Revision and description of the actinopterygian fishes of Devonian Eastern Gondwana.

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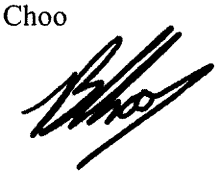
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Author's Disclaimer

This manuscript comprises extensive original research on Devonian fossil actinopterygian fishes combined with the following academic collaborations: Chapter 2 is based on a manuscript co-written with Dr. John Long and Dr. Gavin Young (Long, Choo & Young, 2008), to which I contributed to c.50% of the text and c.95% of the figures. Chapter 4 represents a modified version of a manuscript co-written with Dr. John Long and Dr. Kate Trinajstic (Choo, Long, & Trinajstic, 2009) to which I contributed over 90% to both the text and illustrations.

Many thanks to my collaborators for making this work possible.

Brian Choo



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Abstract

This thesis examines the total diversity of fossil actinopterygian or ray-finned fishes of Devonian Gondwana. The bulk of the material comprises newly prepared specimens from the famous Late Devonian (Frasnian) Gogo Formation of Western Australia, much of which was collected in the 2005 field season. Also examined are specimens from the Middle Devonian deposits of the Aztec Siltstone, Antarctica; the Bunga Beds of New South Wales and the Mt Howitt fossil sites of Victoria.

With the benefit of this new material, I describe new several new genera and species of Devonian actinopterygians and clarify the descriptions of previously described forms. Although still a relatively sparse ichthyofaunal component, the Devonian diversity of the Gondwanan ray-fins was much greater than hithero recognised, with at least five species present in the Gogo Formation. With an improved understanding of early ray-finned anatomy, characters previously considered primitive or of special diagnostic value are re-evaluated.

Newly prepared material from the Aztec Siltstone of Antarctica and the Bunga Beds of New South Wales represent forms similar to *Howqualepis rostridens* from the Givetian of Victoria. The Antarctic form is named *Donnrosenia schaefferi* while the Bunga Beds fossil is questionably assigned as a congener of *Howqualepis.* The similarity of freshwater fossil actinopterygians throughout southeastern Australia and South Victoria Land, Antarctica supports previously described macrovertebrate evidence for a regionally endemic ichthyofauna in the Middle Devonian. Additionally, the pectoral fin of *H. rostridens* is redescribed and is broader in shape and less extensively unsegmented than previously recognised.

Of the five Gogo taxa, the genus *Mimia* Gardiner and Bartram (1977) is renamed *Mimipiscis* nom. nov. due to preoccupation. Newly available material of the type species, *Mimipiscis toombsi*, reveals ontogenetic variability in ornamentation and new data on the parasphenoid and shape of the caudal fin. A second form, *Mimipiscis bartrami* sp. nov., differs from the type species in details of the body shape, squamation, snout, suboperculum and parasphenoid. Two new genera, *Gogosardina* and *Pickeringia* gen. nov. are described. *Gogosardina* is a highly elongate form with a unique arrangement of postrostrals which form the anterior margin of the pineal opening. *Pickeringia* gen. nov. possesses a highly distinctive spinose ornamentation over the skull, scales and lepidotrichia and extremely large vestibular fontanelles. Specimens of *Gogosardina* and *M. bartrami* sp. nov. are known to possess conodont elements within the body cavity suggesting diet and hunting strategies.

A phylogenetic analysis of Devonian ray-fins suggests a limited degree of regional endemism in Eastern Gondwana with unique families present on the Gogo reefs and freshwater habitats in southeastern Australia and Southern Victoria Land, Antarctica. The close similarity of the actinopterygian faunas of Antarctica, New South Wales and Victoria adds to an already large body of evidence suggesting a regionally endemic Gondwanan ichthyofauna in the Middle Devonian.

DEDICATION

This thesis is dedicated to

PEK CHOY AU

1907-1996

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Chapter 1. Introduction

The Actinopterygii, or ray-finned fishes, possess a greater extant diversity than any comparable (subclass level) grouping of modern vertebrates (Fig 1.1). Yet the origins, early diversity and early evolution of this important group of animals remain poorly understood. Fossil actinopterygians tend to be sparse components of pre-Carboniferous fish faunas and their delicate anatomy usually results in poor levels of preservation. At the start of 2006, the Devonian record of Gondwanan actinopterygians was restricted to only three taxa based on articulated remains: *Howqualepis rostridens*, *Mimia toombsi* and *Moythomasia durgaringa*. This gave the impression of scarcity in their southern distribution during the Devonian, contrasting with the abundance and diversity of contemporaneous Gondwanan placoderms and sarcopterygians. In recent decades, a significant amount of fossil material has been recovered from Western Australia, southeastern Australia and Antarctica suggesting a greater variety of Devonian actinopterygians than has previously been recognised. In this project, these new taxa are described, descriptions of established fossil taxa are clarified and the interrelationships of the earliest ray-finned fishes are examined with input from anatomical data provided by new and previously described material.

1.1 Previous work on Gondwanan Devonian ray-finned fishes

The first record of Devonian Gondwanan actinopterygians was for specimens recovered from the glacial moraine at Granite Harbour, Antarctica during the British Antarctic 'Terra Nova' expedition of 1910-13. Among the fossils of several kinds of fishes were isolated 'palaeoniscid' scales that were assigned to 'Order Actinopterygii' by Woodward (1921). The first *in situ* fossil fish material was collected during the Trans-Antarctic Expedition of 1955-58 and included scales and a partial dentary that were considered similar to *Moythomasia*

(White 1968). Despite extensive collections in the 1960s-70s resulting in several articulated specimens, nothing further has been published on the Antarctic material beyond a preliminary life-reconstruction and a photograph of a skull-roof presented by Young (1989a).

The first putative record of Devonian actinopterygians from Australia was recorded by Schultze (1968) who described the scales of *Ligulalepis toombsi* from the Lower Devonian Taemas-Wee Jasper limestones of New South Wales. A partial skull roof and neurocranium was subsequently referred to the genus that was notable in the presence of an eyestalk (Basden and Young 2001). The classification of *Ligulalepis* is currently under scrutiny with recent analyses resolving the taxon as a stem-osteichthyan (Botella et al. 2007, Friedman 2007) or a stem-sarcopterygian (Zhu et al. 2009).

The well preserved fossil ichthyofauna of the Gogo Formation of Western Australia includes the most completely known Devonian actinopterygians. Based on material collected in the 1960s and transported to the British Museum of Natural History (now the Natural History Museum, London), two taxa of Gogo ray-finned fishes were initially described, based mainly on the neurocrania (Gardiner and Bartram 1977) with details of the dermal anatomy presented later in Gardiner (1984). One of these, *Moythomasia durgaringa* (Fig 1.2a) was placed in a widespread genus with representatives in the Late Devonian of Latvia (Gross 1950), Germany (Jessen 1968) and the United States (Gardiner 1963). The second taxon, *Mimia toombsi* (Fig 1.2b) was assigned to a new genus, endemic to the Gogo Formation. (In Chapter 5, the genus *Mimia* is revised to *Mimipiscis*). The squamation of both taxa was described in detail by Trinajstic (1999a,1999b), with isolated scales of these forms being recorded from the Gneudna Formation of the Upper Devonian, Southern Carnarvon Basin in Western Australia. At least one of the Gogo actinopterygians has featured in most

subsequent phylogenetic studies of early ray-finned fishes (Cloutier and Arratia 2004, Friedman and Blom 2007, Gardiner and Schaeffer 1989, Gardiner et al. 2005, Long 1988, Schultze 1992, Schultze and Cumbaa 2001).

Long (1988) provided an extensive description of *Howqualepis rostridens* from the lacustrine, Givetian, Mount Howitt locality in Victoria. Known from multiple complete specimens, this remains the only well-preserved basal actinopterygian from the continental Devonian Lambian facies of southeastern Australia. A phylogenetic analysis resolved this form either as the sister-taxon to *Moythomasia* + Actinopteri or as a more basal form. A recent analysis incorporating the majority of Devonian taxa places *Howqualepis* as the sister-taxon of *Tegeolepis* from the Famennian of Ohio (Friedman and Blom 2006).

1.2 Aims of this project

1.2.1 Redescription of established taxa of Gogo actinopterygians

Mimia toombsi was described in detail by Gardiner (1984). However, newly prepared specimens reveal previously unreported features of the tail and parasphenoid. A specimen, larger than any previously reported individual of *Mimia,* was noted in the collections of the Western Australian Museum mislabelled as *Moythomasia.* This specimen is instead referrable to *Mimia toombsi* and suggests ontogenetically variable features of the ganoine ornamentation on the head, pectoral girdle and scales. From these initial observations it was determined that a redescription of the genus was required.

Some aspects of the dermal osteology of *Moythomasia durgaringa* have only received a cursory examination when compared with the detailed descriptions of the neurocranium

(Gardiner and Bartram 1977, Gardiner 1984). No full reconstruction of the fish, aside from a simplified lateral view of the skull, has ever been presented. Examination of newly prepared material allows for the first complete body reconstruction of this animal and indicates that amendments to the original description are required.. An examination of *Moythomasia* specimens held in Stockhom and London was conducted to test the congeneric status of the Australian and European species.

1.2.2 Diagnosis of novel taxa of Devonian actinopterygian

At least three undescribed taxa of basal actinopterygian are present within fossil collections from the Gogo Formation. One new taxon comprises a highly gracile, small-scaled form known from a handful of specimens collected between 1972 to 2001. Another taxon is a more robust form with unusually spinose ornamentation on the dermal surfaces, represented by a single articulated fossil skeleton recovered from Paddys Valley in 2001. Newly collected examples of *Mimia,* as well as examinations of existing collections, reveals an additional species of actinopterygian currently incorporated within the taxon *Mimia toombsi.* The description and diagnosis of all three novel taxa is undertaken.

The first articulated and potentially diagnostic actinopterygian fossils from the Devonian of Antarctica were recovered in the summer of 1970-71 as part of a Victoria University of Wellington Antarctic Expedition. Additional material, including fairly complete specimens, was collected on subsequent expeditions (1976-77, 1988-89, 1991-92) from new sites in the Cook Mountains (Woolfe et al. 1990; Long and Young 1995).

An articulated actinopterygian specimen was recently collected from the Devonian Bunga Beds near Eden, NSW. The specimen includes sections of postcranial squamation and all of

the fins except for the dorsal. An incomplete pectoral girdle and several branchiostegal rays are also preserved.

An examination of the collections of the Naturhistorischen Reichsmuseum, Stockholm, has revealed additional material of the form that was briefly described by Jessen (1968) as *Moythomasia* cf.*striata* from the Oberer Plattenkalk, Germany. Sufficient material was identified to attempt a full description and reconstruction of this taxon.

1.2.3 Redescription of Pectoral fin anatomy of *Howqualepis rostridens*

The actinopterygian *Howqualepis rostridens* from the Middle Devonian of Mount Howitt, Victoria was described by Long (1988). The initial description describes the pectoral fin as composed almost entirely of long, unsegmented lepidotrichia. A re-examination of the material presented by Long reveals extensive distal and posterior segmentation on the pectoral fins of multiple specimens, warranting a re-examination of this taxon.

1.2.4 Clarifying the relationships of Devonian actinopterygians

The only recent study devoted to interrelationships of the earliest ray-finned fishes was conducted by Friedman and Blom (2006) who analysed thirteen ingroup taxa, representing the totality of all reasonably well known Devonian actinopterygians. This resulted in a number of novel arrangements, including the pairing of *Howqualepis* and *Tegeolepis* as sister-taxa. It also confirmed a close kinship between the Gogo *Moythomasia durgaringa* and the European *M. nitida.*

With the benefit of the material described in this project, an expanded character matrix was assembled based on the Friedman and Blom (2006) study. A phylogenetic analysis, with

the aim to clarify the relationships of the earliest (mainly Devonian) actinopterygians, notably to test the degree of regional endemicity among Gondwanan middle Palaeozoic ray-finned fishes is undertaken.

1.3 Thesis organisation

This thesis has been constructed as a compilation of scientific publications, each representing a single chapter and partially rewritten to form an integrated work. Chapter 2 entails the description of *Donnrosenia schaefferi*, a new genus and species of basal actinopterygian from the Middle Devonian Aztec Siltstone of Antarctica. It also erects a new endemic Gondwanan family, the Howqualepididae. Chapter 3 describes the form from the Bunga Beds of NSW, questionably assigning it to *Howqualepis*, as well as providing additional information on the pectoral fin of *Howqualepis rostridens.* Chapter 4 details *Gogosardina coatesi*, the first new Gogo actinopterygian to be described in thirty years. Chapter 5 revises the Gogo genus *Mimia*, now renamed *Mimipiscis*, and adds a second species to that genus. The preliminary cladistic analysis presented in Chapter 3 is greatly refined. Chapter 6 provides a wealth of new data on *Moythomasia.* An emended diagnosis for this important genus is proposed based on the examination of the genotype material in Stockholm. The Gogo *M. durgaringa* is re-examined and the first rigorous full-body reconstruction is presented. A new species of *Moythomasia* is also erected based on material from the early Frasnian Bergisch-Gladbach site while doubtful taxa referred to the genus are briefly examined. Chapter 7 provides a preliminary description of an additional novel genus and species of Gogo actinopterygian. Chapter 8 summarises and discusses the findings of the preceding chapters, including a phylogenetic analysis of the interrelationships of the Devonian Actinopterygii.

1.4 An introduction to the earliest actinopterygians

The Osteichthyes (bony fishes) are divided into two main subdivisions, the Actinopterygii (ray-finned fishes) and the Sarcopterygii (lobe-finned fishes and tetrapods). With close to 29,000 extant species (Nelson 2006), the actinopterygians comprise the vast majority of modern piscine (= non-tetrapod vertebrate) diversity (Fig 1.1).

Living actinopterygians comprise three distinct lineages (Fig 1.3): the archaic Polypteriformes (bichirs) and Acipenseriformes (sturgeons and paddlefish) alongside the derived and exceptionally speciose Neopterygii. The Polypteriformes retain archaic features including rhombic ganoid scales and fleshy pectoral fin-bases, yet their fossil record only extends back to the Late Cretaceous (Gayet et al. 2003). They are characterised by unique dorsal fin-spine morphology, fusion of the cranial bones and aspects of the pectoral fin skeleton and musculature (ibid). The Acipenseriformes appear in the Jurassic and are characterised by fusion of the premaxilla, maxilla and dermopalatine and a distinctive anterior symphysis of the palatoquadrate (Bemis et al. 1997, Grande and Bemis 1996). The Neopterygii, which appear in the Permian, are characterised by a suite of features contributing to a lightened skeleton and increased sophistication of the jaw mechanism (Patterson 1973, Bartram 1977).

In contrast to the abundance and variety of modern ray-finned fishes, actinopterygians are a minor component of most Devonian fossil assemblages, with only about a dozen genera based on articulated remains described as of 2006.

This study focuses on a variety of fossil taxa from the Middle-Late Devonian which represent some of the earliest known members of the Actinopterygii. Traditionally, all

Devonian actinopterygians have been placed in a grouping known as the Palaeoniscoidei (Goodrich 1904, Gardiner 1967, Pearson 1982), now recognised as representing a paraphyletic grade of basal ray-finned fishes (Gardiner 1984, Patterson 1982, Long 1988). Unambiguous and universally recognised actinopterygian fossils appear in the Middle Devonian (Eifelian-Givetian) where they are largely restricted to freshwater environments. They include *Cheirolepis trailli* (Pearson and Westoll 1979, Fig 1.4) and *Stegotrachelus finlayi* (Gardiner 1963, Swartz 2009), both from the Old Red Sandstone of Scotland and *Howqualepis rostridens* (Long 1988) from Mount Howitt, Victoria. There is an increase in taxa known in the fossil record for the Late Devonian (Frasnian-Famennian), although ray-finned fishes remain a sparse component of most faunas against a high diversity of placoderms, chondrichthyians and sarcopterygians (eg. fewer than 20 described actinopterygian species vs almost 200 Devonian sarcopterygians, Cloutier and Arratia 2004). From Euramerica there are at least two species of *Cheirolepis* (Arratia and Cloutier 1996; Arratia and Cloutier 2004), *Cuneognathus gardineri* (Friedman and Blom 2006), *Kentuckia hlavini* (Dunkle 1964), *Limnomis delaneyi* (Daeschler 2000), several species of *Moythomasia* (Gross 1950, Jessen 1968), *Osorioichthys marginis* (Taverne 1997) and *Tegeolepis clarki* (Newberry 1888; Dunkle and Schaeffer 1973). The only articulated Late Devonian taxa described from outside this region is the single specimen of *Krasnoyarichthys jesseni* (Prokofiev 2002) from Siberia and the exceptionally preserved *Moythomasia durgaringa* and *Mimia toombsi* from the Gogo Formation of Western Australia (Gardiner and Bartram 1977, Gardiner 1984, Fig 1.4). All known Devonian actinopterygian taxa based on reasonably complete articulated remains as of 2006 (including the questionable *Dialipina*) are listed below as Table 1.

TAXON	LOCALITY/HORIZON	AGE	PALAEO-ENVIRONMENT
Cheirolepis canadensis Whiteaves 1881	Escuminac Formation, Quebec	Frasnian	?marginal marine
Cheirolepis schultzei Arratia and Cloutier 2004	Denay Limestone, Nevada	Givetian-Frasnian	marine
Cheirolepis trailli Agassiz 1835	Old Red Sandstone, Scotland	Eifelian-Givetian	freshwater
Cuneognathus gardineri Friedman and Blom 2005	Obrutschew Bjerg Fm, Greenland	Famennian	freshwater
Dialipina salgueroensis Schultze 1968	Bear Rock Formation, NW Territories	Emsian	marine
Howqualepis rostridens Long 1988	Mt Howitt, Victoria	Givetian	freshwater
Kentuckia hlavini Dunkle 1964	Cleveland Shale, Ohio	Famennian	marine
Krasnoyarichthys jesseni Prokofiev 2002	Krasnoyarski Krai, Siberia	Famennian	marine
Limnomis delaneyi Daeschler 2000	Catskill Formation, Pennsylvania	Famennian	freshwater
Mimia toombsi Gardiner and Bartram 1977	Gogo Formation, Western Australia	Frasnian	marine
Moythomasia durgaringa Gardiner and Bartram 1977	Gogo Formation, Western Australia	Frasnian	marine
Moythomasia nitida Gross 1953	Oberer Plattenkalk, Nordhein-Westfalen	Frasnian	marine
Osorioichthys marginis Taverne 1997	Famenne Formation, Belgium	Famennian	marine
Stegotrachulus finlayi Woodward and White 1926	Middle Old Red Sandstone, Shetland	Givetian	freshwater
Tegeolepis clarki (Newberry) 1888	Ohio Shale, Ohio	Famennian	marine

TABLE 1 - All described Devonian actinopterygians based on reasonably complete articulated material as of 2006.

Of the Devonian taxa, *Cheirolepis* is generally considered to be a stem-actinopterygian that is usually resolved close to the base of the clade in most analyses (Friedman and Blom 2006, Gardiner 1984, Long 1988, Taverne 1997). When considered as an actinopterygian rather than a stem-osteichthyan, *Dialipina* is usually resolved as the basal most member of the group. Whether the remaining Devonian taxa fall within the crown-group is largely dependent on the phylogenetic placement of the Polypteriformes, the most primitive extant ray-finned fishes. Their position varies from being the most basal actinopterygians (Lund and Poplin 2002), the most basal actinopterygians save for *Cheirolepis* (Coates 1999, Gardiner 1984, Gardiner and Schaeffer 1989, Gardiner et al. 2005, Taverne 1997) or as more derived forms within a post-Devonian radiation (Lund 2000). *Moythomasia* and *Mimia*, the best known Devonian taxa besides *Cheirolepis*, are normally resolved as stem-members of the Actinopteri (Gardiner 1984, Gardiner et al. 2005, Long 1988, Patterson 1982), the clade which includes all extant taxa save for the Polypteriformes and are characterised by the presence of a perforated propterygium.

The characters that define fossil basal-taxa of actinopterygians are in a state of flux, due in part to the recent recognition of once key diagnostic features in other lineages. Dermal bone ornamentation and scale articulation were once considered key characters of basal Actinopterygii (Gardiner 1984, Maisey 1986, Patterson 1982, Pearson 1982, Schultze 1977, Schultze and Cumbaa 2001) and have been used to assign fragmentary early taxa to this clade. The scales of the majority of unambiguous Palaeozoic ray-finned fishes are rhombic in shape with a distinctive interlocking mechanism of narrow-based dorsal pegs and ventral sockets. The scales and other dermal surfaces are ornamented with ridges of ganoine, a shiny coat composed of layered enamel (Goodrich 1907).

The diagnostic value of both these characters is now in doubt. Rhombic scales with peg-and-socket articulation have long been known from several Devonian sarcopterygians including *Osteolepis* (Gross 1966), *Uranolophus* (Campbell and Barwick 1988) and *Youngolepis* (Zhu and Fan 1995), although the dorsal pegs of these forms are broader-based than those present in most early actinopterygians. As a result, Schultze (1977) claimed that this interlocking system evolved independently in ray-fins and lobe-fins.

A recent important discovery is that of *Guiyu*, a primitive osteichthyan from the late Ludlow (Silurian) Kuanti Formation of Yunnan, China (Zhu, et al. 2009). The fish is known from an almost complete specimen and represents the oldest articulated fossil osteichthyan. With images of the fossils supplied by Prof. Zhu Min (IVPP), I developed a rigorous lateral interpretation of this animal (Fig 1.5a) that served as a model for a life-reconstruction that accompanied the journal submission (Fig 1.5b) and the following descriptions.

Guiyu is notable in displaying a combination of sarcopterygian and (traditionally) actinopterygian characters. The dermal surfaces are covered in extensive ganoine ridging while the large rhombic scales interlock via peg-and-socket articulation. The dorsal peg are narrow-based as in most Devonian actinopterygians and are dissimilar to the broader-based pegs present on the squamation of some early sarcopterygians. In light of these new discoveries, the use of scale ornament and articulation in assigning micro-remains to the Actinopterygii can no longer be employed with confidence.

In contrast, the overall anatomy of the head most closely resembles the basal sarcopterygian *Psarolepis*. The skull possesses traditionally sarcopterygian characters including a broad internasal septum, dermal and endoskeletal intracranial joints, and an

extratemporal bone. The anterior tip of the lower jaw possesses a facet suggesting the presence of a parasymphysial tooth-whorl of the kind present in onychodontiform sarcopterygians. *Guiyu* thus probably represents a very early form of sarcopterygian. With the benefit of this new data, it is likely that the ganoine ornamentation and interlocking squamation of basal actinopterygians are symplesiomorphies retained from their most recent common ancestor with the Sarcopterygii.

Stem-sarcopterygian fossils date from as far back as the Late Silurian of Asia (Zhu and Schultze 1997, Zhu et al. 1999, Zhu et al. 2009) indicating that the two lineages must have diverged more than 420 million years ago. The fossil record of the earliest actinopterygians is elusive in deposits older that the Middle Devonian and all purported fossil ray-finned taxa from before this time are of debatable affinities.

Several taxa from the Late Silurian to Early Devonian have been proposed as early actinopterygians. *Andreolepis* comprises two species based on disarticulated scales, fin spines and dermal platelets from the Ludlow to lower Pridoli of much of Europe (Gross 1968, Märss 2001). The genus *Lophosteus* is known worldwide based on scales, spines and plates (Gross 1969, Schultze and Märss 2004) with assigned material from northern Europe, Canada and Australia, having a temporal range from the Ludlow-Pridoli (Late Silurian) to the Lochkovian (Early Devonian). Scale-taxa from eastern Yunnan in southern China include the Wenlockian *Naxilepis* and a form presently considered congeneric with the Australian *Ligulalepis* (Wang and Dong 1989). Putative actinopterygians from the Early Devonian include *Dialipina*, comprising *D. salgueiroensis* from the Lochkovian of Siberia and *D. markae* from the Emsian of the Northwest Territories, Canada (Schultze 1992, Schultze and Cumbaa 2001). *Ligulalepis toombsi* comprises scales and a referred partial neurocranium

from the Emsian of New South Wales (Basden and Young 2001). The affinities of all pre-Givetian taxa listed above remain contentious and many have been placed outside the Actinopterygii in several recent analyses as either stem osteichthyans (Botella et al. 2007, Friedman 2007, Schultze and Märss 2004) or, in the case of *Ligulalepis*, as a stem sarcopterygian (Zhu, Zhao, Jia, Lu, Qiao, Qu 2009).

Of the taxa mentioned above, only *Dialipina salgueirostris* and *Ligulalepis toombsi* are known from more than isolated scales and platelets. Complete specimens of *D. salgueirostris* have been rcovered, although only a cursory description of this form has been published (Schultze and Cumbaa 2001). It is strikingly different to all other Devonian actinopterygians in possessing two dorsal fins, a triphycercal tail, numerous small bones on the cheek, and in having teeth borne on narrow plates instead of fused to the maxilla, premaxilla and dentary. The Australian *Ligulalepis* possesses highly archaic features, the most obvious being the presence of an eyestalk (Basden and Young 2001), a feature otherwise unknown in the Actinopterygii but present in early sarcopterygians (Zhu et al. 2001), chondrichthyans (Gross et al. 1937) and placoderms (Young 1980). Other features are more characteristic of the basal Sarcopterygii, notably a broad internasal septum and parachordal plates separated from the otic capsule. Indeed the analysis of Zhu et al. (2009) places *Ligulalepis* as a stem-sarcopterygian.

It is probable that scale and ornament-based features used to classify *Dialipina*, *Ligulalepis* and other enigmatic early taxa within the Actinopterygii are actually osteichthyan symplesiomorphies. The classification of all these forms to the Actinopterygii is thus questionable at best. What then remains to distinguish the basal Actinopterygii from the remainder of the Osteichthyes? The following characters have been proposed as

actinopterygian synapomorphies in the past and appear to remain valid:

1) An enclosed canal for the dorsal aorta on the basicranium (Patterson 1975, Gardiner 1984).

2) Narrow interorbital septum (Gardiner 1984).

3) Hole for the basipterygoid process process on the palatoquadrate (Pearson and Westoll 1979, Gardiner 1984).

4) Vaterite otoliths (Gardiner 1984)

5) The majority of the mandibular sensory canal is enclosed within the dentary (Gardiner 1984).

6) Absence of a connection between the sensory canals of the jugal and preoperculum (Rosen et al. 1981, Gardiner 1984)

7) Pelvic radials articulate proximally to a basal plate (Gardiner 1984, Gardiner and Schaeffer 1989).

1.5 Materials and methods

1.5.1 Institutional Abbreviations

The material examined in this thesis belongs to several institutions, represented in the text by the following abbreviations: **AM**, Australian Museum, Sydney; **ANU**, The Australian National University, Canberra; **BMNH**, Natural History Museum, London **MV**, Museum Victoria, Melbourne; **NRM**, Naturhistorischen Reichsmuseum, Stockholm, **WAM**, Western Australian Museum.

1.5.2 Anatomical Abbreviations

adp, anterodorsal process of suboperculum; **An**, angular; **an.f**, anal fin; **ano**, anterior nasal opening; **anpl**, angular pit line; **Aop**, accessory operculum; **ap**, anterior pit-line; **bhc**, bucco-hypophysial canal; **binc**, foramen for dorsal branch of infraorbital sensory canal; **Bpt**, basipterygoid process; **Br. X**, branchiostegal ray (X = number in series counting from suboperculum); **cao**, aortic canal; **cau.f**, caudal fin; **c.ful**, caudal fulcra/scutes; **Cb**, ceratobranchials; **Ch**, ceratohyal; **Clav**, clavicle; **Clth**, cleithrum; **cono**, area where conodont elements have been removed; **cw.lep.** cutwater lepidotrichial segments/fulcra; **Den**, dentary; **dep.f**, depressed field; **d.lep**, dorsal lepidotrichia; **d.scu.** dorsal scute; **Dh**, dermohyal; **Ds**, dermosphenotic; **dor.f**, dorsal fin; **ethc**. ethmoid commissure; **Ex.1**, extrascapular, inner pair; **Ex.2**, extrascapular, outer pair; **Exs**, extrascapular; **F**, frontal; **fepsa**, foramen for efferent pseudobranchial artery; **fhm**, hyomandibular facet; **fhm.VII**, hyomandibular trunk of facial nerve; **fm**, foramen magnum; **f.ful,** fringing fulcra; **foa**, foramen of occipital artery; **focn**, foramen of occipital nerve; **fos**, otico-sphenoid fissure; **fotc**, otico-occipital fissure; **fotn,** foramen of optic nerve; **fv**, ventral otic fissure; **gst X**, groove for supratemporal branch of vagus nerve; **ha**; haemal arches; **hb**, hypobranchial; **Hh**; hypohyal; **hpbt**, hole for basipterygoid process; **hpl**, horizontal pit line; **Hy**: hyomandibular; **inc,** opening for infraorbital sensory canal; **ioc**, infraorbital sensory canal; **It**, Intertemporal; **ivl**, insertion of intervertebral ligament; **jc**, jugal canal; **Ju**, jugal; **Lac**, lacrimal; **L.gu**, lateral gular; **lpr**, lateral postrostral; **man.sc**, mandibular sensory canal; **man.tp**, mandibular toothplate series; **mc**, mandibular sensory canal; **Men**, Mentomeckelian ossification; **mcv**, foramen of middle cerebral vein; **m.gu**, median gular; **mll**, main lateral-line canal; **mp**, median pit-line; **mpr**, median postrostral; **Mx**, maxilla; **N**, nasal; **na**, neural arches; **not**, notochordal canal; **npl**, nasal pit line; **nm**, notochordal (upper) mass of caudal fin; **oatm**, origin of anterior trunk muscle; **ocip**, occipital ossification; **Op**, operculum; **Pa**, parietal; **pal**, palatine; **pal.tp**,

toothplate series of the palatoquadrate; **Par**, prearticular; **Pcl**, postcleithrum; **pec.f**, pectoral fin; **pel.f**, pelvic fin; **pinf**, pineal foramen; **pno**, posterior nasal opening; **Pop**, preoperculum; **por**, postorbital process; **Pm**, premaxilla; **pp**, posterior pit-line; **ppr**, posterior postrostral; **Pr**, postrostral; **Pro,** propterygium; **Ps**, parasphenoid; **Psc**, Presupracleithrum; **pseg,** segmented posterior lepidotrichia on pectoral fin; **Pt**, post-temporal; **Qj**, quadratojugal; **qjpl**, quadratojugal pit line; **R**, rostral; **rpl**, radial plate; **rdp**, rostrodorsal process; **San**, surangular/supra-angular; **sd.lep,** segmented distal lepidotrichia; **Scl**, supracleithrum; **sclr**, sclerotic ring; **soc**, supraorbital canal; **Sop**, suboperculum; **spig**, spiracular groove; **spip**, spiracular toothplate; **spir**, spiracular notch; **St**, supratemporal; **suc**, tube for supraorbital sensory canal; **Sur**, surangular; **tfr,** terminal fringe of fine branching segments on pectoral fin; **v.fon**, vestibular fontanelle; **v.ful**, ventral scutes; **vhl,** ventral hypochordal lobe of caudal fin; **vpl**, vertical pit line; **useg.** unsegmented proximal lepidotrichia on pectoral fin; **III**. notch or foramen of oculomotor nerve; **V**, foramen or canal for trigeminal nerve; **VII**, foramen/canal for facial nerve; **VII.lat**, foramen/canal for lateralis trunk of facial nerve.

1.5.3 Locality details

The Gogo Formation, of the Canning Basin (Fig 1.6), preserves the deep inter-reef basinal facies of a Late Devonian (Frasnian) barrier reef complex (Druce 1975; Playford and Lowry 1966; Teichert 1949; Towner and Gibson 1983). Unweathered sections consist of sequences of siltstone and thin beds of limestone, the latter containing round bedded nodules, ranging in size from around 2.5 to 36 centimetres in diameter. These concretions are composed of silty micritic limestone and are often found to have developed around a fossil fish or invertebrate. The nodules are resistant to weathering and fossil collecting occurs in extensive surface aggregates on the valley floors where the Gogo Formation interfingers with the Saddler Formation in the region. The Gogo fish fauna is world renowned for its high

diversity and outstanding three-dimensional preservation (Long 2007).

The calcareous nodules present within the Gogo Formation sediments formed over solid objects that settled on the anoxic seafloor, including the carcasses of fishes that originally lived in the shallower, oxygenated waters of the reef (Long 2007). As the concretions are resistant to weathering, extensive erosion of the original Gogo Formation sediments has resulted in extensive fields of nodules at or near the soil surface where they may be easily examined for fossils and collected.

The Gogo fossil ichthyofauna represents over forty described species (Long 2007) with the bulk of diversity taken by arthrodire placoderms and dipnoans (lungfishes). Actinopterygians are commonly recovered (pers. observation) but are represented by fewer species. Whereas actinopterygians from other fossil sites are typically recovered as either flattened fish or isolated 3-dimensionally preserved fragments, good specimens from the Gogo Formation comprise entire articulated skeletons with full 3D preservation of both dermal and perichondral tissues.

Actinopterygian specimens collected on the 2005 and 2008 expeditions and examined in this thesis were recovered from the following localities as detailed in Miles (1971, Fig. 1): Embayment Hill, Stromatoporoid Camp, Paddy's Valley (= Paddy's Spring Area of Miles 1971) and Bugle Gap.

The material described in chapter 2 (*Donnrosenia schaefferi*) was collected from the Aztec Siltone of Antarctica, primarily during the 1970-71 expeditions. Further details of this unit are presented in chapter 2.3. The Aztec Siltstone of the Skelton Névé region of the

Transantarctic Mountains has produced a freshwater vertebrate fauna of Givetian age, consisting of placoderms, acanthodians, chondrichthyans and sarcopterygians (Young 1989a, 1991). A detailed summary of the stratigraphy of the Aztec Siltone and locality details of the 1970-71 and earlier expeditions are given by Young (1988, pp. 6-9). Detailed locality maps of vertebrate bearing fossil sites is figured in Young and Long (2005, Fig. 1) of which actinopterygian material is known only from locality 2 (Mount Suess), locality 8 (Mount Crean) and localities 11-12 (Portal Mountain).

The new specimen described in chapter 3 (*?Howqualepis youngorum*) was collected from the Middle Devonian Bunga Beds from close to the shoreline at Bunga Beach in south coastal New South Wales. Young (2007, figs 1, 2) provides a detailed account of the lithology, fossil assemblage and possible age of the Bunga Beds. Further details on the geology of this locality are presented in chapter 3.3.

The existing collections of German *Moythomasia* described in chapter 6 were recovered from the Oberer Plattenkalk in the Heiligenstock quarry, east of Bergisch-Gladbach near Cologne, Germany (Jessen 1973). The age of the fossil fish beds are broadly dated as latest Givetian-earliest Frasnian (Harland et al. 1990)

1.5.4 Collection and preparation of fossils from the Gogo Formation

A field trip to the Gogo Formation was undertaken in 2005. Over a two week period, all major concentrations of surface-concretions were systematically prospected. Nodules were first examined for signs of bone weathering from the surface. These rare nodules were left intact. All other nodules were split, using a geological hammer (Fig 1.7), and those found to contain vertebrate fossil material were collected and transported to Museum Victoria. Field

work yielded 20 specimens of basal actinopterygians, 9 of which were deemed of sufficient quality for preparation.

All specimens used in this study were recovered as neatly split part and counterpart, with each half-nodule mounted face-down on a slab of acrylic resin and prepared from the unexposed side. Specimens were prepared using the acid transfer techniques of Toombs and Rixon (1950). Specimens are placed in 8-10% acetic acid and immersed for 2-3 days, after which the specimens were washed for an equal length of time under running water. Protruding bones were coated with a dilute plastic-based glue (Mowital B30 or Paraloid diluted in ethanol). Bones were cleaned with a fine brush dipped in ethanol prior to each new glue application.

I participated in some of the acid-preparation of most of the Gogo material presented in this thesis, however the majority of the fine-restoration work was carried out by Mr David Pickering and Mr Malcolm Karkeek. Specimens were whitened with ammonium chloride for microscope study and photography.

1.5.5 Fossil preparation on non-Gogo material

The examined material from the Aztec Siltstone of Antarctica comprised specimens collected in 1970-71 by Alex Ritchie and Gavin Young as part of the Victoria University of Wellington Antarctic Expedition (VUWAE 15). The fish material is usually preserved as light coloured bone in a darker siltstone or fine sandstone matrix although the bone is 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* (AM F54363) was prepared this way by Dr A. Ritchie (Australian Museum).

The second articulated specimen (ANU V972) is preserved in a dark slightly calcareous shale, and was partly etched in acetic acid.

The single specimen from the Bunga Beds, NSW was recovered by Gavin Young as a natural mould set within a matrix of dark shale. After collection, the specimen was split into part and counterpart and bone remnants removed. Bone margins were exposed with mechanical preparation and the impressions of the fish were examined using a latex rubber cast whitened with ammonium chloride. Preparation on the fossil was carried out by Mr Ben Young. For comparison, fresh latex casts were made by the author from the following specimens of *Howqualepis rostridens* in Museum Victoria (MV) = P.160745A, P.160782A, P.160788, P.160792B, P.160811, P.160822A, P.160851B, P.160857.

1.5.6 Comparative study

In order to describe and delineate taxa from the Gogo Formation, a survey of Gogo actinopterygians was undertaken in the Western Australian Museum, Perth and the Natural History Museum, London. Specimens of European *Moythomasia* were examined within the Natural History Museum, London to test the congeneric status of *Moythomasia durgaringa*

Specimens examined are listed in the relevant chapters pertaining to each genus. It was determined that several specimens identified as *Mimia toombsi* in existing collections were attributable to undescribed taxa.

1.5.7 Phylogenetic analysis

The phylogenetic analysis presented in Chapter 8 expands on a previous study on the interrelationships of Devonian actinopterygians (Friedman and Blom 2006) by the addition

of newly described Devonian taxa and by the inclusion of a selection of Early Carboniferous forms. The matrix (Appendix III) comprises 82 characters applied to an ingroup of seventeen Devonian and twelve Carboniferous actinopterygians. PAUP 4.0b10 for Microsoft Windows was used to perform a branch-and-bound search, the results processed on Maclade 2.0.



Figure 1.1
A tiny selection of extant actinopterygian diversity. a. Weeping toado (*Torquigener pleurogramma*) and Stripey (*Microcanthus strigatus*); b. Tasselled anglerfish (*Rhyncherus filamentosus*); c. Common seadragon (*Phyllopteryx taeniolatus*); d.Giant gourami (*Osphronemus goramy*); e. Gibbiceps catfish (*Pterygoplichthys gibbiceps*); f. Mudskipper (*Periophthalmus* sp.). All photos by the author.

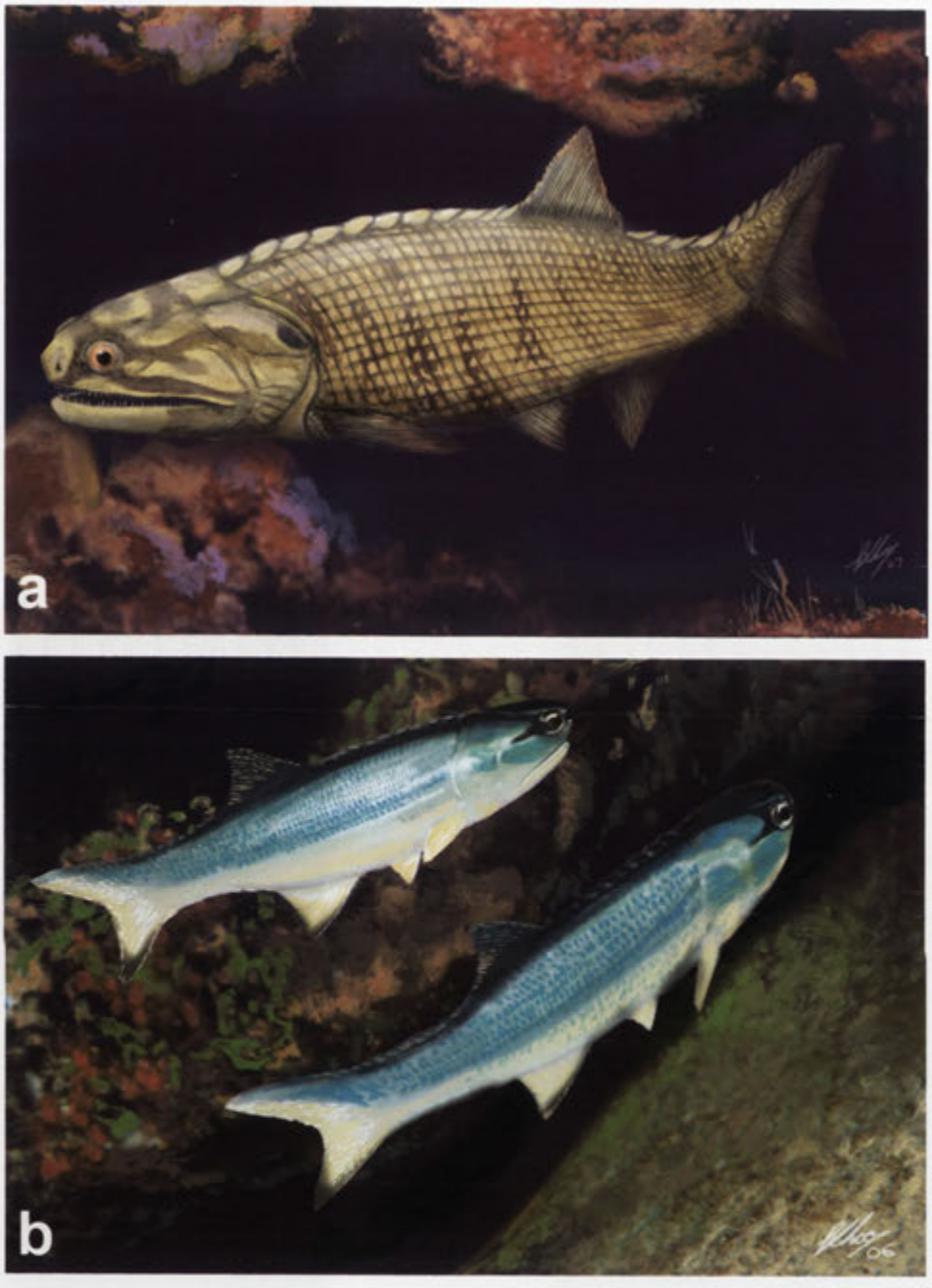


Figure 1.2
The two Gogo actinopterygians described by Gardiner and Bartram, 1977. Life reconstructions of (a) *Moythomasia durgaringa* and (b) *Mimipiscis* (=*Mimia*) *toombsi*.

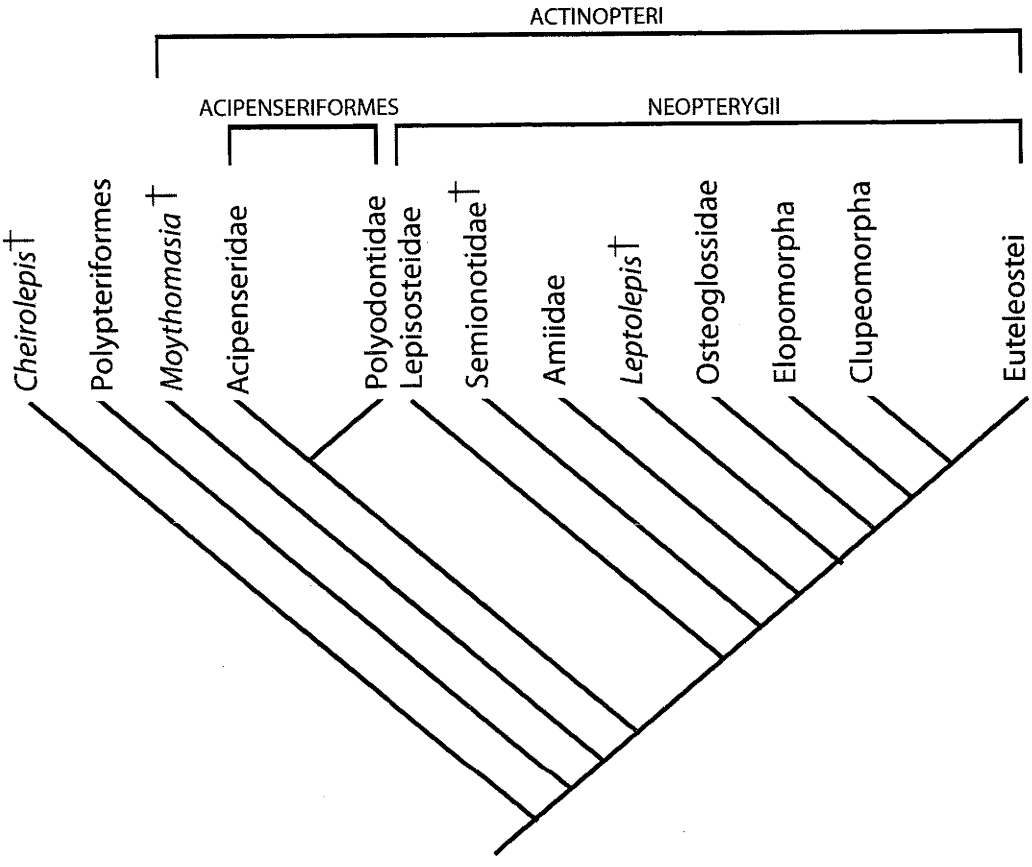


Figure 1.3
Phylogenetic relationships proposed to exist among major groups of actinopterygians. Dagger symbol denotes extinct lineages/taxa. Based on Gardiner (1984) and Maisey (1986).



Figure 1.4
Life reconstruction of *Cheirolepis trailli* from the Eifelian-Givetian Old Red Sandstone, Scotland with the tetrapodomorph *Osteolepis* in the background. At present this is the earliest undisputed actinopterygian known from articulated remains.

