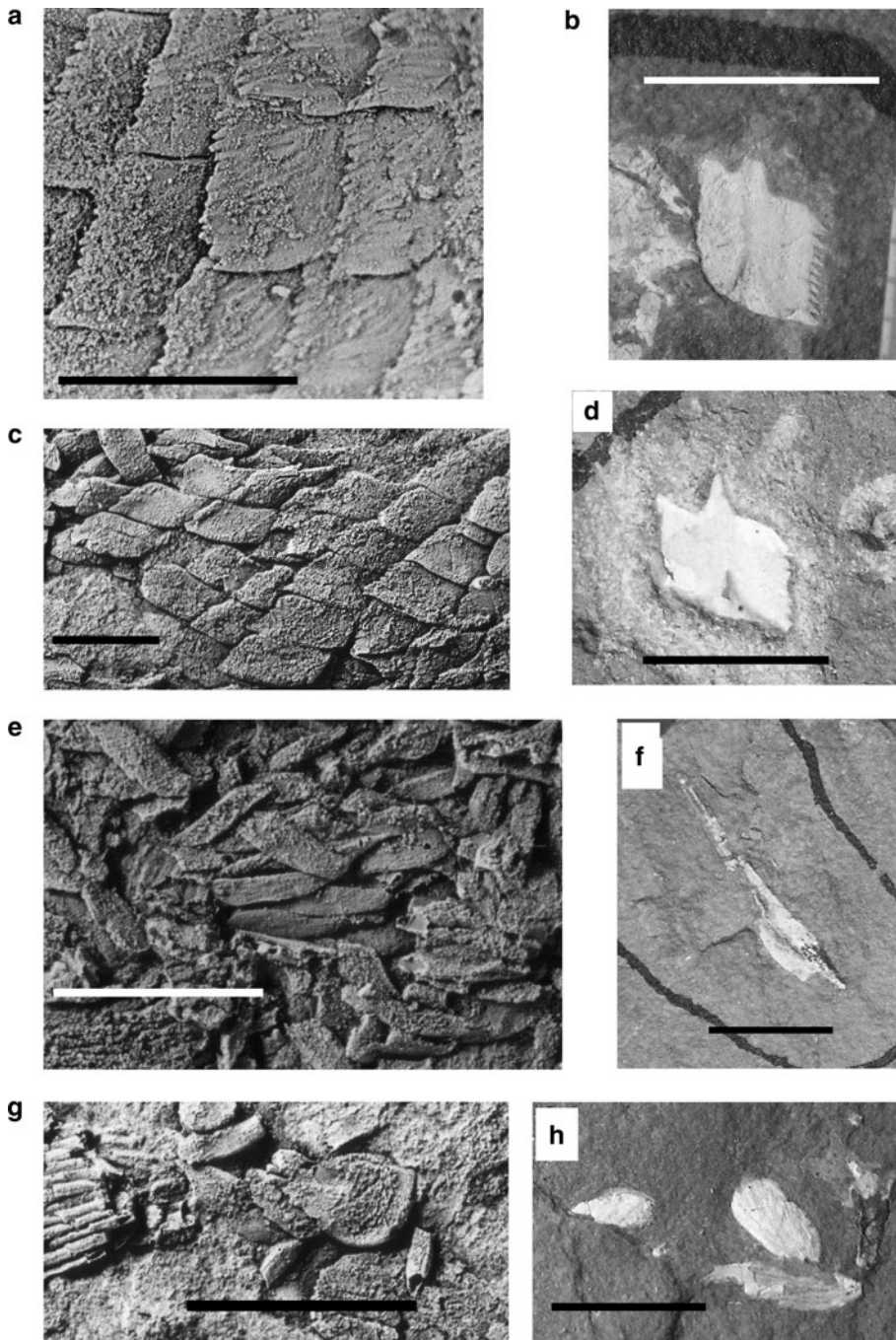
spiracular opening. Among other Gondwanan taxa, only *Howqualepis* has this arrangement (Long 1988), while in *Moythomasia durgaringa* and “*Mimia*” the intertemporal forms the entire dorsal margin of the spiracle.

The narrow supratemporals are as long as the parietals, and considerably larger than the intertemporals. A distinct lateral process (Fig. 4a & b) borders the posterior end of the spiracular notch, a feature also seen in *Howqualepis* (Long 1988). The main lateral line canal runs close to the approximate middle of the bone as in *Cheirolepis* (Pearson & Westoll 1979) rather than staying close to the lateral margin as in most other Devonian actinopterygians. Ornament consists of linear ridges that grade into shorter ridges and tubercles at the lateral margins.

The only identifiable example of the dermosphenotic is visible on ANU V972 (Fig. 3a & b). In overall size and shape it is similar to that of *Howqualepis* and *Moythomasia nitida* (Jessen 1968), being a narrow T-shaped bone of similar length to the frontals, with elongate anterior and posterior extensions. The posterior ramus forms the ventral margin of the spiracle. The canal structure and most of the ornamentation has not been preserved aside from traces of fine anterolateral ridges close to the dorsal margin.

The single pair of extrascapulars is not bordered by the supratemporals as in *Cheirolepis* but instead extend to the lateral margins of the skull roof as in *Howqualepis*. They





**Fig. 8.** *Donnrosenia schaefferi* gen. et sp. nov. Photographs of squamation. **a.** AM F54363 (holotype), Zone A scales in articulation. **b.** ANU 781b, single scale from Zone A. **c.** AM F54363 (holotype), Zone C scales. **d.** ANU 766, isolated scale from Zone B. **e.** AM F 54363 (holotype), Zone H scales. **f.** ANU V771, two caudal fulcra from above the caudal fin. **g.** AM F54363 (holotype), ventral fulcra, anterior to the anal fin. **h.** ANU V772, disarticulated fulcra, original position uncertain.