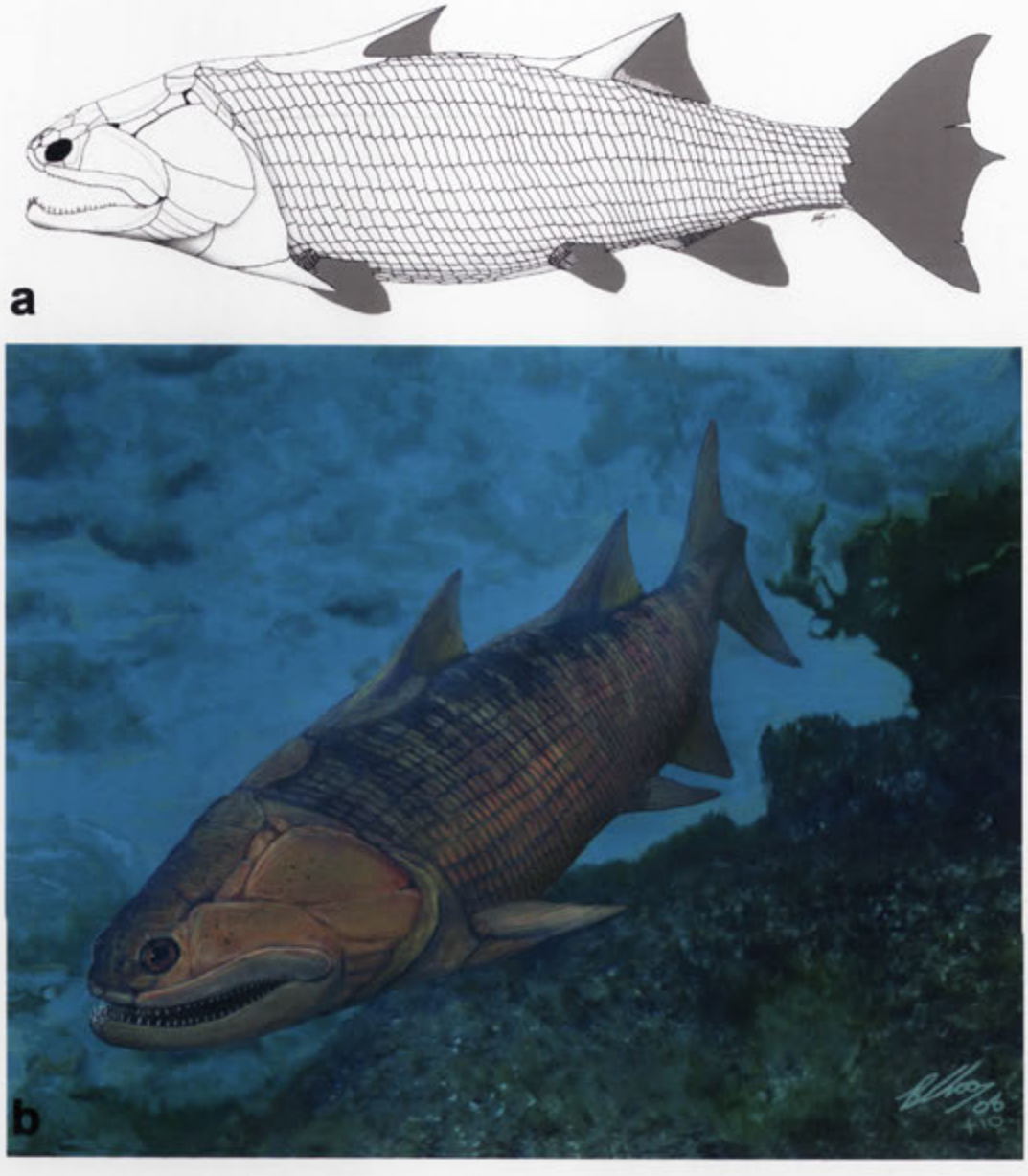


Figure 1.5
(a) Lateral reconstruction and (b) life restoration of *Guiyu oneiros*, a newly discovered basal osteichthyian from the Silurian Kuanti Formation, Yunnan, China.

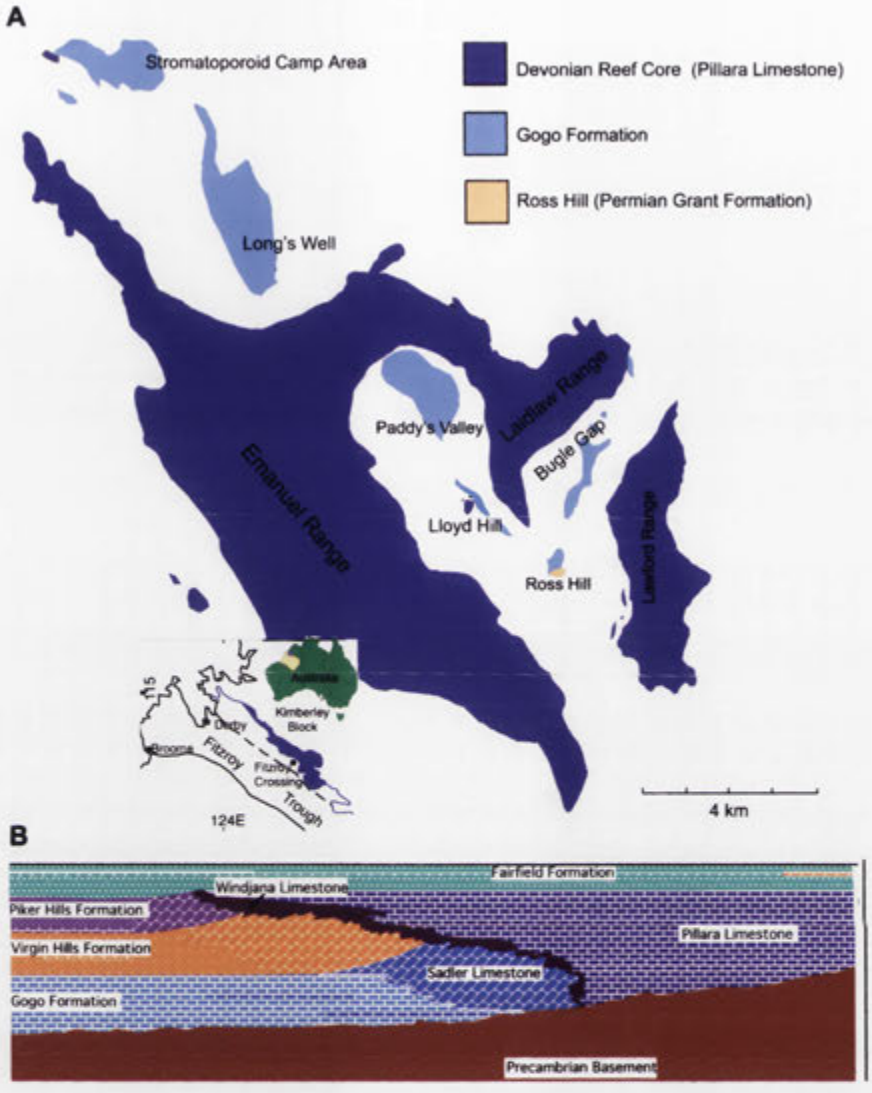


Figure 1.6
(a) Map of the region of Western Australia where nodular concentrations of the Gogo Formation are present along with a (b) generalised stratigraphic section. Modified from an unpublished map supplied by Kate Trinajstic.



Figure 1.7
Photographs taken on the 2005 Gogo expedition. a) Nodule field at Long's Well, b) breaking open a concretion, c) actinopterygian specimen (eventual holotype of *Mimipiscis bartrami* sp. nov. - see Chapter 5) in a nodule freshly broken by the author.

Chapter 2. A new basal actinopterygian fish from the Middle Devonian Aztec Siltstone of Antarctica

2.0 Preamble

This chapter represents a revised and updated version of a manuscript co-authored with both my supervisors and published in Antarctic Science (Long et al. 2008 - see Appendix I), to which I contributed approximately 50% of the text and over 90% of the illustrations. The framework for the original manuscript comprised unpublished notes and diagrams made by John Long, for which he was given primary authorship.

2.1 Abstract

A new basal actinopterygian fish, *Donnrosenia schaefferi* is described from the Middle Devonian (Givetian) Aztec Siltstone of southern Victoria Land, Antarctica. *Donnrosenia* 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 reflexure, porous ornamentation on the clavicle, an elongate body form with macromeric squamation, an absence of obviously paired fringing fulcra on the fins, and pectoral lepidotrichia which are unsegmented for much of their length.

A preliminary phylogenetic analysis based on dermal skeletal features of Devonian actinopterygians was presented in the original manuscript that indicated that *Donnrosenia* and *Howqualepis* were sister taxa from the Middle Devonian of Victoria, Australia, and both were embedded within a possible clade containing the actinopterygians from the Gogo Formation, Western Australia. Further refinement of this analysis (presented in Chapter 7)

continues to support the similarity of *Donnrosenia* and *Howqualepis* but rejects the presence of an all-encompassing actinopterygian clade, regionally endemic to Givetian-Frasnian Gondwana.

2.2 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 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 Ne'ver 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 and Young 1995, fig. 1), 100 km to the south of previously known sites (M.A. Bradshaw, NZARP, event 33; J.A. Long, NZARPANARE expedition).

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

vertebrate groups are represented, including thelodont agnathans (Turner and Young 1992), placoderms (Ritchie 1975, Young 1988, Long 1995, Young and Long 2005), chondrichthyans (Young 1982, Long and Young 1995, Hampe and Long 1999), sarcopterygians (Campbell and Barwick 1986, Young et al. 1992, Johanson and Ahlberg 2001, Johanson 2004), acanthodians (Young 1989b, Young and 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).

2.3 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 and 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 (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 and Turner 2000, fig. 2). Turner (1997) considered the thelodont *Turinia 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 and 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 and 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.

2.4 Systematic palaeontology

Class OSTEICHTHYES Huxley1880

Subclass ACTINOPTERYGII Cope 1887

Family HOWQUALEPIDIDAE Long, Choo and Young 2008

Diagnosis (revised from original manuscript).

Basal actinopterygians with an open spiracular slit bordered by the intertemporal, dermosphenotic and supratemporal. Intertemporal is very small (less than 1/3 the size of parietals). Pineal foramen present on anterior half of the median frontal contact. Dermosphenotic is elongate and tripartite. Suboperculum has a prominent anterodorsal process. Body form is elongate and fusiform. Squamation macromeric; scales are rhombic with linear ganoine ornamentation. Fringing fulcra are spine-like terminal sections of the anterior fin rays, lacking median contact between the hemilepidotrichia. Longest anterior pectoral fin rays are proximally unsegmented for over 60% of their length. Median scute series on dorsal and ventral surface do not extend anteriorly to reach the head.

Remarks.

Gardiner (1993, p. 611–12) united *Mimipiscis* (=*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 and Cumbaa 2001, Friedman and Blom 2006). A new phylogenetic analysis (see Chapter 7) suggests that *Howqualepis* is more closely related to *Donnrosenia* whereas an exclusive sister-group relationship between *Mimipiscis* and the slender-bodied Givetian forms was not recovered.

Genus *Donnrosenia* Long, Choo and Young 2008

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 and Rosen 1980).

Remarks: *Donnrosenia* 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* differs from *Osorioichthys* by its open pineal foramen, single pair of extrascapulars and a lack of a pectoral lobed base. *Donnrosenia* 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. *Donnrosenia* differs from all post-Devonian actinopterygians principally by the presence of the small intertemporal bone within the skull roof table and the large pineal foramen.

Donnrosenia schaefferi Long, Choo and Young 2008

Figs 2.1–2.10

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 and 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 and Young, p. 90

1993 'palaeoniscoid '; Young, p. 248, fig. 9.7

1995 'palaeoniscoid '; Long and Young, table 1

2005 'palaeoniscoid '; Young and Long, table 1

2006 'material from the Aztec Siltstone'; Friedman and Blom, p. 1186

2007 'material from the Antarctic Aztec Siltstone'; Young, p. 996

Diagnosis (revised from Long et al. 2008).

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. Fringing fulcra are spine-like terminal sections of the anterior fin rays, lacking median contact between the hemilepidotrichia. 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.

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.

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Localities and horizon.

AM F54362/3 (holotype) came from Portal Mountain (locality 12 of Young 1988, fig. 3; lat. 7887.2'S, long. 159824'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; 7887.2'S, 159823.5'E), assumed equivalent to Unit 17, Section 10. Material from Mount Crean, Lashly Range (locality 8 of Young 1988, fig. 3; 77853'S, 159833'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).

2.5 Anatomical Description

2.5.1 Skull roof

The skull table (Figs. 2.3 and 2.4) is typical for most Devonian actinopterygians, displaying a similar morphological pattern to that of *Howqualepis* (Long 1988), *Moythomasia* (Jessen 1968, Gardiner 1984) and *Mimipiscis* (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 and Westoll 1979, Arratia and Cloutier 1996, 2004), *Dialipina* (Schultze and Cumbaa 2001) and *Ligulalepis* sp. (Basden and 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 *Mimipiscis*, 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. 2.3a and 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 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. 2.4b) 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 *Mimipiscis* 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. 2.4a and 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 and 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. 2.3a

and 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 are narrow, strap like elements possessing a smooth dorsal overlap region for the parietals (Fig. 2.3c and d). Ornament and the structure of the sensory canal are not preserved.

2.5.2 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 2.2, 2.3a and 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 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. 2.5aand 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 *Mimipiscis 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. 2.5) 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 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 *Mimipiscis* and *Moythomasia* spp. The narrow, anterior suborbital section of the bone is reflexed dorsally 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. 2.1) 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.

2.5.3 Operculo-gular system

The operculo-gular system is well preserved in AM F54363(Fig. 2.1), 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 and 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. 2.5e and f), V765 and V770. They are similar in size and shape to those of *Howqualepis* and *Mimipiscis 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.

2.5.4 Lower jaw

The lower jaw is visible in lateral view in ANU V781a (Fig. 2.5a and b) along with a well-preserved isolated specimen (V815, Fig. 2.5c and 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 it 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.

2.5.5 Pectoral girdle

The cleithrum, clavicle, postcleithrum, and the posteroventral part of the supracleithrum are well preserved in AM F54363 (Fig. 2.1), 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. 2.3c and d) while post-temporals are visible on ANU V2246 (Fig. 2.4c and d).

The supracleithrum is a large, narrow bone that is only a little smaller than the operculum. It consists of a narrow, posteroventral sections 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.

2.5.6 Body and fins

The body form, visible in the holotype and ANU V972, is elongate and fusiform (Figs 2.1 and 2.2). 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 2.1a, 2.7a and 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.

In Long et al. (2008), it was claimed that true fringing fulcra were absent; possessing short, unpaired parallel rays, similar to those found on *Howqualepis*. As discussed in Chapter 3, recent work by Gloria Arratia on similar structures in *Cheirolepis* suggests that these are likely to be represent small paired fulcra with a single enlarged hemilepidotrichium that encloses its counterpart. 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 and 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 and 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.

2.5.7 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 which may be interspaced with minute punctae within the furrows, contrary to the initial description in Long et al. (2008). 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 Trinajstic (1999).

Zone A (anterior lateral flank scales, Fig. 2.8a and 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. Welldeveloped peg and socket joint. Up to fourteen posterior ganoine serrations. Minute pores may be present in the furrows between the ridges on scales on the ventral half of the body.

Zone B (mid lateral flank scales, Fig. 2.8d): 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. 2.8c): 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. 2.8f): 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. 2.2): Visible only as poorly preserved examples on ANU V972. Scales are rhomboidal, about twice as long as high.

Zone F (ventral scales, Figs 2.1 and 2.2): 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. 2.2): 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. 2.8e): Scales are very elongated, up to four times longer than tall. No peg and socket joint. Two or three posterior serrations.

Only a few median 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. 2.8g). 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.

2.6 *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.

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.

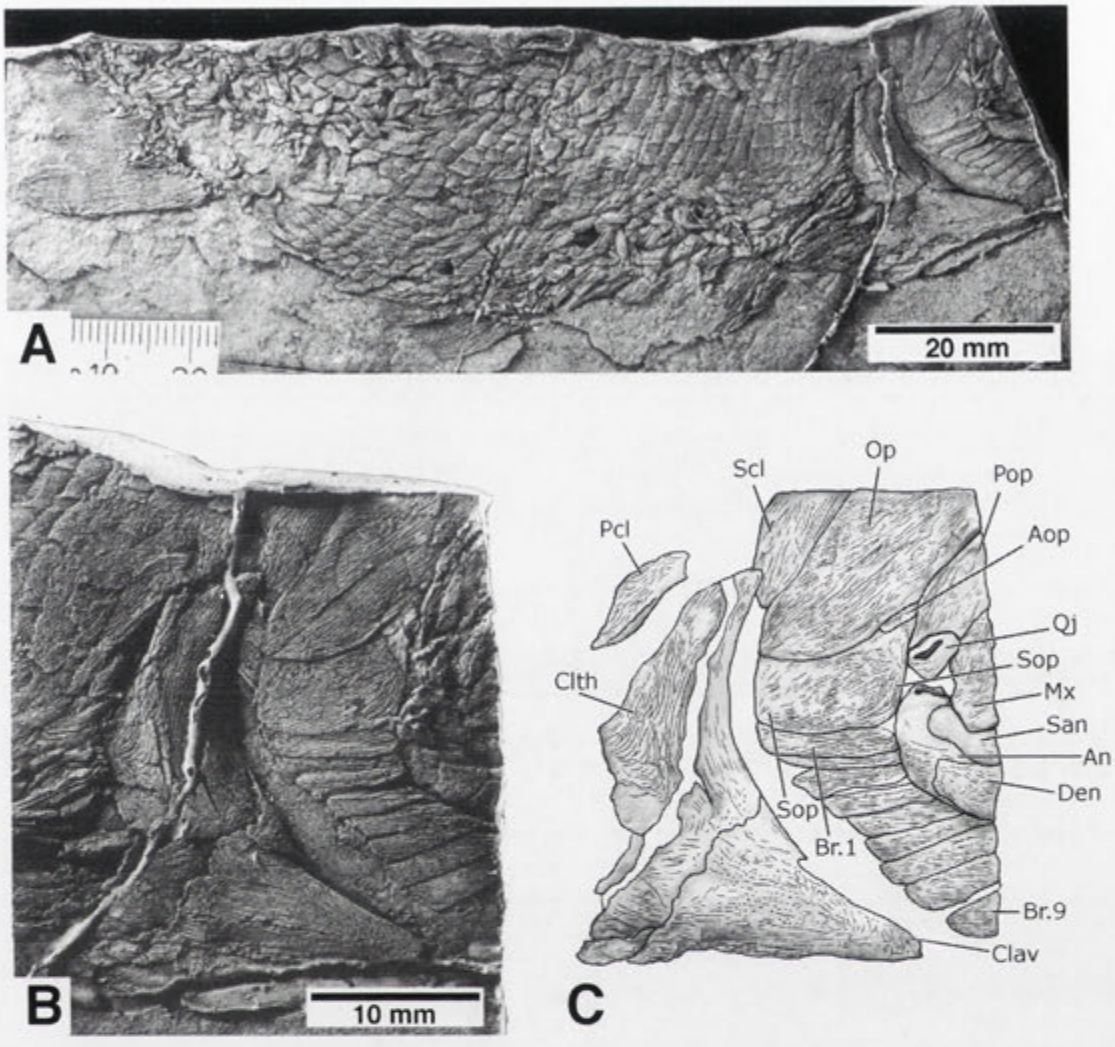


Figure 2.1
Donnrosenia schaefferi. Holotype (AM F54363) in right lateral view. Specimen is a latex cast whitened with ammonium chloride. **a**. photograph of entire specimen. **b.** Photograph. and **c.** drawing of the partial skull, opercular-gular series and pectoral girdle.

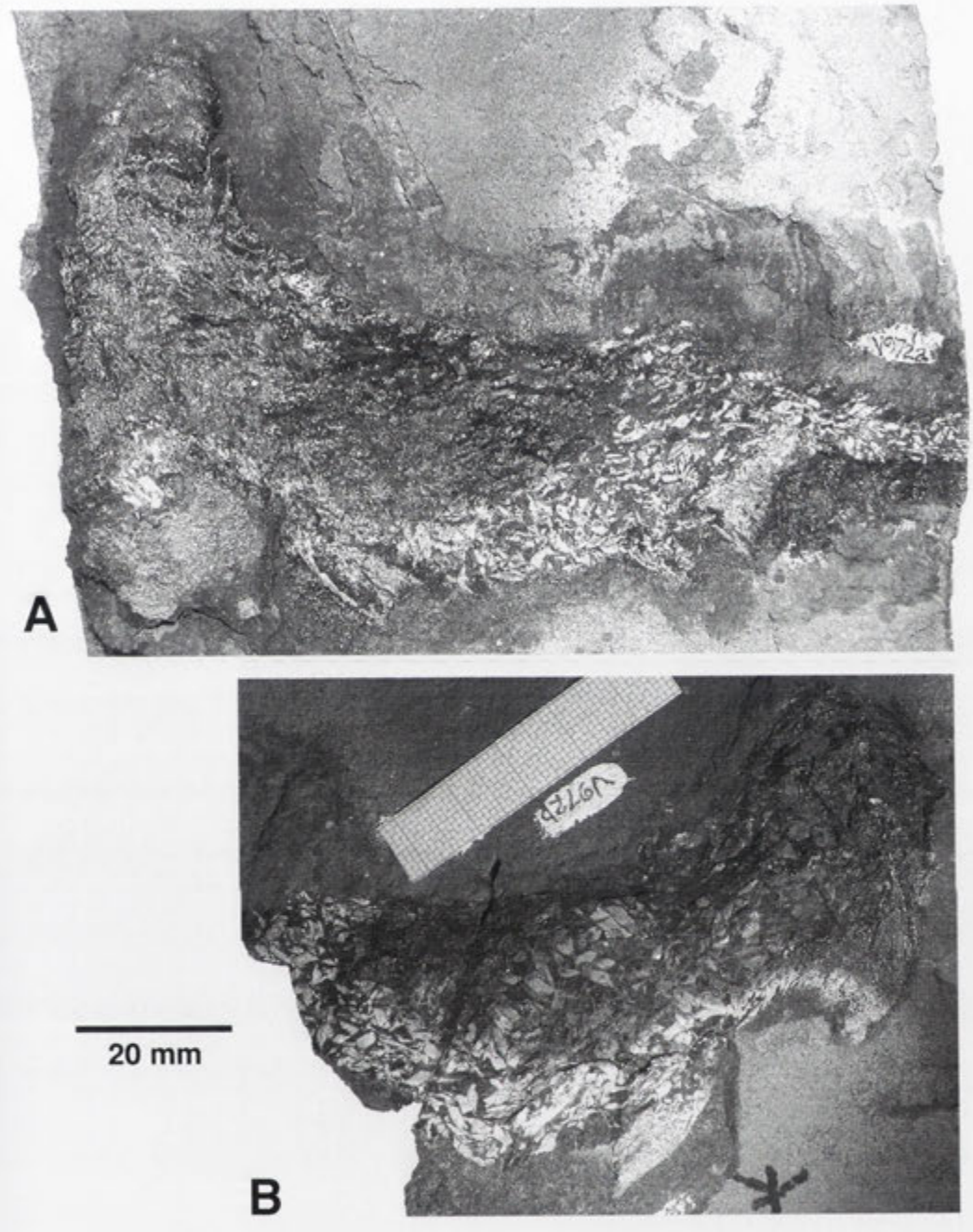


Figure 2.2.
Donnrosenia schaefferi gen. et sp. nov. Photographs of ANU V972. **a**. V972a in left lateral view, **b**. V972b/c in right lateral view. Specimens are bone remains and impressions in the rock.

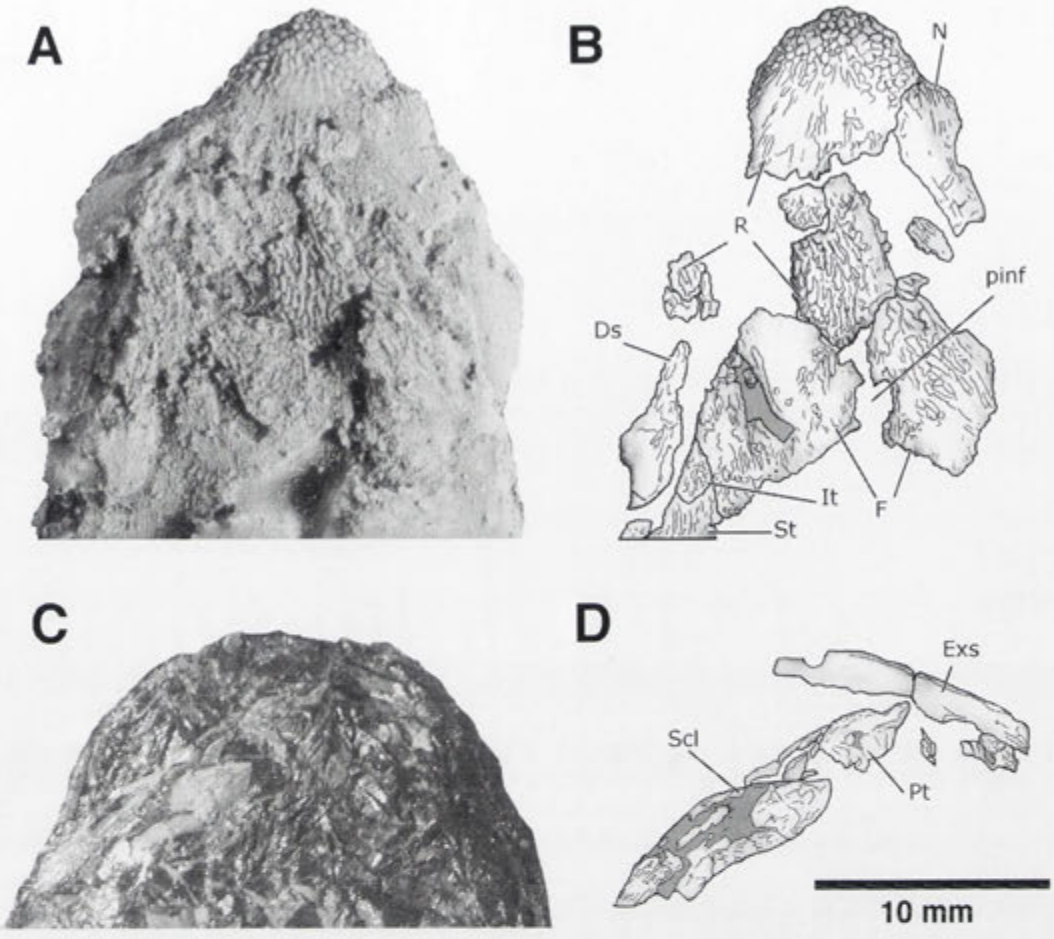


Figure 2.3
Donnrosenia schaefferi. Skull of ANU V972. **a.** Photograph, and **b.** line drawing of V972a showing anterior part of head in dorsal view. **c.** Photograph, and **d.** line drawing of V972b showing posterior elements of the head.

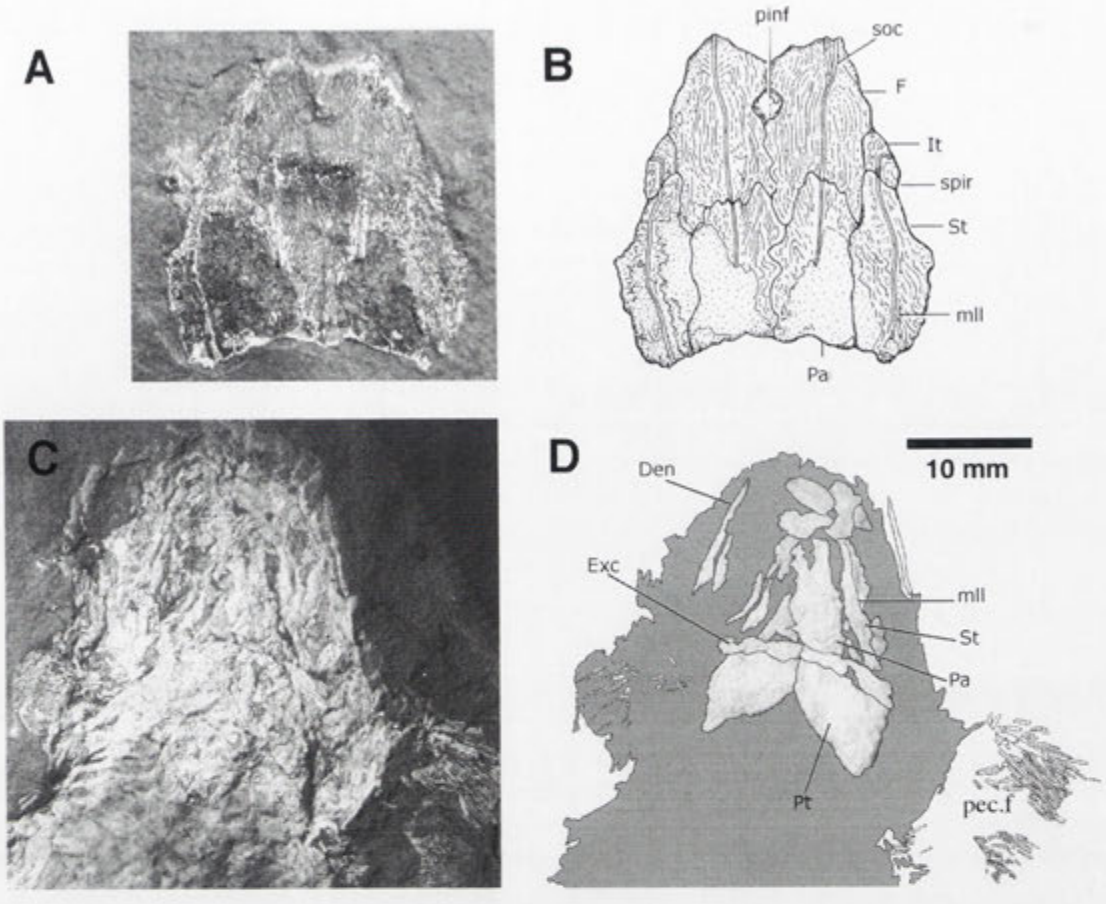


Figure 2.4
Donnrosenia schaefferi. Skulls in dorsal view. **a**. Photograph, and **b**. line drawing of ANU V2246. **c**. Photograph, and d. line drawing of AM F55938. Both specimens presented at the same scale.

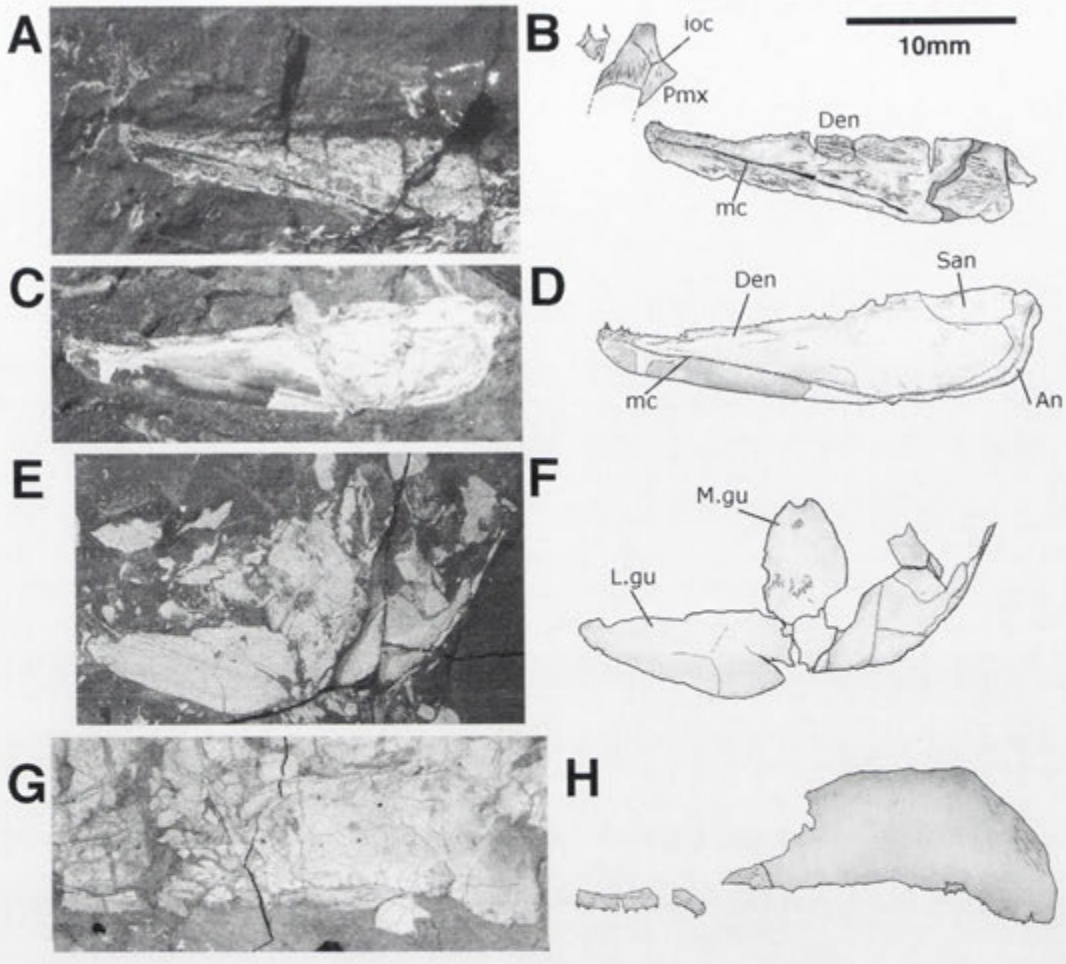


Figure 2.5
Donnrosenia schaefferi. Elements of the head as photographs and line drawings presented to scale. **a., b**. ANU V781a, partial left premaxilla and dentary in lateral view. **c., d.** ANU V815, left lower jaw in lateral view. **e., f.** ANU V781c, Lateral and median gular plates in visceral view. **g., h.** ANU V769, left maxilla in lateral view.

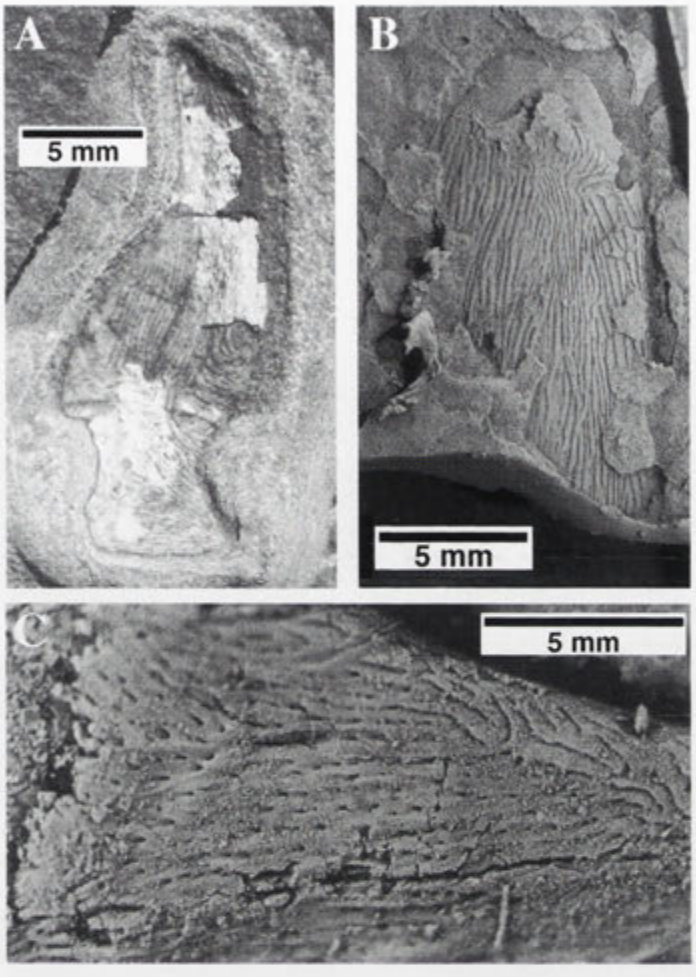


Figure 2.6
Donnrosenia schaefferi. **a.** ANU V763, left cleithrum in lateral view. **b.** ANU V886, left operculum in lateral view. **c.** AM F54363 (holotype), detail of right clavicle in lateral view showing porous ornamentation.

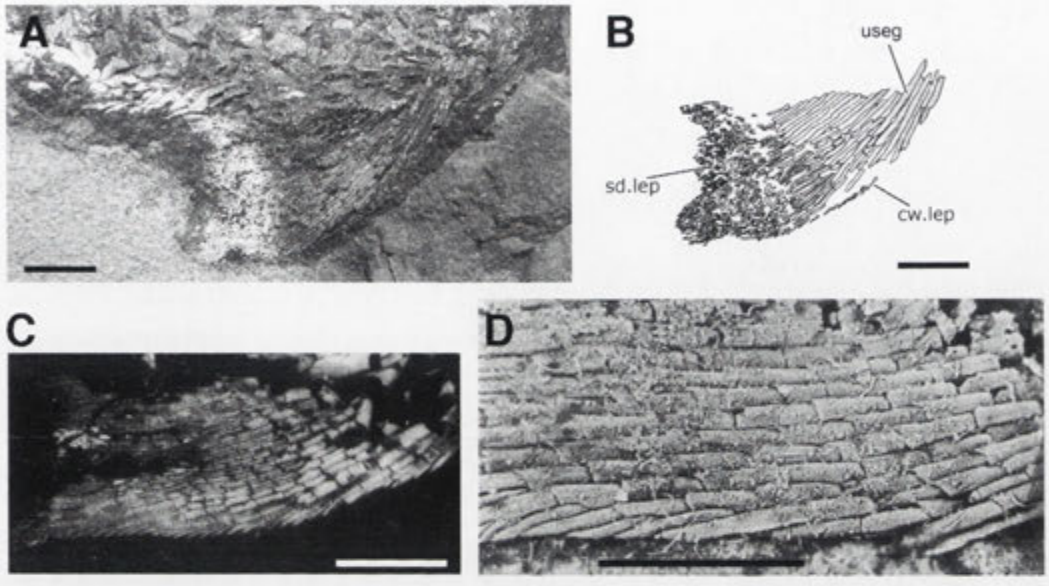


Figure 2.7
Donnrosenia schaefferi. Photographs of fins. **a.–c**. ANU V972b, **a.** right pectoral fin, **b.** right partial pelvic fin, **c.** anal fin. **d.** Holotype AMF54363, anal fin. (AM F54363), anal fin. Scale bar on each image =5 mm.

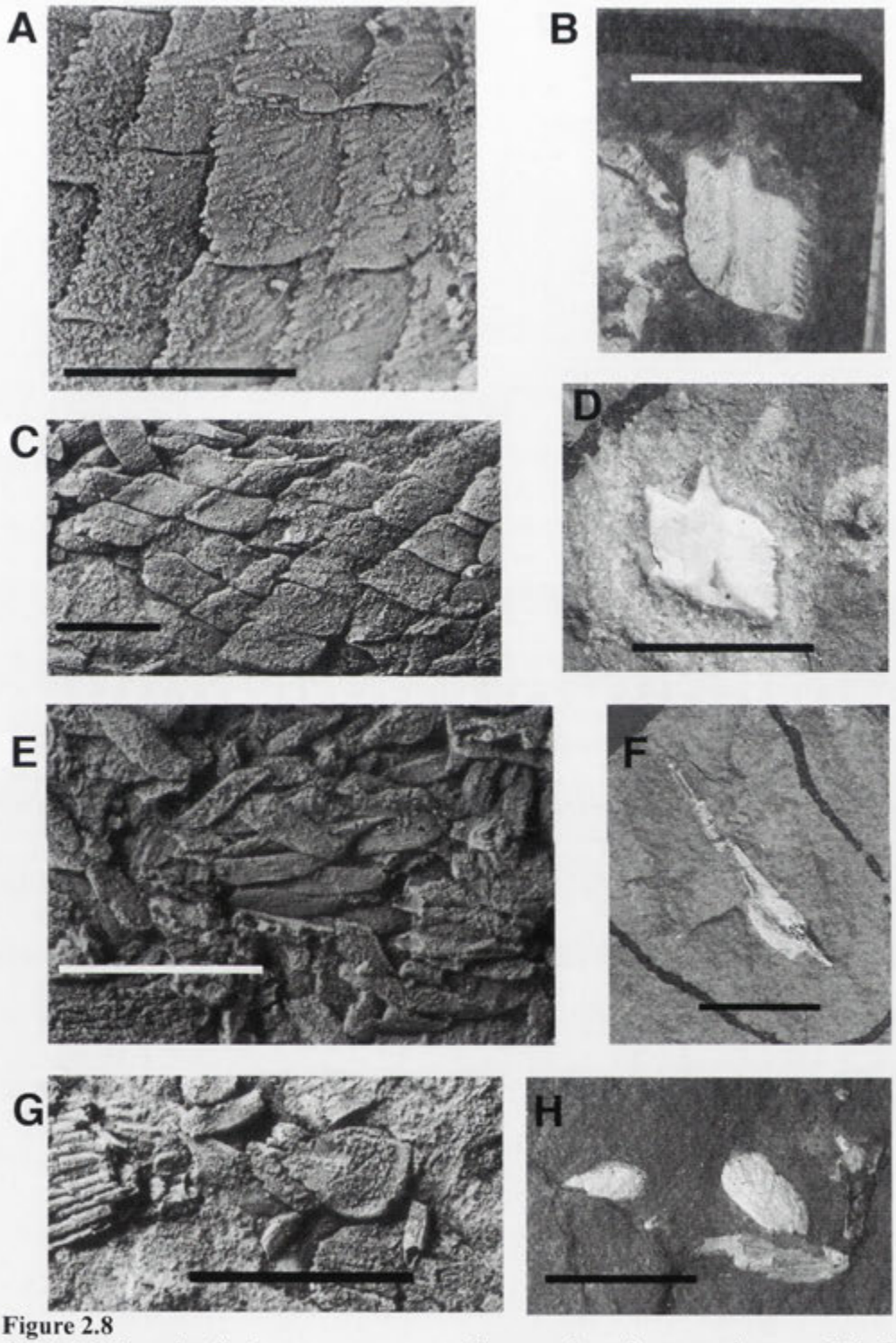


Figure 2.8

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.

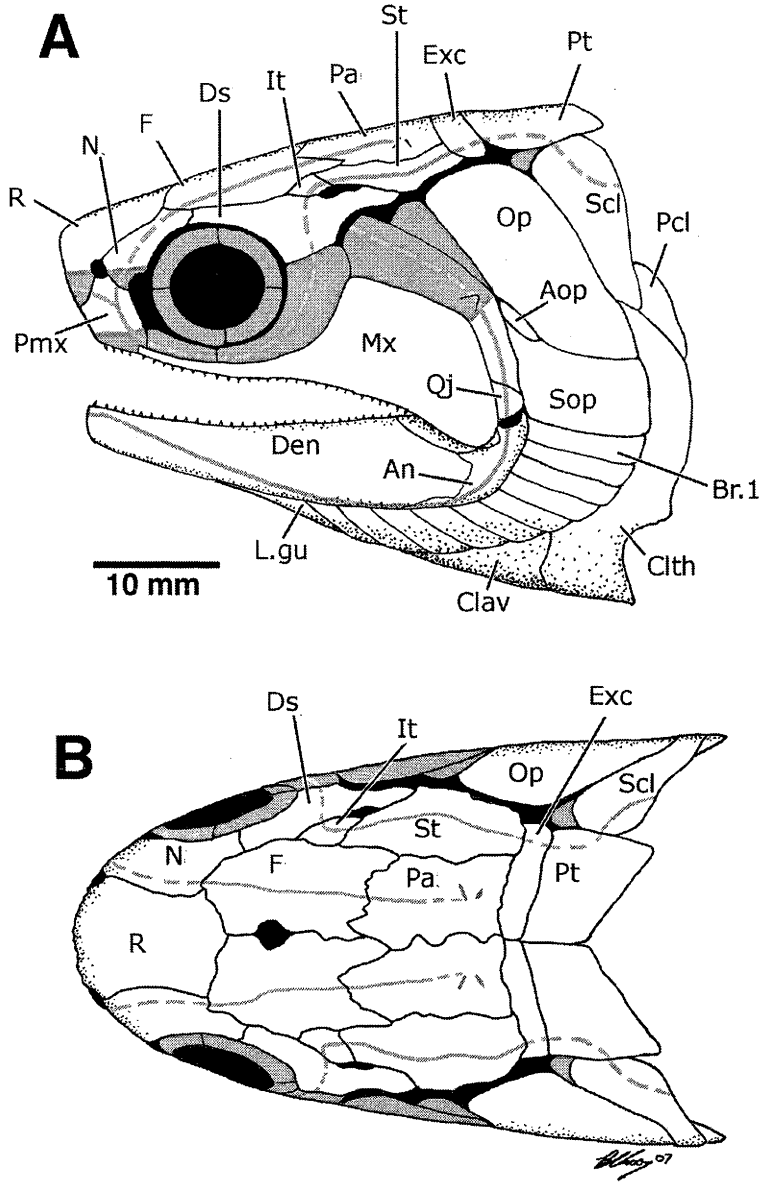


Figure 2.9
Donnrosenia schaefferi. Restoration of the head in **(a)** lateral, and **(b)** dorsal views. Dark grey areas corresponds to missing sections of the skull. Light grey lines refer to the path of the sensory canal, continuous where observed on fossil specimens, broken where inferred from other Devonian actinopterygians.

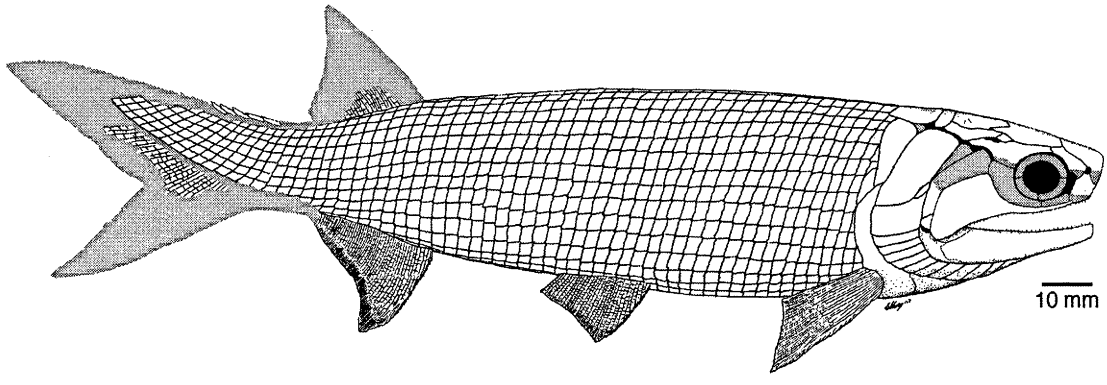


Figure 2.10
Donnrosenia schaefferi. Restoration of the entire fish in lateral view. Grey blank areas refer to missing or poorly preserved sections of the animal.

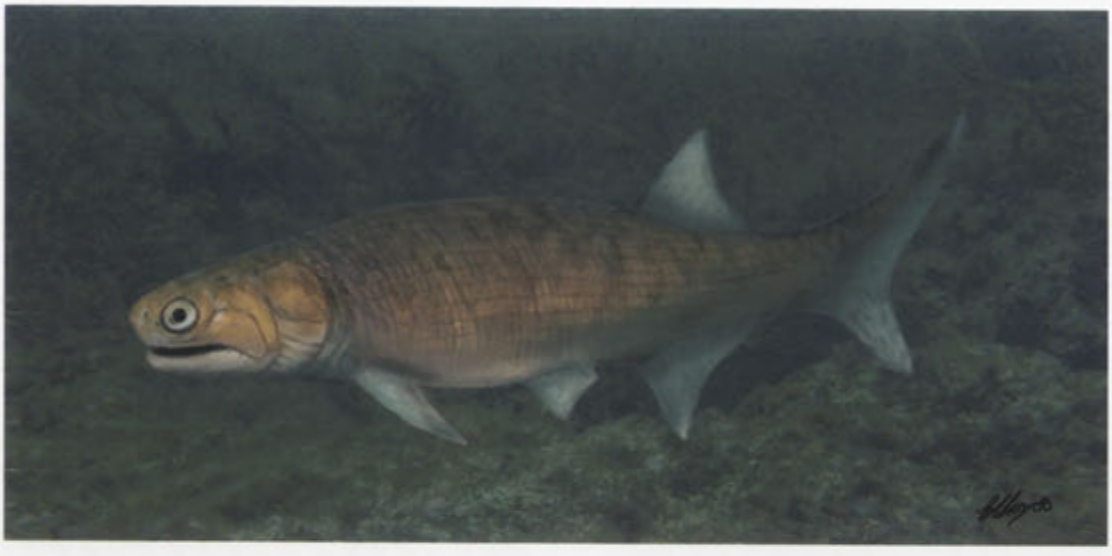


Figure 2.11
Life reconstruction of *Donnrosenia schaefferi*.

Chapter 3. A Basal Actinopterygian Fish from the Middle Devonian Bunga Beds of New South Wales, Australia.

3.0 Preamble

This chapter represents a modification of a manuscript written entirely by myself and published in the Proceedings of the Linnean Society of New South Wales (Choo 2009, see Appendix II). The discussion section has been incorporated into Chapter 8.

3.1 Abstract

A partial articulated skeleton of a basal actinopterygian fish is described from the Middle Devonian Bunga Beds of New South Wales. The specimen represents a new species and is questionably assigned as a congener of *Howqualepis rostridens* from the Middle Devonian of central Victoria. This represents the first record of an articulated postcranium of a Devonian ray-finned fish from New South Wales. The pectoral fin of *Howqualepis* is also redescribed based on a re-examination of Victorian material. The fin is broader in shape and less extensively unsegmented than previously recognised.

3.2 Introduction

Australia is notable in producing some of the finest fossil material of early actinopterygians, the best known of which are exceptionally preserved specimens from the Frasnian Gogo Formation of northern Western Australia. Included within the assemblage are *Moythomasia durgaringa* (Gardiner and Bartram 1977, Gardiner 1984), the currently preoccupied *"Mimia" toombsi* (ibid), *Gogosardina coatesi* (Choo et al., 2009) and at least two additional forms (Choo, in prep).

Southeastern Australian fossil sites have also produced a substantial amount of early ray-finned fishes. The first record of Australian Devonian actinopterygians consisted of the isolated scales of *Ligulalepis toombsi* from the Lower Devonian Taemas-Wee Jasper Limestones of New South Wales (Schultze 1968). The classification of this taxon within the Osteichthyes is currently under scrutiny (see Chapter 1). A subsequently discovered braincase and skull-roof was assigned to this genus (Basden et al. 2000, Basden and Young 2001). Long (1988) described *Howqualepis rostridens* based on numerous specimens from the Givetian Mt Howitt fauna of central Victoria (age revised in Young, 1999).

Adding to this Eastern Australian record is an incomplete but articulated fossil actinopterygian that was recently discovered by Gavin Young from the Middle Devonian Bunga Beds, near the shoreline at Bunga Beach in south coastal New South Wales. This represents the first discovery of an articulated Devonian actinopterygian postrcranium from New South Wales. Subsequent repeated searches failed to recover additional material of this form (Gavin Young, pers. com.).

3.3 Geological Setting

The Bunga Beds represent a thinly bedded sequence of carbonaceous shale and sandstone that comprises the lowest section of an extensively fossiliferous Devonian sequence (Fergusson et al. 1979, Young 2007). Young (2007, figs 1, 2) provides and up to date account of the lithology, fossil assemblage and possible age of the Bunga Beds. The age of the unit is poorly constrained and probably older than the Late Devonian age stated in recent literature (Cas et al. 2000, Giordano and Cas 2001, Rickard and Love 2000).

The dark shales of the Bunga Beds are highly fossiliferous with abundant plant material

and uncommon vertebrate remains (Young 2007, fig. 3), possibly representing a deepwater lacustrine depositional environment. The fossil fish fauna includes ischnacanthid acanthodians (Burrow 1996), several taxa of chondrichthyans including *Antarctilamna prisca* (Young 1982), originally described from the Givetian Aztec Silstone of Antarctica, and a possible tetrapodomorph sarcopterygian (Young 2007, table 1). The fossil ichthyofauna of the Bunga Beds seems impoverished due to the apparent absence of placoderms and dipnoans that are abundant in other southeastern Australian sites of a similar age.

3.4 Systematic Palaeontology

CLASS OSTEICHTHYES Huxley, 1880

SUBCLASS ACTINOPTERYGII, Cope, 1887

Family Howqualepididae Long, Choo and Young, 2008

Genus *?Howqualepis* Long, 1988

?Howqualepis youngorum sp. nov.

Etymology

After Professor Gavin Young (ANU) who discovered the holotype specimen and Mr Ben Young for conducting both the preparatory work as well as the key photography of the specimen. The *-orum* suffix is required when the epithet refers to two or more men or two or more people of mixed genders.

Repository

The type and only known specimen is lodged in the collections of the Department of

Earth and Marine Sciences, Australian National University, Canberra, represented in the text by the prefix **ANU V**.

Holotype.

ANU V2929a, b, an incomplete, partially articulated fish preserved laterally in part and counterpart. Consists of an incomplete opercular-gular series, cleithrum, clavicle, scales and all fins except the dorsal fin (Figs. 1-4). Collected by Gavin Young (ANU) from the Bunga Beds at Bunga Beach, south of Bermagui, New South Wales.

Diagnosis

A *Howqualepis* with more than 54 primary lepidotrichia on the anal fin and porous ornamentation on the cleithrum and clavicle.

Remarks

Tentatively assigned to the genus *Howqualepis.* The extensive unsegmented pectoral lepidotrichia of *?Howqualepis youngorum* sp.nov. separates this taxon from all other Devonian actinopterygians except *Howqualepis rostridens* Long, 1988, *Donnrosenia schaefferi* Long, Choo and Young, 2008, and *Tegeolepis clarki* Newberry, 1888. *?H. youngorum* differs from *Donnrosenia* in that the unsegmented fin-rays account for more than 75% of the total length of the pectoral fin. *?H. youngorum* differs from *Tegeolepis* in possessing macromeric squamation, long-based pelvic fins and a segmented terminal fringe on the pectoral fin. Separable from *H. rostridens* in having porous (as opposed to entirely linear) ornament on the pectoral girdle and in having a larger anal fin (54+ vs 45 primary lepidotrichia).

3.5 Anatomical description

3.5.1 Overall body form

ANU V2929 is preserved in lateral aspect (Fig. 3.1). The anterior part of the specimen terminates at an oblique breakage margin, with elements of the opercular-gular series and pectoral girdle preserved along with the pectoral fin (Fig. 3.2). 2.5 cm behind this is an incomplete pelvic fin with patches of squamation present above and to the rear of the fin (Fig. 3). The largest preserved segment comprises the rear section of the fish, including well preserved anal and caudal fins along with extensive squamation (Fig. 4). The preserved sections suggest a highly elongate, fusiform body form similar to that of *Howqualepis rostridens* (Long 1988) and quite unlike the more compact and robust form of "*Mimia*" or *Moythomasia* (Jessen 1968, Gardiner 1984).

As preserved, the fossil measures slightly less than 12 cm from the anterior preserved edge of the clavicle to the posteriormost caudal scales. Assuming that the missing portions of the fish were of similarly proportions to that of *Howqualepis rostridens*, the complete fish would have measured about 14 cm from snout to caudal peduncle.

3.5.2 Opercular-gular series

A section of the dermal operculo-gular series of ANU V2929 is preserved in articulation and comprises a posteroventral fragment of the operculum, a partial suboperculum, and at least seven branchiostegal rays (Fig.3.2). The anterior portions of most of these elements are missing, the preserved sections terminating at a margin of clean breakage, suggesting that a substantial portion of the fossil, possibly including the skull, was lost prior to collection due to weathering.

The posterodorsal-most bone in the series is tentatively identified as the posterovental fragment of an operculum. It is an oblong bone bone, missing the dorsal and anterior margins. The bone surface is ornamented with short, posterolaterally directed linear ridges. The subopercuIum is rectangular with a convex posterior margin. Ornament consists of short linear ridges that extend to near the posterior bone margin.

At least seven branchiostegal rays are visible on ANU V2929b (Fig. 3.2). The first branchiostegal ray, whose dorsal margin is overlapped by the subopercuIum, is more than twice as thick dorsoventrally as the other bones in the series. The 2nd ray is poorly preserved while the 3rd is narrower than the following two rays. Rays 6 and 7 are very narrow. Ornament on all bones in this series consists of short rostrocaudally directed ridges with little evidence of the tubercular ornament present on the laterally facing branchiostegals of *Howqualepis rostridens* (Long 1988).

3.5.3 Pectoral girdle

A partial cleithrum and clavicle (Fig. 3.2) have a similar overall shape to those of most early actinopterygians. The cleithrum consists of an expanded ventral region with a slender vertically directed blade although the dorsal portion of this structure is missing. The bone is convex postiorly with a moderately deep embayment on the posterior margin for the insertion of the pectoral fin, similar to that of *H. rostridens* (Long 1988. Fig.27). The clavicle is triangular and overlaps the cleithrum posteriorly and is itself dorsally overlapped by the branchiostegal rays.

Preserved sections of ornament on both the cleithrum and clavicle consists of limited areas of short ridges, particularly around the posterior margin of the clavicle and the vertical

blade of the cleithrum, that are largely replaced by rostrocaudally oriented rows of small pores over most of the remainder of the bone surface. This differs from the condition in *Howqualepis rostridens* where the dermal surface of the corresponding area is covered in a mixture of ridges and raised tubercles with no porous ornamentation (Long, 1988. Fig.15). *Donnrosenia* has very similar ornamentation on the clavicle but has entirely linear ornamentation on the cleithrum (Long, Choo and Young, 2008. Fig.6). *Moythomasia durgaringa* and *M. nitida* also have porous ornamentation on the pectoral girdle, but restricted to the ventral faces of the cleithrum and clavicle (Choo, in prep) whereas pores are also present on the lateral surface in ?*H. youngorum.*

3.5.4 Fins

The pectoral fin (Fig. 3.2) is incomplete with no traces of the endoskeletal radial although the visible lepidotrichia are well preserved. The fin is elongate and triangular with more than 14 primary lepidotrichia present. As with *H. rostridens* and *Donnrosenia*, the anterior lepidotrichia are unsegmented for most of their length with secondary division restricted to the region near the fin margin. The trailing edge of the fin is not preserved and it is unclear if the posterior fin rays were fully segmented as in *H. rostridens* (see below). The fin reaches its maximum length at about the seventh primary ray, which is unsegmented for more than 75% of its length as in *H. rostridens*, longer than the c.65% unsegmented region in the fin of *Donnrosenia* (Long et al., 2008). A short section of the leading edge is preserved with spine-like fringing fulcra formed by terminal branching of the leading fin rays. As with *H. rostridens* and *Donnrosenia* (see below) there is no medial contact visible between the distal hemilepidotrichia of each fringing fulcra on any of the fins.

The pelvic fin (Fig. 3.3) is long-based and triangular. It is preserved lateral aspect and

does not appear to be as elongate as in *H. rostridens* although it is unclear if a section of the posterior margin is missing. The fins are located approximately midway along the body between the pectoral and anal fins. Primary lepidotrichia are only preserved for the anterior half of the fin, comprising more than 22 rays suggesting more the 40 primary rays on the entire preserved section. These rays are evenly segmented along their preserved length. Slender spine-like fringing fulcra are present on the leading edge.

The anal fin (Fig. 3.4a, b) is large and triangular in shape. At least 54 primary segmented lepidotrichia are present as opposed to c.45 fin rays on the anal fin of *H. rostridens.* It is unclear if the fin originally had a short posterior fringe trailing behind the main triangular area of the fin as in *H. rostridens*. If this was the case then the complete fin would have probably had over 60 primary lepidotrichia. As in the other fins, shortened spine-like lepidotrichial segments form a serrated cutwater of fringing fulcra on the leading edge.

As was the case in other known Devonian actinopterygians, the caudal fin (Fig. 3.4) was heterocercal in structure with a distinct posterior cleft separating the dorsal lobe (notochordal mass of the fin plus the dorsal hypochordal lobe) from the ventral hypochordal lobe. While little of its dorsal counterpart has been preserved, the ventral hypochordal lobe is elongate and triangular with c.40 primary lepidotrichia preserved. Spine-like fringing fulcra are present on the leading edge. The dorsal fin is not preserved in the holotype although a pair or large, isolated lepidotrichs preserved near the counterpart tail may have originated from that fin (Fig. 3.4d).

3.5.5 Scales and squamation

Articulated macromeric scales, scutes and basal fulcra are preserved from the caudal fin, extending forwards to above the anal fin (Fig. 3.4c, d). There are also isolated patches of scales preserved above and to the rear of the pelvic fins (Fig. 3.3). Very little of the scale ornamentation has been preserved. The visible scale types are described in accordance with the zonation terminology as proposed in in Esin (1990) and employed in Trinajastic (1999).

Area C = flank scales extending from above the pelvic fins to above the anal fin. Scales are elongate and rectangular, with rostrocaudal length being at least twice the height of the scale. Ventral margin is gently convex. The disposition of the peg and socket articulation is unknown in the scales close to the pelvic fins and absent in the scales near the anal fin. Free field ornamentation is poorly preserved but individual scales show remnants of longitudinal furrows. Scales from near the front and rear of the field seem to have two or three serrations protruding along the caudal edge suggesting little or no rostrocaudal decrease in the number of serrations.

Area D = scales anterior to the caudal fin and on the notochordal mass of the caudal fin. Scales anterior to the caudal fin are rhombic in form, becoming smaller and increasingly elongate on the notochordal mass of the fin. Scales near area C have a gently convex ventral margin, becoming less prominent towards the caudal fin until the margin is completely straight at those scales near the caudal inversion. Peg and socket articulation is absent. The free field is smooth with no preserved traces of raised ornamentation. Posterior serrations range from two in scales near area C to none on those scales on the caudal fin.

Area H = scales adjacent to the base of the anal fin. These scales are small, elongate

rhomboids. Peg and socket articulation is not visible and probably absent. There is no evidence of ornamentation or posterior ridges.

Scutes = The only dermal scutes that have been preserved are an articulated series visible anterior to the dorsal caudal lobe and extending over the dorsal margin of the caudal fin (Fig 3.3b, c). Anterior to the caudal fin, the scutes are triangular plates with a caudally-directed apex and are about three times longer than the adjacent flank scales. As the series progresses posteriorly over the notochordal mass of the caudal fin, the scutes narrow and spine-like with extensive overlap between the individual scutes.

3.5.6 Redescription of the pectoral fin of *Howqualepis rostridens*

Long (1988) described the pectoral fin of *Howqualepis rostridens* as consisting of 25 primary lepidotrichia that are unsegmented for most of their extent, save for some secondary division near the fin margin. A complete pectoral fin was not figured and re-examination of this form has revealed the fin to be more extensive than previously recognised (Fig. 3.5). Additionally, the leading edge of the pectoral and other fins was described as having short, parallel rays similar to fringing fulcra, but not paired (ibid). A similar condition in *Donnrosenia* led to Long et al. (2008) to diagnose the Howqualepididae as possessing short spine-like lepidotrichia in lieu of true fringing fulcra.

The anterior two-thirds of the fin consist of c.25 lepidotrichia that possess extensive proximally unsegmented sections that in some specimens display distal bifurcation. At the lateral margins, these primary rays branch into a fringe of narrow, segments. The relative length of the proximal rays to the segmented fringe is variable, with the unsegmented region accounting for between 75-90% of the length of the fin. There appears to be no correlation

between the degree of distal segmentation and the size of the specimen.

Posterior of the unsegmented rays are at more than 10 additional primary lepidotrichia that are segmented from base to margin, again displaying a variable degree of distal branching. The pectoral fin of *H. rostridens* was thus broader in shape and less-extensively unsegmented than has previously been described. In the majority of specimens, the delicate elements of the posterior rays and terminal fringe are scattered or missing, leaving only the thick unsegmented proximal sections in articulation. This configuration of the pectoral fin-rays is similar to that of a number of Carboniferous taxa including *Rhadinichthys* (Moy-Thomas and Bradley Dyne, 1938).

On the leading edge of the pectoral fins of *Howqualepis rostridens*, *?H. youngorum* sp.nov. and *Donnrosenia*, the terminal sections of the otherwise unsegmented marginal fin rays branch at least twice, to forming narrow spine-like elements that are not obviously paired. These elements are called "terminal lepidotrichia" in *Cheirolepis* (Pearson and Westoll 1979) and *Melanecta* (Coates 1998) or "cutwater lepidotrichia" in the Howqualepididae (Long, Choo and Young 2008). In a recent study, such structures fall into Arratia's "Pattern A" class of fringing fulcra, formed from overlapping branched projections of the anteriormost lepidotrichia (Arratia 2009), a condition found in all undisputed Devonian actinopterygians with the exception of *Tegeolepis* which appears to lack any sort of spiny cutwater (Dunkle and Schaeffer 1973). The fulcra of *Cheirolepis*, which are of similar form to those of the Howqualepididae, comprise distally enlarged hemilepidotrichia that partially enclose their paired counterparts (Arratia 2009). The more obviously paired structures present in *Moythomasia* and "*Mimia*" (also falling within "Pattern A") are the result of the terminal segments being of equal length and in medial contact. Given that the

scheme proposed by Arratia (and adopted here) means that all Devonian fringing fulcra are in fact modified spine-like lepidotrichia (merely differing in the nature of contact between the hemilepidotrichia), the diagnosis of Howqualepidiae has been adjusted accordingly in the systematic description.

3.5.7 Revision of the Howqualepididae

Long, Choo and Young (2008), one which Chapter 2 is based on, erected the Howqualepididae, comprising *Howqualepis rostridens* from Mount Howitt, Victoria and *Donnrosenia schaefferi* from the Aztec Siltstone of Antarctica. ANU V2929 appears to represent a third taxon within this clade. All three fish have an elongate body form with macromeric squamation; long-based pelvic fins; small fringing fulcra without medial contact between the distal hemilepidotrichia, and extensive unsegmented primary lepidotrichia that comprise most of the length of the pectoral fin. Among the other Devonian actinopterygians, only *Tegeolepis clarki* (Dunkle and Schaeffer 1973) possesses extensive unsegmented pectoral lepidotrichia but is distinguished from the Gondwanan forms in lacking a terminal segmented fringe on the pectoral fins, in possessing micromeric squamation and having small, short-based pelvic fins.

Assigning the Bunga Bed taxon to a genus is difficult owing to the lack of key skull characters that are used to characterise *Howqualepis rostridens* from the similar *Donnrosenia.* For example, *H. rostridens* possesses an extremely long maxillary blade, a dentigerous rostral and small, dorsoventrally compressed premaxillae (Long 1988). *Donnrosenia* displays a short, deep maxillary blade, dorsoventrally prominent premaxillae, a small accessory operculum and much smaller teeth than *Howqualepis* (Long, Choo and Young 2008).

ANU V2929 is considered to be closer *H. rostridens* in having more extensive unsegmented pectoral lepidotrichia and relatively smaller scales than *Donnrosenia.* The pectoral fins of ANU V2929 are more similar to that of *H. rostridens* in that both forms possess unsegmented lepidotrichia that account for over 75% of the maximum length of the fin. Those of *Donnrosenia* account for less than 70% of the maximum fin length (Long, Choo and Young 2008. Fig.7).

Based on these anatomical similarities and pending the discovery of skull material for this taxon, ANU V2929 is tentatively assigned to *Howqualepis*. The Bunga Bed form is not conspecific with *H. rostridens* and is distinguished in having a larger anal fin with a greater number of primary lepidotrichia and in possessing porous dermal ornamentation of the pectoral girdle.

The presence of a grade of Devonian actinopterygian so far found exclusively in Middle Devonian freshwater deposits of southeastern Australia and Victoria Land, Antarctica highlights the close biogeographical similarity between the fossil faunas of these two regions. The apparent absence of these ray-finned fishes in Devonian sites outside this area also adds to a growing body of fossil evidence that indicates a regionally endemic freshwater vertebrate fauna within Middle Devonian Eastern Gondwana. Similarities in key taxa of placoderms (Young 1988, Young and Long 2005), acanthodians (Long 1983, Young 1989b, Young and Burrow 2004), chondrichthyans (Young 1982, 2007; Long and Young 1995) and dipnoans (Long 1992, 2003) have been well documented.

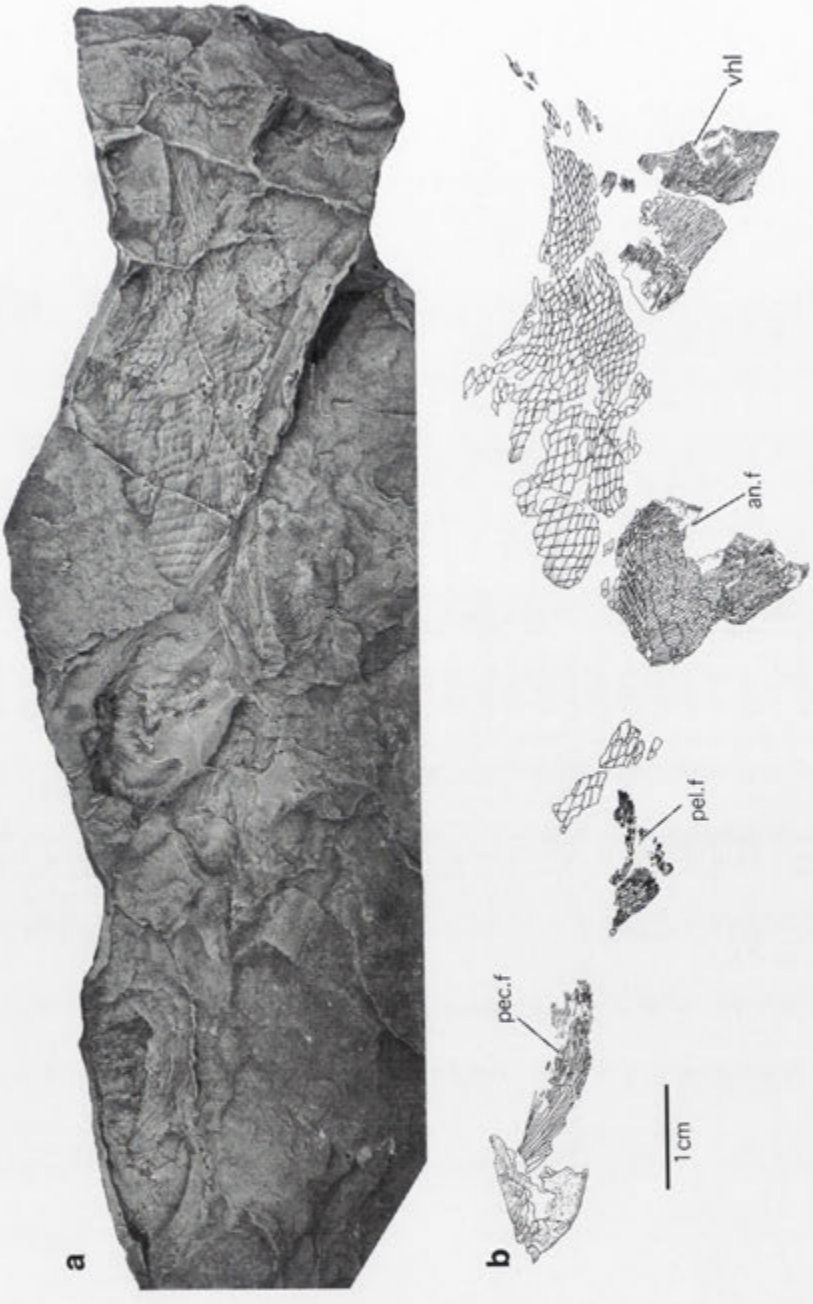


Figure 3.1
?Howqualepis youngorum sp. nov. **a.** photograph and **b.** line drawing of holotype (ANU V2929A) showing the entire preserved fossil in lateral view. The specimen is a latex cast whitened with ammonium chloride.

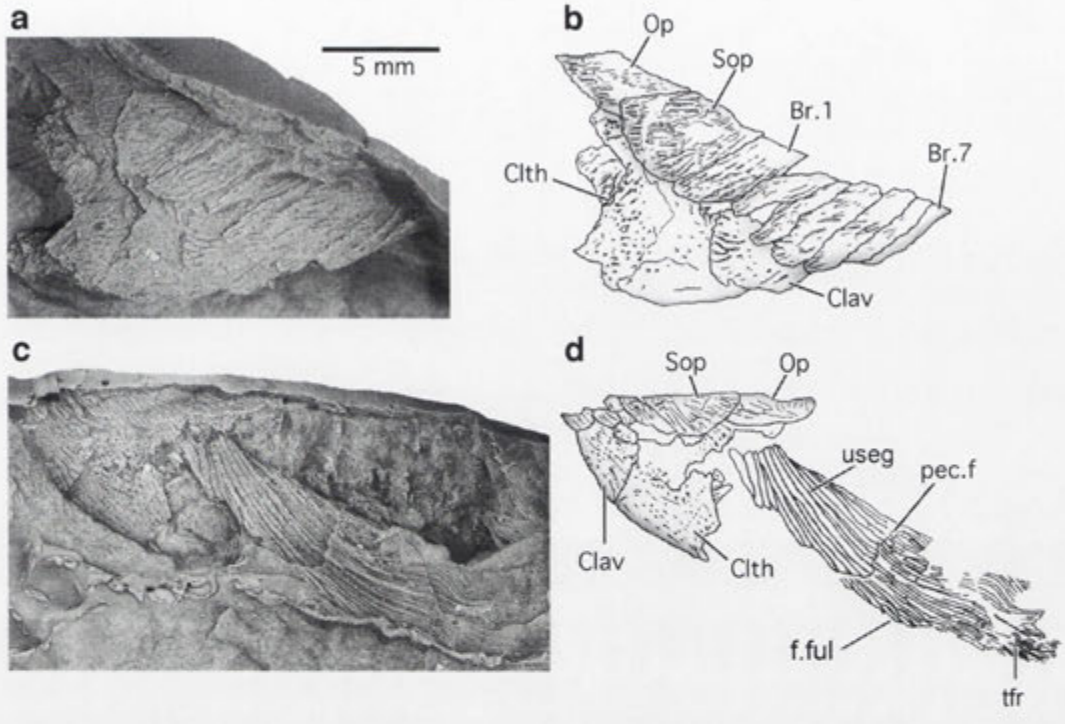


Figure 3.2
?*Howqualepis youngorum* sp. nov. **a.** photograph and **b.** line drawing of the pectoral girdle and opercular-gular series of the holotype counterpart (ANU V2929B), **c.** photograph and **d.** line drawing of pectoral girdle, opercular-gular series and pectoral fin of the holotype (ANU V2929A).

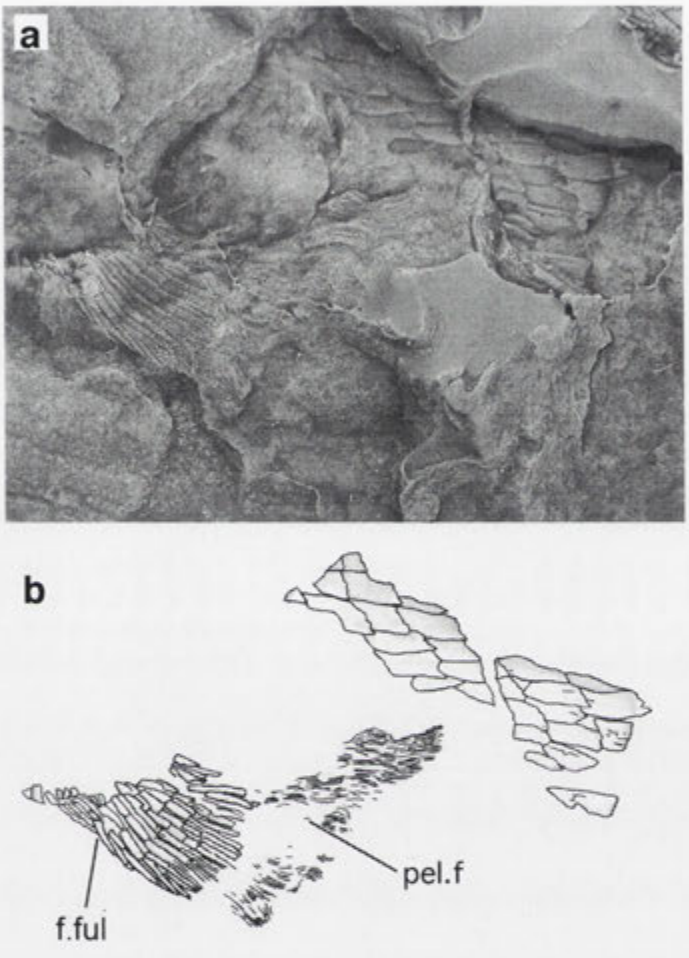


Figure 3.3
?*Howqualepis youngorum* sp. nov. **a.** photograph and **b.** line drawing of the pelvic fin and associated squamation on ANU V2929A.

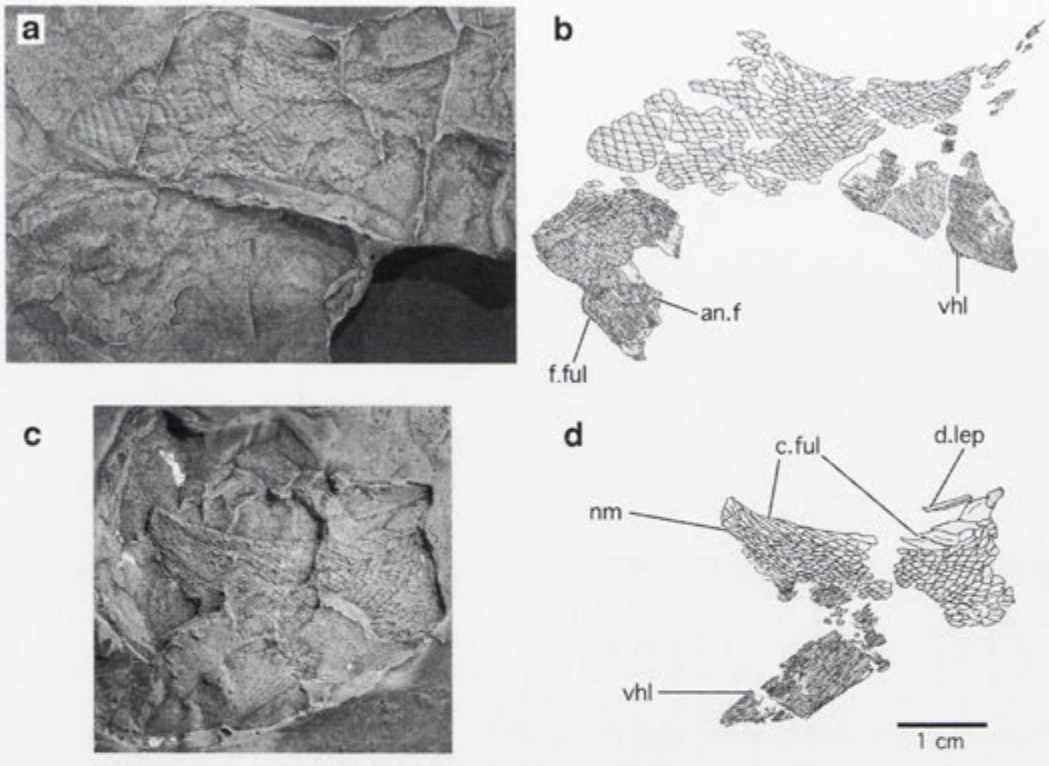


Figure 3.4
?*Howqualepis youngorum* sp. nov. **a.** photograph and **b.** line drawing of the anal and caudal fins of ANU V2929A, **c.** photograph and **d.** line drawing of the caudal fin of the holotype counterpart (ANU V2929B).

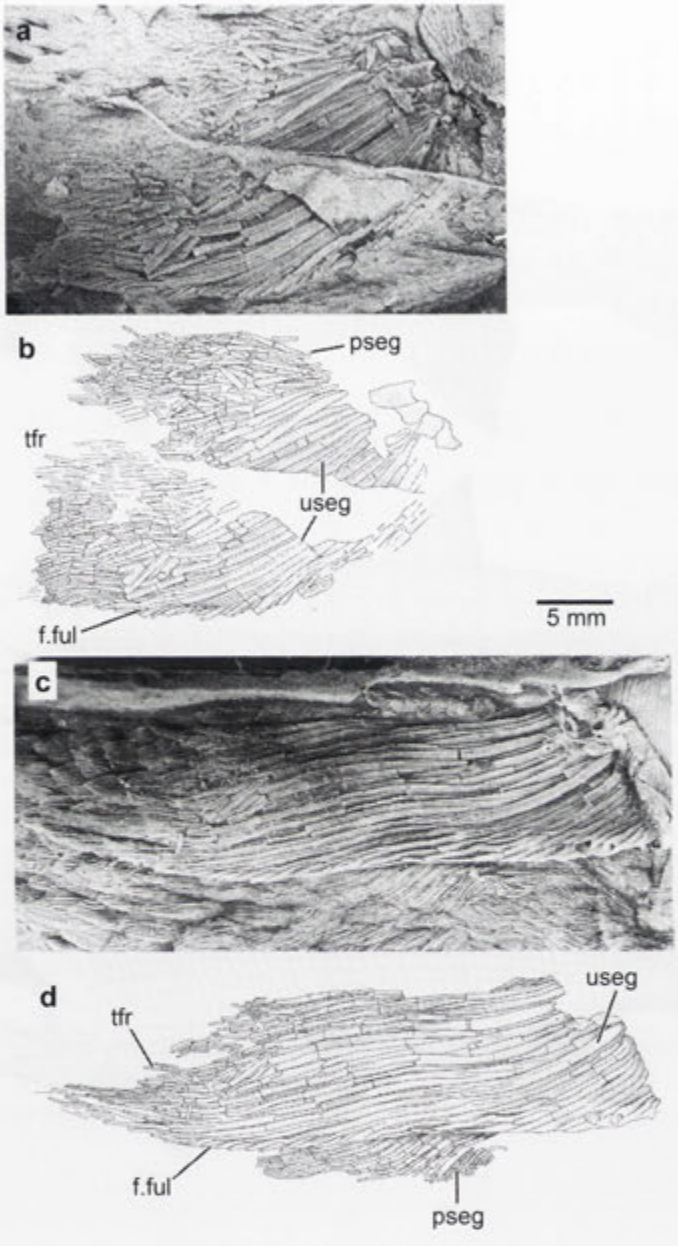


Figure 3.5
Pectoral fin of *Howqualepis rostridens*. **a.** photograph and **b.** line drawing of the fin of MV P.160857. **c.** photograph and **d.** line drawing of the fin of MV P.160851B. In this specimen, the posterior section has partially torn off and folded to be visible ventral of the anterior edge of the fin.

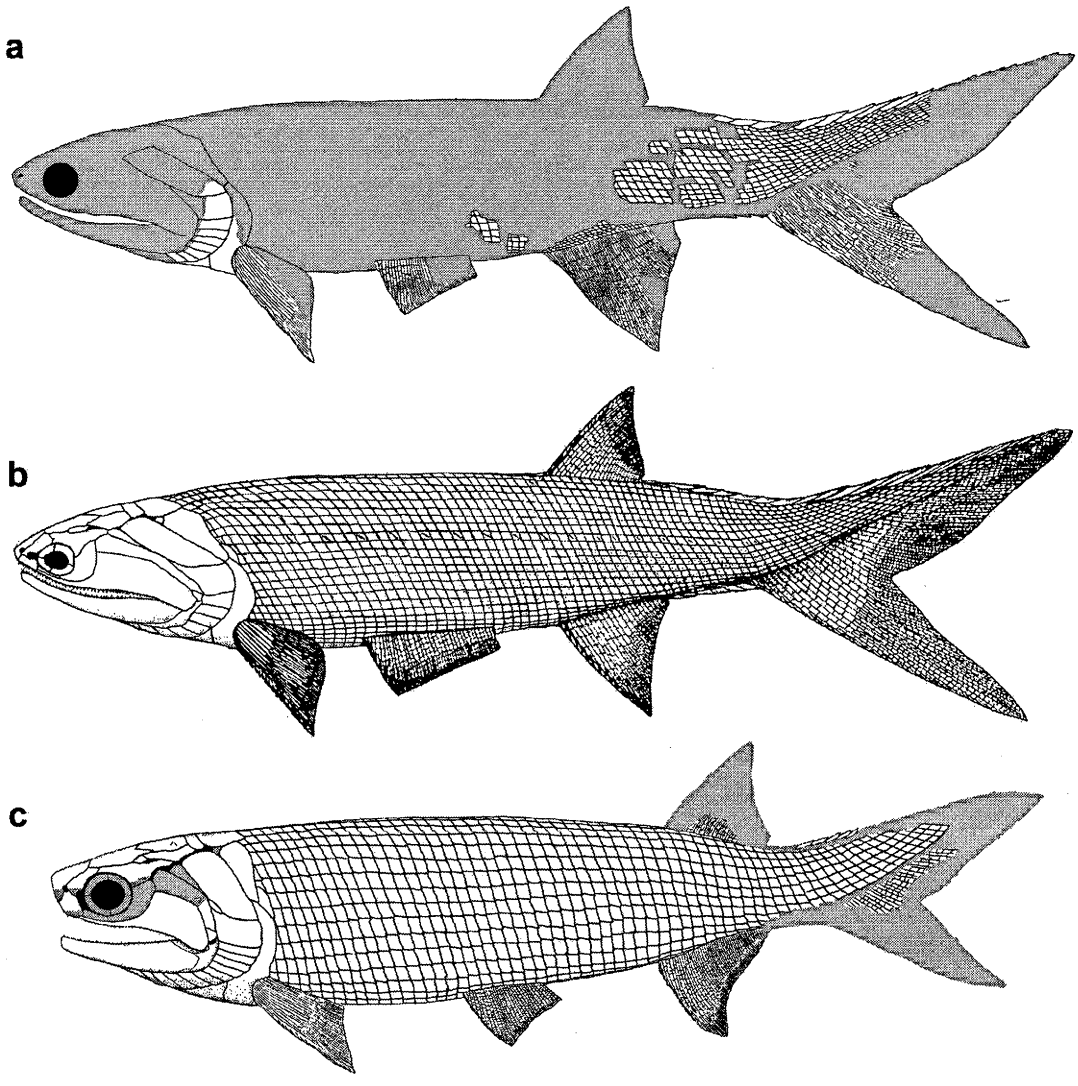


Figure 3.6
Comparison of the three known species of the Howqualepididae. Reconstructions presented in lateral view and are not to scale. Unknown parts of the anatomy are represented by dark grey areas. **a.** *?Howqualepis youngorum* sp.nov., based on the preserved extent of the holotype with outline based on *H. rostridens*, c.14cm long. **b.** *Howqualepis rostridens* from Mount Howitt, Victoria (modified after Long, 1988). Size of specimens range from 20-50cm. **c.** *Donnrosenia schaefferi* from the Aztec Siltstone, Southern Victoria Land, Antarctica (from Long et al., 2008), c. 14cm long.



Figure 3.7
Life reconstruction of *Howqualepis rostridens* from the Givetian of Victoria. *?H. youngorum* was likely to have been a very similar looking animal.

Chapter 4. A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia

4.0 Preamble

This chapter represents a modified version of a manuscript co-authored with John Long and Kate Trinajstic recently published in *Acta Zoologica*, to which I contributed more than 90% of the text and illustrations (Choo et al. 2009). John Long discovered and prepared the original specimen and provided unpublished preliminary observations. Kate Trinajstic provided the SEM images and written description of the scales.

4.1 Abstract

A new basal actinopterygian, *Gogosardina coatesi* gen. et sp. nov., is described from the Upper Devonian Gogo Formation of the Canning Basin, Western Australia. The new taxon is known from four prepared specimens that display the typical exceptional preservation of fossil vertebrates from the region. *Gogosardina* gen. nov. possesses a series of four small postrostrals, no surangular and a highly gracile body covered with over 140 vertical rows of very small scales, all ornamented with separate horizontal ganoine ridges. One specimen contains conodont elements lodged among the branchial arches, indicating dietary habits and a possible cause of death.

4.2 Introduction

Research into the Late Devonian (Frasnian) Gogo fish fauna of the Canning Basin, Western Australia has greatly contributed to our understanding of the anatomy and interrelationships of early vertebrates owing to an extraordinary level of fossil preservation.

Exceptional specimens are recovered as three-dimensional articulated skeletons with exquisite dermal, perichondral and, in rare cases, soft tissue preservation (Trinajstic et al. 2007). To date, over 40 species of placoderms, actinopterygians and sarcopterygians have been described in the assemblage (Long 2006). In contrast to the diverse placoderm and dipnoan fauna, recorded actinopterygian diversity has, to date, been low. This work partly redresses this by providing the first comprehensive description of *Gogosardina* gen. nov., the first new actinopterygian described from the Gogo Formation in over thirty years. Moreover, these remains have considerable significance in providing the identification of isolated scales from a previously unknown palaeoniscoid found throughout the Canning Basin (Trinajstic and George in press).

Complete specimens of early actinopterygians are a sparse component of most pre-Carboniferous vertebrate assemblages and are currently known from only a dozen described Devonian genera. In Australia, articulated Devonian actinopterygians are rare with the only complete specimens consisting of the Gogo material, plus *Howqualepis* from the Givetian Mt. Howitt locality in central Victoria (Long 1988). The actinopterygian fauna of the Gogo Formation has, to date, been represented by only two taxa: *Moythomasia durgaringa* Gardiner and Bartram 1977 and *Mimia toombsi* Gardiner and Bartram 1977 (renamed *Mimipiscis* in Chapter 5). Additional anatomical information was presented by Gardiner (1984) and their squamation described in detail by Trinajstic (1999a, 1999b).

The presence of at least three additional taxa of Gogo actinopterygians has become apparent based on superb material recovered by Western Australian Museum expeditions to the region from 1986-2003 as well as the 2005 Museum Victoria expedition. The material described herein represents one of these, initially recognized as a novel form based on a

specimen collected by J.A. Long in 2001. In addition, a well preserved conodont apparatus was recovered in the branchial regions of one specimen, giving a rare insight into the lifestyle and diet of these animals.

The Gogo material has been of exceptional importance in being the most complete Palaeozoic examples of ray-finned fishes, with 3-dimensional preservation of the full dermal skeleton combined with rarely recovered fine details of the neurocranium. Both of the previously described taxa have featured in the majority of recent phylogenetic analyses of early ray-finned fish (Cloutier and Arratia 2004, Coates 1999, Friedman and Blom 2006, Gardiner and Schaeffer 1989, Long 1988, Schultze and Cumbaa 2001, Taverne 1997). Given the typically imperfect preservation of forms from outside the Gogo, the interrelationships of early actinopterygians remain poorly resolved (Cloutier and Arratia 2004). The material described herein will be incorporated into future phylogenetic studies of early actinopterygians (Choo, in prep).