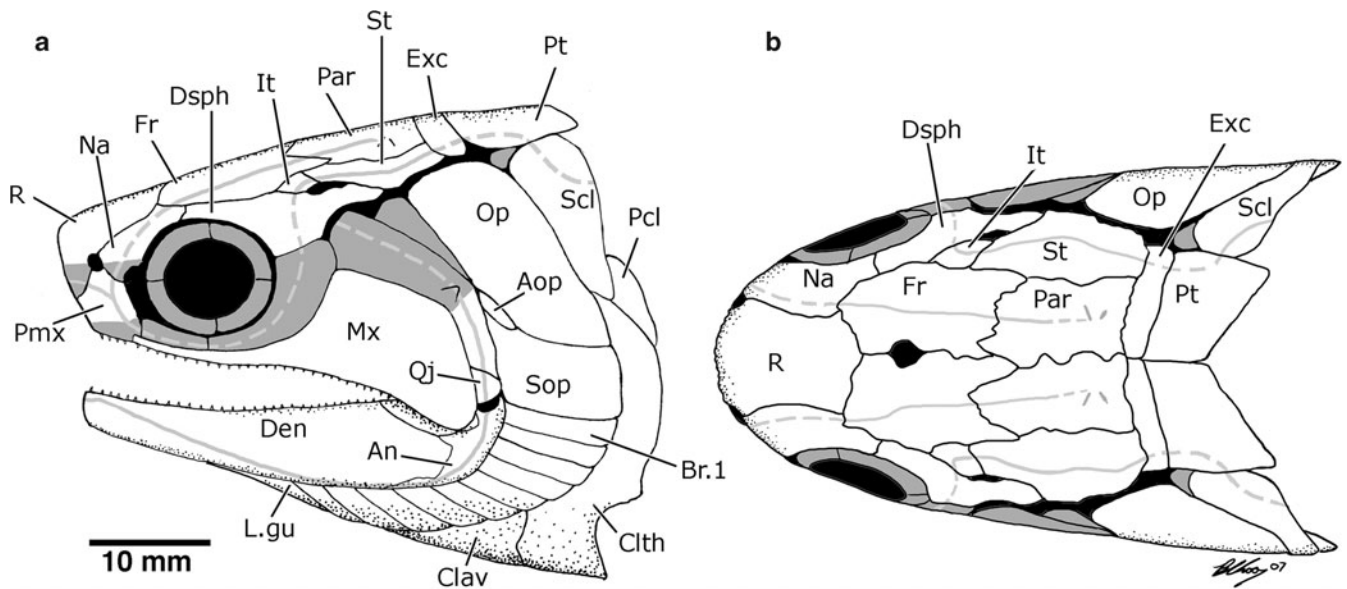
are narrow, strap like elements possessing a smooth dorsal overlap region for the parietals (Fig. 3c & d). Ornament and the structure of the sensory canal are not preserved.

#### Snout and cheek

The snout is preserved in ANU V972a, which has been partially acid-prepared to show the rostral bone and nasals in dorsal view (Figs 2, 3a & b). The rostral bone is broad and rounded at its apex, abruptly narrowing after it bends

downwards to form the anterior-facing rostral lamina. The terminal edge is not preserved and it is unknown whether the rostral possessed a dentigerous tip and contributed to the biting margin as in *Howqualepis* and *Moythomasia durgaringa*. Posteriorly, the rostral narrows slightly to meet the parietals. Ornamentation consists of coarse linear ridges breaking into scattered rounded tubercles near the anterior margin.

The nasals are imperfectly preserved on V972 and are situated laterally to the rostral, forming the posterior border



**Fig. 9.** *Donnrosenia schaefferi*, gen. et sp. nov. Restoration of the head in (a) lateral, and (b) dorsal views. Dark grey areas corresponds to missing sections of the skull. Light grey lines refer to the path of the sensory canal, continuous where observed on fossil specimens, broken where inferred from other Devonian actinopterygians. Abbreviations: An = angular, Aop = accessory operculum, Br.1 = 1st branchiostegal ray, Clav = clavicle, Clth = cleithrum, Den = dentary, Dsph = dermosphenotic, Exc = extrascapular, Fr = frontal, It = intertemporal, L.gu = lateral gular, Mx = maxilla, Na = nasal, Op = operculum, Qj = quadratojugal, Par = parietal, Pcl = postcleithrum, Pmx = premaxilla, Pt = post-temporal, R = rostral, Scl. supracleithrum, Sop = suboperculum, St = supratemporal.

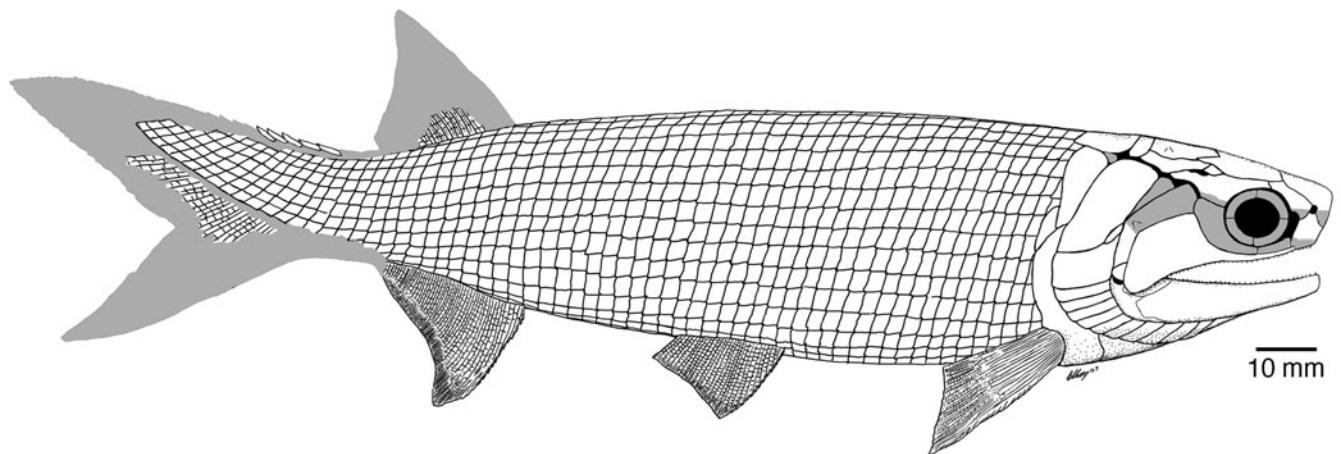
of the incurrent naris. They are narrow in dorsal view and of similar length to the rostral. Scattered patches of linear ornament are preserved.

A partial left premaxilla is visible in ANU V781a (Fig. 5a & b), missing its ventral edge. It is a comparatively larger and taller bone than the dorsoventrally compressed premaxilla of *Howqualepis*. In its relative size and roughly square shape, it appears more similar to that of "*Mimia*" *toombsi* (Gardiner 1984). A section of the infraorbital sensory canal is visible

close to the lateral edge, branching to be transmitted anterodorsally, presumably into the rostral, and dorsally into the nasal.

Ornament consists of short anterodorsally directed ridges and scattered tubercles.

The maxilla is well-preserved in ANU V769 (Fig. 5) and V781, while AM F54363 preserves only the posterior corner of the maxilla where it can be seen immediately anterior to the glenoid fossa of the mandible. The bone has



**Fig. 10.** *Donnrosenia schaefferi*, gen. et sp. nov. Restoration of the entire fish in lateral view. Grey blank areas refer to missing or poorly preserved sections of the animal.

an expanded postorbital blade slightly deeper in its posterior region than immediately before the suborbital section. In this regard it is not as slender as the maxillae seen in either cheirolepidids, *Howqualepis* and *Limnomis*, but is more akin to the shape seen in “*Mimia*” and *Moythomasia* spp. The narrow, anterior suborbital section of the bone is gently reflexed upwards as in *Howqualepis*. Only scattered sections of dentition are preserved, mostly on the suborbital extension, which consists of numerous minute teeth on the outer edge and an inner row of larger, conical laniary teeth. The inner teeth are considerably smaller than those of *Howqualepis* and are only about four times longer than the outer teeth.

Only small sections of ornament are preserved, including very short, rostrocaudal ridges in the anterior extension, and short to medium-length ridges lying parallel to the posterodorsal margin of the postorbital blade.

The partially preserved preopercular bone in AM F54363 (Fig. 1) shows the posterior corner. From both its preserved shape, and the dorsal margin of the maxilla, it can be restored to be similar to the bar-like preopercular seen in most other Devonian actinopterygians. None of the infraorbital bones of the cheek have been identified in the material.

#### *Operculo-gular system*

The operculo-gular system is well preserved in AM F54363 (Fig. 1), which shows a large opercular, rectangular subopercular, small sliver-like accessory opercular element, and at least nine branchiostegal rays. The posteroventral two-thirds of the operculum is visible in AM F54363 while a complete isolated specimen (ANU V886) shows it to be a relatively deep and narrow bone as seen in cheirolepidids, *Howqualepis* and *Limnomis*.

The subopercular is slightly longer than deep, with a strongly concave dorsal margin and a relatively straight ventral margin. The accessory opercular element sits anterodorsal to the subopercular and is splint-like in form, unlike the more prominent accessory opercular element seen in the cheirolepidids (Arratia & Cloutier 2004).

The branchiostegal ray ventral to the subopercular is the narrowest relative to its length. The next two are relatively short, after which the anterior-most series increases in size towards the front of the head. The eighth and ninth rays are relatively deep bones that are also very large relative to the position of the lower jaw in that articulated specimen. A similar condition is seen in *Moythomasia nitida* (Jessen 1968) and in *Limnomis* (Daeschler 2000).

Several examples of gular plates have been preserved, including examples on ANU V973 (Fig. 5e & f), V765 and V770. They are similar in size and shape to those of *Howqualepis* and “*Mimia*” *toombsi* (Gardiner 1984) being large, lanceolate elements consisting of two larger, asymmetrical, lateral bones framing a smaller, symmetrical median bone. The median gular is about half as long as the

laterals but is almost as equally broad as them. Ornament and pit-lines have not been preserved.

#### Lower jaw

The lower jaw is visible in lateral view in ANU V781a (Fig. 5a & b) along with a well-preserved isolated specimen (V815, Fig. 5c & d). The posterior region of the lower jaw as preserved in AM F54363 displays the suture for the surangular and angular bones. The dentary is robust in form and deep posteriorly, quite unlike the gracile jaw of *Howqualepis*, with the mandibular sensory-line canal arching anteriorly away from the ventral edge to cross the middle of the bone at its anterior extremity. The teeth are not well preserved, but where seen are quite small, unlike the large laniary teeth seen in *Howqualepis*. Ornament consists of horizontally directed linear ridges on the angular and posterior dentary. The ridges are longer along the rest of the dentary. The supra-angular, which was overlapped by the maxilla in life, is devoid of ornamentation.

#### Pectoral girdle

The cleithrum, clavicle, postcleithrum, and the posteroventral part of the supracleithrum are well preserved in AM F54363 (Fig. 1), plus isolated cleithrum and clavicles are seen in the material (ANU V763, V784). An almost complete right supracleithrum is present in ventral view on ANU V972b (Fig. 3c & d) while post-temporals are visible on ANU V2246 (Fig. 4c & d).

The supracleithrum is a large, narrow bone that is only a little smaller than the operculum. It consists of a narrow, posteroventral section that expands anterodorsally towards a broad dorsal end, the edge of which is overlapped by the post-temporals. The path of the lateral line canal has not been preserved and the ornament on the visible section on the holotype consists of posteroventrally directed linear ridges.

The postcleithrum is large when compared to those of other Devonian actinopterygians. It is a robust, crescentic bone with an ornamented region approximately twice the size of the adjacent flank scales. A smooth ventral overlap surface is visible for articulation with the cleithrum.