4.3 Notes on preparation

The process of fossil preparation is detailed in Chapter 1.5.4. The holotype specimen suffered extensive damage during preparation due to the failure of the resin base to properly bond with the fossil bone. It currently consists of isolated scales, dermal elements of the skull, pectoral girdle along with impressions of the articulated fish with bone remnants set within the resin base. A fragmentary neurocranium survives with attached parasphenoid, right lower jaw and right maxilla.

All articulated specimens were whitened with ammonium chloride prior to principle photography with the exception of MV P228849b which was left unwhitened in the interest

of preserving the delicate conodont apparatus present within the fish's body. Scanning electron micrographs were produced of scales removed from the holotype specimen.

4.4 Systematic palaeontology

Class Osteichthyes Huxley 1880

Subclass Actinopterygii Cope 1887

Genus *Gogosardina* nov.

Diagnosis

As for type species (monotypic genus).

Type Species

Gogosardina coatesi, sp. nov.

Locality and horizon

Gogo Formation, Western Australia, lower Frasnian, Upper Devonian.

Etymology

"Gogo sardine"; referring to the Gogo Formation and the highly gracile body form of the fish which superficially resembles that of some extant clupeid teleosts.

Gogosardina coatesi sp. nov.

(Figs 4.2-4.14)

Diagnosis

Stem actinopterygian with skull roof having parietals, frontals and supratemporals of roughly equal rostrocaudal length; triangular intertemporals forming dorsal margin of spiracular slit; four small postrostral units (3 anterior and 1 posterior); posterior postrostral forms anterior margin of the pineal foramen; rostral stout and tapers anteriorly. Lower jaw comprises large dentary and small angular which meet in the smooth maxillary overlap area with a zigzag suture; surangular absent. Parasphenoid with diamond-shaped posterior shelf which underlies the ventral otic fissure; ascending processes absent. Opercular elongate and four sided; subopercular with a well-developed anterodorsal process; first three branchiostegal rays of uniform height. Body elongate and fusiform; fringing fulcra present on at least the pectoral, pelvic and anal fins; pectoral fin-rays proximally unsegmented; pelvic fins short-based; dorsal and anal fins large and long-based. Scales small and barely macromeric with c.145 scale rows from occipit to caudal inversion; all scales have a free field ornament of separate horizontal ganoine ridges.

Etymology

For Mike Coates in recognition of his many contributions to palaeoichthyology.

Holotype

WAM 07.12.2. Originally an entire fossil fish, now consisting of a partial neurocranium with attached partial parasphenoid, right maxillary and lower jaw; dermal elements of the skull, left lower jaw, opercular-gular system, pectoral girdle and numerous scales along with a partially articulated counterpart mounted in resin, consisting of scales, skull roof, and resin impressions of other bones. Collected in 2001 by John A. Long near Embayment Hill.

Referred Specimens

MV P227023 (a+b) : Articulated fish resin-mounted as separate part and counterpart; almost complete fish including that, in one half-mount, contains a well preserved neurocranium that is not fully prepared at the time of writing. Collected by John A. Long at Stromatoporoid Camp in 1986.

MV P228269 : Partial articulated postcranium resin-mounted as separate part and counterpart. Skull lacking skull-roof and neurocranium recovered as disarticulated pieces. Collected by Gavin Young at Paddy's Valley in 1972.

MV P228849 (a+b) : Articulated fish resin-mounted as separate part and counterpart. Almost complete, lacking only the snout, skull-roof, neurocranium, most of the dorsal fin and much of the ventral body area including the pelvic and anal fins. Collected by John A. Long in Paddy's Valley in 2001.

BMNH P.53241 : Unprepared specimen comprising the anterior half of a fish. Collected in 1967 near Stromatoporoid Camp, Gogo Station (H.A.T. 67/47, see Miles, 1971: fig.1)

4.5 Anatomical Description.

MV P228849 represents the most complete, fully prepared specimen and has a standard length of c.11 cm with a lower jaw that is 1.8cm long. MV P227023 and P228849 are of a similar size. MV P.228269 represents the largest known specimen with a jaw length of 2.35 cm.

The neurocranial anatomy of *Gogosardina* is not presented in this description as it

requires further preparation of one specimen (MV P227023a) and high-resolution CT scanning before it can be fully studied; but will form a separate work in conjunction with other braincase material from the additional new taxa recovered from the Gogo Formation.

4.5.1 Skull roof.

The holotype is the only specimen that has a complete skull roof with the postrostrals in place. The skull roof (Figs. 4.7, 4.13) is comprised of the following paired elements: frontals, parietals, dermosphenotics (now destroyed), intertemporals and supratemporals. There are also a series of anamesic postrostral elements and an unknown number of extrascapulars.

Postrostrals (Fig. 4.7). The postrostral series is only preserved on the type specimen. It consists of a laterally-arranged trio of small anterior bones that narrow to a single, posterior unit. The combined postrostral series sutures anteriorly to the rostral, anterolaterally to the nasals and laterally to the frontals. The posterior margin of the posterior unit forms the anterior margin of the pineal foramen. The (anterior) median unit is rectangular, flanked on each side by rhombic lateral postrostrals. The posterior postrostral is hexagonal and more than twice the size of the anterior units. Dermal surfaces are ornamented with linear rostrocaudal ridges.

Frontals (Fig. 4.7). Narrow bones of similar length to the parietals. The paired bones meet for the posterior 40% of their length in a smooth median suture, with a large central embayment for the pineal foramen. Anterior to the foramen, the medial margin is deflected anterolaterally, suturing with the posterior postrostral and a lateral postrostral. Overlapped anteriorly by the nasal and posteriorly by the parietal. The supraorbital canal enters the bone

from the middle of the posterior margin and is deflected anterolaterally at the level of the pineal foramen. Ornament consists of fine rostrocaudally-directed linear ridges, becoming shorter and more radial near the anterolateral margins.

Parietals (Fig. 4.7). Bones of roughly equal rostrocaudal length to the frontals and supratemporals. Dorsally convex and about 1.4 times longer than broad. Smooth marginal contact with neighbouring parietal, intertemporal and supratemporal, zig-zag anterior suture with the frontal. Rostrocaudally oriented anterior pit-line continuous with the supraorbital canal which exits the bone anteriorly. The middle pit-line sits close to the anterior pit-line and is directed towards the anterolateral suture with the intertemporal. The posterior pit-line is widely separated from the other two and is directed posteromedially. Dermal ornament consists of linear rostrocaudal ridges.

Supratemporals. (Fig. 4.7). Narrow bones which sutures medially with the parietal and anteriorly to the intertemporal. Dermal surface is poorly preserved on the type specimen and the path of the path of the infraorbital sensory canal is not visible.

Intertemporals. (Fig. 4.7). Narrow, triangular bones, one fifth the length of the parietals. Ornament not preserved. Slight embayments on their lateral surfaces in dorsal view suggest that they formed at least part of the dorsal margin for an open spiracular slit.

Dermosphenotic. Originally preserved on the holotype but destroyed during preparation. Based on preliminary sketches, they were tripartite structures similar to the dermosphenotics of *Mimipiscis* and *Moythomasia durgaringa.*

Extrascapulars. Broken pieces of dermal bone with linear ornamentation from the type specimen probably represent fragments of the extrascapulars. Their original size, shape and number cannot be determined.

4.5.2 Snout

The anterior section of the skull has been preserved on the holotype and MV P.228269 (Fig. 4.8). It comprises paired, medially abutting dentigerous premaxillae, nasals and a single median rostral.

Rostral. (Fig. 4.8A-D). Small median bone of a similar size to the premaxillae. Short dorsal lamina folds downwards and abruptly narrows anteriorly to a tip set against the median premaxillary suture. Distinct posteroventral kinks where the ethmoid canal exits the bone. Dorsoposterior margin is convex, forming an embayment for the anterior postrostrals. Lateral margins straight, suturing with the nasals except for circular emarginations for the anterior nostrils. External surface consists of linear ridges along the dorsal surface, grading into an irregular, vermiculate pattern of short ridges and tubercles on the anterior face. Ethmoidal commisure is visible externally as an arc of pores and internally as an open groove.

Premaxilla. (Fig. 4.8A-D). Flat, anterior facing bones with a small lateral aspect. Meets counterpart in a short, straight median suture. Inward sloping anterior margins of both premaxillae form a V-shaped recess for the median rostral. Posterior face forms anteroventral margin of the orbit and there is a small unornamented overlap surface for the anterior maxillary tip and probably the lacrymal. The dentigerous margin for each bone consists of large, conical teeth set in rounded sockets. Sharpened tubercles form an outer row

of variably sized smaller teeth. The infraorbital sensory canal enters the premaxilla posteroventrally, branching 80% up into the bone with one branch exiting via the anterodorsal margin into the rostral, the other via the posterodorsal margin into the nasal. Complex ornamentation consists of posteroventrally directed linear ridges along the lateral face which grade into a vermiculation of short, irregular ridges and tubercles on the anterior aspect. Small tubercles close to the biting margin. The smooth internal surface is slightly concave with the infraorbital canal represented by a sharply defined tube.

Nasal. (Fig. 4.8E-H) Narrow bones positioned dorsal and anterior to the premaxillae and lateral to the median rostral. Sutures with both these bones are straight, broken only by the notch on the dorsal margin for the posterior border of the incurrent naris. Lateral margin is gently concave, forming the anterodorsal margin of the orbit. The bone narrows at a slender dorsal lamina which sutures with the dermosphenotic. The external surface is covered in short-to medium length longitudinal ridges. The course of the supraorbital sensory canal is visible externally as a longitudinal row of widely spaced small pores with a short anterior pit-line and viscerally as an open groove.

4.5.3 Cheek and Infraorbitals

The cheek comprises a large maxilla, preoperculum and small quadratojugal. The jugal represents the only infraorbital unit among the available material. There is space for a slender lacrimal between the jugal and premaxilla, but such a bone has not been identified.

Jugal. (Figs. 3,8I-L). Crescentic bone with a concave anterodorsal surface that forms posteroventral border of the orbit. Narrow at anteroventral suborbital extremity, broad posterodorsal surface. The infraorbital canal changes from a horizontal suborbital

orientation to a vertical postorbital aspect as it passes through the bone. Dermal ornament consists of short linear ridges.

Maxilla. (Figs. 4.3,4.9) The maxilla is of a type similar to *Mimipiscis*, consisting of a narrow suborbital ramus and an expanded postorbital blade. The suborbital portion is long and low, expanding to meet the postorbital blade in a shallow curve. The postorbital region is rectangular, with a pronounced posteroventral extension that overlaps the lower jaw in articulation. The occlusal margin is dentigerous along the entire length, consisting of an inner row of more than 25 large, acrodin-capped conical teeth and an outer row of numerous small teeth. Ornament consists of long ridges on the dorsal two-thirds of the maxillary blade and short, irregular ridges on the ventral one-third of the blade and on the suborbital ramus.

Preoperculum. (Figs 4.3,4.8M-N) An acutely angled bone, overlapped on its ventral margin by the postorbital section of the maxilla. Robust anterodorsal horizontal ramus tapers towards the junction with the narrow, near-vertical posterior ramus. Anterior head is straight and meets the jugal. The posterior extremity is pointed and overlaps the quadratojugal. The preopercular canal runs close to the posterodorsal margin of the posterior 75% of the bone, exiting dorsally. Short vertical and horizontal pit-lines are present at the junction between the horizontal and posterior rami. Ornament of short linear ridges with scattered tubercles.

Quadratojugal. (Fig. 4.8M-N) A small subrectangular bone overlapped anteriorly by the posteroventral corner of the maxilla and dorsally by the preoperculum. The quadratojugal pit-line is visible as a short, slanting surficial groove, oriented parallel to the posteroventral margin of the maxilla. Ornament restricted to a small portion of the surface and consists of very short linear ridges.

4.5.4 Parasphenoid and Palatoquadrate

Parasphenoid. (Fig. 4.9) Only the posterior half of the parasphenoid is preserved in the holotype. This tooth-covered bone is elongate with a broad posterior shelf extending to the level of the ventral otic fissure, similar to the configuration in *Moythomasia durgaringa* (Gardiner 1984, Fig. 51). As with *Mimipiscis toombsi* (ibid, Fig. 50) there are no ascending processes.

Palatoquadrate. (Figs. 4.4,4.11) A long structure fused into a single unit with no trace of separate ossification centres in available specimens. It is very similar to the palatoquadrate in large specimens of *Mimipiscis toombsi*, being roughly triangular with a circular hole for the basipterygoid process near the anterodorsal margin. Behind a narrow, suborbital ramus there is a tall postorbital plate whose posterior margin is fixed to the mesial surfaces of the preopercular and quadratojugal. The spiracular groove runs backwards from just posterior to the hole for the basipterygoid process and follows the contours of the ventral margin of the preoperculum. An extensive dentigerous dermal plate covers more than two-thirds of the medial surface, completely fused into a single ossification. It is of similar form to that of *Mimipiscis* (Gardiner 1984: Fig. 54 and 56) except that the dorsal margin of the dermopalatines, which is straight in *Mimipiscis*, forms a strongly undulating outline.

4.5.5 Operculo-gular system

Dermohyal. (Figs. 4.3, 4.8M-N) Small, roughly triangular bone consisting of a rounded anteroproximal section tapering to a narrow posterior apex. Ornament consists of small tubercles and short posteroventrally oriented ridges.

Operculum. (Fig. 4.3) Large, near-symmetrically lenticular bone with convex anterior and posterior margins meeting at narrow anterodorsal and posteroventral corners. Entire ventral margin overlaps the dorsal margin of the subopercular. Lower 30% of the anterior margin overlaps the subopercular, followed further upwards by a small area of contact with the dermohyal. The left operculum of MV P.228849 possesses two circular pits on the dermal surface close to the middle of the bone that might represent sensory pits. These pits are however not present on other examples of this taxon. Ornament consists of short to medium-length linear ridges arranged posterolaterally. The visceral is surface smooth except for small round depression near anterodorsal corner, corresponding to the presumed opercular cartilage housing in *Mimipiscis toombsi* (Gardiner 1984).

Subopercular. (Figs. 4.3, 4.11) Rectangular bone about 70% the size of the operculum. Although shape varies among specimens, the length of the bone is always more than double the height. Has a prominent, prong-shaped anterodorsal process that functionally replaces the accessory operculum of certain other early actinopterygians (eg. *Cheirolepis* and *Moythomasia nitida*) and gives the bone a strongly convex dorsal margin. Isolated circular depressions close to the anterior margin probably represent laterosensory pits. Ornament consists of horizontal, posterolateral linear ridges that flex into a posterodorsal orientation at the anterodorsal process.

Branchiostegal rays. (Fig. 4.3) A complete branchiostegal series has not been preserved but at least eight are visible on MV P228849a. The first branchiostegal ray is a slender and elongate bone, its concave shape conforming to the ventral contours of the subopercular. The next two rays are marginally shorter than the first, but show no variation in height. The branchiostegal rays possess only a slight overlap with their neighbours and there is no evidence of extensive unornamented hyoid processes or overlap surfaces as present in

Mimipiscis (Gardiner 1984: Fig. 97) and *Cheirolepis* (Pearson and Westoll 1979: 363).

Gulars. (Fig. 4.3) An incomplete lateral gular is viscerally exposed in MV P228849a as an angular unit below the left dentary.

4.5.6 Lower Jaw

The lower jaw is effectively indistinguishable to that of *Mimipiscis* (Gardiner 1984, Fig. 90), consisting of a long dentary, angular, pre-articular and coronoids. There is no surangular.

Dentary. (Figs. 4.3, 4.4, 4.9, 4.10, 4.11). The largest bone on the lower jaw, consituting more than 85% of the dermal surface. Dentition consists of more than 20 large, conical, laniary teeth with an outer row of much smaller, numerous tubercle-like teeth. The posterodorsal section is unornamented, part of a smooth semi-circular excavation that is overlapped by the posteroventral corner of the maxilla. The dentary meets the angular in this excavation with a zig-zag shaped suture. The pores of the mandibular sensory canal run close to the ventral margin of the bone throughout its length, with a slight dorsal deflection into the middle of the bone close to the anterior tip. Dermal ornament of long ridges near the ventral margin, becoming increasingly short and irregular dorsally and grading into tubercles near the biting margin.

Angular. (Figs. 4,9,10A-B) A short, crescent-shaped bone that forms the posterior and posteroventral dermal surface of the lower jaw. The mandibular canal follows the outer margin and there is a prominent angular pit-line close to the crescentic, ornamented suture with the dentary. Aside from the smooth section beneath the maxillary-overlap, the

ornamentation consists of short ridges and tubercles.

Meckelian ossifications and mesial dermal bones. (Figs. 4,10C-D,11) The Meckelian cartialage is ossified into a single unit in the holotype and MV P228849. The endochondral articular region is free of dermal bone with two circular depressions for the insertion of the quadrate condyles. The coronoids and prearticular are completely fused in all prepared specimens. The combined series forms a flat and elongated denticulated surface that covers about half of the mesial surface of the lower jaw, excluding the articular region and the ventromedial surface. The anterior coronoids bear a row of pointed, conical teeth.

4.5.7 Hyoid and Branchial Arches

The hyomandibula (Fig. 4.8M-N) is a large, gently curved element of solid endochondral bone onto which the dermohyal is firmly attached along the anterodorsal flank. A perichondrally-lined canal for the hyomandibular trunk of the facial nerve runs obliquely through the bone. Delicate tubular sections of perichondral bone, sometimes with attached toothplates, represent broken segments of the ceratohyal, interhyal and hypohyal. Four branchial arches are present (Figs. 4.4, 4.5, 4.11). Each bone is a perichondral structure with minimal endochondral ossification. The first four ceratobranchials are elongate, rod-like units of similar size with deep ventral longitudinal grooves. The anterior two have extensive toothplates. The fifth ceratobranchial is more slender and lacks a longitudinal groove, probably comprising the sole unit in the fifth arch as in *Mimipiscis* (Gardiner 1984: Fig.108). Scattered hypobranchials are elongate bones bearing an expanded proximal end for attachment to the basibranchial.

There are 12 of a possible 15 elements that comprise a complete apparatus of a prioniodinid conodont animal within the branchial cavity of MV P228849 (Figs. 4,11)

4.5.8 Pectoral Girdle

Comprises the post-temporals, supracleithra, postcleithra, cleithra and clavicles. Presupracleithra and a ventral median clavicle are expected to have been present, as in the other Gogo actinopterygians, but have not been identified.

Post-temporal. (Fig. 4.3). The only identified example consists of a partial left post-temporal on MV P228849, comprising the posterolateral corner of the bone. Ornament consist of a linear short-to-medium length rostrocaudally-oriented ridges.

Supracleithrum. (Figs. 4.3,4.4,4.11). A long and narrow element with a broad, rounded dorsal end with a smooth overlap surface for the post-temporal. The bone gently tapers towards the ventral tip which overlays the dorsal tip of the cleithrum. The main lateral line canal enters dorsally at the middle of the dorsal margin and exits approximately three-quarters down the posterior margin. Ornament consists of linear ridges with short, irregular or circular ridges near the anterior margin.

Cleithrum. (Figs. 4.3,4.4,4.11) Large, tall bone with an expanded, convex ventral region and a slender, crescentic vertical blade. The anterior apex is almost completely ornamented with only a very narrow overlap surface for the supracleithrum, unlike the more extensive overlap surfaces in *Mimipiscis* (Gardiner, 1984) or *Howqualepis* (Long, 1988). Convex posterior margin with a deep posteroventral notch for the insertion of the pectoral fin. The entire anterior margin below the level of the vertical blade is a smooth overlap surface for the

clavicle. Dermal ornamentation comprises short ridges on the vertical blade, longer ridges at the pectoral swelling and a mixture of long ridges interspaced with elongated tubercles on the ventral face.

Clavicle. (Figs. 4.3,4.4,4.11). A long, semi-conical bone with a tall, convex posterior which rigidly overlaps the cleithrum and narrows towards the anterior apex. Bends sharply inwards to a large flat ventral sheet that presumably contacts its counterpart. Dermal ornament of short ridges, becoming longer at rear of the ventral surface and on the posteroventral lateral surface.

Postcleithrum. (Figs. 4.3) The postcleithrum is comparatively large with the ornamented surface of the bone being four times larger than the ornamented free fields of the adjacent flank scales. Unlike the postcleithrum of *Mimipiscis* (Gardiner 1984: Fig.127), the ornamented surface comprises the majority of the unit with minimal overlap surfaces.

4.5.9 Body and fins

The head of *Gogosardina* occupies roughly 25% of the body length from the snout to the base of the caudal peduncle, the body being about 5 times as long as it is deep. This gives an elongate, streamlined appearance akin to *Howqualepis* (Long 1988) and *Donnrosenia* (Long, Choo and Young 2008), unlike the more robust, shorter bodies of contemporary Gogo forms.

Axial Skeleton. (Fig. 4.5) The axial ossifications are delicate structures comprised of perichondral bone. The anterior vertebral column comprises separate paired dorsal neural arch elements though anterior ventral haemal arch elements have not been positively identied. Each neural arch comprises a long distal neural spine, expanding ventrally to a

medial face devoid of perichondral-lining and a spatulate epineural process on the lateral face. Articulated haemal arches are present near the caudal fin of MV P.227023b as unpaired, semi-cylindrical structures.

The dorsal lobe of the caudal fin of MV P.228849a (Fig. 4.3) contains more than 18 hypurals. They are broad, spatulate structures, decreasing in size caudally, that protrude below the scale covering to be embraced by the lepidotrichia. They are broader and more robust than the hypurals of Mimipiscis (Gardiner 1984: Fig.124) and appear to be the only significant difference in axial anatomy between these two genera.

Pectoral fins (Figs. 4.3,4.6) The endoskeletal radials have not been preserved. About 27 primary lepidotrichia (visible on BMNH P.53241, Fig. 4.6) were present. The longest fin rays have unsegmented proximal sections that accounted for close to half of their length, with the rays becoming distally articulated. Posterior fin rays appear to have been fully segmented to the base. Disarticulated spine-like structures appear to be fringing fulcra similar to those present on *Mimipiscis.*

Pelvic fins. (Fig. 4.5) The pelvic fin is poorly known, the only examples being impressions in MV P.227023a. The pelvic fin is small and short-based, situated marginally closer to the anal fin than the pectoral fins.

Anal fin. (Fig. 4.5) A large triangular fin, supported by at least 14 long, closely packed radials, more than twice the number present in *Mimipiscis.* More than 41 primary lepidotrichia were present. Fringing fulcra are present on the leading edge.

Dorsal fin. (Fig. 4.3) Poorly preserved and of uncertain shape, based on broken proximal lepidotrichia. Based on the distribution of the dorsal scutes on MV P228849, the fin was of similar length to the anal fin. The leading edge of the dorsal fin appears to have been slightly anterior to the level of the leading edge of the anal fin.

Caudal fin. (Figs. 4.3,4.4,4.5) Large heterocercal tail with long, slender dorsal and ventral hypochordal lobes. The maximum extent of both lobes has not been preserved. About 30 lepidotrichia are present on the ventral hypochordal lobe while the dorsal lobe is too incompletely known for an accurate count. Fringing fulcra are present on the leading edge of the ventral lobe.

4.5.10 Scales and Squamation

The scales of *Gogosardina* are very small but macromeric. At least 145 rows are present on MV P228849 (Fig. 4.3). The scales undergo a marked decrease in size (with a corresponding increase in numbers) about halfway down the length of the fish, with flank scales at the level of the dorsal fin being about a third of the size of more anterior example. Scale size continues to decrease caudally to a size less than one sixth of the anterior scales. As a result of this, the squamation of *Gogosardina* is not arranged in continuous horizontal rows that extend down the entire length of the fish.

The squamation of *Gogosardina* is divided into the nine areas designated by Esin (1990) (Fig. 4.12I). Esin's method provides a uniform reference for the identification of palaeoniscoid scales and has been successfully used by Burrow (1994) to attribute various forms of *Ligulalepis* scales to particular body areas and by Trinajstic (1999,a, b) to refer isolated scales from the Gneudna Formation to the Gogo taxa *Moythomasia durgaringa* and

Mimia toombsi.

Area A. (Fig. 4.12A). Scales are rectangular with the dorsal-ventral height greater than the rosto-caual length. The anterior margin is straight with the rostro-dorsal process high although unlike *M. durgaringa* it does not extend above peg. The peg is high with a rounded apex and a wide peg base, which is 1/3 the width of the scale. The keel is well-developed and the socket is deep and long forming a strong interlocking mechanism between scales. The anterior margin of the free field consists of narrow, discrete ganoine ridges, which terminate in up to 9 acutely pointed serrations that overhang the posterior margin. The ridges slope in a dorsal to ventral-caudal direction at approximately 20°. The ridges are plain when compared to *M. durgaringa* (Trinasjtic 1999a) and *Mimipiscis* (Trinajstic 1999b) with only fine, raised stria along the dorsal and ventral margins of each ridge. There is a decrease in the scale depth, and in the number of terminal serrations from area A to area B, and from the median line of area A to the dorsal and ventral margins.

Area B. (Fig. 4.12B) Similar to area A scales, these scales are also higher then long with the free field ornamented with up to 8 separate ganoine ridges which terminate in acutely pointed serrations beyond the body of the scale. The anterior portion of each ridge is ornamented withnarrow, raised striae. The keel, peg and socket are well developed, indicating the scales are closely articulating making the anterior portion of the palaeoniscoid body relatively inflexible. There are pores along the depressed field of the scales and smaller pores between the ganoine ridges that make up the free field.

Area C. (Fig. 4.12C) Through the transitional region from area B to area C a change in scale-shape is observed with the rostro-caudal length exceeding the dorsal-ventral height. The free

field ornament remains similar to area B scales, the main difference being in the reduced number of ridges with no greater then 6 ridges present. Anteriorly, the ridges slope in a dorsal to ventral-caudal direction at approximately 10° but caudally the ridges appear to be almost straight. The ventral margin of each scale is gently convex. The rostro-dorsal process is high extending above the peg. The peg and socket are reduced, and located midway along the dorsal margin of those scales close to area B and further reduced or absent in scales close to area D. Where the peg is present it has a wide base, extending across the dorsal margin of the free field.

Area D. (Fig. 4.12D) Scales in area D are rhombic in form and become more elongate towards the caudal fin. The ridges are reduced in number to four in scales near area C and one, in scales close to the caudal fin. The ridges terminate in acute serrations that extend beyond the body of the scale. These scales have very poorly-defined, low ridges instead of distinct pegs providing weak articulation between scales and permitting greater flexibility in the caudal region of the fish.

Area E. (Fig. 4.12E) These scales are taller than long with a high, wide-based peg, extending the length of the free field, and no rostro-dorsal process. The free field ornament consists of three separate, parallel ganoine ridges that terminate in acute points, which do not extend beyond the body of the scale. The ornament on the ganoine ridges is most pronounced on scales from this body area. The keel and socket are well developed and these scales were closely articulated making the anterior-dorsal region of the fish relatively rigid.

Area F. (Fig. 4.12F) The scales are elongated with a low peg and the corresponding socket is shallow. The rostro-dorsal process is high with a rounded apex in scales closest to the fin

margins and high with an acutely pointed apex in scales closer to areas B and C. The ornament on the free field consists of separate ridges running slightly downward in the direction of the rear corner of the scale. Posteriorly the ridges extend beyond the body of the scale and terminate in acute points.

Area H. (Figs 4.12H) Scales are elongated, their length exceeding their height two to three times. The peg is low and extends along the dorsal margin of the scale with the corresponding socket being shallow and the keel is reduced when compare to area A–C scales. There is no rostro-dorsal process. The depressed field is wide, providing a secure attachment in the skin around the mobile fins (Burrow 1994). The ornament is consistent with that present on other scales.

Areas G. (Figs 4.12G). The scales in this area are almond-shaped. The free field is slightly raised above the wide depressed field. Scales from area G (Fig. XG) have an ornament of separate ridges with fine striae on the dorsal and ventral margins of each ridge. The ridges do not extend beyond the margin of the scale. There is no peg or socket visible on this scale type, however there is a small anterior notch.

Remarks. The scale types described for *Gogosardinus* can be attributed to the specific body areas designated by Esin (1990). There is a transition from high, narrow scales to low, wide scales from anterior to posterior, and from the midline to the dorsal and ventral margins of the fish. This scale morphology is consistent with those described for other palaeoniscoids (Long 1988, Esin 1990, Burrow 1994, Trinajstic 1999a, b). There are certain characteristics of scale morphology that remain consistent on scales from different parts of the fish's body (Esin 1990). The scales from *Gogosardina* all have a free field ornament of separate ganoine

ridges, making isolates scales easy to identify. This pattern is different from the two other Gogo paleaoniscoids, *Moythomasia durgaringa* and *Mimipiscis toombsi,* in which the free field ornament became less ornate from the anterior to the posterior of the fish, with caudal scales only having fine striations around the anterior of the free field (Trinajstic 1999a, b).

Body scutes. (Figs. 4.3,4.4,4.5) Only a few dorsal scutes anterior to the dorsal fin on MV P228849 are preserved. Three are present in articulation, immediately anterior to the remnants of the fin on MV P228849a (Fig. 4.3), each slightly overlapping the one behind it. They are large plate-like structures with the anteriormost being over 20 times larger than the adjacent flank scales. Each scute has a pointed posterior margin that becomes a short spine on the scute at the anterior dorsal base. Broken plate-like fragments near the skull suggest that the dorsal fulcral series extended anteriorly to the occipit. Each scute in the dorsal series is ornamented with up to 17 longitudinal ridges. Posterior of the dorsal fin, the scutes are narrower and more triangular (Fig. 4.3, 4.4, 4.5). As the series progresses posteriorly, the scutes become increasingly narrow and with a greater degree of overlap. Over the notochordal mass of the caudal fin, the scutes are spine-like and almost completely overlap one another.

Ventral scutes are poorly preserved. Two disarticulated examples in between the caudal and anal fin of MV P228849b (Fig.4.4) are triangular in shape and similar to the anterior elements in the upper caudal series. No scutes have been preserved anterior of the anal fin.

4.6 Discussion

4.6.1 Comparisons with other early actinopterygians

Based on preliminary observations, *Gogosardina* appears most similar to *Mimipiscis*, also

from the Gogo Formation. Both represent the only genera of stem-actinopteran known to lack ascending processes on the parasphenoid. Both lack a surangular and possess a zigzag suture of the angular and dentary in the maxillary overlap area. At present, two distinct species are present in material currently designated as *Mimipiscis toombsi*. The relationship of *Gogosardina* to *Mimipiscis* will be examined with the description of the second species of the latter genus (Choo, in prep). The new genus is distinguishable from both species of *Mimipiscis* in having a more elongate body form, smaller scale-size, in lacking anastomosing ridges on the anterior flank scales and in the contribution of the postrostral series to the margin of the pineal foramen.

Gogosardina is distinguishable from all other actinopterygians due to the unique arrangement of postrostrals wedged between the frontals, with the posterior unit forming the anterior margin of the pineal foramen. Among other Devonian forms, it differs from *Cheirolepis* in the absence of fleshy basal-lobes on the pectoral fin and possessing macromeric squamation (Pearson and Westoll, 1979; Arratia and Cloutier, 1996). It differs from *Osorioichthys* in the absence of fleshy pectoral lobes, suborbitals and surangulars, along with the presence of postrostrals and a pineal foramen (Taverne, 1997). It differs from *Kentuckia* in the absence of accessory operculae, having parietals of a similar length to the frontals and a pineal foramen (Dunkle, 1964). It differs from *Tegeolepis* in having macromeric squamation, segmention on the pectoral fin-rays and large lateral gulars (Dunkle and Schaeffer, 1973). It differs from *Donnrosenia* and *Howqualepis* in having a dorsal scute series that extends to the occipital region, short-based pelvic fins, in lacking a surangular and having more extensive distal segmentation on the pectoral fin (Long 1988, Long et al. 2008). It differs from *Moythomasia durgaringa* and *M. nitida* in its elongate body form, lacking any porous ornamentation and in possessing postrostrals (Gardiner 1984, Jessen 1966). It differs

from *Krasnoyarichthys* in lacking an accessory operculum, in having a less extensive series of ventral scutes and having longer, narrower branchiostegal rays (Prokofiev, 2002). It differs from *Stegotrachelus* in its more gracile body form, possessing postrostrals and having a prominent anterodorsal process on the suboperculum (Gardiner 1963). It differs from *Limnomis* and *Cuneognathus* in possessing pelvic fins and postrostrals, while lacking curved anterior ridges on the flank scales (Daeschler 2000, Friedman and Blom 2006). *Gogosardina* is distinguishable from the majority of post-Devonian actinopterygians in having a large pineal foramen and the absence of a dermopterotic.

4.6.2 Postrostral units in early actinopterygians

In contrast to the sarcopterygians where such bones are primitively present, the presence of distinct postrostrals (anamesic bones posterior to the rostral and anterior to the frontals) is an unusual feature within the actinopterygians and is restricted to a handful of fossil genera. The postrostral configuration *Gogosardina* as presented in the description (three laterally-arrayed anterior bones followed by a single posterior unit which forms the anterior margin of the pineal foramen) is highy distinctive and thus of diagnostic importance.

The postrostral series of *Cheirolepis canadensis* is superficially similar to that of *Gogosardina* in overall configuration, consisting of a median postrostral flanked by lateral units, followed by a variable number (0-3) of median posterior postrostrals (Arratia and Cloutier, 1996). The postrostral series of *Gogosardina* differs from *C. canadensis* in that the lateral units suture with the frontals laterally rather than posteriorly and in that the posterior bone is the largest in the series. Conversely, *Cheirolepis trailli* has a single postrostral ossification (Pearson and Westoll, 1979), but its shape and positioning more closely matches the extent of the entire postrostral series of *Gogosardina* with the bone nestled in a V-shaped

anterior recess between the frontals. No species of *Cheirolepis* possesses such a large, open pineal foramen as *Gogosardina*, the structure being either absent, much smaller or covered by a pineal plate.

A single large postrostral is present in *Mimipiscis bartrami* from the Gogo Formation (see Chapter 5). It conforms to the dorsal lamina of the larger rostral of *Mimipiscis toombsi* and sutures posteriorly with the frontals.

Postrostrals are present in a number of Carboniferous forms. The guildayichthyids (*Guildayichthys* and *Discoserra*) have a pair of anterior postrostrals that contribute to the anterior nasal openings along with a single, large posterior postrostral (Lund, 2000). The tarassiids (*Tarrasius* and *Paratarrasius*) have a single median postrostral that does not contact the frontals (Lund and Poplin, 2002). *Kalops* has an extremely large single postrostral that contributes to the anterior nasal openings and excludes the small rostral from the dorsal surface of the skull (Poplin and Lund, 2002).

That the postrostral series of *Gogosardina* is only preserved in a single damaged individual invites scrutiny regarding the validity of our reconstruction. In the skull roof of the majority of Devonian actinopterygians, the pineal foramen is fully enclosed by the paired frontals. This configuration is impossible in *Gogosardina* as there is no trace of a median suture anterior to the pineal foramen in the type specimen and the frontals of MV P.227023a do not meet anteriorly, indicating that one or more ossifications were nestled between the frontals. However, the possiblity that the four structures identifed as separate postrostrals actually represent the fragments of a lesser number of bones cannot be ruled out without further specimens.

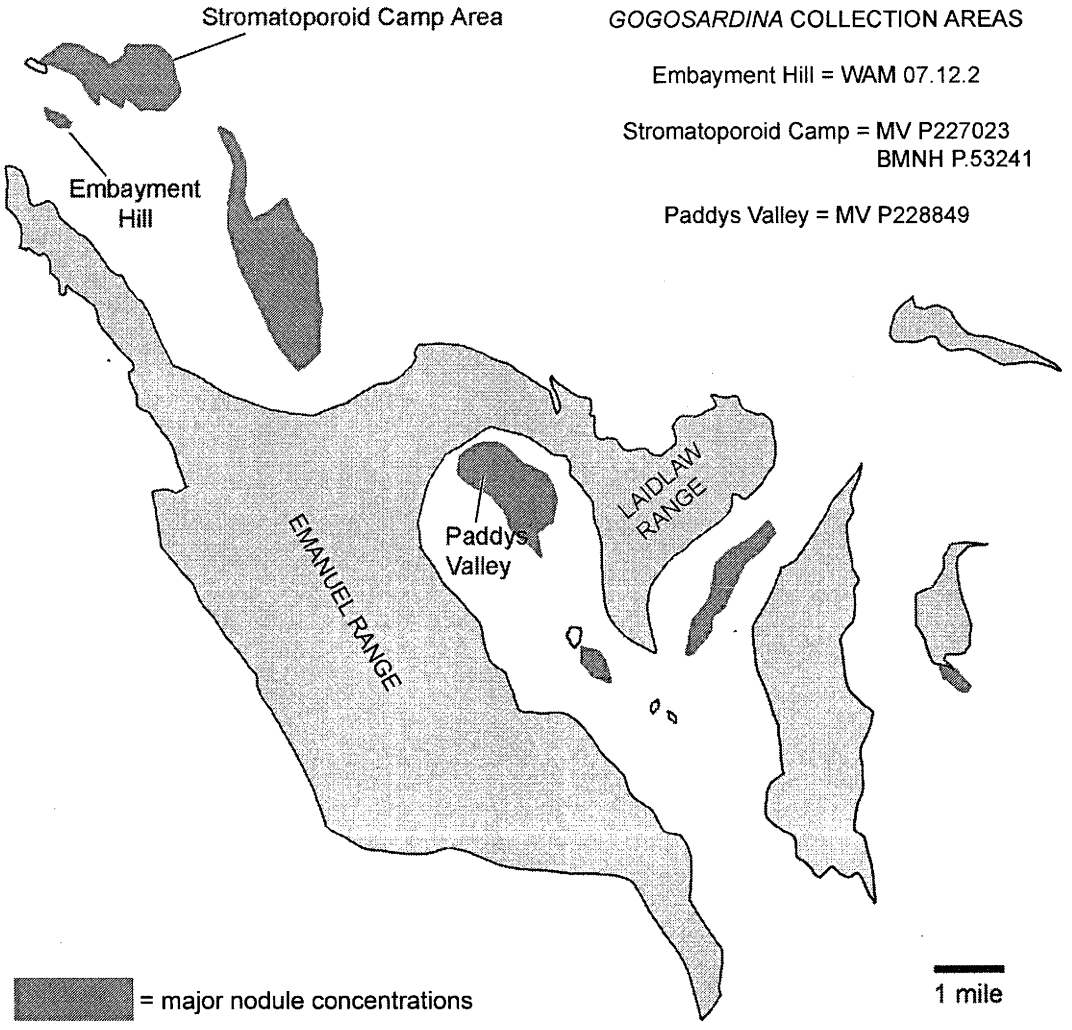


Figure 4.1
Simplified map of the Gogo Formation, Western Australia, showing the collection areas which have produced specimens of *Gogosardina* gen. nov.

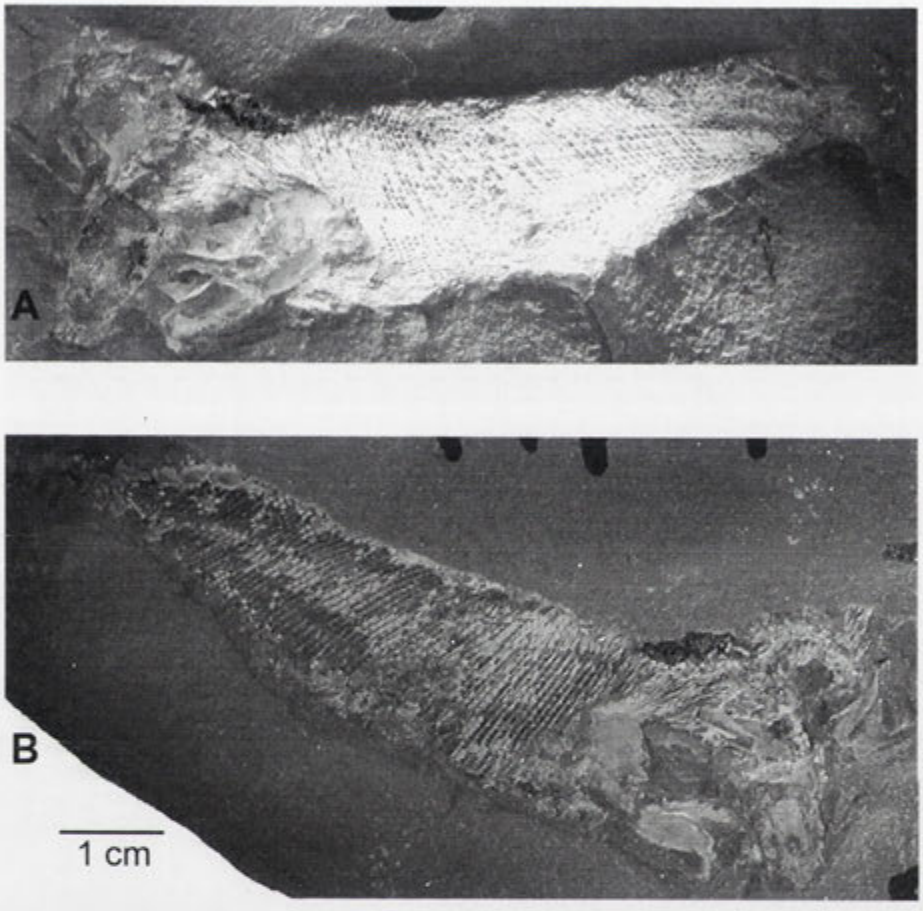


Figure 4.2
Gogosardina coatesi gen. et sp. nov. Holotype (WAM 07.12.2) prior to preparation. **-a**. main specimen in lateral view. **-b**. counterpart in lateral view. Arrows indicate position of skull roof.

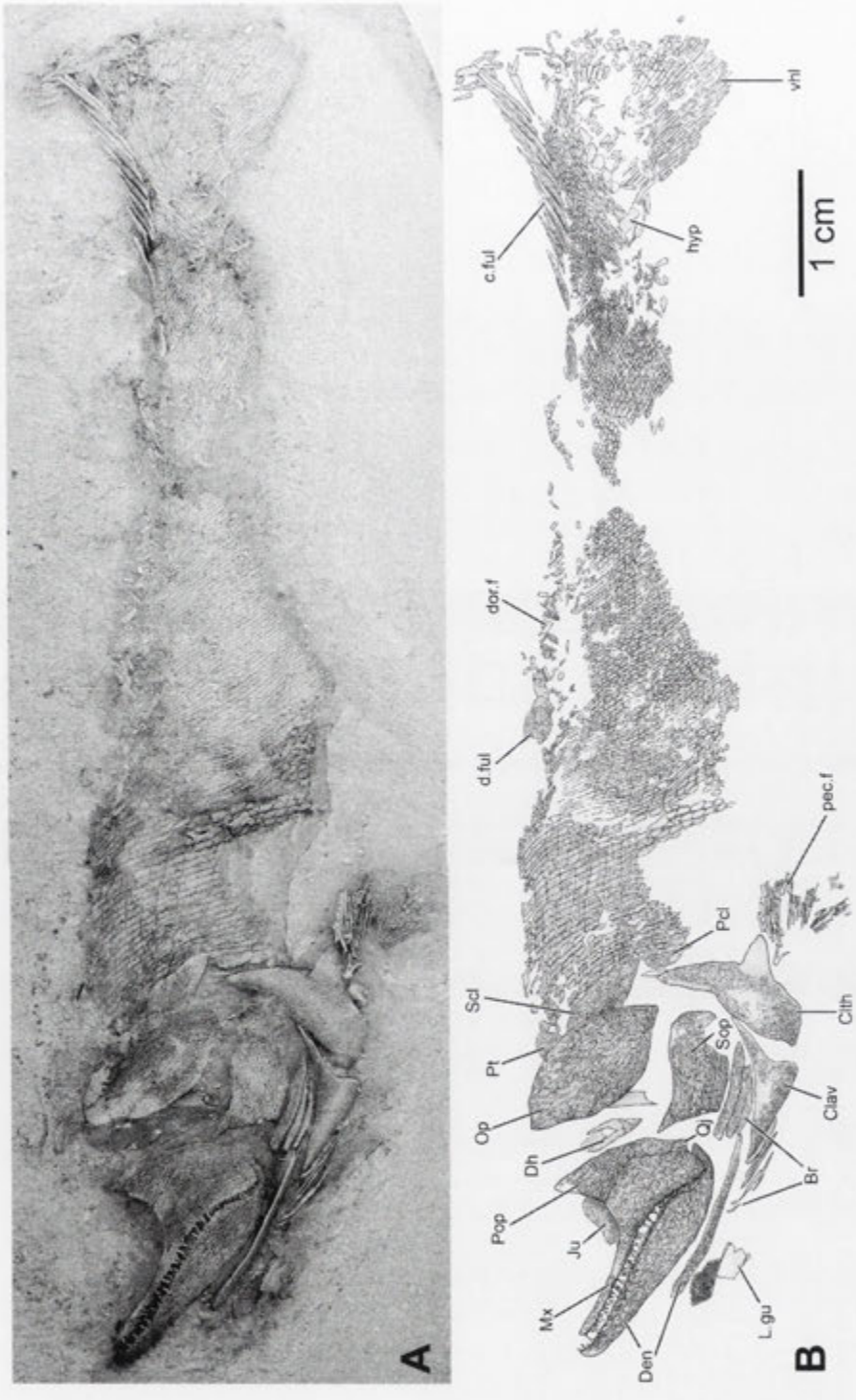


Figure 4.3
Gogosardina coatesi gen. et sp. nov. MV P.228849a in lateral view. -**a**. photograph of specimen. -**b**. interpretive drawing of specimen.