The cleithrum is of characteristic shape for a Devonian actinopterygian, with an extensive infolded postbranchial lamina and a dorsally pointed apex. There is a well-defined notch for the pectoral fin seen on ANU V763. The clavicle is seen from two specimens (AM F54363, ANU V784) and is similar in shape to those of other Devonian actinopterygian clavicles. The ornamentation consists of fine rostrocaudally directed ridges along the dorsal margin and ventral areas, which are remodelled on the lateral face into lines of large individual pores.

The post-temporals are of typical shape for basal actinopterygians, being paired rhomboidal bones situated

posterior to the skull roof. The anterior margins are straight and are overlain by the extrascapulars. Ornamentation and the sensory canals are not preserved in the only known examples.

#### Body and fins

The body form, visible in the holotype and ANU V972, is elongate and fusiform (Figs 1 & 2). The head of V972 occupies about 25% of the total body length from rostrum to caudal-fin base and the body is four times as long as it is deep. Among Devonian actinopterygians, only *Howqualepis*, *Tegeolepis*, *Kentuckia* and *Cheirolepis* are known to have a similarly elongated configuration, with other taxa possessing deeper, shorter bodies. ANU V972 measures *c.* 13.5 cm in length from the tip of the snout to the caudal inversion. The holotype, measuring 11 cm from the posterior of the lower jaw to the rear of the anal fin, would have been close to 15 cm in length when complete.

The holotype and ANU V972 display well preserved pectoral fins (Figs 1a, 7a & b). They are triangular in shape with *c.* 20–25 primary lepidotrichia, reaching their maximum extent at the seventh row. The lepidotrichia are unsegmented proximally along over 60% of their length and display simple branching along the fin margin. True fringing fulcra are absent; instead, the leading edge of the fin has a row of short, unpaired parallel rays, similar to those found on *Howqualepis*. The previous reconstruction by Young (1989a, fig. 3C) erroneously depicts an extensively segmented pectoral fin, the result of a misidentified partial pelvic fin on ANU V972b.

The pelvic fins (Figs 1a, 2 & 7c) are located equidistantly between the pectoral and anal fins. These are long-based, with *c.* 25–28 rows of segmented lepidotrichia that display very fine terminal branching. The fins are of a low, triangular shape with the length of the seventh, most elongated lepidotrich being roughly equal to the rostrocaudal extent of the fin. Short, spine-like lepidotrichia adorn the leading edge.

The anal fin (Figs. 2a & 7d) is well preserved only in the holotype. It is large and long-based, consisting of a large anterior triangular area followed by a low posterior flange. The preserved extent of the holotype fin displays over 50 lepidotrichia although the posterior edge of the fin is not preserved. A cutwater of short lepidotrichia is present on the leading fringe.

Evidence on the dorsal and caudal fins is only provided by the incomplete examples on ANU V972. The dorsal fin is represented by isolated fin radialia, indicating an approximate position slightly anterior to the start of the anal fin. No information is available regarding the size or shape of the dorsal fin. The heterocercal caudal fin is preserved as a series of over fifty incomplete primary lepidotrichia arising from the ventral surface of the caudal region of the body. No terminal elements of the fin have

been preserved, preventing an accurate assessment of its shape.

#### Scales and squamation

No specimen displays complete, undisrupted body squamation although well-preserved scales in articulation are present on the visible flank of the holotype which displays about 32 vertical scale rows between the cleithrum and the anterior edge of the anal fin. The scales are rhomboidal with anterior flank scales possessing a well developed peg and socket articulation. They are ornamented on the free field with diagonal bony ganoine ridges that extend to the posterior scale margin as a series of serrations. The ridges are simple, linear structures lacking pores or raised striae. A description of the scales will be presented here falling into regions conforming to the pattern of squamation described by Esin (1990) and used in Trinajstić (1999).

Zone A (anterior lateral flank scales, Fig. 8a & b): Scales are rectangular with height exceeding length by about 1.5 times. The ventral edge is straight with an anteroventral corner having a 40 degree dorsal inclination. Well-developed peg and socket joint. Up to fourteen posterior ganoine serrations.

Zone B (mid lateral flank scales, Fig. 8d): Scales are nearly square with height only slightly greater than length. Well-developed peg and socket joint. Up to twelve posterior ganoine serrations.

Zone C (posterior lateral flank scales, Fig. 8c): Scales rectangular and twice as long as high. Peg and socket joint absent or poorly developed. Up to seven posterior ganoine serrations.

Zone D (caudal scales, Fig. 8f): Scales rhomboid, becoming increasingly elongate on the caudal fin of ANU V972a. No peg and socket joint. Posterior serrations few (at most three) or absent on the caudal lobe.

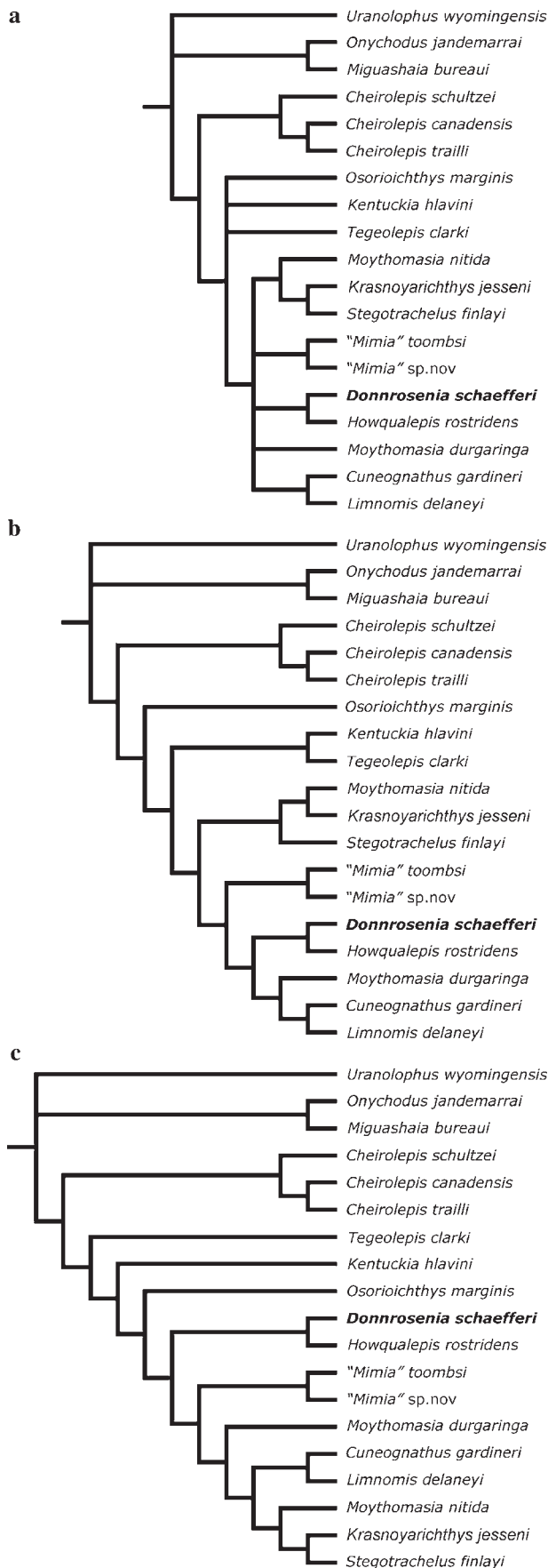
Zone E (dorsal scales, Fig. 2): Visible only as poorly preserved examples on ANU V972. Scales are rhomboidal, about twice as long as high.

Zone F (ventral scales, Figs 1 & 2): Scales are elongate, over 2.5 times as long as high. Weakly developed peg and socket joint. At least four posterior serrations.

Zone G (scales adjacent to dorsal fin base, Fig. 2): Visible only as poorly preserved examples on ANU V972. Scales are rhomboid to sub-oval in shape. No peg and socket joint.

Zone H (scales adjacent to anal fin base, Fig. 8e): Scales are very elongated, up to four times longer than tall. No peg and socket joint. Two or three posterior serrations.

Only a few fulcral scutes have been preserved, mostly as disarticulated elements (Fig. 8h). They are relatively small



and only slightly larger than the neighbouring scales. Three ventral scutes are visible immediately anterior to the holotype anal fin (Fig. 8g). These are disc-shaped structures that lack serrations with the posterior scute being more elongated. These seem to be the anteriormost fulcra in the ventral series.

Narrow basal scutes are visible anterior to the dorsal fin of ANU V972; however, their absence near the head of this specimen along with the skull elements of ANU V769, V770 and V781 suggests that the dorsal series did not extend to the skull. Caudal fulcra, visible on ANU V972 and V771 (Fig. 8f) are narrow and spinous with heavy overlap between the individual scutes.

## Discussion

### *Donnrosenia* and early descriptions of Antarctic 'palaeoniscids'

Using the articulated material collected in 1970–71 we can reassess the earlier descriptions of isolated palaeoniscoid scales by Woodward (1921) and White (1968). Woodward (1921, p. 60) described four scales and a possible dentary belonging to a 'palaeoniscid' from Granite Harbour, which he considered to 'closely resemble scales from the Upper Devonian of North America ... referred provisionally to *Rhadinichthys*'. Gardiner (1963) considered such scales to belong to *Moythomasia*, while White (1968, p. 24) noted similarities to the scales of Carboniferous genera, and considered Woodward's material, and isolated scales from the two localities he studied, to each belong to separate species (called Palaeoniscids type I, II, III). However, the type I and type II material is similarly preserved in a dark shale of a similar lithology to the material from the lower part of the Aztec Siltstone at Mount Crean. This agrees with evidence from other groups that the moraine material at Granite Harbour was derived from basal beds of the Aztec Siltstone (Young 1988).

The 'Palaeoniscid type III' of White (1968) was based on impressions on a single sample of sandstone, but these are poorly preserved and it is not evident that they represent actinopterygian remains (GCY, personal observation). They are rectangular elements up to 5 mm tall, about 1.5 times higher than long, with no visible peg and socket joint. There are at least 14 horizontal ridges, but the posterior margin is smooth with no protruding serrations.

**Fig. 11.** **a.** Strict consensus tree of two most parsimonious cladograms depicting Devonian actinopterygian relationships. **b.** Cladogram whose topology suggests an exclusive Eastern Gondwanan clade of actinopterygians during the Givetian–Frasnian, with Euramerican representatives appearing in the Famennian. **c.** Alternative cladogram depicting the Eastern Gondwanan Devonian Actinopterygians as successive outgroups to a diverse Northern Hemisphere assemblage.

Apart from these, most of the previously described Devonian actinopterygian material from Antarctica can be provisionally referred to *Donnrosenia*. Of the material figured by Woodward (1921, pl. 1), P.12589 (his fig. 30) is a ventral scale (Zone F), P.12576 (fig. 32) is a scale from near the base of the anal fin (Zone H), and the rhombic scale P.12563 (fig. 31) is probably from the anterior part of Zone D of a small individual. P.12591 (fig. 34) seems to conform to the dentary of *Donnrosenia* although it is difficult to be certain based on the small drawing.

Of the scales reported by White (1968), the type 1 material (which includes P.12563, now re-numbered as P40673) consists of rhombic scales lacking pegs or posterior serrations; these could represent Zone D squamation of a small individual. Type 2 scales, with well-developed pegs on the dorsal margin, roughly square shape and prominent posterior serrations (P49174, P49175) could be Zone B flank scales.