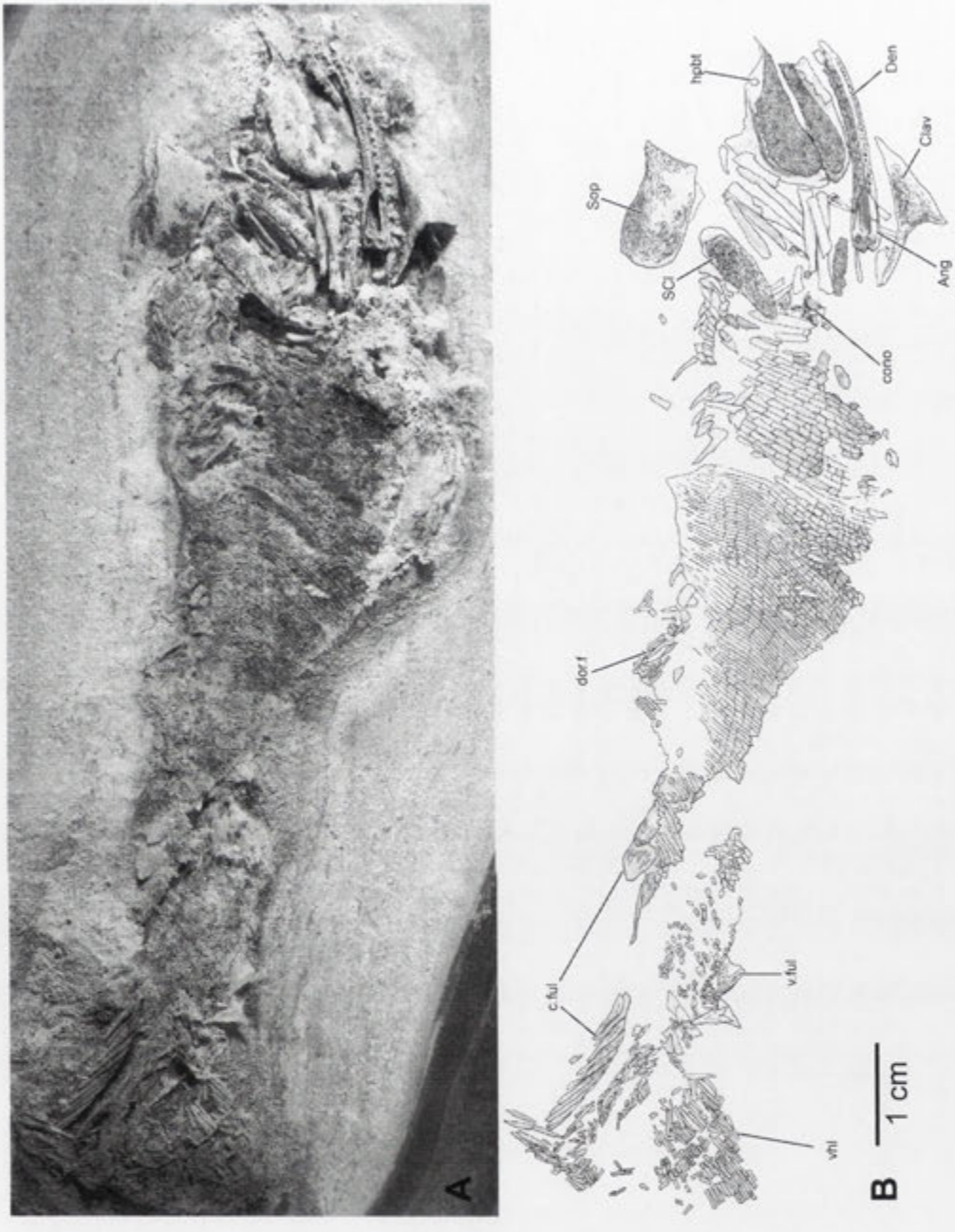


Figure 4.4
Gogosardina coatesi gen. et sp. nov. MV P.228849b in lateral view, counterpart of the specimen presented in Fig.2. -**a**. Photograph and -**b**. interpretive drawing of specimen.

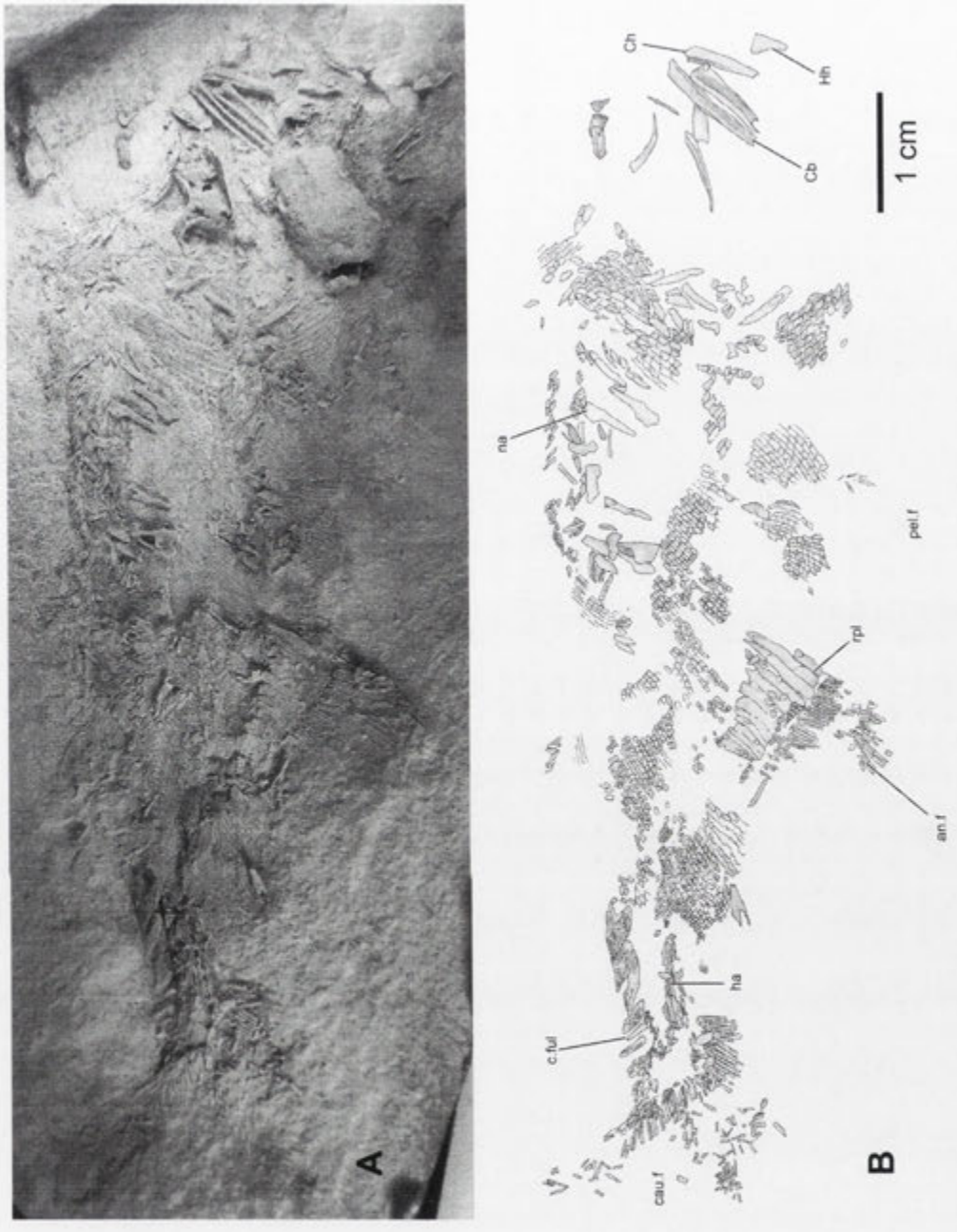


Figure 4.5
Gogosardina coatesi gen. et sp. nov. MV P.227023b in lateral view. -**A**. Photograph and -**B.** interpretive drawing of specimen.



Figure 4.6
Gogosardina coatesi gen. et sp. nov. BMNH P.53241, unprepared specimen in lateral view.

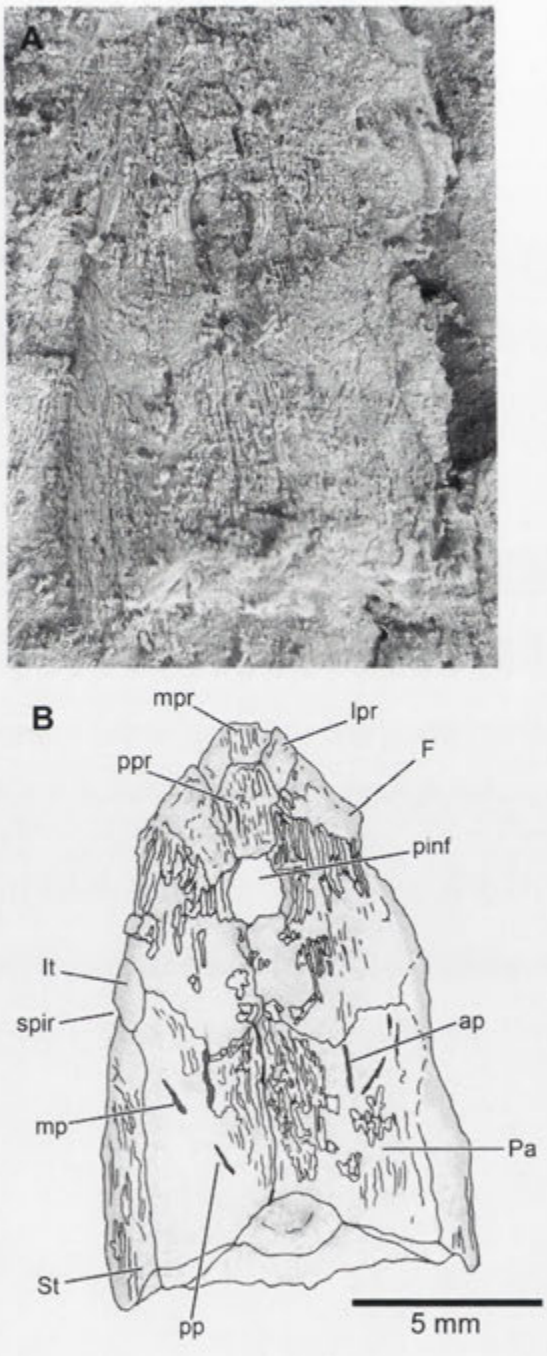


Figure 4.7
Gogosardina coatesi gen. et sp. nov. Skull roof of the holotype (WAM 07.12.2) in dorsal view. -A. Photograph and -B. interpretive drawing. Specimen represents bone impressions set in a resin base with attached fragments of dermal bone.

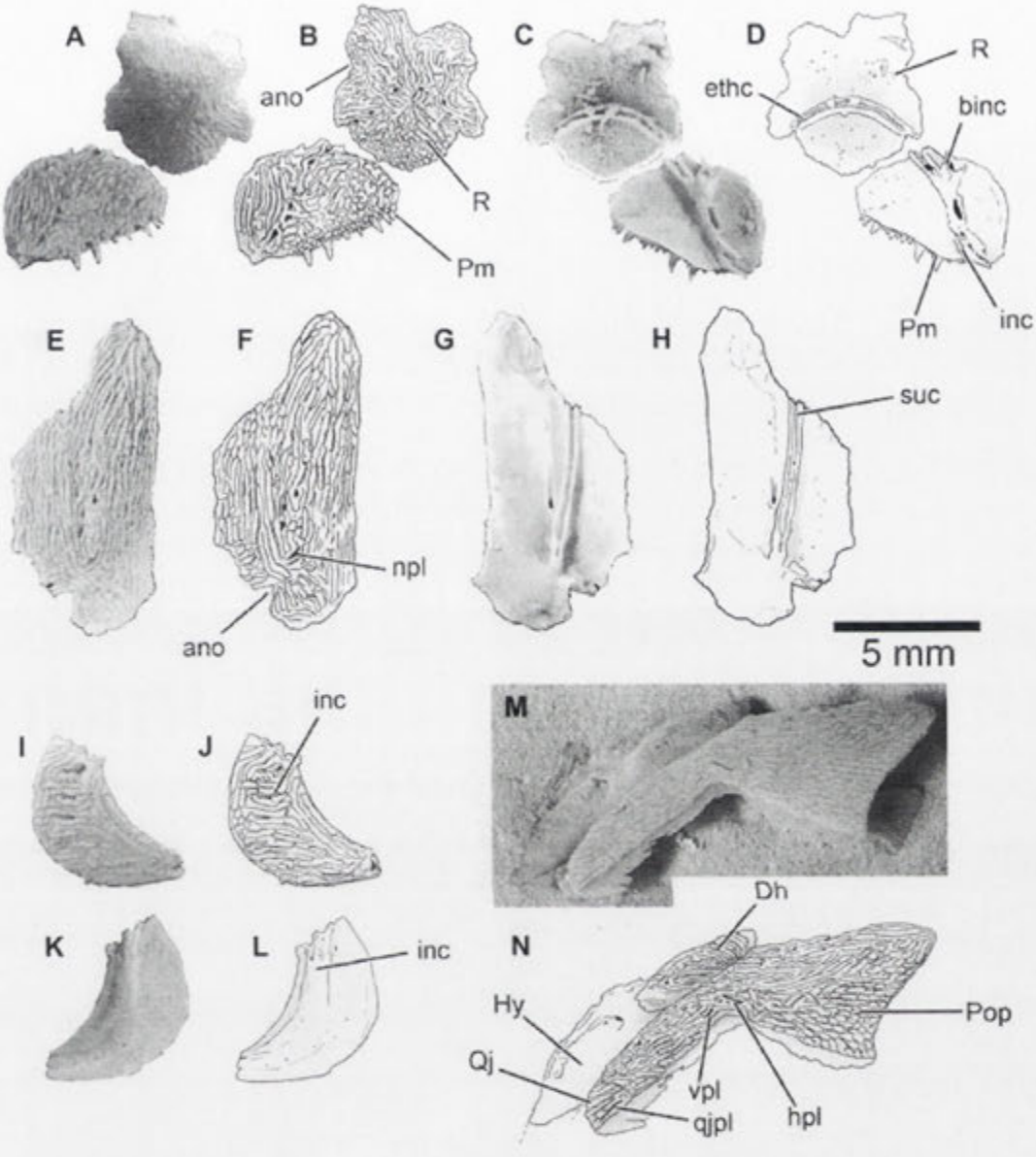


Figure 4.8
Gogosardina coatesi gen. et sp. nov. MV P.228269. **A,** Photograph and **B,** drawing of the rostral and right premaxilla in anterior view, presented as if flattened out in one plane. **C,** Photograph and **D,** drawing of the same bones in medial view. Left nasal; **E,** photograph and **F,** drawing in lateral view. **G,** Photograph and **H,** drawing in medial view. Right jugal presented in lateral view as a **I,** photograph and **J,** line drawing. **K,** Photograph and **L,** drawing of jugal in medial view. **M,** Photograph and **N,** drawing of preoperculum, quadratojugal, dermohyal and partially exposed hyomandibular.

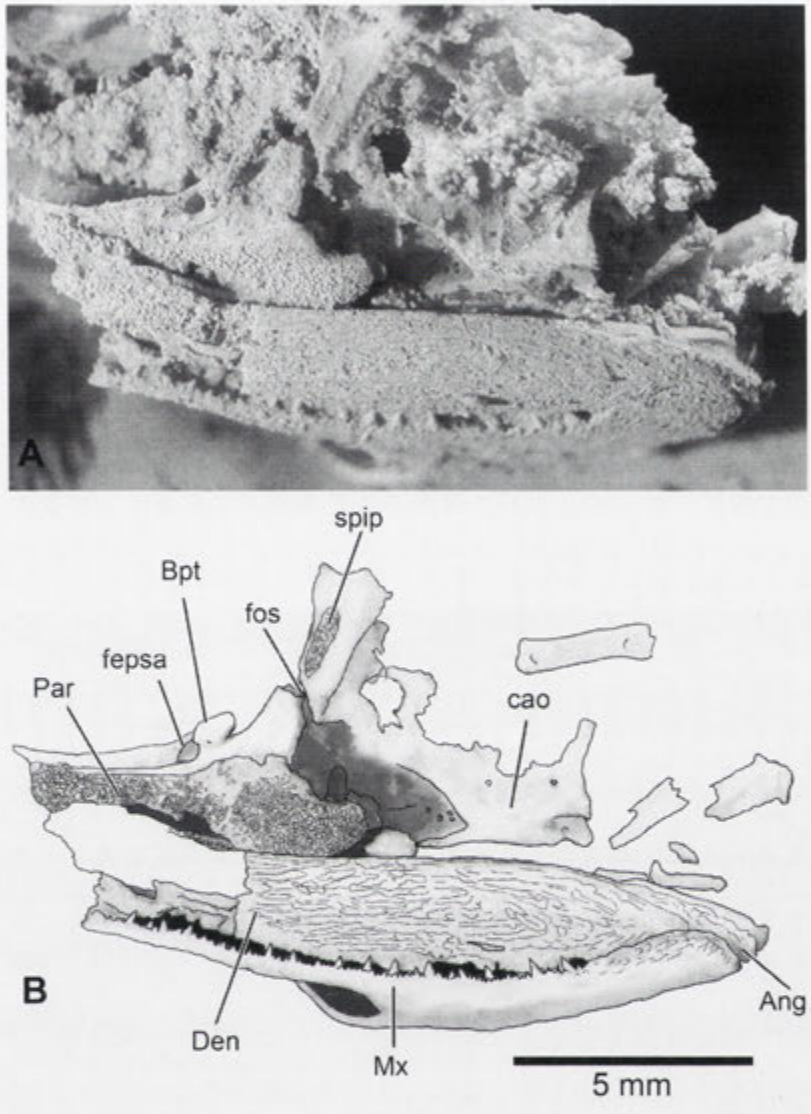


Figure 4.9
Gogosardina coatesi gen. et sp. nov. Fragmentary neurocranium with parasphenoid of holotype specimen (WAM 07.12.2). **A,** photograph and **B,** drawing of the specimen in ventral view.

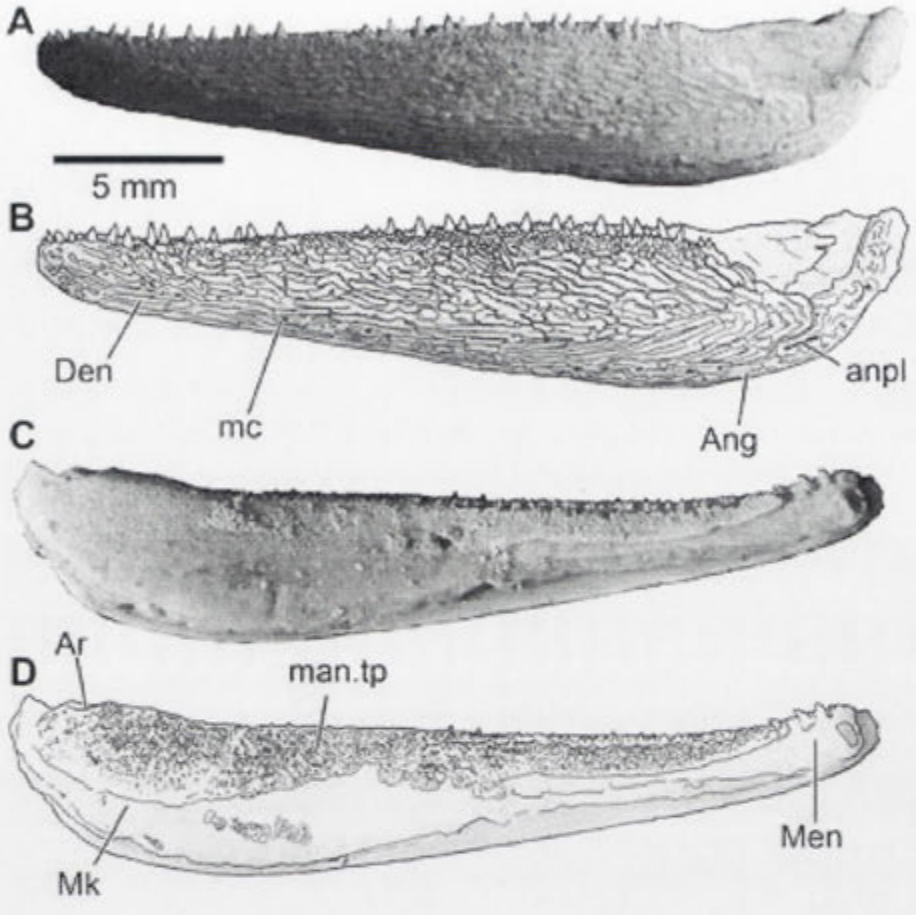


Figure 4.10
Gogosardina coatesi gen. et sp. nov. MV P.228269. **A,** Photograph and **B,** drawing of left lower jaw in lateral view. **C,** Photograph and **D,** drawing of left lower jaw in medial view.

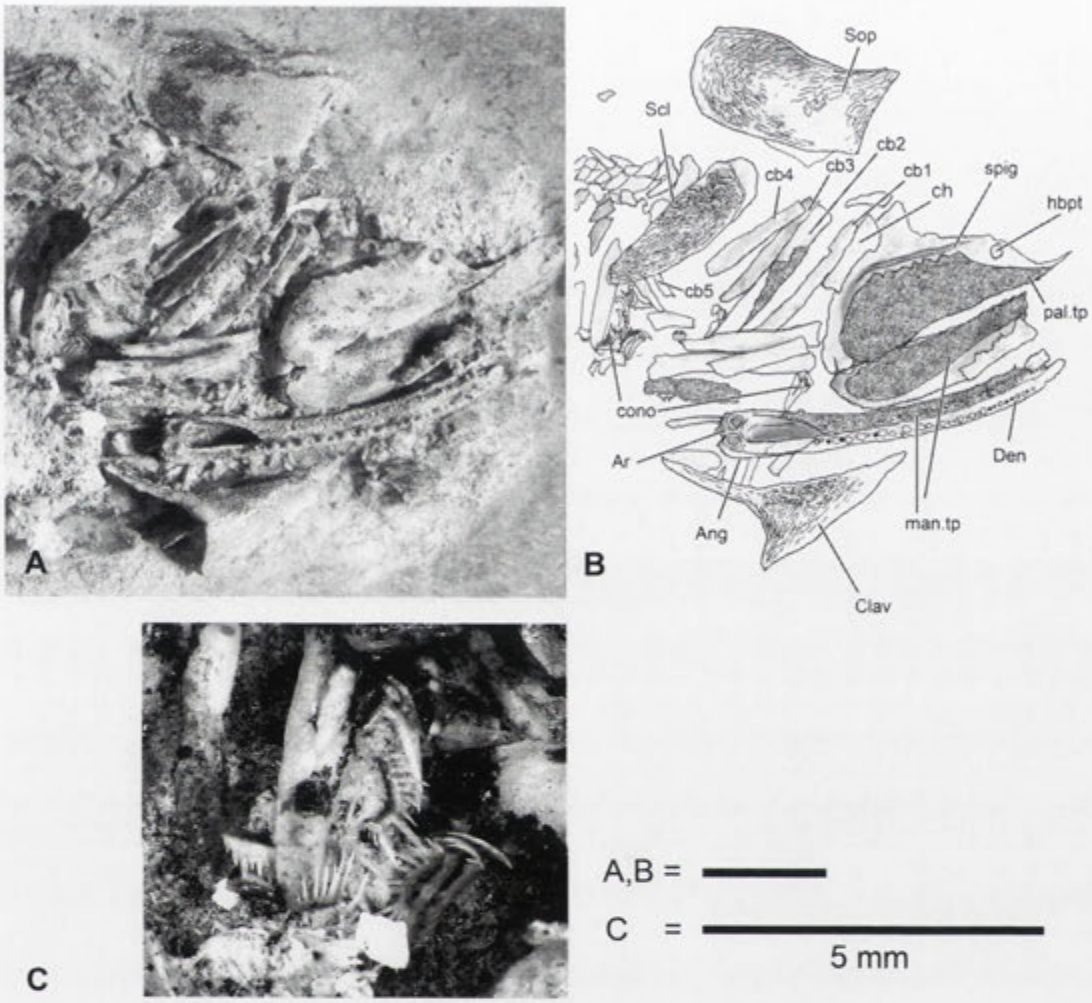


Figure 4.11
Gogosardina coatesi gen. et sp. nov. Details of the head, branchial arches and pectoral girdle of MV P.228849b. with various bones visible in mesial (left palatoquadrate and lower jaw), dorsal (right lower jaw) or lateral aspect. **A,** Photograph and **B,** interpretive drawing of the specimen. **C.** enlargement of branchial area revealing embedded conodont elements.

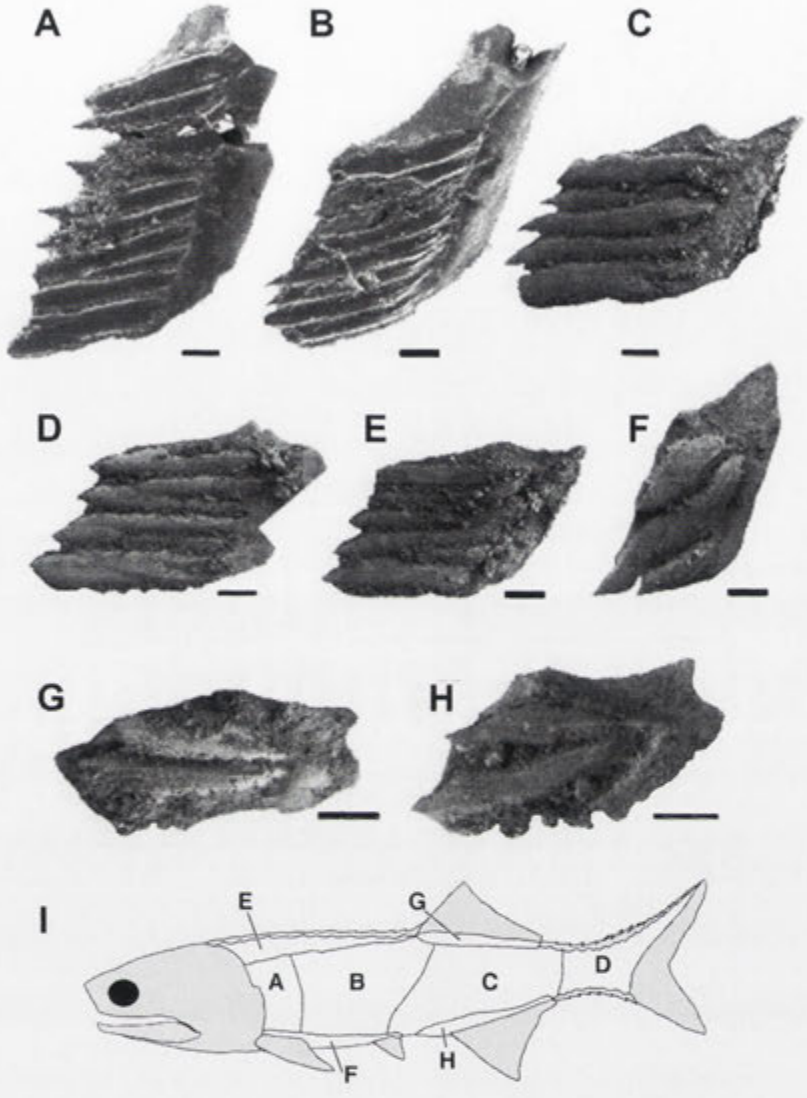


Figure 4.12
Gogosardina coatesi gen. et sp. nov. Representative scales removed from the right side of the holotype (WAM 07.12.2) in lateral view. -**A**. Zone A scale from the anterior flank. -**B.** Zone B scale from the mid-flank. -**C.** Zone C scale from the rear flank. -**D**. Zone D scale from near the base of the caudal fin. -**E.** Zone E scale from the anterior dorsal surface. -**F**. Zone F scale from the anterior ventral surface. -**G.** Zone G scale from near the base of the dorsal fin. -**H.** Zone H scale from near the base of the anal fin. -**I.** Simplified diagrammatic outline of *Gogosardina* showing the distribution of the major areas with morphologically distinct scale types after Esin (1990). Scale bars for A-F = 100 ugs. Scale bars for G-H = 200 ugs.

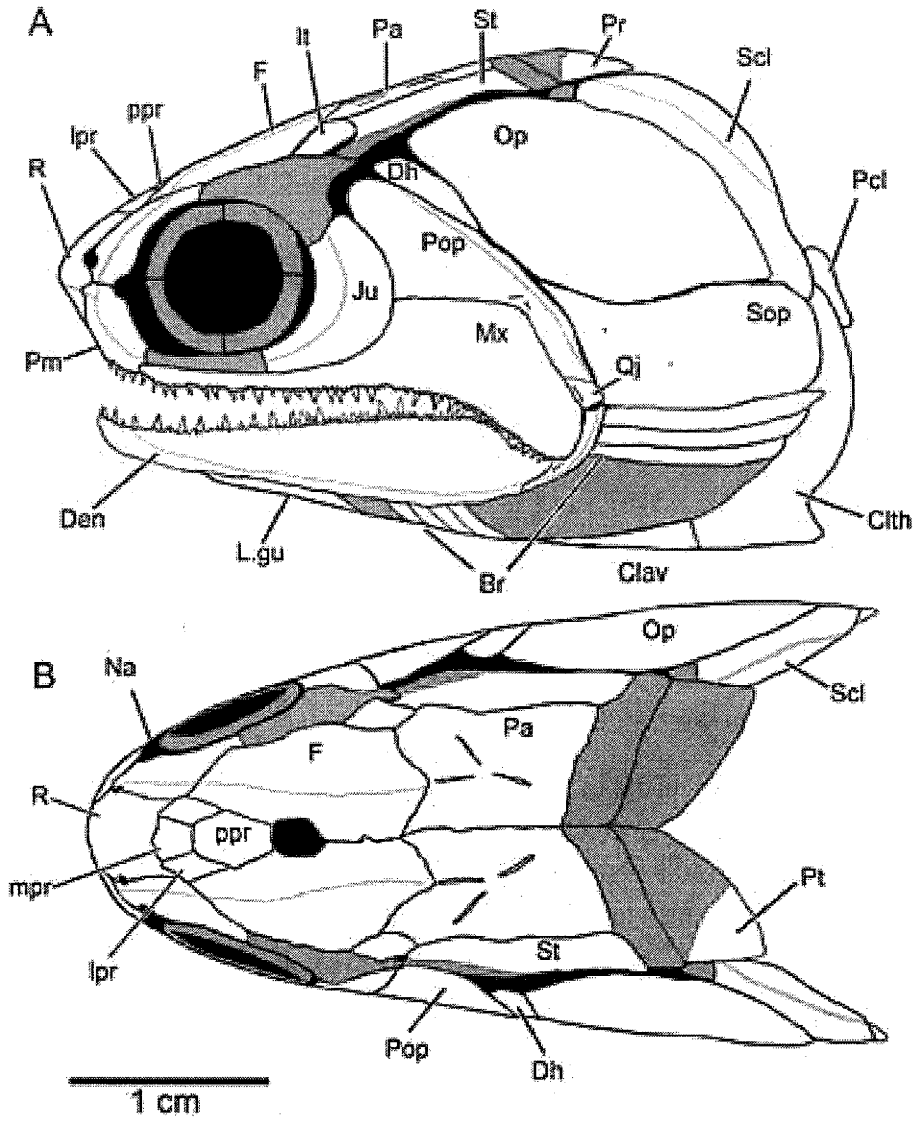


Figure 4.13
Gogosardina coatesi gen. et sp. nov. Restoration of the head in **-A.** lateral and **-B.** dorsal view. Light grey lines correspond to preserved sections of the sensory canals. Dark grey corresponds to areas that have not been preserved.

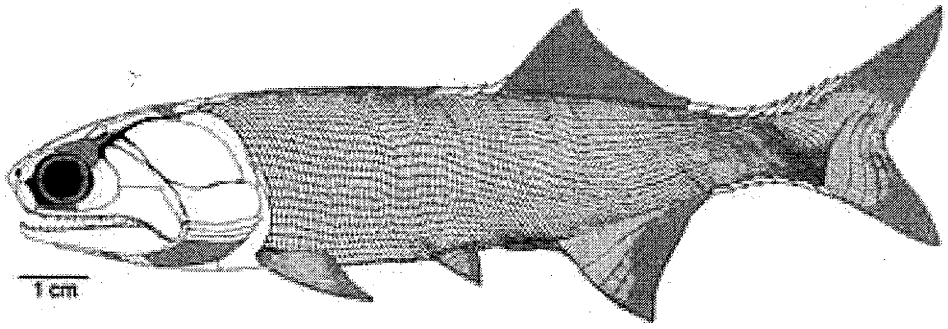


Figure 4.14
Gogosardina coatesi gen. et sp. nov. Restoration of the entire fish in lateral view. Dark grey corresponds to missing parts of the anatomy.



Figure 4.15
Life reconstruction of *Gogosardina coatesi* gen. et sp. nov. on the Gogo Reef.

Chapter 5. A replacement name and a new species for the basal actinopterygian *Mimia* from the Upper Devonian Gogo Formation of Western Australia.

5.0 Preamble

This chapter comprises an unpublished manuscript, with myself as sole author, that is currently undergoing review for publication in the Proceedings of the Royal Society of Edinburgh.

5.1 Abstract

The Devonian actinopterygian fish *Mimia* Gardiner and Bartram (1977) is renamed *Mimipiscis* nom. nov. due to preoccupation of that genus by the butterfly *Mimia* Evans (1953). In addition to an emended diagnosis of the type species, *Mimipiscis toombsi* (Gardiner and Bartram 1977), a second form, *Mimipiscis bartrami* sp. nov., is described from the Upper Devonian (Frasnian) Gogo Formation of Western Australia. It differs from the type species in details of the body shape, squamation, snout, suboperculum and parasphenoid. Additional material of *Mimipiscis toombsi* includes the first complete tail for the genus and an exceptionally large specimen with unusual ornamentation. Newly prepared fossil material suggest a hithero greater diversity of stem-actinopterans in the Gogo fossil fish fauna than previously recognised.

5.2 Introduction

The Late Devonian (Frasnian) Gogo Formation of Western Australia is a famous lagerstätte that has produced a fossil ichthyofauna of rich diversity and exceptional preservation (Long 2006). Early actinopterygian or ray-finned fishes make up a significant

proportion of the vertebrate fossil collections from the region. Conversely, they have been viewed as representing only a small portion of the Gogo faunal diversity, with only two taxa: *Mimia toombsi* and *Moythomasia durgaringa.* These forms were initially diagnosed based primarily on neurocranial anatomy (Gardiner and Bartram 1977) and described in fine detail by Gardiner (1984). They are the most completely known Palaeozoic actinopterygians and their ancestry underpins the most recent phylogenetic analyses of early ray-finned fish (Cloutier and Arratia 2004, Coates 1999, Friedman and Blom 2006, Gardiner and Schaeffer 1989, Long 1988, Schultze and Cumbaa 2001, Taverne 1997).

The nomen *Mimia* was originally erected by Evans (1953) as a genus of Mexican hesperiid butterfly. This invalidates the use of the name *Mimia* (Gardiner and Bartram, 1977) as a genus of fossil fish. I therefore substitute the name ***Mimipiscis* nom. nov.** for the Gogo actinopterygian.

The presence of additional taxa of Gogo actinoptergians became apparent with the recent collection and preparation of superb specimens in the collections of Museum Victoria and the Western Australian Museum. The description *Gogosardina coatesi* Choo, Long and Trinajstic, represents the first new taxon of Gogo ray-finned fish to be named in over thirty years (Choo, Long and Trinajstic, 2008). During the 2005 Museum Victoria expedition to the Gogo Formation, the author discovered a nearly complete specimen with a skull that closely resembled that of *Mimipiscis toombsi*, but with differences in squamation and body shape. This prompted a re-examination of existing collections within Australian and British collections, after which it became apparent that material assigned to *M. toombsi* contained two distinct congeneric species (as well as examples of the new mimiid genus). In addition to a revised description and additional anatomical observations of the type species, the second

form of *Mimipiscis* is detailed herein.

5.3 Notes on preparation

Principle acid preparation and restoration was carried out by MV preparator, David Pickering. The end results were fully exposed skeletons supported within clear acrylic bases. Specimens were whitened with ammonium chloride for microscope study and photography. Digital images of the fossils were supplied by Erich Fitzgerald (Figs 5.4 and 5.6), Lucinda Gibson (Fig. 5.15) and the author.

5.4 Systematic palaeontology

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii Cope, 1887

Family Mimiidae Gardiner, 1993

Remarks. Gardiner (1993) united *Mimipiscis* (= *Mimia*) from Gogo and *Howqualepis* from the Givetian of Victoria within Mimiidae, but did not provide a diagnosis. Subsequent studies have consistently failed to find a sister-relationship between these two genera exclusive to other early actinopterygians (Cloutier and Arratia 2004, Friedman and Blom 2006). Long et al. (2008) united *Howqualepis* and *Donnrosenia* from Antarctica in the novel family Howqualepididae. A provisional diagnosis of the Mimiidae, excluding *Howqualepis*, is detailed below. As redefined, the family contains the two species of *Mimipiscis* and *Gogosardina coatesi*, all from the Gogo Formation, Western Australia.

Diagnosis. The family contains basal actinopterygian (palaeoniscoid grade) fishes with an open spiracular slit bordered by the intertemporal, dermosphenotic and supratemporal. Large pineal foramen present. Surangular absent. The dentary and angular meet on the smooth maxillary overlap surface in a zigzag suture. Ascending processes on the parasphenoid absent. Anterior lepidotrichia of the pectoral fins are unsegmented for between 40-60% of their length. Basal and fringing fulcra present. Flank scales with peg and socket articulation. Dorsal scutes extend from the occipit to dorsal fin. Genera included *Gogosardina* and *Mimipiscis* nom. nov.

Mimipiscis nom. nov.

[= *Mimia* Gardiner and Bartram, 1977]

Type species. *Mimipiscis toombsi* Gardiner and Bartram 1977

Etymology. For the Mimi dreamtime beings of Arnhem Land aboriginal folklore and the Greek *piscis* for fish.

Diagnosis. As for *Mimia* in Gardiner (1984) with the following amendments: Postrostral singular or absent. Prong-like anterolateral extension of the supratemporal contributes to the ventral margin of the spiracular opening. Anterior flank scales with anastomosing linear ridges and an absence of extensive porous ornamentation. Body form is robust and fusiform.

Holotype. WAM 70.4.245.

Other specimens examined. WAM 86.9.687. MV P.221806

Mimipiscis toombsi (Gardiner and Bartram 1977)

= *Mimia toombsi* Gardiner and Bartram 1977

Diagnosis (emended). A *Mimipiscis* with approximately 75 scale rows, flank scales with prominent raised striae on the ganoine ridges. Postrostral absent. Tubercular ornament on anterior face of the rostral. Parasphenoid terminates at or just before the ventral otic fissure. Small, pointed anterodorsal process on the subopercular. Lateral margin of the post-temporal of much shorter length than anterior margin. Posterior Zone E scales rectangular with well developed peg and socket. Anterior margins of the dorsal and anal fin directly aligned with one another.

5.5. Description of *Mimipiscis toombsi*

The dermal and neurocranial anatomy of *Mimipiscis toombsi* has been comprehensively described by Gardiner (1984). The scales were described by Trinajstic (1999b). Additional observations based on more recently prepared material are presented here.

5.5.1 A large specimen of *Mimipiscis toombsi*

A large (by Gogo standards) actinopterygian was collected by John Long at Paddys Valley in 1986 and prepared by him at the Western Australian Museum. It was registered as WAM 86.9.687 as an example of *Moythomasia durgaringa*. The prepared specimen comprises a partially articulated fish mounted in resin, including the maxillae, palatoquadrate, lower jaws, opercular-gular series, pectoral girdle and scales representing about 40 transverse rows (Fig. 5.1).

A re-examination has established the specimen to be an example of *Mimipiscis.* There is an absence of a surangular, a zigzag suture of the dentary and angular in the maxillary overlap field, an absence of the porous ornamentation present in *M. durgaringa*, while the anterior flank scales have prominent raised striae. As preserved, WAM 86.9.687 measures about 13.5 cm from the anterior tip of the maxilla to the rearmost visible scales. Scaling up from smaller, more complete specimens suggests a total length of about 22 cm from the snout to caudal inversion, representing a fish far in excess of the 15 cm maximum size stated in Gardiner (1984). This makes the specimen one of the largest of Gogo actinopterygians, rivalled only by a few individuals of *Moythomasia durgaringa.*

The dermal osteology has no visible differences in shape or proportions to larger (10 cm or greater) specimens of *Mimipiscis toombsi.* The suboperculum has a small anterodorsal process, there are raised striae on the ridges of the flank scales and there are about 40 scale rows anterior to the dorsal fin (suggests a total of less than 80 vertical scale rows). WAM 86.9.687 is thus assigned to *M. toombsi.*

There are however notable differences in the dermal ornamentation of WAM 86.9.687 to other specimens of this taxon. The ornament on the pectoral girdle comprises closely packed tubercles and very short ridges of ganoine that become more pointed on the ventral surface (Fig. 5.1b). This differs from the condition in most other individuals of this taxon, where the cleithrum and clavicle possess long, well-spaced ridges (Gardiner 1984: Fig. 126). There is also a region of tubercles on the supracleithrum in the centre and posteroventral margin of the bone. Elsewhere on this bone, the tubercular ornament changes to the linear arrangement more typical for this taxon (Gardiner 1984: Fig. 125).

Isolated patches of short ridges and tubercles also appear among the elongate ornamentation in some larger individuals of *M. toombsi* (personal observation, BMNH P56491, P56507 and others). The shortening of the ganoine ridges on the bones of some large specimens of this species appears to have been taken to extreme levels on the exceptionally large WAM 86.9.687. The scales of WAM 86.9.687 (Fig. 5.1c) are more densely ornamented with proportionally smaller ridges than in other examples, with the ridges terminating in up to 16 posterior serrations on the anterior scales vs the normally reported maximum of 10 (Gardiner, 1984; Trinajstic, 1999b; both based on specimens less than 15 cm long). This could conceivably be the result of ontogenetic variability where the increase in scale-size from a more common-sized (in collections) individual does not correspond with an increase in the size of the ganoine ridges, with additional ridges developing to accommodate the greater scale area.

5.5.2 The tail of *Mimipiscis toombsi*

MV P.221806 was collected in 2005 by Tim Senden (ANU) at the area south of Lloyd Hill. It represents a complete specimen of *Mimipiscis toombsi* with an overall length of 11 cm (Fig. 5.2), and is notable for having a complete caudal fin. An examination of other specimens in Australian and the BMNH failed to produce another whole tail, with the lower hypochordal lobe usually being incomplete or disrupted. Gardiner (1984) briefly describes the caudal fin as deeply cleft and inequilobate, restoring the tail accordingly (ibid, Fig. 145). The heterocercal tail of P.221806 has more than 55 closely set primary lepidotrichia that are extensively segmented with distal branching. Both the upper notochordal mass and the lower hypochordal lobe are of a similar size and shape to each other, making the fin equilobate and functionally homocercal. A revised tail based on this information is presented on the lateral reconstruction of *M. toombsi* (Fig. 5.16b).

5.5.3 Revised description of the parasphenoid

A ventral view of the parasphenoid of BMNH P53247 was provided in the original description of *Mimipiscis toombsi* (Gardiner and Bartram 1977: Fig.2; Gardiner 1984: Fig.50) which depicts the posterior section of the bone as a pair of narrow posterolateral arms (of unequal length) flanking a small median shelf. Paired notches devoid of denticles, located at the juncture of the arms and the shelf, were interpreted as points of insertion for the subcephalic muscles (Gardiner 1984).

Examination of additional specimens of *M. toombsi* has shown that the posterior section of the parasphenoid of BMNH P53247 is broken posteriorly. The presence of a more extensive posterior shelf is indicated in a number of specimens (Fig. 5.3a,b), with a complete posterior margin being preserved on the counterpart of MV P.221806 (Fig. 5.3c,d).

The anterior, multifid section consists of a narrow, median tongue flanked by two broader lobes with a variable degree of further subdivision. In some specimens, these lobes branch into a number of small, digitate subdivisions (eg. BMNH 53247, Fig. 5.3e), in others they form discrete, square-tipped lobes (eg. BMNH 53223, Fig. 5.3a).

The posterior section of the parasphenoid forms a depressed triangular shelf. From an area just aft of the bucco-hypophysial canal, the shelf flares outwards in a delta-wing shape. The posterolateral tips of this shelf have a slight dorsal flexure and in some specimens may extend to below and behind the spiracular canal. Medially, the posterior shelf terminates at or just anterior to the level of the ventral otic fissure in a smooth posterior edge that in some specimens is folded into a number of small, finger-like projections. The entire buccal surface of the posterior section is covered in small denticles.

Thus the posterolateral arms and small median section presented in the original description (Fig. 5.3e) actually consists of the remnants of a large, triangular posterior shelf, the "arms" representing the lateral margins of this shelf (Fig. 5.3f). The unornamented sections described as attachment areas for the subcephalic muscles by Gardiner are probably the result of damage to the parasphenoid of BMNH P53247. They are not visible on any specimen of this taxon in which the posterior section is complete.

This revised reconstruction of the parasphenoid of *M. toombsi* displays greater degree of similarity to that of *Moythomasia durgaringa* (Fig. 5.12c) which also has a depressed, denticulated posterior shelf. Unlike *Moythomasia*, the posterior shelf of *M. toombsi* is not flanked by true ascending processes, nor are there recesses for paired parotic toothplates (Gardiner 1984: Fig. 51).

5.6. Systematic palaeontology of a new species of *Mimipiscis*

Mimipiscis bartrami sp. nov.

(Figs. 5.5-5.16 inclusive)

1977 : *Mimia toombsi* (in part) ; Gardiner and Bartram : figs 2 and 2B (occipital and otic region incorporated into composite reconstruction).

1977 : "palaeoniscoid"; Nicholl: figs 2 and 3.