#### Phylogenetic analysis

A preliminary phylogenetic analysis of 19 taxa and 71 characters was conducted using PAUP v.4.0b10 (for Macintosh) and MacClade 2.0 (see Appendix). The taxa comprised 16 Devonian actinopterygians known from reasonably complete material, and an outgroup of three Devonian sarcopterygians. The study was based on that presented in Friedman & Blom (2006), which was concerned only with the interrelationships of Devonian actinopterygians, excluding younger taxa. Our character matrix (Fig. A1) was based on the 54 characters of Friedman & Blom (2006), with 17 additional characters, largely restricted to the dermal osteology. As detailed neurocranial information among Devonian taxa is currently restricted to those forms from the Gogo Formation, these characters are not considered. Future studies will incorporate a wider selection of taxa as well as neurocranial anatomy.

Data obtained from recently discovered Gogo material is included; an undescribed second species of “*Mimia*”, plus details from freshly prepared complete specimens of *Moythomasia durgaringa*. New data is also forthcoming regarding *Stegotrachelus finlayi* (Brian Swartz, personal communication 2007) and revised aspects of the anatomy of this taxon that contradict previous reconstructions (e.g. Gardiner 1963, fig.12) are coded as unknown pending the publication of these findings. The revised coding rendered characters 12 and 14 of Friedman & Blom’s (2006) matrix parsimony uninformative. All characters were treated in the Acctran mode and analysed using a branch and bound search algorithm.

A strict consensus of two trees was created of 180 steps with a consistency index of 0.4722 (0.4663 with removal of parsimony uninformative characters), a homoplasy index of 0.5243 (0.5337 with removal of parsimony

uninformative characters), a retention index of 0.6507, and a rescaled consistency index of 0.3073 (Fig. 11a). Both trees grouped *Howqualepis* and *Donnrosenia* as sister taxa, on which basis we have united them in one family.

Beyond the consistent similarities between certain taxa (i.e. *Limnomis* + *Cuneognathus*, *Howqualepis* + *Donnrosenia*) the broader relationships among stem actinopterygians remain ambiguous and poorly resolved. This could be an indication that many key early actinopterygian taxa are currently missing from the fossil record, unsurprisingly given the absence of articulated remains from Early Devonian sediments. Alternatively, it could suggest an extremely rapid diversification event amongst the Devonian actinopterygians shortly after they diverged from the rest of the Actinopterygii.

In the first of our trees (Fig. 11b) *Donnrosenia* and *Howqualepis* are united by seven unambiguous synapomorphies: characters 13, contact between the intertemporal and supratemporal anterior to the frontal/parietal contact (CI = 0.5, state change from 0 to 1); 22, reflexed anterior tip on dentary (0.25, 0 to 1); 37, absence of true fringing fulcra (0.500, 2 to 1); 44, extensive unsegmented lepidotrichia on the pectoral fins (0.5, 1 to 2); 45, long based pelvic fin insertion (0.5, 0 to 1); 48, few dorsal ridge scales anterior to the dorsal fin (0.5, 2 to 1); and 68, elongate body form (0.5, 1 to 0).

In our alternative tree (Fig. 11c), this relationship is supported by only four unambiguous synapomorphies: characters 13, 22, 44 and 54, a T-shaped dermosphenotic with a long posterior ramus (0.5, 1 to 2). This evidence forms the basis for our diagnosis of the family Howqualepididae presented above.

The sister relationship between *Howqualepis* and *Tegeolepis* resolved in Friedman & Blom (2006) was not supported in either of our trees. Both trees also recovered a novel clade consisting of *Stegotrachelus*, *Krasnoyarchthys* and *Moythomasia nitida*, henceforth referred to as “the *Stegotrachelus*-grade assemblage”. The Gogo form *Moythomasia durgaringa* did not form a clade with the European *Moythomasia nitida*, nor did it fall within the *Stegotrachelus*-grade assemblage, indicative of notable dissimilarities in the dermal skeleton of the two taxa as revealed by newly prepared material from the Gogo Formation (BC, in preparation).

While the interrelationships of Devonian Actinopterygii remain poorly resolved, it is notable that the topology of the first of the recovered trees nested *Howqualepis* + *Donnrosenia* amongst the Western Australian Gogo taxa (*Moythomasia durgaringa* and “*Mimia*”) as well as the small, short-bodied *Cuneognathus* and *Limnomis*, suggesting a novel clade exclusive of the Northern Hemisphere Devonian actinopterygians with the exception of the aberrant short-bodied Euramerican freshwater forms. The *Stegotrachelus*-grade assemblage forms the sister group with this clade.

If this is an accurate representation of evolutionary relationships, then the Middle to Late Devonian ray-finned fishes of eastern Gondwana could represent an endemic radiation of both marine and freshwater forms descended from a single ancestor that originated in the Northern Hemisphere. This clade would appear to be absent from Euramerica until the appearance of *Cuneognathus* and *Limnomis* in the late Famennian.

In the first tree, this primarily Gondwanan clade is supported by four unambiguous synapomorphies: characters 57, a snout shaped like a sharp bump (CI = 1.0, state change of 0 to 1); 61, possession of a quadratojugal (0.333, 0 to 1); 66, a functionally homocercal caudal fin, a state that is reversed in *Cuneognathus* + *Limnomis* (0.5, 0 to 1); and 67, an anterodorsal process on the suboperculum (0.333, 0 to 1).

The Gondwanan clade is not supported by the second tree (Fig. 11c). Instead, *Moythomasia durgaringa*, “*Mimia*”, and the *Howqualepis* + *Donnrosenia* clade form successive outgroups to a novel clade comprising the *Stegotrachelus*-grade assemblage along with *Cuneognathus* + *Limnomis*. This result would suggest much less regional endemism in the Devonian evolution of basal actinopterygians than is suggested by the first tree. The possibility of an endemic Gondwanan radiation of Devonian stem-actinopterygians deserves further investigation, and a more robust phylogenetic study incorporating a wider selection of taxa is currently in progress.