1984 : *Mimia toombsi* (in part) ; Gardiner : figs 3, 6, 14,16, 20, 50 (occipital and otic region incorporated into composite reconstruction), 82,121,122 and 127.

2008 : *Mimia* sp.nov ; Long, Choo and Young.

Locality and horizon.

The nodule fields at Stromatoporoid Camp Area, Long's Well, Paddy's Valley and Bugle Gap (see Fig.1 and Miles 1971, Fig.1 for a more detailed map), Gogo Formation, Late Devonian (lower Frasnian), near Fitzroy Crossing, Western Australia.

Etymology

For the late Alan Bartram in recognition of his pioneering work on *Mimipiscis toombsi* and other fossil actinopterygians.

Diagnosis

A *Mimipiscis* with approximately 110 scale rows, flank scales without raised striae on the ganoine ridges. Postrostral present. Vermiculate ornament on small rostral. Posterior shelf of parasphenoid extends past the ventral otic fissure. Long, prong-like anterodorsal process on suboperculum. Length of lateral margin of post-temporal more than half that of the anterior margin. Anterior margin of the anal fin shifted posterior to that of the anterior margin of the dorsal fin. Posterior Zone E scales are tall and narrow, lacking peg-and-socket articulation

Holotype. WAM 08.9.1 (a + b): An almost complete body and head with incomplete braincase preserved in counterpart (Figs. 5.5, 5.6, 5.7, 5.13, 5.16). Collected in 2005 by the author at Bugle Gap.

Other material

MV P.227027 (a+b):Partial skull with fragmentary braincase. Articulated postcranium, lacking the tail (Figs. 5.8, 5.9 and 5r.16) . Collected in 2005 by John Long at Paddys Valley. MV P.228270 (a+b): Almost complete fish, lacking tail (Figs. 5.10b and 5.12). Collected in

1972 by Gavin Young at Paddys Valley. CPC 17220 (a+b): In the ANU collections. Partially prepared almost complete fish preserved with conodont elements recovered from the body cavity (Fig. 5.10a).

The following specimens in the BMNH collection, originally identified as *Mimia toombsi*, are referred to *Mimipiscis bartrami*: P53250, P53254, P53259, P56489, P56491, P56492, P56496, P56500, 70.4.246 (a WAM number?).

5.7. Description of *Mimipiscis bartrami* sp.nov.

5.7.1 Snout

The rostral (Figs. 5.7 and 5.12) is short and of a similar size to each of the paired premaxillae. It sutures posteriorly with the postrostral with a wavy margin. There is a narrow, unornamented overlap surface for the anterior margin of the postrostral. A recess for the anterior nasal opening corresponds to a sharp ventral downcurve, forming a rounded protruding snout-tip. The bone narrows anteriorly to a tip that is set against the median premaxillary suture. Dermal ornamentation consists of an irregular vermiculate pattern of ganoine ridges, the anteroventral tubercles that are present on the rostral of *M. toombsi* (Gardiner 1984, Fig. 42) are absent. The ethmoidal commisure is visible externally as an arc of small pores.

The premaxilla (Figs. 5.7 and 5.11) is small and flat, forming the occlusal margin of the snout with its opposite number. There is a single row of pointed, conical teeth inwards of a row of much smaller accessory teeth on the outer edge. Acrodin caps are visible on the largest teeth of all dermal occlusal margins. The premaxillae meet in a short median suture,

forming a smooth v-shaped recess that excludes the rostral from the jaw margin. The infraorbital sensory canal enters near the posterior edge of the bone and exits the anterodorsal margin midway through the suture with the rostral. Ornamentation consists of short posterolaterally directed ridges that grade into tubercles at the biting edge.

The nasals (Figs. 5.7 and 5.11) are long bones, situated lateral to the postrostral, which narrow posteriorly to suture with the dermosphenotic. The dorsal margin is straight save for a notch for the anterior nasal opening. The concave lateral margin forms the anterodorsal border of the orbit. Ornament consists of longitudinal ridges along the dorsal lamina, grading towards smaller ridges closer to the anterior margin. The supraorbital sensory canal is visible as a longitudinal row of small pores with a short anterior pit-line adjacent to the anterior nasal opening. The nasals are effectively identical to those of *M. toombsi* (Gardiner 1984: Fig. 43)

5.7.2 Skull roof

The skull roof of *Mimipiscis bartrami* contains paired frontals, intertemporals, parietals, dermosphenotics and supratemporals, along with a single anamesic postrostral. The dermal ornamentation of all skull roofing bones is composed primarily of rostrocaudally directed linear ridges.

The postrostral (Figs. 5.7 and 5.12) is a rectangular bone that occupies a similar area to the dorsal lamina of the rostral of *M. toombsi* and accounts for about 20% of the skull length in dorsal view. It sutures posteriorly to the frontals and laterally with the nasals. Unlike the similarly postrostral of *Kalops* (Poplin and Lund, 2002), there is no contribution to the posterior nasal openings. It differs from *Gogosardina* which has a series of four small

postrostrals that contribute to the margin of the pineal foramen (Choo, Long and Trinajstic 2009).

The paired frontals and parietals are of similar length, differing from the condition in *M. toombsi* where the frontals are the largest bones on the skull roof (Fig. 5.7). They narrow anteriorly towards an irregular margin that forms a v-shaped recess for the postrostral. An excavation for the large pineal foramen is present halfway down the smooth medial margin. The supraorbital canal enters the bone in the middle of the posterior margin and is deflected laterally at the level of the pineal foramen, exiting anterolaterally into the nasal.

Each parietal (Figs. 5.7 and 5.11) is roughly rectangular in outline with a smooth median margin. The bone has a jagged anterior margin where it contacts the frontal. The three pit lines are fully separated, the anterior being the smallest and is continuous with the supraorbital canal, exiting the bone via a tongue-shaped projection as with *M. toombsi* (Gardiner 1984: Fig. 80). Ornament consists of long, rostrocaudally directed linear ridges that are deflected by the pit lines.

The triangular intertemporal (Fig. 5.11) is the smallest bone in the skull roof and is about one half the length of the parietal. It sutures with the frontal medially, the parietal posteromedially and the the supratemporal posteriorly. The sensory canal exits the bone posteriorly into the supratemporal and anterolaterally into the dermosphenotic.

The supratemporal (Fig. 5.11) is narrow; situated lateral to the parietal and posterior to the intertemporal. As with *M. toombsi* (Gardiner 1984: Fig. 82) there is an anterolateral flange that forms the posterior margin of the spiracular opening. The sensory canal traverses

the bone near the lateral margin, presumably originating in the extrascapular and continuing anteriorly into the intertemporal.

The dermosphenotic, as in *M. toombsi* (Gardiner 1984: Fig. 68), is a T-shaped, roughly triangular bone that meets the posterior edge of the nasal via a shelf-like anterior ramus. There is a narrow ventral extension suturing with the anterodorsal margin of the jugal. The posterior ramus is a short, narrow structure whose dorsal surface has an excavation for the anterolateral margin of the spiracular opening. The configuration of the infraorbital sensory canal is identical to that of *M. toombsi*, entering in the dorsal margin from the intertemporal, exiting ventrally into the jugal and with a short anterior branch.

There is a single pair of extrascapulae (Fig. 5.7) that meet medially in a short suture although the bones do not taper inwards as much as those of *M. toombsi* (Gardiner, 1984: Fig. 84).

5.7.3 Cheek and infraorbitals

The palatoquadrate (Fig. 5.11a) is long and roughly triangular, and is very similar to that of *Mimipiscis toombsi* (Gardiner, 1984: Fig.56). The dermal elements on the medial surface of palatoquadrate are fully ossified in all specimens making the isolation of individual bones impossible. It is covered in numerous minute teeth except for a single row of large pointed teeth on the fluted dermopalatine series. There is no evidence for accessory vomerine toothplates.

There are two infraorbitals: the jugal and lacrimal. The jugal (Fig. 5.7) is a large, crescentic dorsal infraorbital unit. It tapers anteroventrally to meet the lacrimal while the

convex posteroventral margin overlaps the edges of the preoperculum and maxilla. The orbital margin is evenly concave with no notch. The infraorbital canal shifts from a near vertical to a near horizontal orientation within the bone. Ornament comprises short to medium linear ridges that follow the contour of the orbit near the anterodorsal margin, becoming more rostrocaudally directed on the remainder of the bone. A right lacrimal is preserved in mesial view on the holotype (Fig. 5.7). As with the lacrimal of *M. toombsi* (Gardiner, 1984: Fig. 72) it is a small thin bone that tapers anteriorly. The infraorbital sensory canal runs the entire length of the bone.

5.7.4 Neurocranium and parasphenoid

The neurocranium of *Mimipiscis bartrami* has been prominently figured and thoroughly described by Gardiner as that of *Mimia toombsi* (Gardiner 1984: Figs. 3, 6, 14, 16 and 20). Beyond individual variation, there appear to be no consistent differences between the braincases of the two species.

The parasphenoid and the associated basisphenoid are visible in ventral view on the holotype (Figs. 5.6 and 5.13) as a slender, rectangular element. As with the parasphenoids of *Cheirolepis* (Pearson and Westoll, 1979) and *Mimipiscis toombsi*, there are no ascending processes. Except where described below, the buccal surface is covered in minute, tooth-like denticles.

Anterior to the basipterygoid processes, the parasphenoid is blade-shaped. The bone flares rostrally to terminate at a tripartite structure of two broad square-tipped extensions lying immediately adjacent to a narrow, median ramus whose anterior tip is not preserved. The left (right in ventral view) lateral anterior extension of the holotype is further subdivided

on the smooth lateral margin into multiple digitate structures. The anterior parasphenoid is similar in overall form to that of *Mimipiscis toombsi* (Fig. 5.4a) and differs from the anterior tripartite extensions of *Moythomasia durgaringa* and *Howqualepis* (Fig. 5.14) in which the lateral extensions are widely separated from the median tongue. The buccohypophyseal opening is roughly level with the basipterygoid processes. There are small square-tipped lateral extensions of the parasphenoid on the basipterygoid processes which are absent in *M. toombsi.*

Posterior to the basipterygoid processes, the parasphenoid is more extensive than that of *Mimia toombsi* with a denticulated rectangular median shelf, the posterior margin extending well past the position of the ventral otic fissure. Flanking this shelf on either side is a depressed (in ventral view) flange of smooth endochondral bone. Vomerine toothplates like those of *Mimia toombsi* have not been preserved. Nor is there any evidence of the paired parotic toothplates seen in *Moythomasia durgaringa.*

5.7.5 Lower jaw

The external dermal surface of the lower jaw consists of a dentary and angular with pre-articular and coronoids on the medial side. As in *Cheirolepis* (Peason and Westoll, 1979), *Gogosardina* (Choo, Long and Trinajstic 2009) and *Mimipiscis toombsi*, there is no surangular. Where present, ornamentation consists of long parallel ridges of ganoine along the ventral and lateral surfaces, with small ridges and tubercles at the dorsal margin and near the anterior tip of the mandible. Near the posterior end of the jaw is a semicircular excavation conforming to the overlapping posteroventral edge of the maxilla. Sections of both the angular and the dentary meet in this region, their surfaces smooth and devoid of ornamentation. The lower jaw of *Mimipiscis bartrami* is effectively indistinguishable from

that of *M. toombsi* and Gardiner's (1984, Fig. 90-91) description applies equally to both taxa.

5.7.6 Operculogular series

The operculum (Figs. 5.7, 5.8 and 5.11) is a large diamond-shaped bone, roughly twice the size of the subopercular. The ventral margin is distinctly convex and overlaps the dorsal margin of the subopercular while the anterior margin contacts the dermohyal. Ornament of both the operculum and subopercular consists of medium to long linear ridges with a predominantly posterolateral orientation.

The subopercular (Figs 5.6, 5.7, 5.8, 5.11) is roughly rectangular with a concave dorsal margin that is devoid of ornamentation where overlain by the opercular. There is a pronounced, anterodorsal process, similar to that present on *Howqualepis* (Long 1988) and the new mimiid (Choo, Long and Trinajstic 2009). It is comparatively longer than the pointed anterodorsal corner present on *M. toombsi* (Gardiner 1984, Fig. 97). Isolated sensory pits are present near the dorsal and posterior margins at midlength along the bone.

More than nine branchiostegal rays are present (Figs. 5.5 and 5.8). They are similar in form and ornamentation to those of *M. toombsi* (ibid; Fig.97). The gulars consist of paired lateral units that are much larger than the adjacent branchiostegal rays, flanking a much smaller median gular (Fig. 5.8).

5.7.7 Pectoral girdle

The post-temporal (Figs. 5.7 and 5.8) is a four-sided rectangular bone that tapers slightly inwards towards a narrow median suture with its counterpart. There is a narrow unornamented anterolateral overlap surface for the extrascapular. The main lateral line canal

passes through bone near the anterolateral corner. Ornamentation consists of curved linear ridges. It differs from the more narrow post-temporal of *M. toombsi* (Gardiner, 1984: Fig. 125) in that the rostrocaudal length is similar to the width while that of *M. toombsi* is almost twice as wide as it is long.

The presupracleithrum (Fig.5.7) is a small triangular bone wedged between the posterodorsal corner of the operculum, the anterolateral corner of the post-temporal and the anterodorsal corner of the supracleithrum. Ornament consists of short linear ridges that run parallel to the nearest margin of the bone.

The supracleithrum (Fig. 5.7) is a long, slender bone with a straight posterior margin. It broadens dorsally where it is overlapped by the post-temporal. The main lateral line canal enters from the dorsal margin via the post-temporal and posteroventrally, exiting approximately two-thirds the way down the posterior margin. Ornamentation consists of posteroventrally directed linear ridges with shorter, circular ridges at the anterior margin.

The postcleithrum (Gardiner 1984: Fig. 127A, as *Mimia toombsi*) is a small sliver-like bone situated behind the pectoral girdle. It is similar in form to that of *Mimipiscis toombsi* but is of a similar size to the adjacent flank scales and difficult to discern when in articulation.

The cleithrum (Figs 5.6 and 5.9) is a large bone with a tall vertical blade and a strongly concave anterior margin. The posterior margin is strongly convex with a deep embayment for insertion of the pectoral fin. At the level of this embayment, the ventral region of the bone sharply curves in medially. There is a prominent smooth overlap surface on the anterior

margin for the clavicle. Ornamentation is complex with vertically directed ridges near the dorsal apex and anterior margin of the vertical blade, grading into circular patterns near the posterior margin. At the level of the pectoral embayment, thicker ridges run posteroventrally with rostrocaudally directed ridges on the ventral surface.

The clavicle (Figs 5.6, 5.7 and 5.9) is large and semiconical, with the posterior margin wrapping around the cleithrum.The bone has distinct vertical and ventral laminae separated by sharp, medially directed curvature. The vertical face is triangular in profile with a tall ascending process while the ventral lamina is broad and flat, coming into close proximity of its opposite counterpart. Ornament consists rostrocaudally directed wavy ridges. There is a space for a small interclavicle, but such a bone has not been identified in the available material.

5.7.8 Body form and fins

The head occupies a little under one third of the total length to the base of the caudal fin, which in the holotype measures approximately 9.5 cm (Figs. 5.5 and 5.6). MV P.227027 is incomplete, but slightly larger with a probable length of a little over 10 cm when complete (Figs. 5.8 and 5.9). The body form is stout and fusiform, being about three times as long as it is deep. Near-complete fish that are preserved in lateral view display a distinct hunch-backed profile that is absent or less pronounced in similarly preserved specimens of *M. toombsi* (Figs. 5.5 and 5.10). This suggests that *M. bartrami* was either wider bodied (appearing deeper when laterally compressed) or that it possessed a dorsal contour that arched steeply upwards from the behind the skull. The latter interpretation is presented in the lateral life reconstruction (Fig. 5.18).

The pectoral fins (Figs. 5.8 and 5.9) have large unsegmented proximal sections that are better preserved than the remainder of the fin. Small fringing fulcra are present along the leading edge. More than 24 primary lepidotrichia are visble on available specimens. The longest anterior fin rays display segmentation and terminal branching on the distal 40-60% of their length. Small, lepidotrichial segments suggest the presence of additional, more extensively segmented posterior rays Disarticulated endoskeletal radials are present including a large, perforated propterygium on MV P.227027.

Small, short-based pelvic fins are present approximately 45% down the length from the pectoral girdle to the start of the caudal fin (Fig. 5.5). At least 18 lepidotrichia were present. The dorsal fin (Fig. 5.10b) is triangular and situated in the posterior half of the body. There are more than 30 segmented lepidotrichia and the leading edge contains fringing fulcra that alternate with lepidotrichial tips.

The anal fin is poorly preserved on available specimens. While it is impossible to determine the shape of the fin, the distribution of the broken fin rays and the ventral scutes reveal the front edge of the fin to be at a point posterior to the leading edge of the dorsal fin. This differs from the condition in *M. toombsi* (Fig. 5.17) where the fins are directly opposite one another and more similar to the configuration seen in *Krasnoyarichthys* (Prokofiev, 2002) and *Moythomasia durgaringa* (Choo, in prep). Of the caudal fin, only the anteriormost section of the lower hypochordal lobe is visible on the holotype (Fig. 5.5), comprising about a dozen rays. Fringing fulcra are preserved on the leading edge.

5.7.9 Squamation

The entire body is clad in rhombic scales with ganoine ornamentation. They are arranged

in transverse rows up to the line of inversion on the base of the tail with no anteromesial redirection on the underside as in *Moythomasia nitida* (Jessen, 1972) and *Howqualepis* (Long, 1988). There are over 110 vertical scale rows between the cleithrum and the caudal inversion in contrast to c.75 scale rows on *Mimipiscis toombsi* (Gardiner, 1984). As in *Gogosardina* (Choo, Long and Trinajstic, 2009), the size of the scales undergo several abrupt reductions in size (with a corresponding increase in numbers within each vertical row) down the length of the fish. The ganoine ridges bear only a few raised striae, unlike the prominent ridging present on the scales of *Mimipiscis toombsi* (Trinajstic, 1999b).

In the following description, the squamation is divided into the nine areas designated by Esin (1990) and employed by Burrow (1994) and Trinajstic (1999a,b) to attribute isolated scales of Devonian actinopterygians to specific areas of the body.

Area A. (Fig. 5.15 a,b,f) Scales are narrow and rectangular, with a height to length (h/l) ratio ranging from more than 4:1 in the anterior scales to 3:1 in examples near area B. The anterior margin is gently concave in first row scales near the postcleithrum, straight in the remainder. The rostro-dorsal process is low and pointed while the peg is high with a rounded apex. In anterior scales (Fig.15.a), the peg and rostrodorsal process are widely separated from the free field via a depressed dorsal extension that accounts for 40% of the vertical height of the scale. Anterior scales may also have an anteroventral extension which may either be smooth and depressed or bear a ventrally directed ganoine ridge. Keel and socket are well developed. The depressed field is narrow in first row scales and widens to between 30-50% of scale-length in more posteriorly positioned scales. Ornamentation consists of anastomosing narrow ganoine ridges that terminate in up to 8 posterior serrations on the caudal margin. Each ridge is smooth and devoid of accessory striations. There is a decrease in depth and ornament of

the scales near area B, with a reduction in the number of posterior serrations.

Area B. (Fig. 5.15 c,g) Scales are rectangular in shape with h/l ratio varying from 2:1 for scales close to area E to 2.5:1 for mid-flank scales. Rostro-dorsal process, keel, peg and socket are well developed. The peg is high with a rounded apex. The depressed field accounts for about 20-25% of the scale-length. Ornament consists of 5-7 separate ganoine ridges that terminate in acutely pointed denticles.

Area C. (Fig. 5.15 h,i) There is a great reduction in scale size from area B to C, with flank scales at the level of the dorsal and anal fins being about 1/5 the size of scales at at the same vertical level anterior to the dorsal fin. Scales are longer than tall with an h/l ratio of 1:1.5. Rostro-dorsal process absent or weakly developed. Anterior and ventral margins are straight. Peg is short and wide based while the keel is well developed. Depressed field is 25% the length of the scale. Free field ornamentation is similar to area B scales, but with the number of ridges reduced to 3-4.

Area D. (Fig. 5.15 j) Area D scales are rhombic in shape, becoming increasingly elongate towards the caudal fin. Ganoine ridges reduced to two in scales close to area C, and a single ridge close to the caudal fin. Pegs, sockets and keels greatly reduced or absent. Depressed field is narrow. Examples from the notochordal mass of the caudal fin are not preserved.

Area E. (Fig. 5.15 d,k,l) There is much variability in scale size and shape within the dorsal surface between the head and dorsal fin. Anterior scales have an h/l ratio of 2:1 with a wide depressed field accounting for at least 25% of scale-length. Rostro-dorsal process is high and is of equal height to the scale body in the anterior-most examples. The peg, socket and keel

are well developed. Each scale has between 4-7 separate ridges which may either protrude as caudal denticles or terminate before the caudal margin. From the middle to the rear of area E, the scales are tall and narrow with an h/1 ration of 5:1. Peg, socket and rostro-dorsal process are greatly reduced or absent. Depressed field is narrow and nearly the entire lateral surface of the scale is ornamented. Ornamentation consists of anastomosing ganoine ridges that terminate before reaching the caudal margin on the dorsal half of the scale and protrude as posterior serrations on the lower half.

Area F. (Fig. 5.15 e) Scales are rostrocaudally elongate with h/1 ratio ranging from 1:2 to 1:3. Peg, socket and keel are poorly developed while the rostro-dorsal process is high. There are two to three separate ridges with one or two posterior serrations which extend beyond the body of the scale.

Area G and H. Scales in these areas are either not preserved or poorly exposed on available specimens. Scales are rhombic in shape with 2 separate ganoine ridges which taper to posterior points usually do not protrude past the scale-body. No pegs or sockets are visible.

Ridge scutes. (Fig. 5.15m) Median scutes are present on both the dorsal and ventral surface. Dorsal scutes are overlapping disc-shaped structures, becoming narrow at the base of the dorsal fin, with about 10 longitudinal ridges on their surfaces. Each is over 10 times larger than the adjacent dorsal scales. A complete series is not preserved, but given their size, there would have been 18-20 originally present between the dorsal fin and supratemporals. There are 2 large ventral scutes anterior to the anal fin and at least 6 between the caudal and anal fins.

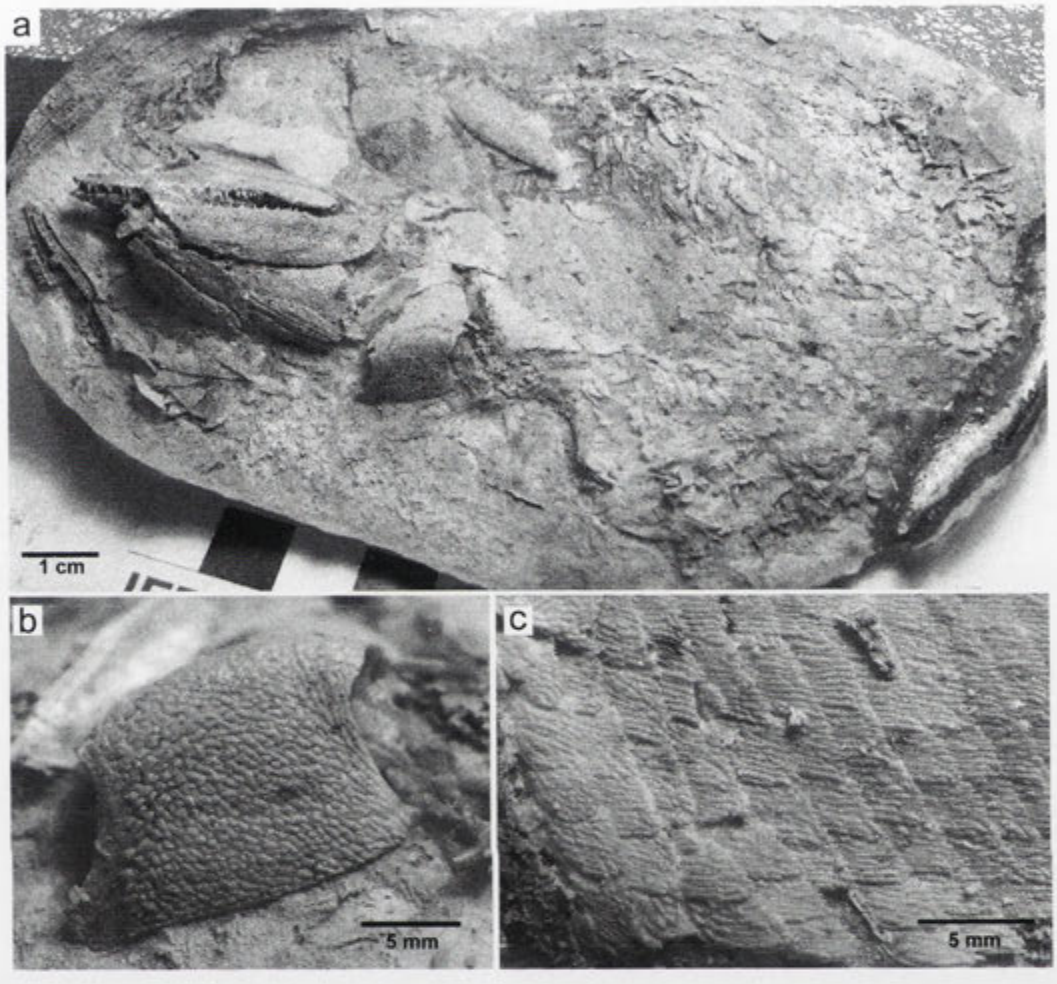


Figure 5.1
Mimipiscis toombsi. Photographs of WAM 86.9.687. **(a)** The entire specimen in left lateral view. **(b)** View of ventral surface of cleithrum showing tubercular ornament. **(c)** Detail of anterior flank scales.

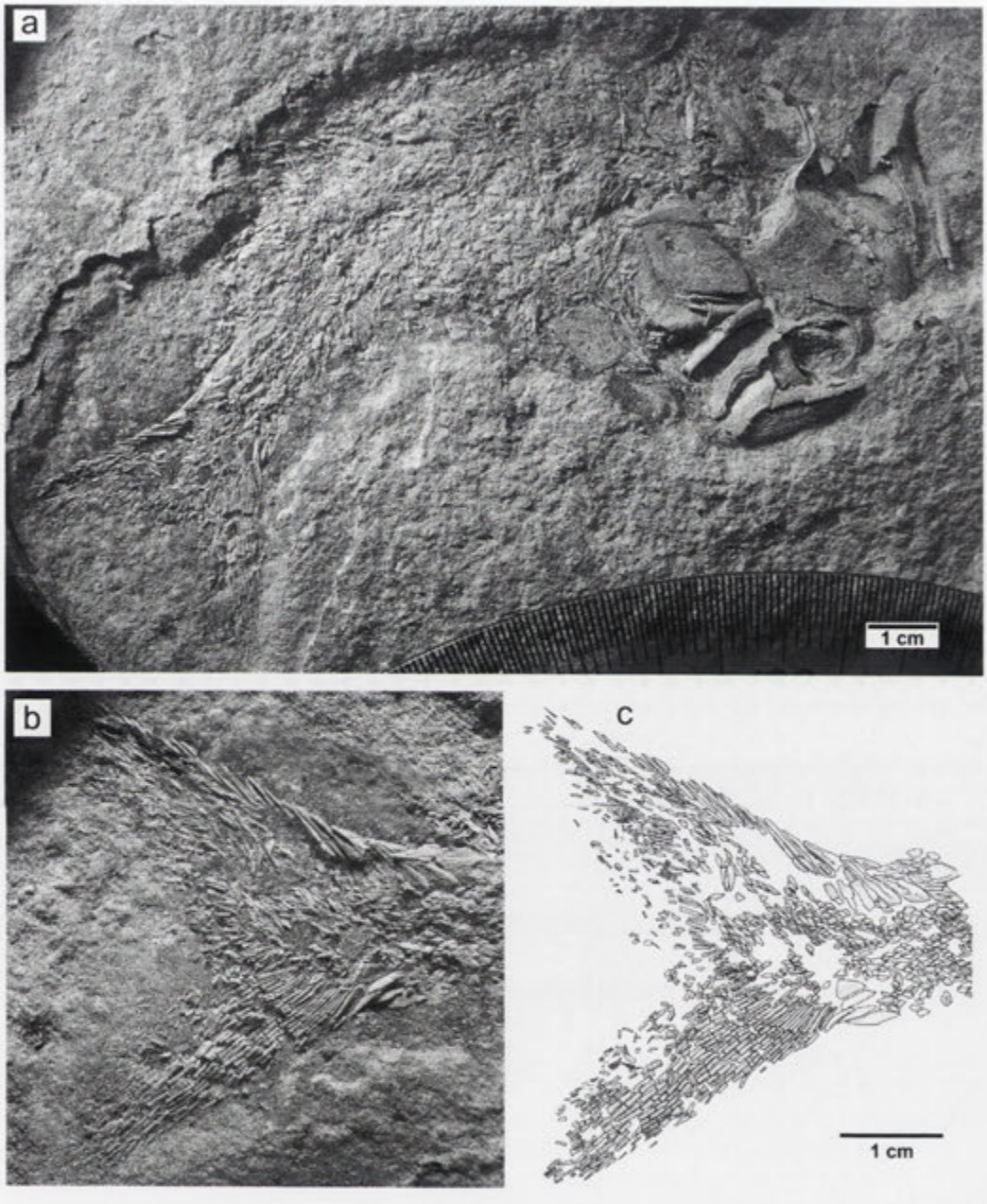


Figure 5.2
Mimipiscis toombsi. MV P.221806a. **(a)** Photograph of entire specimen. The fish has been flattened in right dorsolateral view. **(b)** Photograph and **(c)** drawing of the caudal fin in right lateral view.

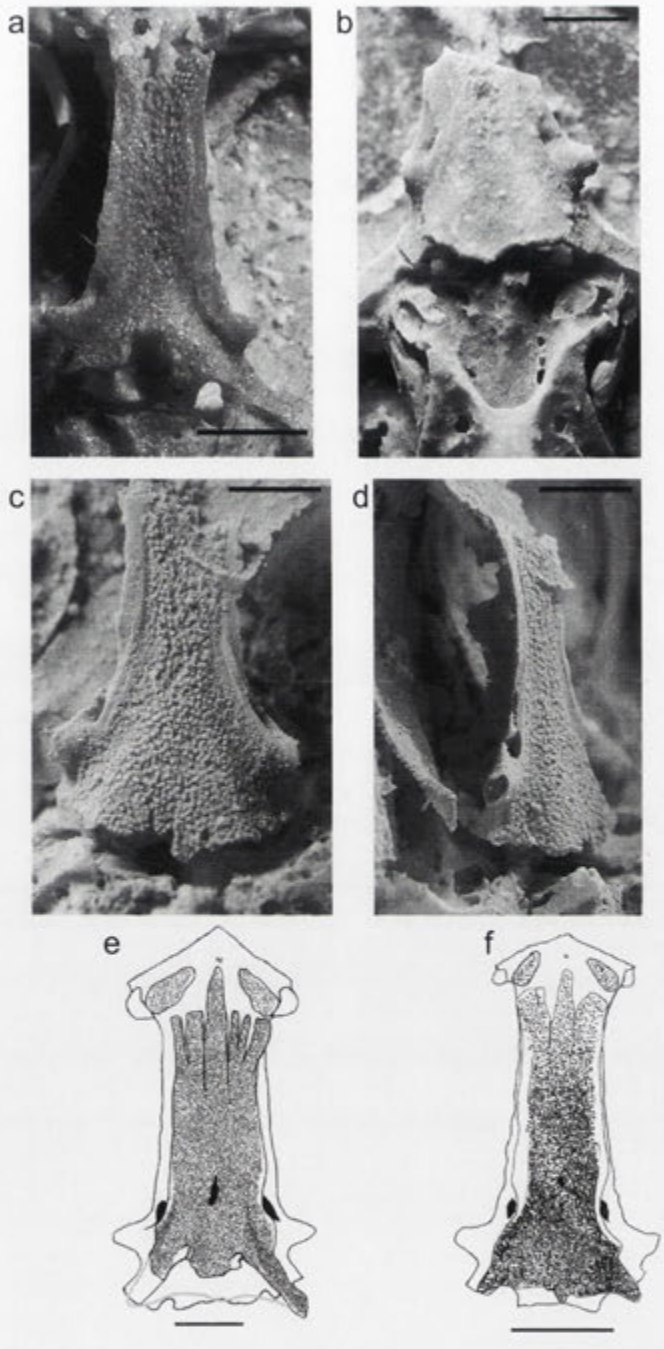


Figure 5.3
Parasphenoids of *Mimipiscis toombsi*. **(a)** Photograph of the whole parasphenoid of BMNH P53223 in ventral view. The bone is complete save for a small median section of the posterior shelf. **(b)** Posterior section of the parasphenoid of MV P.227028 in ventral view. **(c)** Posterior and **(d)** left lateral views of the parasphenoid of MV P.221806b. The anterior 25% of the bone is missing. **(e)** Reconstruction of the parasphenoid of BMNH P53247 as presented by Gardiner and Bartram (1977). Grey line added to delineate probable original full extent of the posterior shelf. **(f)** Reconstruction of the complete parasphenoid of *Mimipiscis toombsi*. Based on BMNH P53247 with missing sections of the posterior shelf based on MV P.221806b.

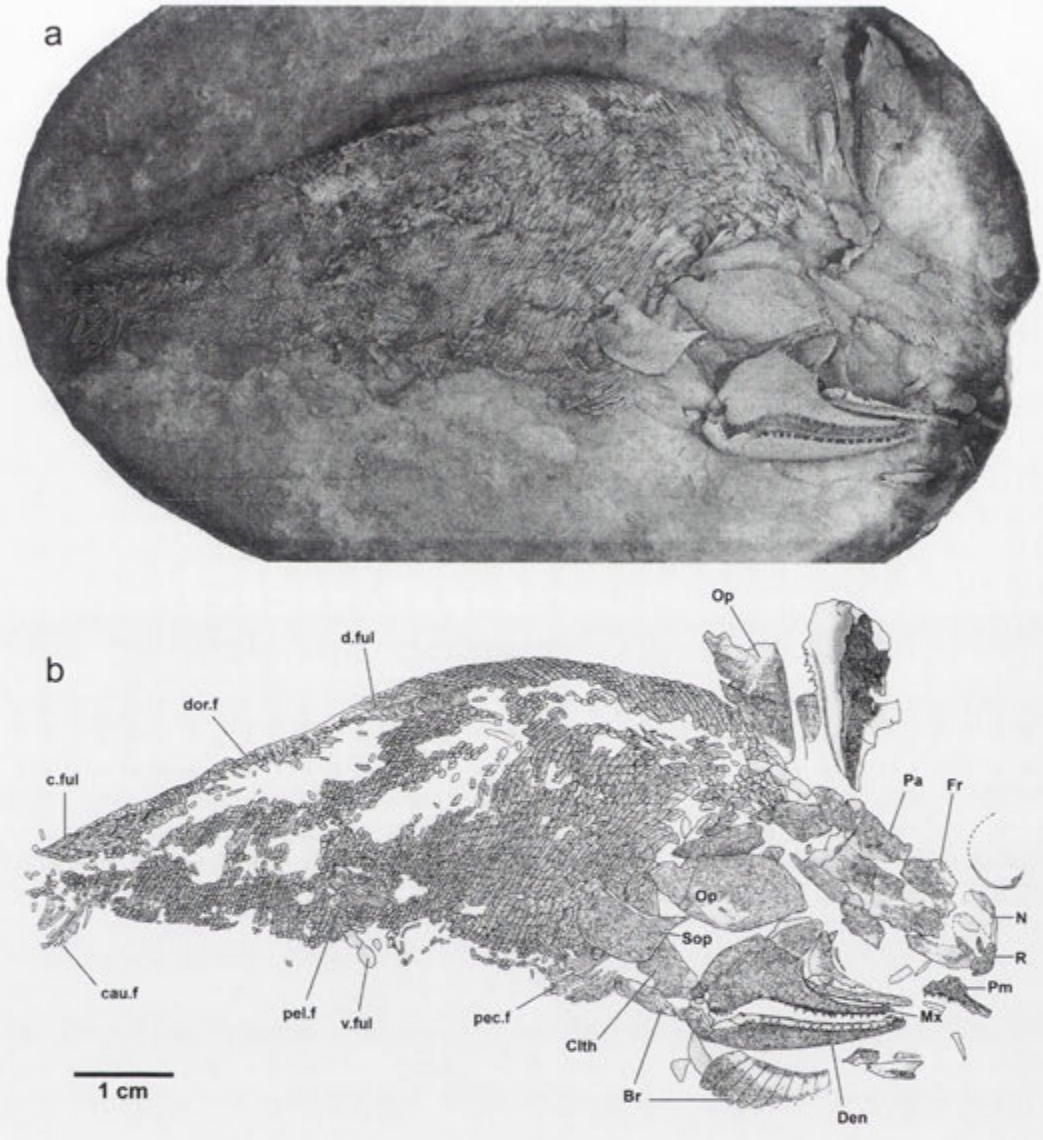


Figure 5.4
Mimipiscis bartrami sp. nov. **(a)** photograph and **(b)** interpretive drawing of WAM 08.9.1a (holotype) in right lateral view.

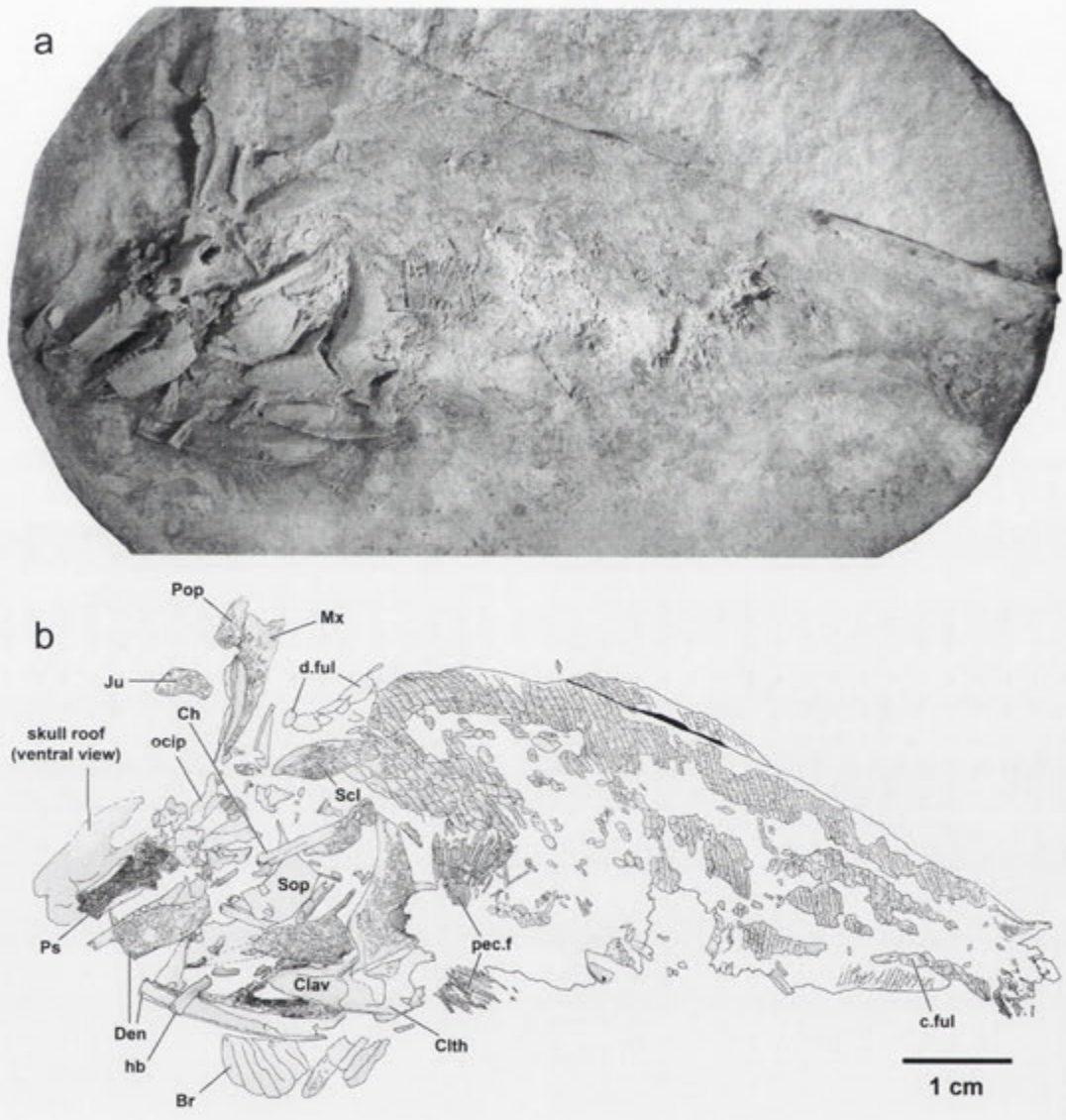


Figure 5.5
Mimipiscis bartrami sp. nov. **(a)** photograph and **(b)** interpretive drawing of WAM 08.9.1b (holotype counterpart) in left lateral view.

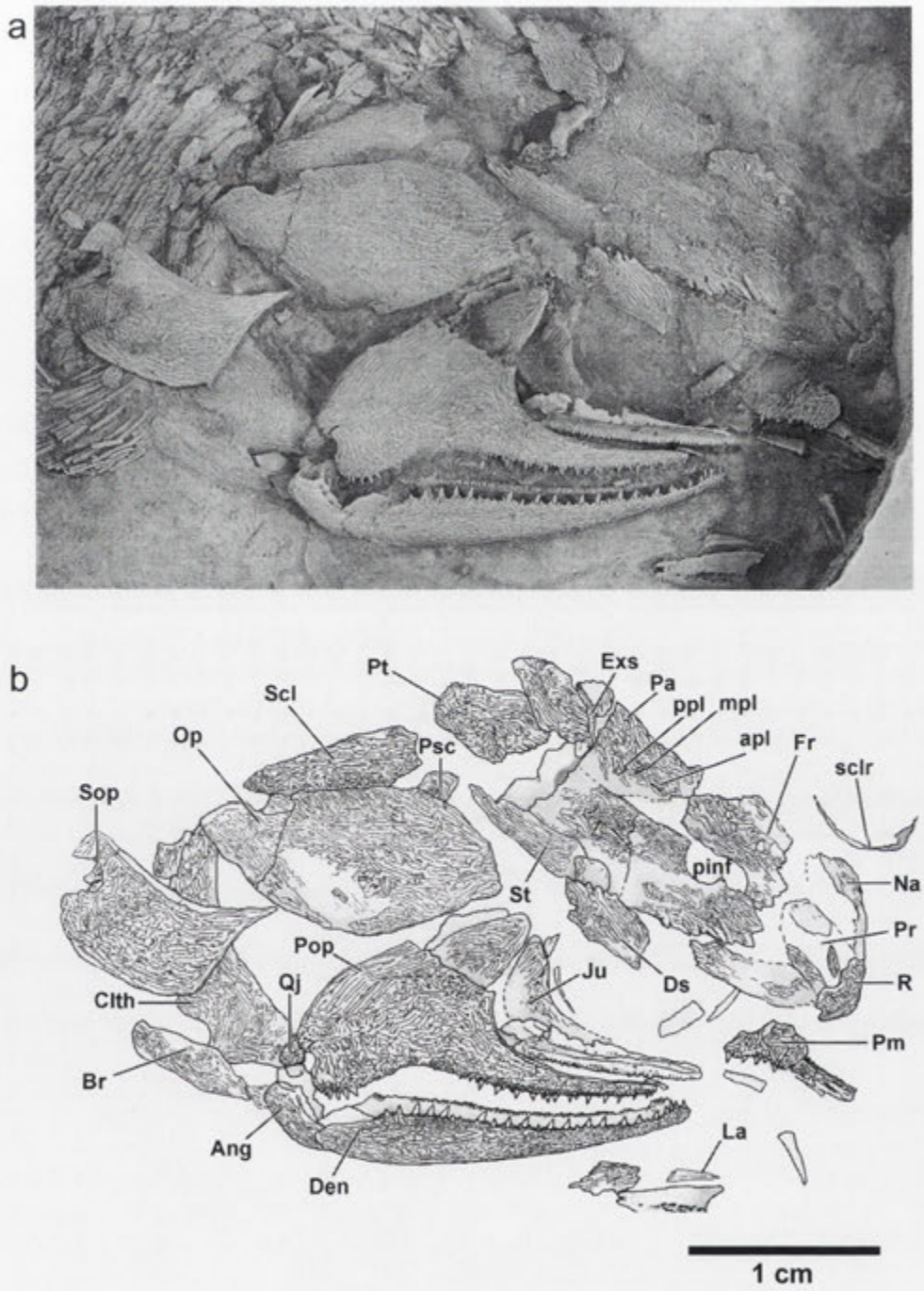


Figure 5.6
Mimipiscis bartrami sp. nov. **(a)** photograph and **(b)** interpretive drawing of the skull of WAM 08.9.1a (holotype) in right lateral view.

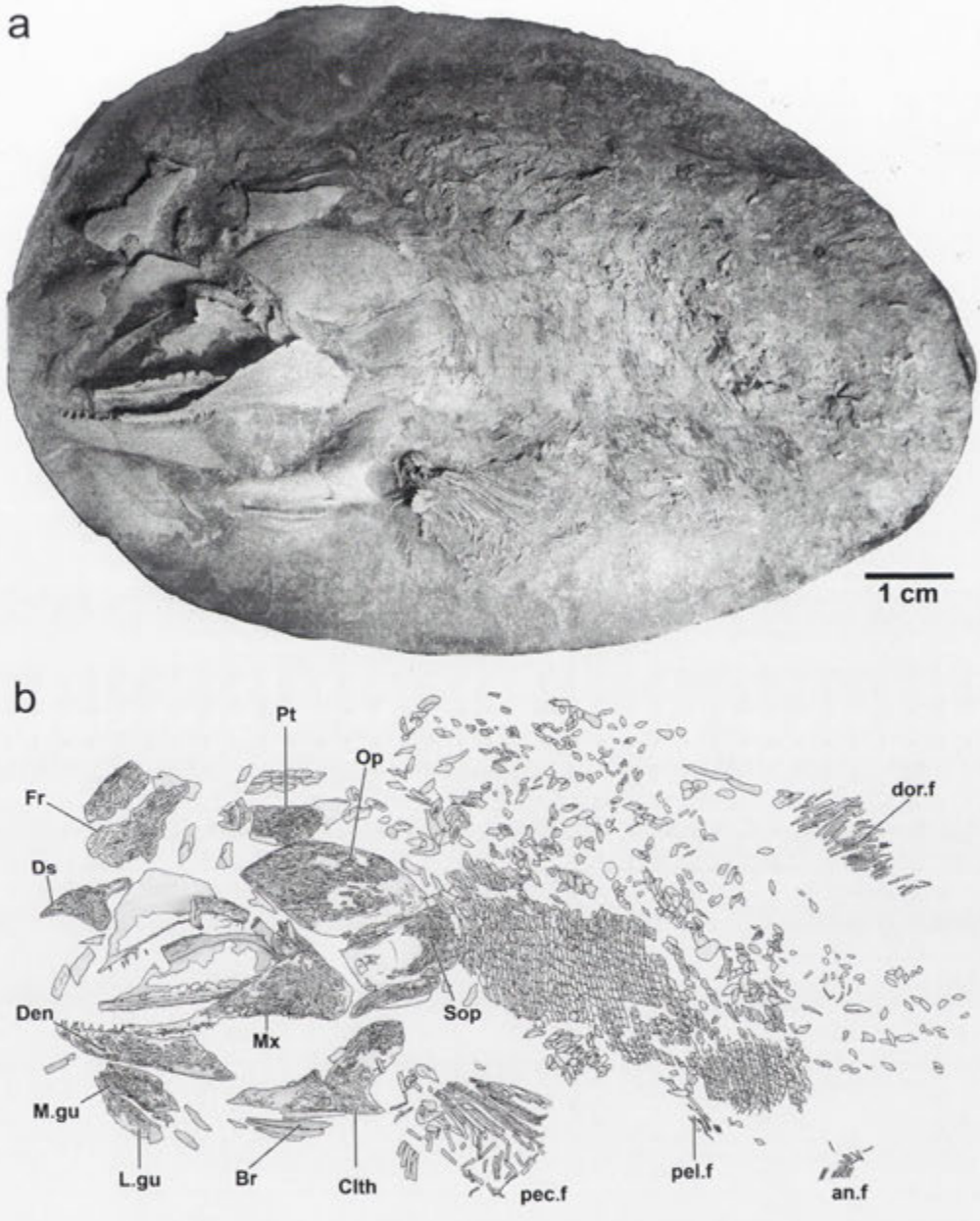


Figure 5.7
Mimipiscis bartrami sp. nov. **(a)** Photograph and **(b)** interpretive drawing of MV P.227027a in left lateral view.

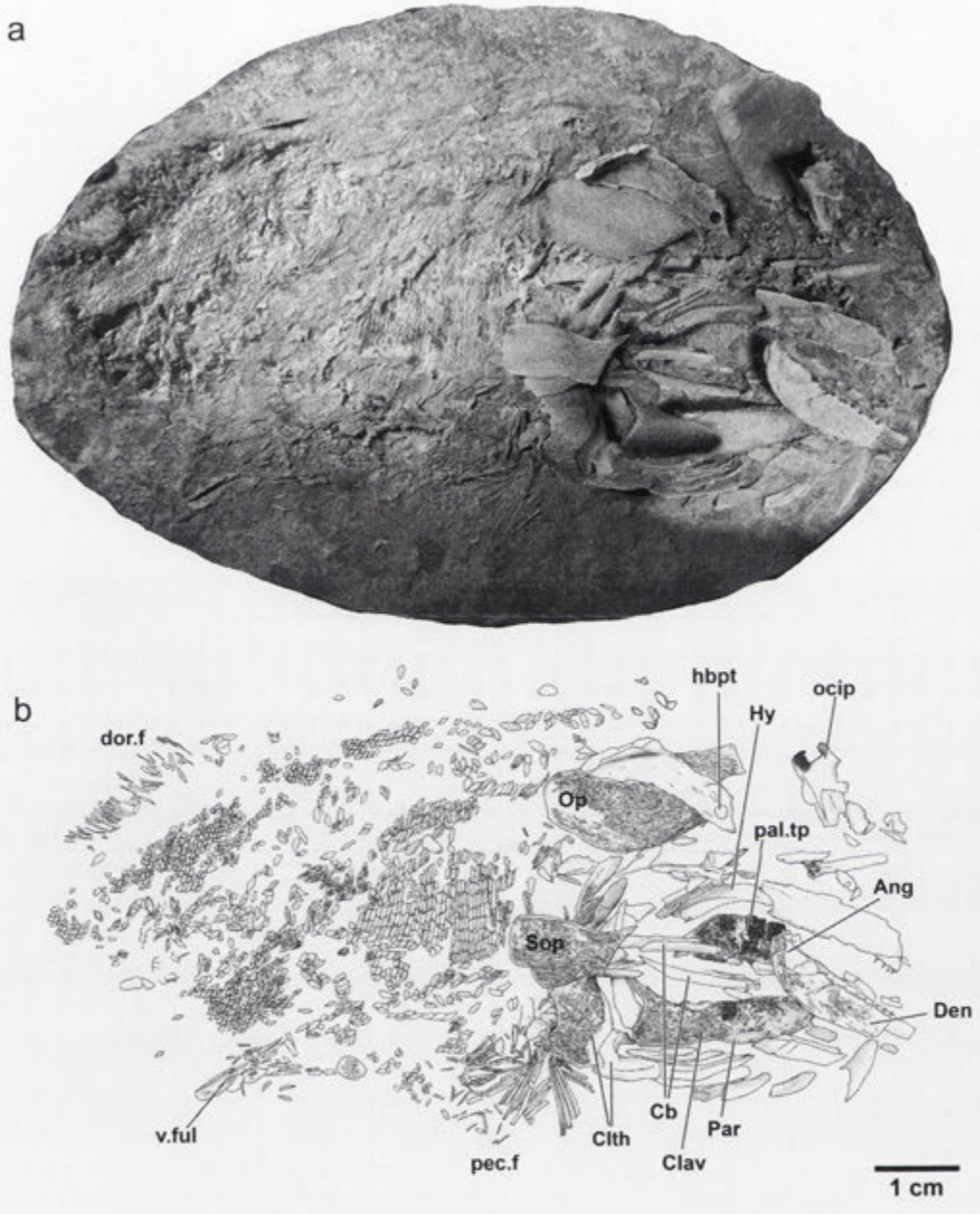


Figure 5.8
Mimipiscis bartrami sp. nov. **(a)** Photograph and **(b)** interpretive drawing of MV P.227027b in right lateral view.

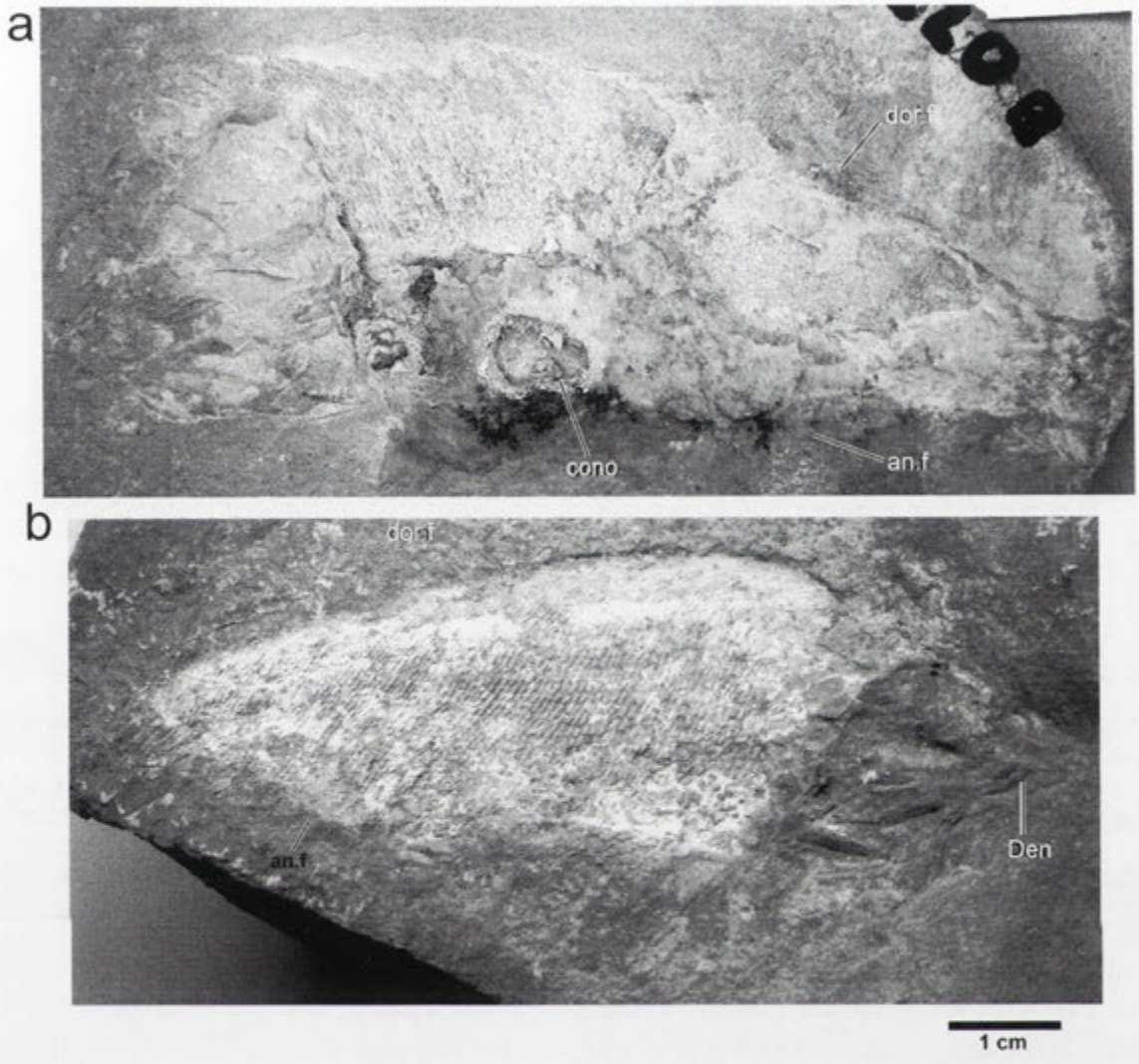


Figure 5.9
Mimipiscis bartrami sp. nov. **(a)** Photograph of CPC 17220 with arrow pointing to conodont elements in the stomach cavity. **(b)** Photograph of MV P.228270 in right lateral view prior to preparation.

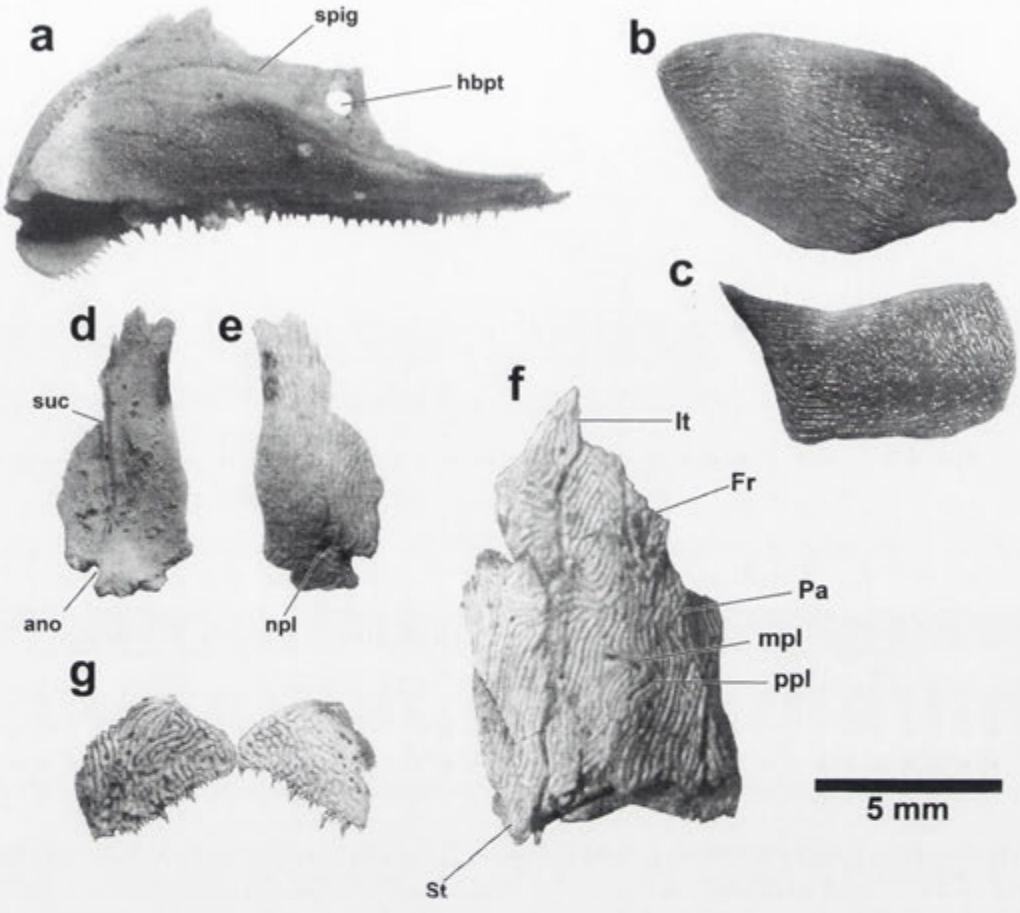


Figure 5.10
Mimipiscis bartrami sp. nov. Photographs of miscellaneous dermal skull elements.
(a) BMNH P56489, left palatoquadrate and associated dermal bones in medial view. (**b**) Left operculum and **(c)** suboperculum of BMNH P56489 in lateral view. Left nasal of BMNH P56489 in (**d**) ventral and **(e)** dorsal view**. (f)** Partial skull roof in dorsal view and **(g)** anterior view of premaxillae of specimen 70.4.246 (within the BMNH collections but apparently a WAM catalogue number).

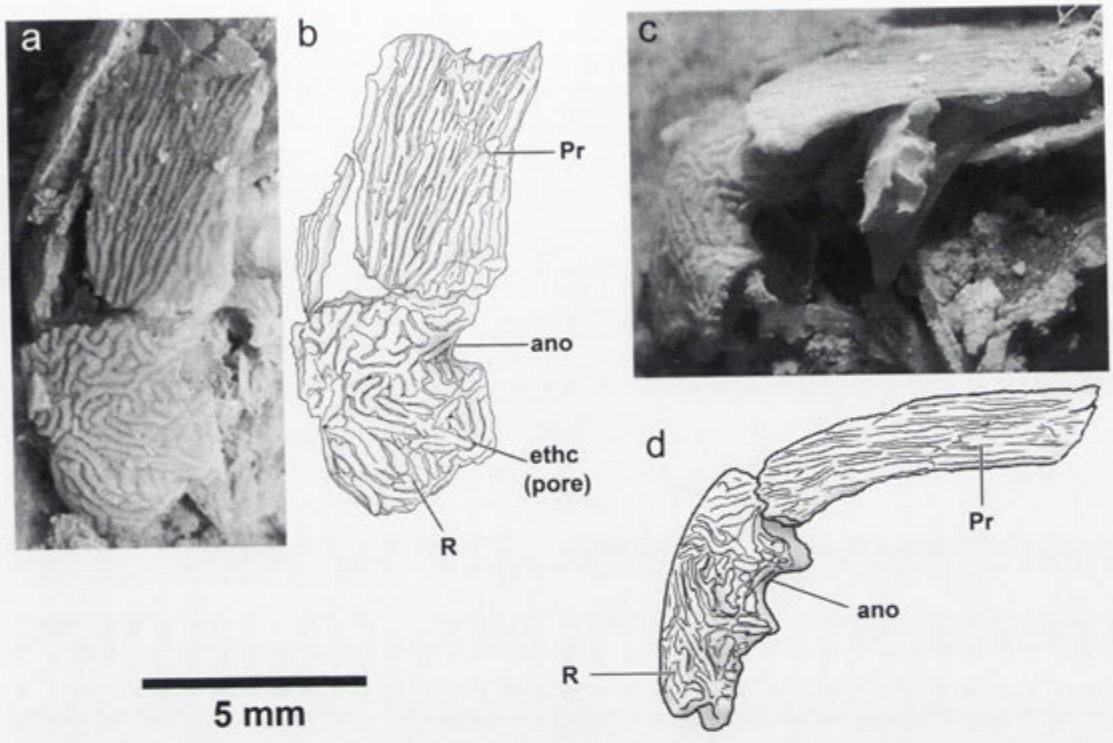


Figure 5.11
Mimipiscis bartrami sp. nov. **(a)** Photograph and **(b)** interpretive drawing of rostral and postrostral of MV P.228270 in anterodorsal view. The bones have been flattened into a single plane. **(c)** Photograph and **(d)** interpretive drawing of the same pair of bones in left lateral view.

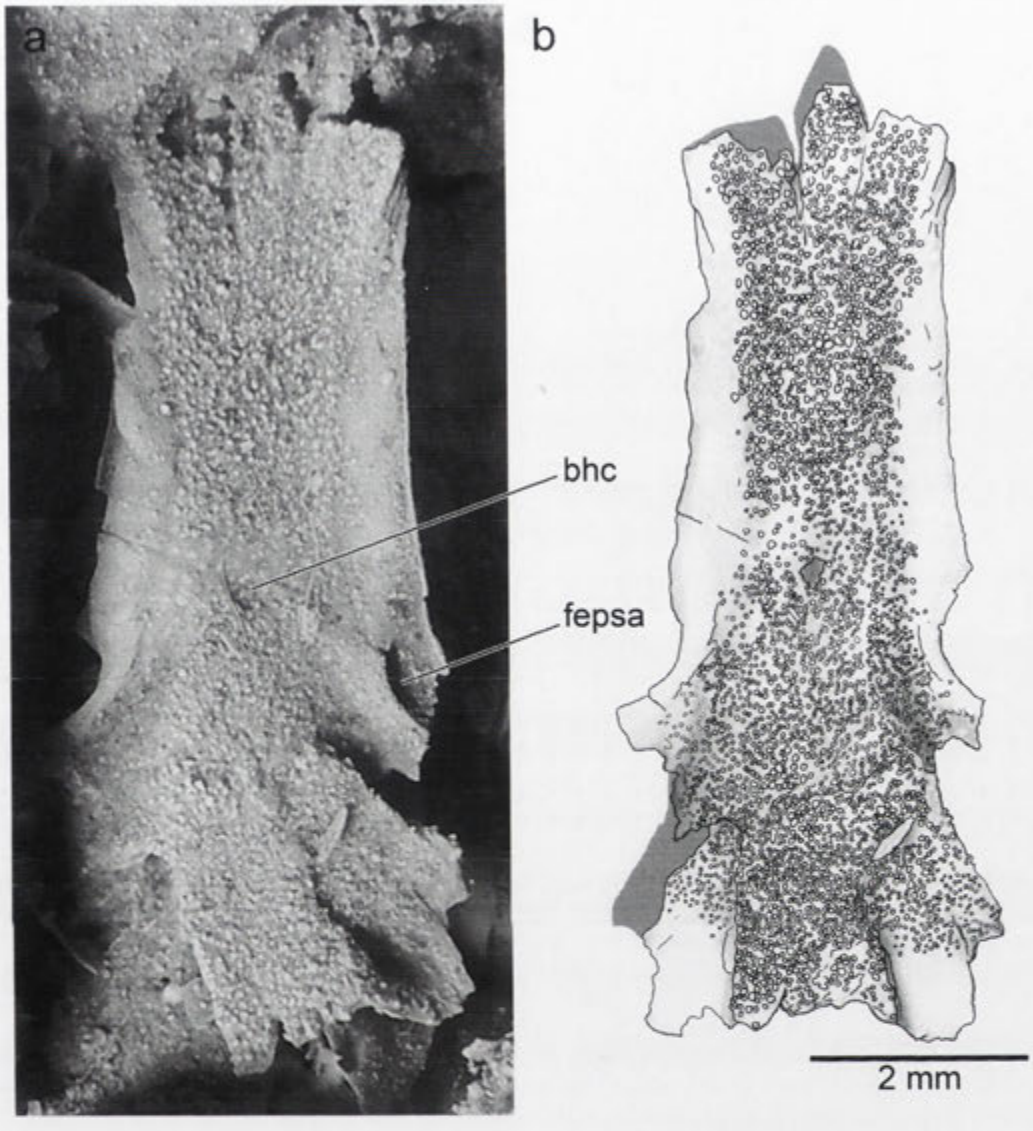


Figure 5.12
Mimipiscis bartrami sp. nov. **(a)** Photograph of the parasphenoid of the holotype counterpart (WAM 08.9.1b) in ventral view. The posterior section of the bone is broken and rotated counterclockwise. **(b)** Reconstruction of the parasphenoid with the posterior section realigned. Grey areas represent missing areas.

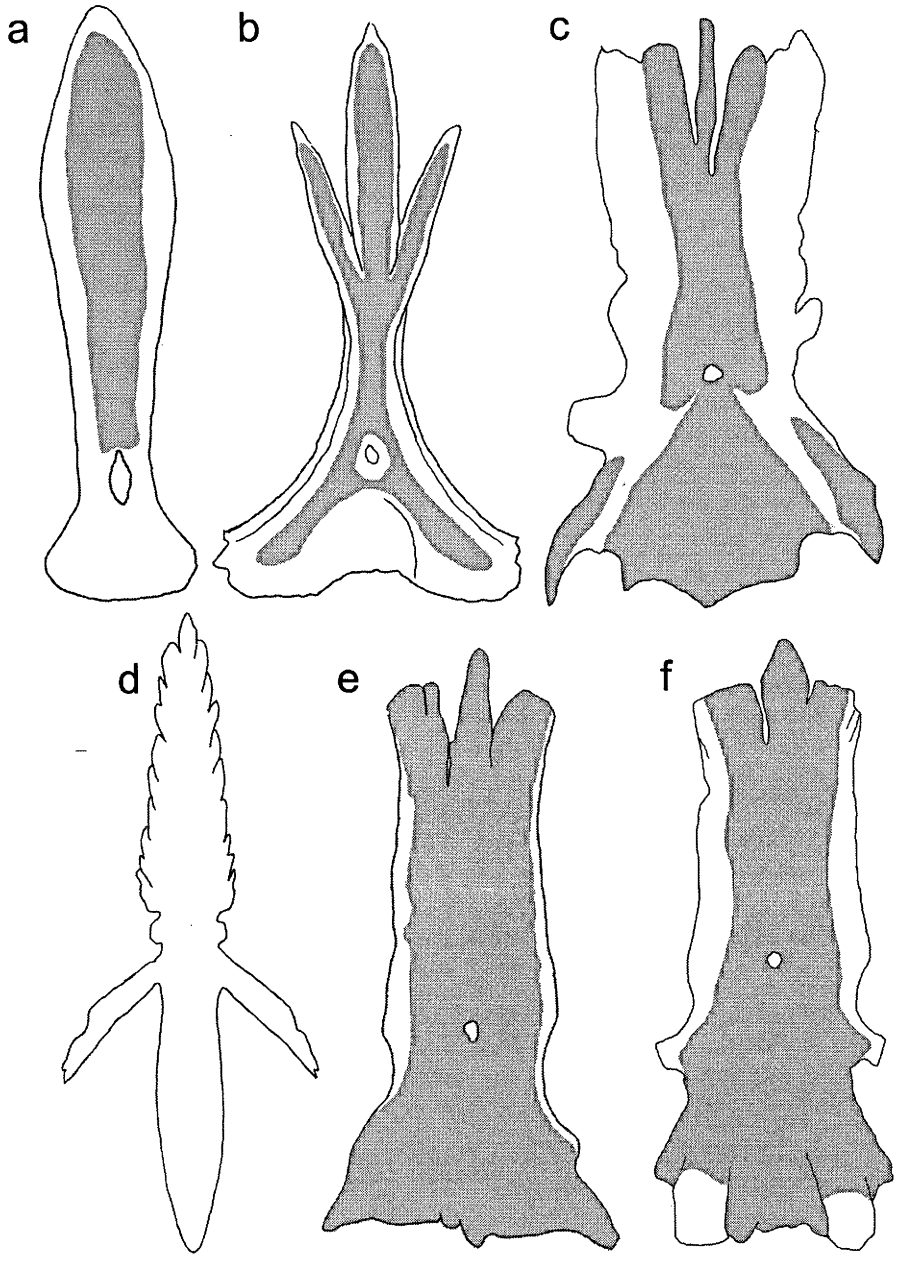


Figure 5.13
Comparisons of the parasphenoids of Devonian actinopterygians depicted in ventral view, except for that of *Tegeolepis* which is in dorsal view. Grey areas correspond to denticulated regions (not known for *Tegeolepis*). **(a)** *Cheirolepis trailli* (after Pearson and Westoll, 1979), **(b)** *Howqualepis rostridens* (after Long 1988), **(c)** *Moythomasia durgaringa* (after Gardiner 1984), **(d)** *Tegeolepis clarki* (after Dunkle and Schaeffer 1973), **(e)** *Mimipiscis toombsi* and **(f)** *Mimipiscis bartrami* sp. nov. Parasphenoids not drawn to scale.

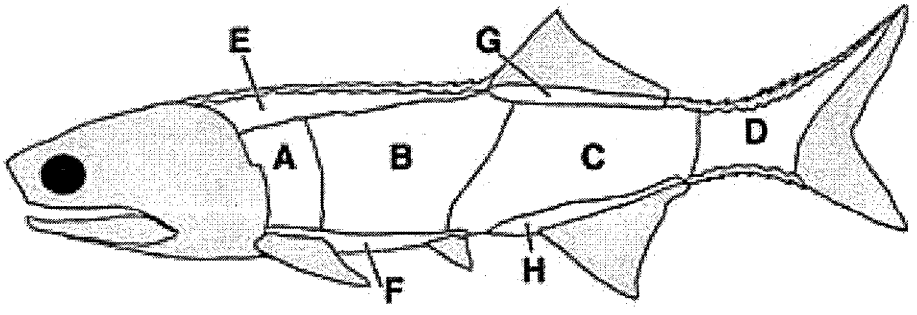


Figure 5.14
Diagrammatic outline of a basal actinopterygian fish, based on *Gogosardina coatesi* (Choo, Long and Trinajstic 2008), detailing distribution of major areas of morphologically distinct scale types as erected by Esin (1990).

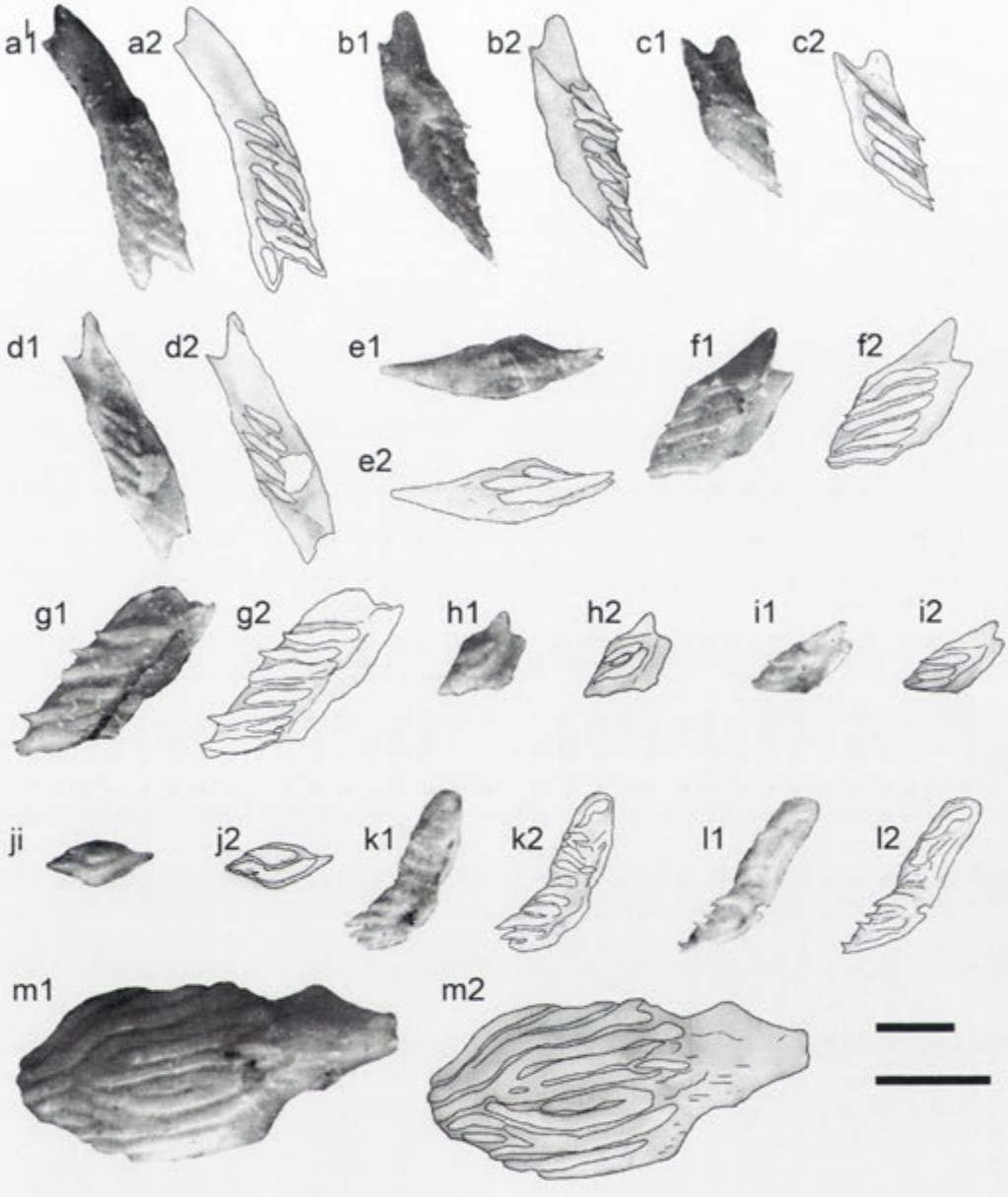


Figure 5.15
Body squamation of *Mimipiscis bartrami* sp. nov. Each individual scale is depicted as a photograph (letter +1) and an interpretative drawing (letter + 2). **(a-e)** Scales the left side of MV P.227027a: **(a)** First row scale from the anterior region of area A, **(b)** scale from posterior region of area A, **(c)** scale from anterior of area B, near transition zone with area E **(d)** scale from anterior of area E and **(e)** scale from area F. Scales from the right side and median dorsal area of holotype (WAM 08.9.1a): **(f)** scale from area A near transition zone with area E, **(g)** posterior area B scale, **(h+i)** area C scales, **(j)** scale from anterior of area D, (k+l) scales from the posterior of area E, close to the anterior margin of the dorsal fin, (m) median dorsal scute, anterior of the dorsal fin.

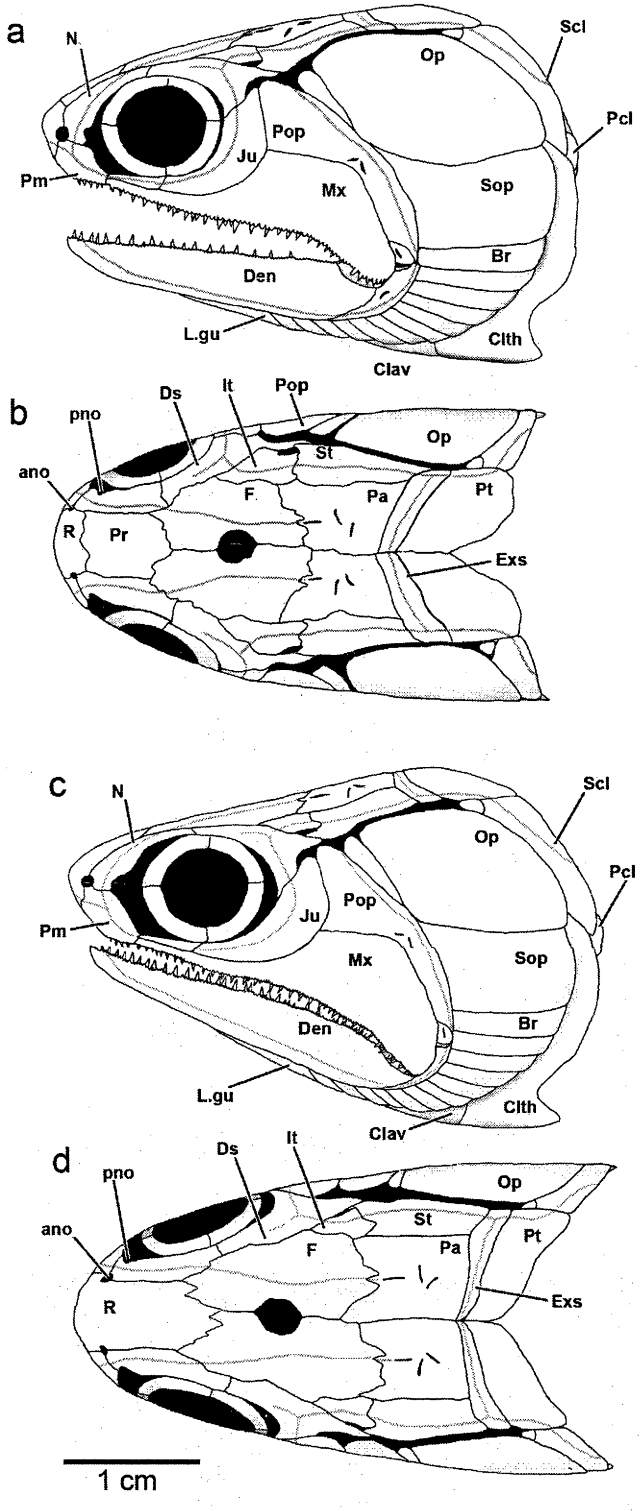


Figure 5.16
Skull reconstructions of *Mimipiscis* spp. Skull reconstruction of *Mimipiscis bartrami* sp. nov. in **(a)** lateral and **(b)** dorsal view. Skull reconstruction of a similar sized specimen of *Mimipiscis toombsi* in **(c)** lateral and **(d)** dorsal view.

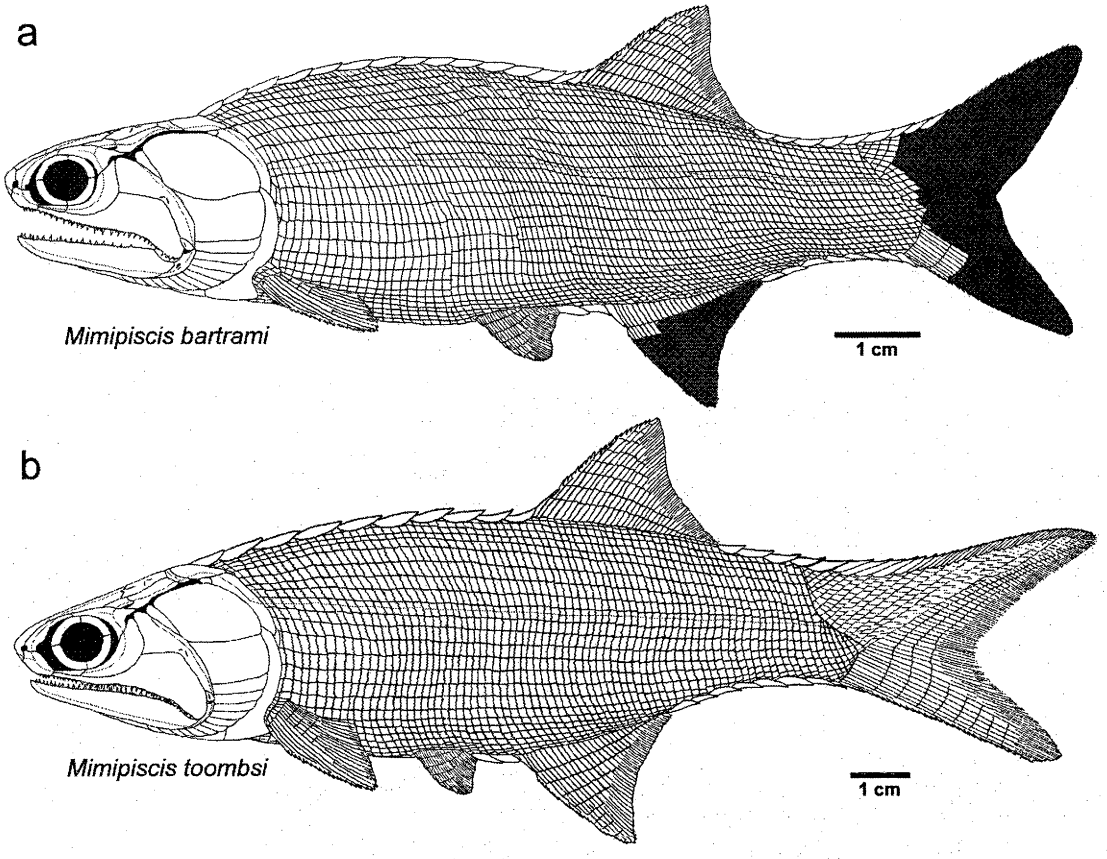


Figure 5.17
Full body reconstructions of **(a)** *Mimipiscis bartrami* sp. nov. and **(b)** a similar sized specimen of *Mimipiscis toombsi* (modified from Gardiner 1984) in left lateral view. Dark grey areas correspond to missing areas of the anal and caudal fin.

Chapter 6. Review of the Devonian actinopterygian genus *Moythomasia* with special attention to the dermal anatomy of *M.durgaringa* of the Gogo Formation of Western Australia and the description of a new species from Bergisch-Gladbach, Germany.

6.0 Preamble

This chapter represents an unpublished manuscript, with myself as sole author, of the basal actinopterygian *Moythomasia*. It has been submitted for review to the Journal of Vertebrate Paleontology.

6.1 Abstract

The Gogo taxon *M. durgaringa* is re-examined and the first rigorous reconstruction of the postrcranial anatomy is attempted. Three European taxa are considered valid, the type species *M. perforata* from Latvia along with *M. nitida* and *M. lineata* sp. nov. from Bergisch-Gladbach, Germany. A revised diagnosis of the genus is presented based on details directly comparable with the Latvian genotype, including unique cranial ornamentation and a lack of median-branching of the occipital canal on the extrascapulae. The four species examined share no unique derived features of the squamation, rendering all scaled-based taxa assigned to this genus invalid.

6.2 Introduction

Moythomasia Gross 1950 is a genus of basal actinopterygians with assigned fossil material from the Late Devonian of Europe, North America and Australia. The type species was described by Gross (1942) on the basis of two skull roofs with associated scales from the

marine Upper Devonian of Kokenhusen, Latvia as *Aldingeria perforata* (Fig. 6.1). Due to nomenclatural preoccupation by another fossil actinopterygian (Moy-Thomas, 1942), the Latvian genus was renamed *Moythomasia* (Gross, 1950). The original specimens are present on a remarkable block also containing the skull roofs of the sarcopterygians *Lativius* and *Strunius*, along with the plates of several antiarch placoderms (Fig. 6.1a). Gross (1953) added three additional species based on material from the Frasnian of Germany. Of these, *Moythomasia striata* (Fig. 6.2) and *M. laevigata* were based on isolated scales from Wildungen (Kellwasserkalk) while *M. nitida* (Fig. 6.3) comprised an incomplete skull and articulated skeleton from near Bergisch-Gladbach (Oberer Plattenkalk). Gardiner (1963) subsequently added two poorly known North America taxa from New York, previously assigned to both *Palaeoniscus* (Hussakof and Bryant, 1918) and *Rhadinichthys* (Gross, 1933). *M. antiqua* (Williams) was yet another scale-based taxon while *M. devonica* (Clarke) comprised parts of the skull, pectoral girdle and scales. More recently, palaeoniscoid scales from the Middle or Late Devonian of northwest Iowa have been classified as *?Moythomasia* sp. (Storrs, 1987).

Jessen (1968) provided a thorough description of *M. nitida* based on additional material from Bergisch-Gladbach. Briefly described in the same publication were three large specimens; tentatively assigned to *M. striata* based on similarities in the squamation. Aside from an analysis of the endoskeletal pectoral girdle and fin, only a brief description was provided of the second form, including an attempted reconstruction of the skull (Fig. 6.3b).

Gardiner and Bartram (1977) provided a preliminary neurocranial description of two actinopterygians: *Moythomasia durgaringa* and *'Mimia' toombsi* (renamed in Chapter 5 as *Mimipiscis toombsi*) from the Gogo Formation of Western Australia. A more detailed

examination of was subsequently provided by Gardiner (1984). The neurocrania of both taxa were described in detail, as was the rest of the anatomy of *Mimipiscis toombsi*. However many aspects of the dermal anatomy of *Moythomasia durgaringa* received only limited attention. The only reconstruction of the skeleton was a simplified view of the head in lateral view (Fig. 6.4a) with no attempt to restore the full body. Since then, the only significant examination of this form has been Trinajstic's (1999a,b) description of the squamation. It has recently become apparent that at least five actinopterygian species are represented in the Gogo assemblage, including *Gogosardina coatesi* (Choo et al., 2008), a second species of *Mimipiscis* (Chapter 5) and the new genus described in Chapter 7.

At present *Moythomasia nitida* represents the only species in this genus that has been provided with a thorough dermal reconstruction, although aspects of this reconstruction have been called into question (position of spiracular opening in Pearson 1982 and Moy-Thomas and Miles 1971, the configuration of the lepidotrichia and fulcra by Arratia, 2009). The form referred to as *M.* cf.*striata* by Jessen (1968) has received little attention despite the availability of well-preserved material. While the neurocranium, squamation and some aspects of the skull of *M. durgaringa* has been closely examined, much of the remainder of the animal is incompletely described. The partial description of two well-preserved Devonian actinopterygians has had a negative effect on phylogenetic studies of this group of fishes. The Bergisch-Gladbach taxon referred to as *Moythomasia* cf.*striata* has been conspicuously absent from all phylogenetic studies of early actinopterygians. The most comprehensive recent analysis of Devonian ray-finned fishes incorporates the braincase characters of *M. durgaringa* but codes many postcranial features as unknown (Friedman and Blom 2006), despite this species being known from complete specimens. Alternatively, the head of *M. durgaringa* is sometimes combined with the body of *M.nitida* to create an artificial construct

as in Trinajstic (1999b, Fig. 2) or Cloutier and Arratia (2004), where the character coding appears to combine the neurocranial anatomy of *M. durgaringa* with the dermal skeleton of *M. nitida* (a form which preserves no neurocranial data).

This study presents previously undescribed aspects of the dermal anatomy of *Moythomasia durgaringa* as well as a fuller description of Jessen's *M* cf.*striata*. The 2005 Museum Victoria field expedition to the Gogo Formation recovered several outstanding specimens of *M. durgaringa*, allowing for a detailed reconstruction of this animal.

In addition to the three specimens figured by Jessen, an examination of the collections of the Naturhistorischen Reichsmuseum, Stockholm produced additional individuals of *M.*cf.*striata* among the Bergisch-Gladbach material. The distinctiveness of this form to the contemporary *M. nitida* along with differences in scale morphology to the true *M. striata* has resulted in the creation of a new species of *Moythomasia.* The status of scale-taxa (*M. striata*, *M. laevigata* and *M. antiqua*) and the fragmentary *M. devonica* are briefly discussed in Chapter 8.

6.3 Materials and methods

The following specimens of *Moythomasia durgaringa* were collected in the 2005 Gogo expedition: MV P.221788 (collected by Lindsay Hatcher at Paddy's Valley, prepared by M, Karkeek), MV P.221789 (collected by Mike Nossal in the area south of Lloyd Hill, prepared by D. Pickering), MV P.221790 (collected by John Long at Longs Well, prepared by D. Pickering), MV P. 221799 (collected by Tim Senden at Paddy's Valley, prepared by D. Pickering), MV P.227029 (collected by the author at Paddy's Valley, prepared by Malcolm Karkeek).

6.4 Systematic palaeontology

Osteichthyes Huxley, 1880

Actinopterygii Cope, 1887

Genus *Moythomasia* Gross, 1950

[= *Aldingeria* Gross, 1942]

Type species. Moythomasia perforata (Gross)

Diagnosis (emended) - Basal actinopterygian fishes with an open pineal foramen. Intertemporals are of similar length to parietals. Parietal in contact with the intertemporal via a distinct anterolateral margin. Posterior corner of supratemporal is markedly pointed and extends beyond the posterior margin of the parietal. Skull ornamented with rostrocaudally-directed linear ridges bearing small serrations or barbs. Macromeric ganoid squamation with well-developed peg and socket articulation. The three species known from complete dermal remains (*M. nitida*, *M. durgaringa* and *M. lineata* sp.nov.) share the following characters that are not available for comparison in the type species (*M. perforata*) = Lacrimal expanded anteriorly. Tripartate dermosphenotic forming the ventrolateral margin of the spiracular slit. Supraorbital sensory canal terminates in the nasal at a level between the anterior and posterior nares. Two pairs of extrascapulae present with no median branching of the occipital sensory canal. Median dorsal scutes extend from the occipit to the dorsal fin. Ventral scutes do not extend anteriorly past the pelvic fins with paired scutes anterior to the anal fin. Basal and fringing fulcra present. Heterocercal and highly inequilobate tail.