#### Biogeographical implications

That *Donnrosenia* should display such a close relationship with the Australian *Howqualepis* to the exclusion of other actinopterygians of a similar age reinforces an already strong biogeographical affinity between the Middle Devonian fossil fish faunas of southern Victoria Land, Antarctica, and south-eastern Australia. Strong similarities in key taxa of antiarchs (Young 1988), phyllolepid (Young & Long 2005), acanthodians (Long 1983, Young 1989b, Young & Burrow 2004), sharks (Young 1982, 2007, Long & Young 1995) and dipnoans (Long 1992, 2003) have already been well documented.

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APPENDIX

Characters and character states - Characters 1–54 are effectively unmodified from those presented in Friedman & Blom (2006) except for character 23 where possessing more than 2 infradentaries has been reduced to a single rather to two states, character 28 which has been expanded to incorporate states implemented in Gardiner *et al.* (2005, Character 10) and character 54 in which the presence of a T-shaped dermosphenotic has been expanded into two states based on the length of the posterior ramus. Characters 55–63 and 69–71 are based on those presented in Cloutier & Arratia (2004) that were deemed applicable with regards to the taxa examined. The remaining additional characters were formulated based on examination of original and published material. Unknown characters are depicted as “?” in the matrix table. Inapplicable characters are depicted as “-”. Multistate coding is represented as “\” (0/1) and “/” (1/0).

1. Premaxillae, contact at midline: present (0); absent (1).
2. Premaxillae, shape of: wider than deep (0); depth approximately equal to width (1).
3. Postrostrals: present (0); absent (1).
4. Single median dermal bone contacts premaxillae ventrally, nasals laterally, and frontals or postrostrals posteriorly: absent (0); present (1).
5. Transverse ornamentation on medial rostral or dermal cover of ethmoid region: absent (0); present (1).
6. Posterior nostril in complete communication with orbital fenestra: absent (0); present (1).
7. Premaxillae, contributes to posterior nostril: absent (0), present (1).
8. Number of bones carrying supraorbital canal between premaxilla and frontals: multiple (0); single (1).
9. Pineal foramen: present (0); absent (1).

	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	4			
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	
<i>Cheirolepis canadensis</i>	?	0	0	0	?	?	?	?	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	?	0	0	/	1	0	0	1	0	0	1	0	0	0		
<i>Cheirolepis schultzei</i>	0	0	0	0	?	?	?	0	0	1	0	2	-	-	0	0	1	0	1	1	1	1	0	0	0	?	0	?	/	?	0	0	1	0	0	1	?	?	0	0	
<i>Cheirolepis trailli</i>	0	0	0	0	?	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	0	0	0	?	0	0	1	1	0	0	1	0	0	1	0	0	1	0	
<i>Cuneognathus gardineri</i>	?	?	1	1	1	?	?	?	1	0	1	2	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	/	1	0	0	1	0	1	2	1	1	?	?
<i>Donnrosenia schaefferi</i>	?	1	1	1	0	?	?	?	1	0	0	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	/	0	1	1	0	0	0	1	0	?	?	1
<i>Howqualepis rostridens</i>	1	0	1	1	0	1	1	1	0	0	2	0	1	0	0	1	0	1	1	1	0	1	1	1	0	1	1	1	/	1	1	1	0	0	0	1	0	1	?	?	
<i>Kentuckia hlavini</i>	?	?	1	1	0	?	?	?	1	1	2	1	0	1	0	?	0	1	0	?	?	0	?	0	0	0	2	?	/	0	0	1	1	0	0	0	2	0	1	?	
<i>Krasnoyarchichthys jesseni</i>	?	?	?	?	?	?	?	?	?	1	2	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	/	0	1	1	0	0	0	2	0	0	?	?
<i>Limnomis delaneyi</i>	1	1	1	1	1	0	1	0	1	0	2	0	0	0	?	0	0	1	0	?	?	?	?	?	?	?	?	?	/	0	0	1	0	0	1	2	1	1	?	?	
"Mimia" toombsi	0	1	1	0	1	1	1	0	0	0	2	0	0	0	0	0	1	0	0	?	?	0	2	0	1	0	0	0	1	/	1	1	1	0	0	0	2	0	1	1	?
"Mimia" sp.nov	0	1	1	1	0	1	1	1	0	0	2	0	0	0	0	0	0	1	0	?	?	0	2	0	1	0	?	0	1	/	1	1	1	0	0	0	2	0	1	1	?
<i>Moythomasia durgaringa</i>	1	1	1	1	0	1	0	1	0	1	2	0	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	1	2	0	1	1	0	0	0	2	0	1	1	?
<i>Moythomasia nitida</i>	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?	2	0	1	1	0	1	0	2	0	1	1	?
<i>Osorioichthys marginis</i>	0	0	1	1	?	0	1	1	1	0	1	0	0	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	/	?	?	?	?	?	?	?	?	?	?	?	
<i>Stegotrachelus finlayi</i>	0	?	1	1	0	1	0	1	0	1	2	?	?	?	?	0	0	0	0	1	1	0	?	?	?	?	?	?	/	0	1	1	0	0	0	2	0	0	?	?	
<i>Tegeolepis clarki</i>	0	0	1	1	0	?	?	?	1	1	0	1	0	0	?	0	0	0	?	?	?	0	1	1	0	0	1	2	1	/	1	1	1	1	0	0	0	?	?	?	?
<i>Onychodus jandemarrai</i>	0	0	0	1	0	0	0	0	1	0	0	0	-	?	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
<i>Miguashaia bureauui</i>	0	0	?	?	?	?	?	?	0	1	0	0	-	?	0	?	?	?	?	?	?	0	1	2	0	0	0	0	?	?	0	0	0	0	-	0	0	0	?	?	?
<i>Uranolophus wyomingensis</i>	?	?	?	0	0	-	0	?	?	1	1	2	?	-	?	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?	0	0	0	0	?	?	?	?	?	?	?

Fig. A1. Character matrix for Devonian osteichthyans used in the cladistic analysis.

10. Parietals (sarcopterygian postparietals): rectangular (0); subquadrate (1).
11. Relative lengths of frontals and parietals (sarcopterygian parietals and postparietals): roughly equal size (0); frontal much longer than parietal (1).
12. Relative lengths of supratemporal and intertemporal: intertemporal shorter than supratemporal (0); intertemporal of equal or greater length than supratemporal (1).
13. Contact between intertemporal and supratemporal anterior to that between the frontal and parietal: absent (0); present (1).
14. Contact between intertemporal and nasal excludes dermosphenotic from contact with frontals: absent (0); present (1).
15. Number of paired extrascapulars: 1 pair (0); 2 pairs (1).
16. Lacrimal, anterior expansion of: absent (0); present (1).
17. Jugal, notch in anterior margin of: absent (0); present (1).
18. Jugal and maxilla separated by non-canal bearing ossifications: absent (0); present (1).
19. Accessory operculum: absent (0); present (1).
20. Lateral gulars: large with rounded posterolateral profile (0); equal in area to three or few branchiostegal rays, with prominent posterior and lateral angles.
21. Course of mandibular canal: traces ventral margin of lower jaw along entire length (0); arches dorsally in anterior half of jaw (1).
22. Dentary with reflexed distal tip: absent (0); present (1).
23. Infradentaries, number of: more than two (0); two (1); one (2).
24. Enlarged series of parasymphysial teeth on dentary: absent (0); present (1).
25. Acrodin on teeth: absent (0); present (1).
26. Remodelled porous ganoine on lower jaw: absent (0); present (1).
27. Ossification of mentomeckelian region: present (0); absent (1).
28. Ascending process: absent or incipient, confined between basipterygoid process and incisure (0); terminates below spiracular canal (1); meets mouth of spiracular canal (2). (G,S&M)
29. Parasphenoid multifid anteriorly: no (0); yes (1).
30. Ganoine: absent (0); nonprismatic (1); prismatic (2).
31. Number of scale rows: fewer than 60 (0); greater than 60 (1).
32. Scales with peg and socket articulation: absent (0); present (1).
33. Anterodorsal extension of scales: absent (0); present (1).
34. Scales: macromeric (0); micromeric (1).
35. Scales with well developed pores on ganoine surface: absent (0); present (1).
36. Curved ridges along anterior margin of scales: absent (0); present (1).
37. Fringing fulcra: absent (0); unpaired, modified lepidotrichs (1); true paired fringing fulcra (2).
38. Pelvic fins: present (0); absent or greatly reduced (1).
39. Presupracleithrum: absent (0); present (1).
40. Horizontal plate of scapulocoracoid: absent (0); present (1).
41. Anterior rays embrace protopterygium: no (0); yes (1).
42. Metapterygium elongated relative to preceding radials: no (0); yes (1).
43. Pectoral fins inserts: into basal lobe (0); directly into lateral flank (1).
44. Pectoral fin segmentation: anteriormost pectoral lepidotrichia segmented proximally (0); segmented only distally or unsegmented (1); all lepidotrichia with long, unsegmented regions (2).
45. Pelvic fin insertion: short-based (0); long-based (1).
46. Epichordal lobe of caudal fin: present (0); absent (1).
47. Fulcra/ridge scales along dorsal ridge of caudal fin: present (0), absent (1).
48. Dorsal ridge scales anterior to dorsal fin: absent (0); few limited to region immediately anterior to fin (1); dorsal fulcra from dorsal fin to occipit. (2).
49. Ventral ridge scales between hypochordal lobe of caudal fin and anal fin: absent (0); present (1).
50. Ventral keel scales anterior to anal fin: absent (0); few, immediately anterior to anal fin (1); many, extending below abdominal region.
51. Relative positions of anal and (second) dorsal fin; anal shifted anteriorly relative to dorsal (0); fins opposite one another (1); anal shifted posteriorly relative to dorsal (2).
52. Dorsal fins. number of: two (0); one (1).
53. Dermohyal: absent (0); present (1).
54. T-shaped dermosphenotic: absent (0); present, posterior ramus short, less than 1/3 rostrocaudal length of entire bone (1); present, posterior ramus long, at least 1/3 of length of bone. (2).
55. Premaxillae, contributes to orbital margin: false (0); true (1).
56. Premaxillae, relation to lacrimals: posterior contact with lacrimals (0); ventral contact (1); not in contact (2).

57. Snout shape: rounded (0); sharp bump (1); pointed snout (2).
58. Rostral, shape of median: widening anteriorly (0); equal anteriorly and posteriorly (1); narrowing anteriorly (2).
59. Intertemporal, contact with parietal/post-parietal: absent (0); present (1).
60. Intertemporal, contact with nasal: absent (0); present (1).
61. Quadratojugal: present (0); absent (1).
62. Operculum, shape of: first axis longer than second axis (0); both axes roughly equal (1); second axis longer than first axis (2).
63. Operculum, position of: dorsal to preoperculum (0); posterior to preoperculum (1).
64. Operculum, relative size: at least twice as high as suboperculum (0); less than twice the height of suboperculum (1).
65. Lateral extrascapular in alignment with dorsal margin of the operculum and is not separated from it by other ossifications. false (0); true (1).
66. Caudal fin, shape of: hypochordal lobe shorter than upper lobe (0); hypochordal lobe almost equal or equal to upper caudal lobe Tail is functionally homocercal. (1).
67. Suboperculum, anterodorsal process: The suboperculum is considered to have an anterodorsal process if the anteriormost section of the bone in articulation is a sharp point where the dorsal and anterior faces meet at an angle of 40 degrees or less. absent (0); present (1).
68. Body form: elongate, entire length at least 4 times greater than height (0); stout, entire length less than 4 times greater than height (1).
69. Single median extrascapular: present (0); absent (1).
70. Tabular: present (0); absent (1).
71. Branchiostegal rays: absent (0); present (1).