Remarks - Primary diagnosis is based primarily on the proportions of the skull-roofing bones

as the remainder of the anatomy is unknown in the type species (*M. perforata*). Neurocranial diagnosis proposed by Gardiner (1984) is applicable only to *M.durgaringa*, as braincase anatomy is unknown for all other taxa.

In possessing an open pineal foramen on the median margins of the frontals, *Moythomasia* is distinguishable from *Cheirolepis* (pineal foramen absent or located within pineal plate - Arratia and Cloutier, 1996, Pearson and Westoll, 1979) *Osorioichthys* (Taverne 1997), *Tegeolepis* (Newberry 1888), *Kentuckia hlavini* (Dunkle 1964) and the majority of post-Devonian actinopterygians. Having intertemporals of a similar length to the parietals distinguishes from *Osorioichthys, Tegeolepis,* the Howqualepididae (Long 1988, Long et al. 2008) and the Mimiidae (Chapter 5). The flank scales of *Stegotrachelus* are distinguishable from *Moythomasia* in possessing a single diagonal rib (Aldinger 1937). Anterolateral parietal contact with intertemporal separates *Moythomasia* from *Cheirolepis*, *Tegeolepis*, howqualepidids. Macromeric squamation distinguishes it from *Cheirolepis* and *Tegeolepis*. Well developed dorsal pegs on the flank scales separates the genus from *Cuneognathus* (Friedman and Blom, 2006) and *Limnomis* (Daeschler, 2000). The linear dermal ornament on the skull of all valid *Moythomasia* spp., consisting of long ridges serrated with small barbs appears unique and is not present in any of the genera mentioned above. The new genus described in Chapter 7 has similar serrations on the cranial dermal ornament, but differs in having numerous small pointed denticles on the skull roof rather than elongate linear ridges.

Moythomasia perforata (Gross) 1942

(Fig. 6.1)

Holotype - NRM P.6240 (Fig. 6.1). Skull roof preserved in dorsal view.

Additional Material Examined - NRM: P.4607, P.17797

Diagnosis (revised) - A *Moythomasia* where the anterior margins of the frontals form a V-shaped recess for the rostral. Parietals marginally smaller than frontals. Flank scales ornamented with separate linear ridges with rows of punctae in inter-ridge furrows.

Geology - Late Devonian (early Frasnian), Snetnaya Group, Kokenhusen, Latvia. Locality description in Gross (1942).

Description - As in Gross (1942, 1950, 1953)

Moythomasia nitida Gross 1953

(Fig. 6.2,6.22)

Material Examined - NRM: P.4803, P.4911, P.4921, P.4931, P.4935, P.4961, P.4964, P.4969, P.4973, P.4978, P.4982, P.5217, P.5237, P.5252, P.5259, P.5264, P.5289, P.5305, P.5311, P.5314, P.5316, P.5318, P.5320, P.5322, P.5342, P.5359, P.5376, P.5384, P.5385, P.5734, P.5966, P.5976, P.6047, P.6852.

Diagnosis (revised) - A *Moythomasia* up to c.15cm long, with c.55 vertical scale rows from head to caudal peduncle. Anterior frontal margins form a straight contact against the posterior margin of the rostral. Porous dermal ornamentation on ventral surfaces of the lower jaw, opercular-gular series and pectoral girdle. Rostral with squared off anteroventral margin that is excluded from the biting margin by the premaxillae. Posterolaterally directed ridges on the dorsal lamina of the rostral. Parietals marginally smaller than or of similar size to the

frontals. Postorbital maxillary blade with curved dorsal margin. Quadratojugal absent. Suboperculum more than ½ the size of the operculum, with small squared-off anterodorsal margin against the adjoining accessory operculum. Two postorbitals anterior to preoperculum. Ornamentation on anterior face of preoperculum dorsoventrally oriented. Dentary teeth of similar size to maxillary teeth. Mandibular sensory canal dorsally deflected on the anterior half of the dentary. Body form robust with the dorsal and anal fins positioned opposite to one another. Pectoral lepidotrichia evenly segmented to fin base. Flank scales ornamented with anastomosing ridges combined with punctae.

Geology - Late Devonian (early Frasnian), Oberer Plattenkalk, Bergisch-Gladbach, Nordrheine-Westfalen, Germany. Locality details in Gross (1953) and Jessen (1968).

Description - As in Jessen (1968) with the following amendments: As has been pointed out by Moy-Thomas and Miles (1971) and Pearson (1982), the spiracular opening was depicted by Jessen (1968) in too posterior a position. The posterior ramus of the dermosphenotic and the intertemporal contribute to the spiracular margin. A distinct angular on the posteroventral lower jaw is clearly visible on larger specimens (Jessen 1968, Plate 14.1).

Moythomasia durgaringa Gardiner and Bartram 1977

(Fig. 6.4, 6.5, 6.6, 6.7, 6.8, 6.9, 6.10, 6.11, 6.12, 6.13, 6.22)

Holotype - WAM: 70.4.244. Incomplete fish preserved in counterpart.

Additional Material Examined - BMNH: P.53216, P.53217, P.53218, P.53219, P.53221, P.53227, P.53236, P.53255, P.56475, P.56477, P.56478, P.56479, P.56480, P.56493,

P.56502, P.56510. MV: P.221788, P.221789, 221790, P.221799, P.227029.

Diagnosis - A *Moythomasia* up to 25cm long, with c.45 vertical scale rows from head to caudal peduncle. Anterior margins of the frontals form a V-shaped recess for the rostral. Porous dermal ornamentation on ventral surfaces of the lower jaw, opercular-gular series and pectoral girdle. Rostral tapers anteroventrally to a dentigerous tip that contributes to the biting margin of the mouth. Irregular short ridges on the dorsal lamina of the rostral. Postorbital maxillary blade with angular dorsal margin. Quadratojugal present. Suboperculum more than ½ the area of the operculum, with small sharp anterodorsal process. Accessory operculae and suborbitals absent. Ornamentation on the anterior face of preoperculum posteroventrally oriented. Dentary teeth 30-60% larger than maxillary teeth. Mandibular canal aligned close to the ventral margin of the dentary. Body form robust with dorsal fin positioned anterior to anal fin. Pectoral lepidotrichia proximally unsegmented for 25-30% of their length. Flank scales ornamented with anastomosing ridges combined with punctae.

Moythomasia lineata sp.nov.

(Fig. 6.3, 6.14, 6.16, 6.17, 6.18, 6.19, 6.20, 6.21, 6.22)

Moythomasia cf.*striata*	Jessen, 1968 (Figs.5-8, Plates 15-17)
Moythomasia nitida (in part)	Jessen, 1973 (Plate 19.1)

Holotype - NRM P.4848 (Fig. 6.14, 6.15, 6.20). Anterior 1/3 of a large specimen, wanting skull roof and snout.

Paratypes - NRM: P.4804 (entire 33mm long fish), P.4805 (anterior 2/3 of medium-sized specimen with 13mm long lower jaw), P.4937 (entire 45mm long fish), P.4994 (small specimen lacking head), P.5260 (entire 43mm long specimen), P.5293 (posterior half of large specimen), P.5332 (entire 40mm long fish), P.5718 (entire small fish), P.5964 (nearly complete c.45mm long fish wanting snout and skull roof), P.6191 (large disarticulated skull with lower jaw length of 29mm).

Etymology - In reference to the simple linear ornament on the scales and dermal skull bones.

Diagnosis - A *Moythomasia* up to c.20cm long, with c.63 vertical scale rows from head to caudal peduncle. Anterior margins of the frontals form a straight contact against the posterior margin of the rostral. Linear ganoine ridges present on the head and scales, with no significant porous remodelling anywhere on the dermal surface. Rostral with squared off anteroventral margin that is excluded from the biting margin by the premaxillae. Posterolaterally directed ridges on the dorsal lamina of the rostral. Postorbital maxillary blade has an angular dorsal margin. Suboperculum less than ½ the size of the operculum, with pointed anterodorsal process. Accessory operculae and postorbitals absent. Dentary teeth 40-70% larger than maxillary teeth. Mandibular sensory canal is dorsally deflected on the anterior half of the dentary. Ornamentation on the anterior face of the preoperculum dorsoventrally oriented. Body form elongate with dorsal fin positioned anterior to anal fin. Pectoral lepidotrichia evenly segmented to fin base. Flank scales ornamented with separate linear ridges without punctae.

Remarks - NRM P.4804 represents the best preserved of the three large specimens examined by Jessen (1968) and was thus selected as the type specimen. Although more complete

smaller specimens are available, the individual bones are not as well preserved or as easily visible as in the holotype.

Doubtful taxa of Moythomasia - *Moythomasia striata*, *M. laevigata* and *M. antiqua* are based solely on disarticulated scales and cannot be reliably assigned to this genus. These forms must be regarded as *nomen dubia* and are briefly covered in Chapter 8. The available material of *Moythomasia devonica* is similar to that of *M.nitida* (as stated by Gardiner, 1963) and includes several partially articulated specimens. Further examination is required to determine the status of this taxon.

6.5 Description of the dermal osteology of *Moythomasia durgaringa*

The neurocranium has been thoroughly described by Gardiner (1984) and the squamation by Trinajstic (1999a,b). As with other species in this genus, the linear ganoine ridges on the skull are usually marked with small pointed barbs (Gardiner and Bartram, 1977). These are absent in areas where the linear ornament has been remodelled into porous reticulation (Fig. 6.9, 6.10).

6.5.1 Skull roof

Dermal ornamentation for all skull-roofing bones (Fig. 6.9, 6.10) consists of short-to-medium length linear ridges that follow a roughly rostrocaudal orientation. Pointed, tooth-like tubercles may occur at the lateral margins. Extrascapulae as described by Gardiner (1984, Fig. 87), with the additional observation that the lateral extrascapular on large individuals (Fig. 6.9b-c) becomes more mediolaterally elongate with little change in the relative size of the medial pair.

The frontals account for c.60% of the rostrocaudal length of the skull-roof. They meet in a wavy median suture with a V-shaped anterior recess for the rostral. The supraorbital canal enters the bone via the parietals with a slight lateral deflection at the midway before exiting into the nasals. The pineal foramen is broader than long and sits in the anterior third of the median suture, accounting for less than 15% the length of the suture. This contrasts with the larger, circular and centrally located opening of *Mimipiscis*.

The parietals are subquadrate and about half the size of the frontals. Anterior suture with the frontal is jagged, the other margins are smooth including the anterolateral contact with the intertemporal. Triradiate pit-lines occur in the middle of the bone, the anterior pit-line is always separate while the middle and posterior grooves may coalesce in some specimens.

Supratemporals are elongate and marginally longer than the parietals. A small anterolateral flange contributes to the rear of the spiracular opening. It differs from the more extensive process of *Mimipiscis* which also forms the ventral margin of the spiracular opening. The bone narrows posteriorly, extending well past the posterior margin of the parietal. Post-temporals are rectangular, tapering slightly inwards towards median contact with its counterpart.

6.5.2 Cheek region

Gardiner's (1984, Figs. 73,74) description of the jugal and lacrimal remains unchanged. Infraorbital ornamentation combines linear ridges on the lower orbital margins, short ridges on the ventral margins and dorsal extremity of the jugal, long ridges perpendicular to the orbital margin on the posterior of the jugal and tubercles on the anteroventral lacrimal

The maxilla consists of a broad postorbital blade behind a narrow suborbital ramus. The postorbital blade has dorsal and posterodorsal margins that meet at a distinct junction of about 120° degrees, similar to the maxilla of *Mimipiscis* (Gardiner 1984) and *Moythomasia lineata* sp.nov. but differs from *M. nitida* where there is gentle curvature from the dorsal to posterior margins. The occlusal margin bears a row of stout, conical teeth that are smaller (c.40-60% shorter) than the corresponding dentary teeth and are situated inward of numerous small tooth-like denticles. With the exception of the anterodorsal overlap surface for the infraorbitals, ornament consists of long linear ridges on the dorsal surface that follow the dorsal contours of the bone that are replaced by short ridges and tubercles near the ventral margin (Gardiner 1984, Fig. 66). On large specimens, (Fig. 6.9, 6.10) these short ridges thicken and fuse to form a continuous reticulation with embedded pores.

The preopercular is a strongly inflexed bar that broadens anteriorly. The anterior face of the anterodorsal section has a pronounced concavity to receive the jugal (Fig. 6.10). The posterior extremity of the posteroventral section narrows towards a juxtaposition with the quadratojugal. The ventral margin has a smooth area that underlies the maxilla. The sensory canal exits dorsally, 60-70% along the posterodorsal margin and there is a well developed cuspate pit-line at the level of inflexure. Ornamentation consists of horizontal linear ridges that are deflected at the dorsal and posteroventral edges to follow the bone outline. This contrasts with the preoperculae of *Moythomasia nitida* and *M. lineata* sp.nov. in which the ridges on the anterior surface are vertically oriented (Fig. 6.18, Jessen 1968, Plate 14.1).

The quadratojugal is a small, subrectangular bone with a well-developed cuspate pit line (Fig. 6.10a). It is less than 10% the size of the preopercular and smaller than as figured by Gardiner (1984: Fig. 103). Ornament consists of short horizontal ridges with the anterior half

of the bone being smooth and overlain by the maxilla.

The dermosphenotic (Fig. 6.9) is a tripartite bone that narrows to an anterior contact with the nasal, has a straight dorsal margin that contacts the intertemporal, and a short posterior ramus that is sigmoidal in lateral view with a narrow overlap margin for the jugal. There is variation in the shape of the posterior section of the bone that forms the posterolateral margin of the spiracular opening. In some smaller specimens (Gardiner 1984, Fig.69), the bone does not extend posteriorly beyond the contact with the jugal, with the spiracular opening directly above the ventral ramus. In most specimens, there is an elongated posterior ramus of variable length, with the spiracular opening more posteriorly positioned. The route of the sensory canal is identical to that of *Mimipiscis* (Gardiner 1984) while ornament consists of linear ridges that become progressively shorter posteriorly.

6.5.3 Lower jaw

(Fig. 6.9, 6.10) Description unchanged from Gardiner (1984) with the following amendments: dermal ornament of the lower jaw consists tubercles near the biting margin, linear ridges on the angular and posterior dentary that coalesce on the remainder of the lateral surface into a smooth mass with numerous embedded pores. The mandibular sensory canal is aligned close to the ventral margin of the dentary with only a slight dorsal flexure at the anterior end.

6.5.4 Opercular-gular series

The opercular-gular series of *Moythomasia* received only a cursory treatment by Gardiner (1984, p.339). The operculum (Fig. 6.5, 6.6, 6.11) is an elongate four-sided bone that is articulated in a less-vertical position (c. 45° to the horizontal) than previously reconstructed

(Fig. 4). It is 40-55% larger than the suboperculum, which it overlaps ventrally with margin that may be straight or convex. Ornamentation consists of short-to-medium length ridges that become increasingly fine posteroventrally.

The suboperculum is highly variable in shape and a pair from a single individual fish may look strikingly different to each other (Fig. 6.11a,d). The bone may be subquadrate to rectangular in shape with a hook-like anterodorsal process anterior to a small semicircular embayment on the dorsal surface. Ornament consists of short-to-medium length ridges and pointed tubercles. Prominent lateral sensory pores are present in some specimens.

The twelve branchiostegal rays again show considerable variablity in shape between individual fish, although the 1st ray (immediately ventral to the suboperculum) is consistantly larger (by c.30-40%) than the remainder in the series (Fig, 6.11h). The posterodorsal-most rays have short ridges that grade into the typical porous ventral ornament for this taxon (as described for the lower jaw) at the 2rd to 4th bone in the series.

6.5.5. Pectoral girdle

As described in Gardiner (1984), with the following amendments: The supracleithrum is large, being as long as the posterodorsal margin of the operculum (Fig. 6.11f-g). Broader at the dorsal end with a prominent smooth overlap surface for the post-temporal. The main lateral line canal. visble as a thickened region on the smooth visceral surface, enters at the dorsal margin from the post-temporal, running posteroventrally to exit 75-90% down the length of the bone into the lateral-line scales. This is considerably further down than as presented in Gardiner's reconstruction (Fig. 4a). Linear ornament runs parallel to the anteroventral margin close to the opercular contact, transforming to shorter rostrocaudally-

directed ridges elsewhere on the lateral surface. The cleithrum and clavicle are lineated on their lateral surfaces, the ornament changing on the ventral surface into a smooth mass studded with numerous pores (Gardiner 1984, Fig. 131).

6.5.6 Body and fins

The body is robust and fusiform, with the head occupying about 30-35% of standard body length (Fig 6.5, 6.6, 6.7, 6.8). Body depth c.35-40% of standard length (snout tip to caudal inversion). Largest known specimens are about 23cm long. Fins are as described by Gardiner (1984) with the following amendments: The proximal pectoral fin rays segments are longer than the others, accounting for 20-25% of the length from base to fin-tip (Fig. 6.12a). The dorsal fin (Fig. 6.12b) is situated 55-60% of the distance from the occipit to the anterior of the caudal fin, at a position anterior to the level of the anal fin, not directly opposite the anal fin as stated by Gardiner (1984). The tail (Fig. 6.12c,d) is heterocercal with a triangular lower hypochordal lobe that is. Scale morphology is as described by Trinajstic (1999a). Immediately anterior of the anal fin are two partially overlapping pairs of large, wedge-shaped ventral scutes (Fig. 6.12e,f). Situated anterior to these are narrow, elongated scales that presumably surrounded the vent. Only a single pair of rounded pre-anal scutes are visble on *M. nitida* and *M. lineata* sp.nov. (Jessen 1968, 1973)

6.6 Description of *Moythomasia lineata* sp.nov.

With few exceptions (notably the pectoral girdle on the holotype), little endoskeletal information of this taxon is preserved. As in other species of *Moythomasia*, most of the linear ganoine ridges on the skull possess barb-like serrations (Fig. 6.16c)

6.6.1 Skull roof

The skull roof (Fig. 6.18) has only been preserved in smaller specimens and is ornamented with rostrocaudally-directed linear ridges. Frontals are rectangular in shape, with the lateral margins converging anteriorly to a straight suture with the rostral. They account for c.50% of the length of the skull roof. The supraorbital canal runs a straight course through the middle of the bone from nasal to parietal. A small pineal foramen is set between the frontals, 40% down the length of the median suture. The rectangular parietals are c.45% the length of the frontals. The tripartite pit-lines are located well away from the bone margins and are separate in all available specimens.

The supratemporals (Fig. 6.15, 6.18) are elongate rectangles that taper posterolaterally to points well behind the parietals. The supraorbital sensory canal runs close to the lateral margins of the bones. Anterolateral flaps with ventral flexure embrace the rear tip of the dermosphenotic and form the posterior margin of the spiracular opening. Intertemporals (Fig. 6.18) are triangular bones that are almost as long as the parietals. There is a slight embayment on the posterolateral margin, forming the dorsal margin of the spiracular opening. There are two pairs of short extrascapulae, the lateral examples being twice the width of the mesial pair. The lateral extrascapulae transmit the occipital canal from the supratemporals to the parietals close to their lateral edges. As in other *Moythomasia* spp., there is no evidence of a mesial branch of this canal.

6.6.2 Snout

The ornamentation of the snout (Fig. 6.16, 6.17) consists of linear ridges, grading into tubercles on the anterior face of the rostral and medial halves of the premaxillae. As in *M. nitida,* the ridges on the dorsal lamina of the rostral radiate posterolaterally from the midline

of the bone, unlike *M. durgaringa* where the ridges have a more irregular aligment.

The rostral (Fig. 6.16a-b) is a large rectangular element that arches into distinct dorsal and anterior laminae. The bone is squared-off at both ends, the anterior-margin is excluded from the mouth by the premaxillae while the posterior-margin sutures against the frontals. Notches on the lateral margins form the anterior margins of the anterior nares. The premaxillae (Fig 6.16a-b, 6.18) are square-shaped and straight-edged on all sides. Conical laniary teeth on the biting margin are situated mesial to a row of minute pointed tubercles. The posterodorsal edge contributes to the orbital margin while there is no contact with the posterior naris. An ethmoidal commisure of the sensory canal is not visible any specimen.

Nasals (Fig. 6.16a-b, 6.18) are elongate bones, lateral to the rostral against which it forms the posterior margin of the anterior nares. Excavations on the posteroventral margin form the anterior margins of the posterior nares. The supraorbital canal runs close to the medial section of the bone and terminates at the level of the posterior nasal opening.

6.6.3 Cheek

The infraorbital series (Fig. 6.16) consists of a large crescentic jugal posterior to a small lacrimal that flares dorsally at the contact with the premaxilla as in the other completely known *Moythomasia* sp. and *Howqualepis* (Long, 1988). Ornament consists of short ridges and tubercles on the lacrimal and posterior jugal, on the jugal grading into linear ridges anterior of the infraorbital canal

The maxilla (Fig. 6.14, 6.15, 6.16, 6.18) is of similar shape to that of *M. durgaringa* with the exception that the suborbital ramus is more slender and elongate. The conical maxillary

teeth are substantially smaller than their counterparts on the dentary. Ornament on the postorbital blade consists predominantly of posteroventrally directed long linear ridges, abruptly shifting to a rostrocaudal orientation at the dorsal margin and anterior margins and grading into tubercles alongside the dentigerous ventral surface. Short ridges and tubercles are present on the narrow suborbital ramus.

The preoperculum (Fig. 6.15, 6.18) is acutely angled, with its ventral margin following the contours of the maxilla. The anterior margin is straight and contacts the jugal and dermosphenotic. The preopercular canal runs close to the posterodorsal margin of the bone, extending from the narrow posterior extremity before terminating about 65-70% up the length of the bone. Pit-lines are not visible on available specimens. Ornament consists of short ridges on the posterior ramus that follow the long margins of the bone and almost vertical ridges on the anterior ramus. A quadratojugal is not visible on any specimen of *M. lineata* sp.nov. or *M. nitida.*

6.6.4 Lower jaw

The lateral surface of the lower jaw (Fig. 6.15, 6.16, 6.18) consists of a large dentary, a narrow posteroventral angular and a smooth surangular that is confined to the area overlapped by the maxilla. The lower jaw is straight and robust, of a similar shape to that of *M. durgaringa*. Ornament is comprised entirely of medium to long linear ridges, grading to tubercles near the biting margin. The porous remodelling of the type present on *M. durgaringa* and *M. nitida* is absent. Stout, conical teeth on the dentary are more than twice the size of the maxillary teeth whereas the upper and lower dentition of *M. nitida* is of a similar length. The mandibular sensory canal runs close to the ventral margin of the angular and posterior dentary, then arches strongly in the anterior third of the dentary.

6.6.5 Opercular-gular series

The dermohyal (Fig. 6.15, 6.18) is a stout, wedge-shaped bone with a broad anteroproximal section tapering to a narrow posterior apex, wedged between the operculum and preoperculum. The operculum (6.15, 6.16, 6.18) is a long, parallelagram-shaped bone of similar proportions to that *Howqualepis* and more acutely angled than the operculae of congeneric forms. Linear ornamentation is predominantly rostrocaudal except for anterior ridges that align against the anteroventral margin. The rectangular suboperculum (Fig. 6.15, 6.18) is slightly less than half the size of the operculum. It is more elongate than in congeners and is more similar to that of *Mimipiscis* with a curved posterior margin and a pointed anterodorsal process. Ornament consists of short ridges and tubercles. More than 10 branchiostegal rays (Fig 6.15, 6.16) are present, becoming increasingly slender anteriorly with the 1st bone below the suboperculum being twice as thick as the next in the series. The lateral gulars are rectangular and more the thrice the length of the narrow median gular. Ornamentation on the ventral gular elements consists predominantly of short ridges.

6.6.6 Pectoral girdle

The pectoral girdle (Fig. 6.15, 6.18) consists of paired cleithra, clavicles, supracleithra, post-temporals and postcleithra. The pectoral endoskeletal anatomy of the holotype was described by Jessen (1968). The large cleithrum is nearly twice as tall as its maximum length and was probably articulated in a near-vertical position. It tapers dorsally to an acute tip overlain by the supracleithrum while the embayment for the pectoral fin was moderately deep, of similar shape to that of *M. nitida* and *Howqualepis* (Long, 1988) and less acutely angled than that of *M. durgaringa*. Clavicles are stout and triangular while an interclavicle has not been identified. Ornament on the cleithra and clavicles is incompletely preserved, with rostrocaudally-directed ridges on the ventral surface and near the anterior margin of the

cleithrum while straight Post-temporals are parallelagrams with medial and lateral margins of similar length, unlike those of *M. nitida* which taper medially. Rostrocaudal ornament of short-to-medium ridges are deflected posterolaterally near the lateral margins.

The supracleithrum (Fig. 6.15, 6.18) is similar in shape, relative size and path of the lateral-line canal to that of congeneric forms. Linear ornament of short-to-medium ridges is oriented posteroventrally over most of the surface, becoming short and rostrocaudal near the posterodorsal margin. A small, triangular presupracleithrum (Fig. 6.15, 6.18) is wedged between the supracleithrum, the post-temporal and the operculum. A crescent-shaped postcleithrum is visible on the holotype (Fig 6.15), distinguishable from the adjacent scales by being 50% larger and ornamented with posteroventral instead of horizontal ridges.

6.6.7 Body and fins

The largest known specimens (including the holotype) are incomplete and have an estimated standard length of about 20cm. Body is fusiform, with the head occupying 30-35% of standard body length (Fig 6.18, 6.19). Specimens of *Moythomasia nitida* with a similar skull-size are immediately distinguishable by their much shorter, more robust bodies (Fig. 6.3). The body depth is 25-30% of standard body length, giving the *M. lineata* a more slender appearance.

The radial skeleton of the pectoral fin consists of a perforated propterygium followed by five elongate radials and a large metapterygium supporting three or four preaxial radials (Jessen 1968, Plate 15-16). There are more than 26 primary lepidotrichia on the triangular pectoral fin (Fig. 6.15). Paired-fringing fulcra present on the leading edge of all fin-lobes composed of lepidotrichia.

Poorly preserved small pelvic fins are visible on a few smaller specimens. It is a short-based fin with at least 20 primary lepidotrichia, located at the approximate mid-point between the pectoral and anal fins. The triangular dorsal fin possesses 40-43 fin rays and lies on the posterior half of the body, slightly anterior to the anal fin as in *M. durgaringa* but unlike *M. nitida* where these two fins are directly opposite one another. The anal fin has over 30 lepidotrichia and appears more markedly pointed than that of *M. nitida.* The heterocercal caudal fin has a deep posterior cleft between the longer upper and the shorter triangular lower lobe. It contains more than 80 closely set lepidotrichia, the anteriormost 6-8 of which are unsegmented, the remainder of which are extensively jointed. The proximal first segments on the upper lobe and 1-3 segments on the lower hypochordal lobe are elongated to more than three times the length of the following square segments in the series, extending to a zone of fine-branching at the distal fringe.

Between 60-64 transverse rows of scales are present from the occipit to the inversion line at the caudal base. Median ridge scales are present from the from the occipit to the anterior of the dorsal fin, from the dorsal fin to the posterior tip of the notochordal mass of the caudal fin, and from the posterior of the anal fin to the lower hypochordal lobe.

The scales of *Moythomasia lineata* are of similar shape to those of *M. durgaringa* and *M. nitida* but with strikingly different ornamentation (Fig, 6.20, Jessen 1968, Plate 15.3) Scales over the anterior 2/3 of the body have well-developed peg-and-socket articulation. As in *M. perforata*, the scales are ornamented with well-separated linear ridges that run rostrocaudally from the anterior margin of the free field to terminate in a series of posterior serrations (more than 12 in anterior flank scales of the holotype). The ridges are separate along their entire

length with no anastomosing as in *M. durgaringa* and *M. nitida*. There are no punctae or pores present.

The scales of *M. lineata* differ from those of *M. striata* (Fig 6.2) in the following characteristics. The scales of *M. lineata* have narrow depressed fields, accounting for less than 20% of the rostrocaudal length of the scale whereas the depressed fields of *M. striata* are much broader, comprising at least 25% of the length. The scales of *M. striata* often have an extremely large, dorsally directed rostro-caudal process that may exceed the height of the peg. The rostro-caudal process of *M. lineata* is much smaller, anterodorsally directed and is not significantly elevated above the dorsal margin of the free field. The many scales of *M. striata* often possess short ridges that run diagonally from the dorsal to posterior margin of the free field. This is not visible in any scales of *M. lineata* where the dorsalmost ridges run parallel to the dorsal margin of the free field.

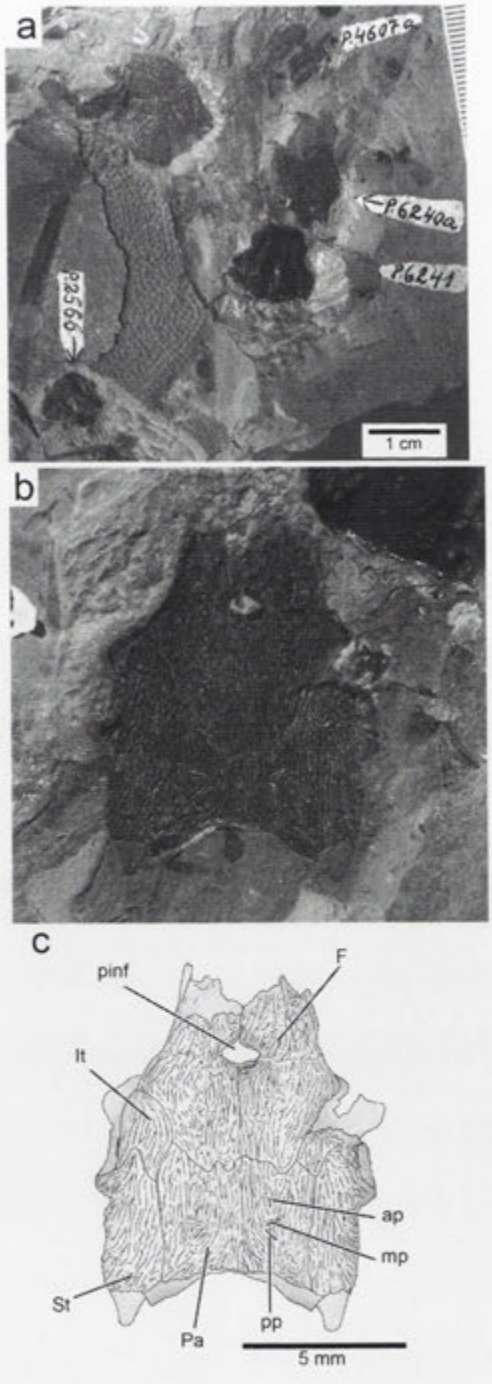


Figure 6.1
Moythomasia perforata (Gross). **a**. Detail of block containing skull roofs of NRM P.6240a (holotype) and P.4607a. Also in the block are skull roofs of the sarcopterygians *Latvius grewingki* (P.6241) and *Strunius rolandi* (P.2566) as well as the plates of several antiarch placoderms. **b.** Photograph and **c.** interpretive diagram of the holotype skull roof of *M. perforata* in dorsal view.

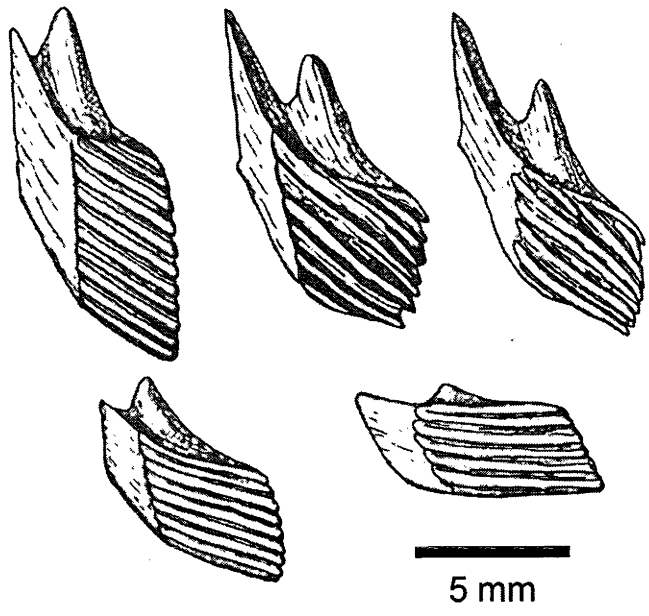


Figure 6.2
Moythomasia striata Gross. Drawings of isolated scales from Gross (1953).

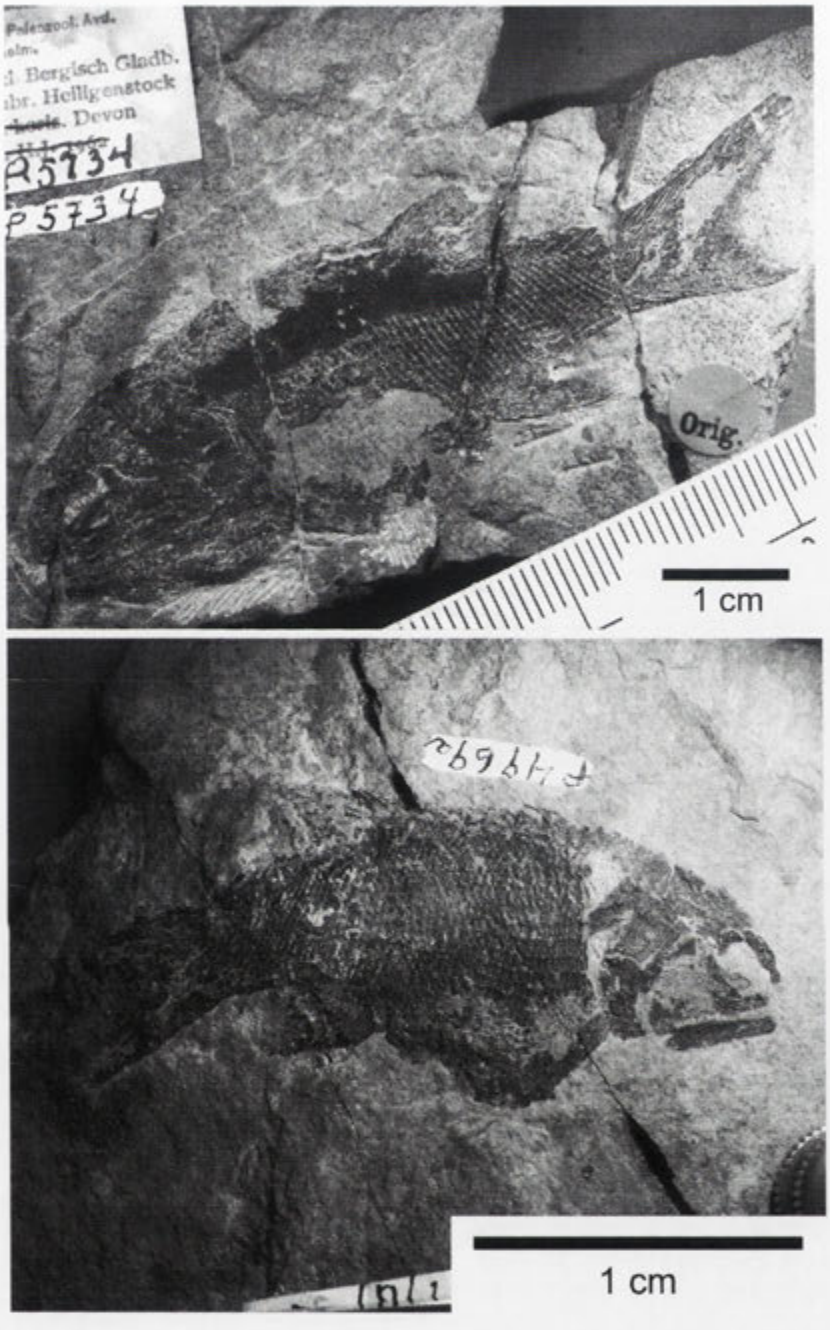


Figure 6.3
Moythomasia nitida Gross. Photographs of specimens **a.** NRM P.5734 in left lateral and **b.** NRM P.4969a in right lateral view.

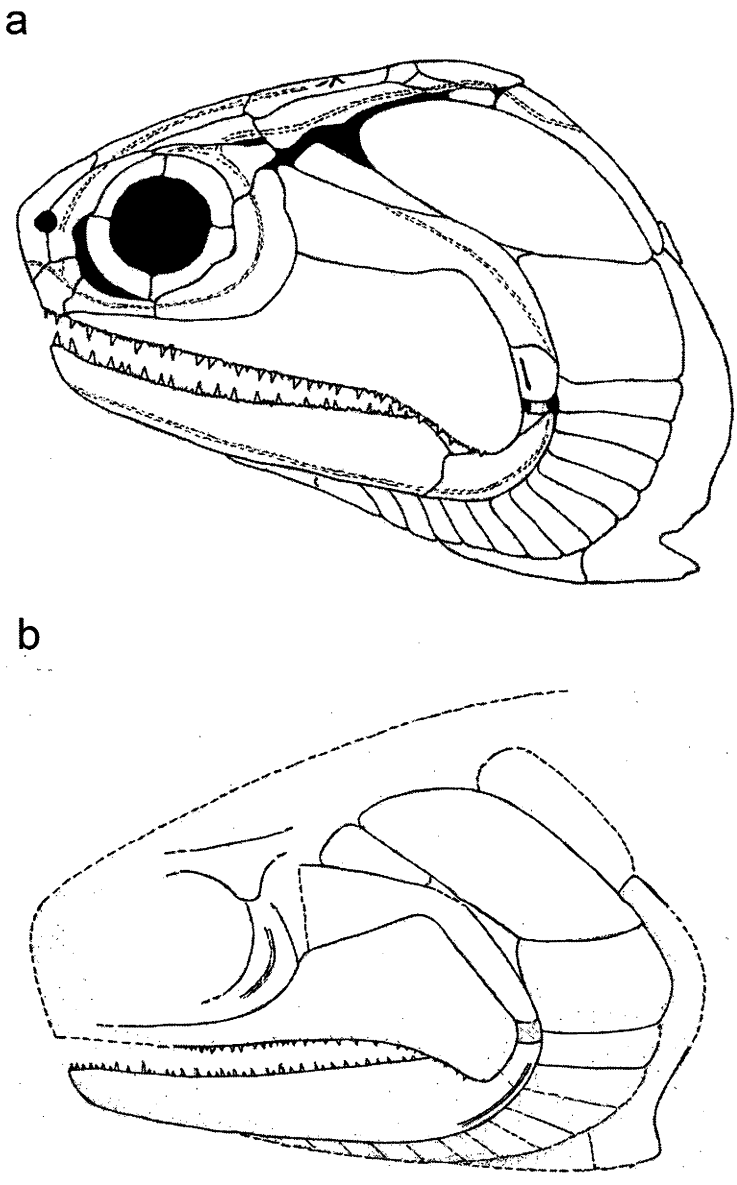


Figure 6.4
a. *Moythomasia durgaringa* Gardiner and Bartram. Reconstruction of the skull in lateral view as presented by Gardiner (1984: Fig.103). **b.** Reconstruction of the skull of *Moythomasia lineata* sp.nov (= *M.* cf. *striata*) from Jessen (1968:Fig. 5A). Not depicted to scale.

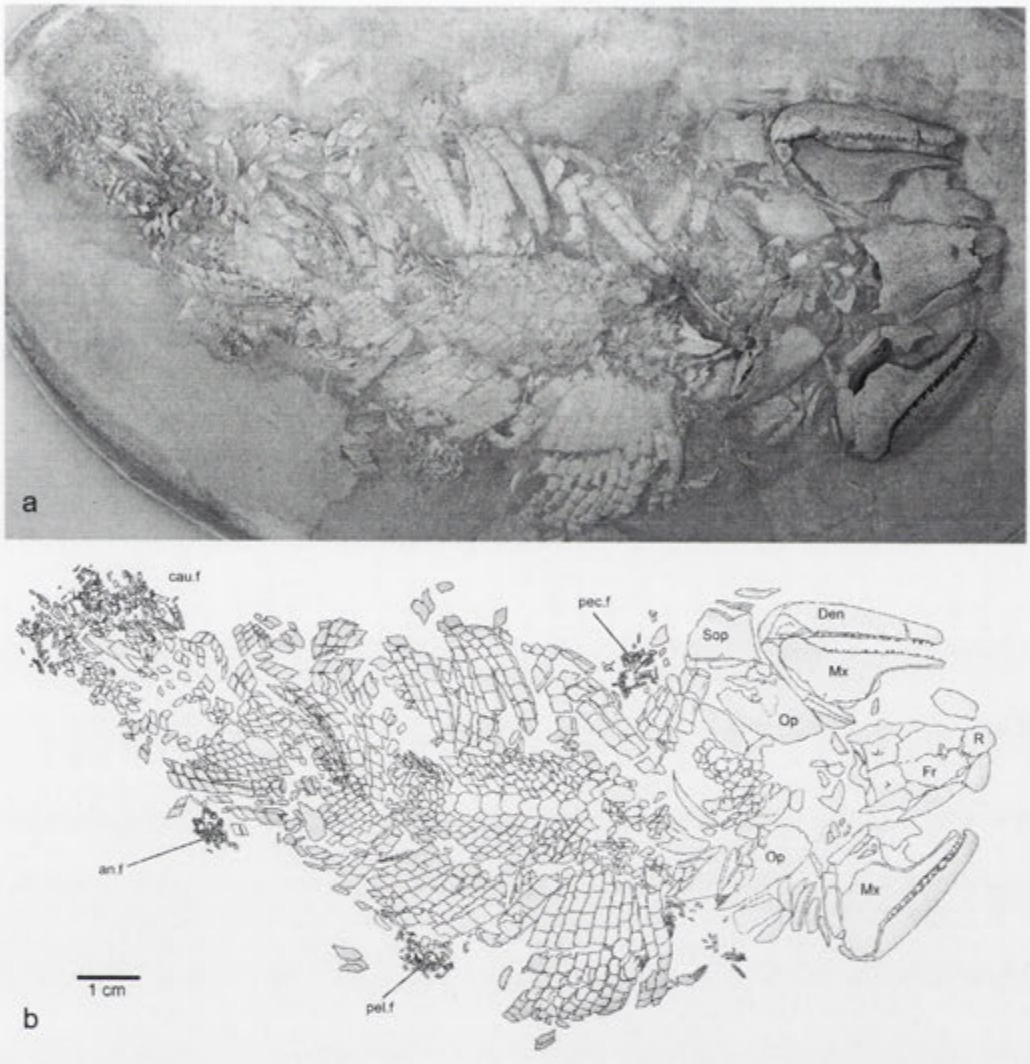


Figure 6.5
Moythomasia durgaringa Gardiner and Bartram. **a.** Photograph and **b.** reconstruction of MV P.221788a in dorsal view.

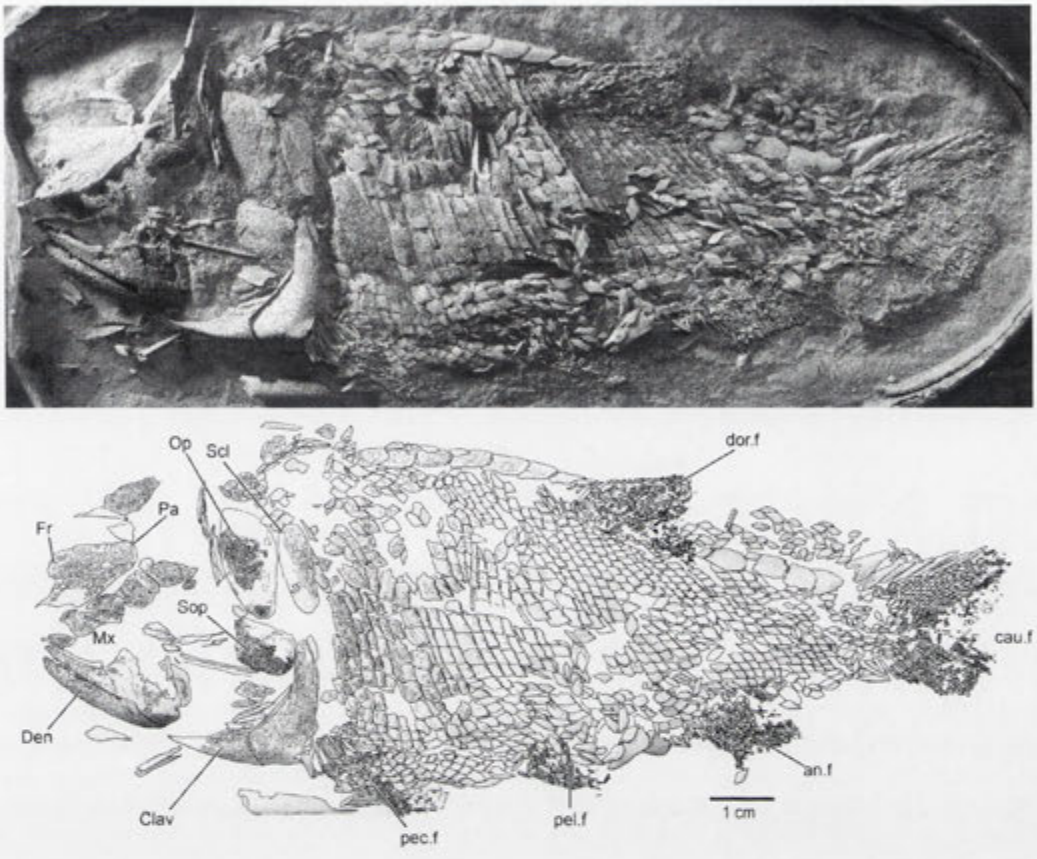


Figure 6.6
Moythomasia durgaringa Gardiner and Bartram. **a.** Photograph and **b.** reconstruction of MV P.221789a in left lateral view.

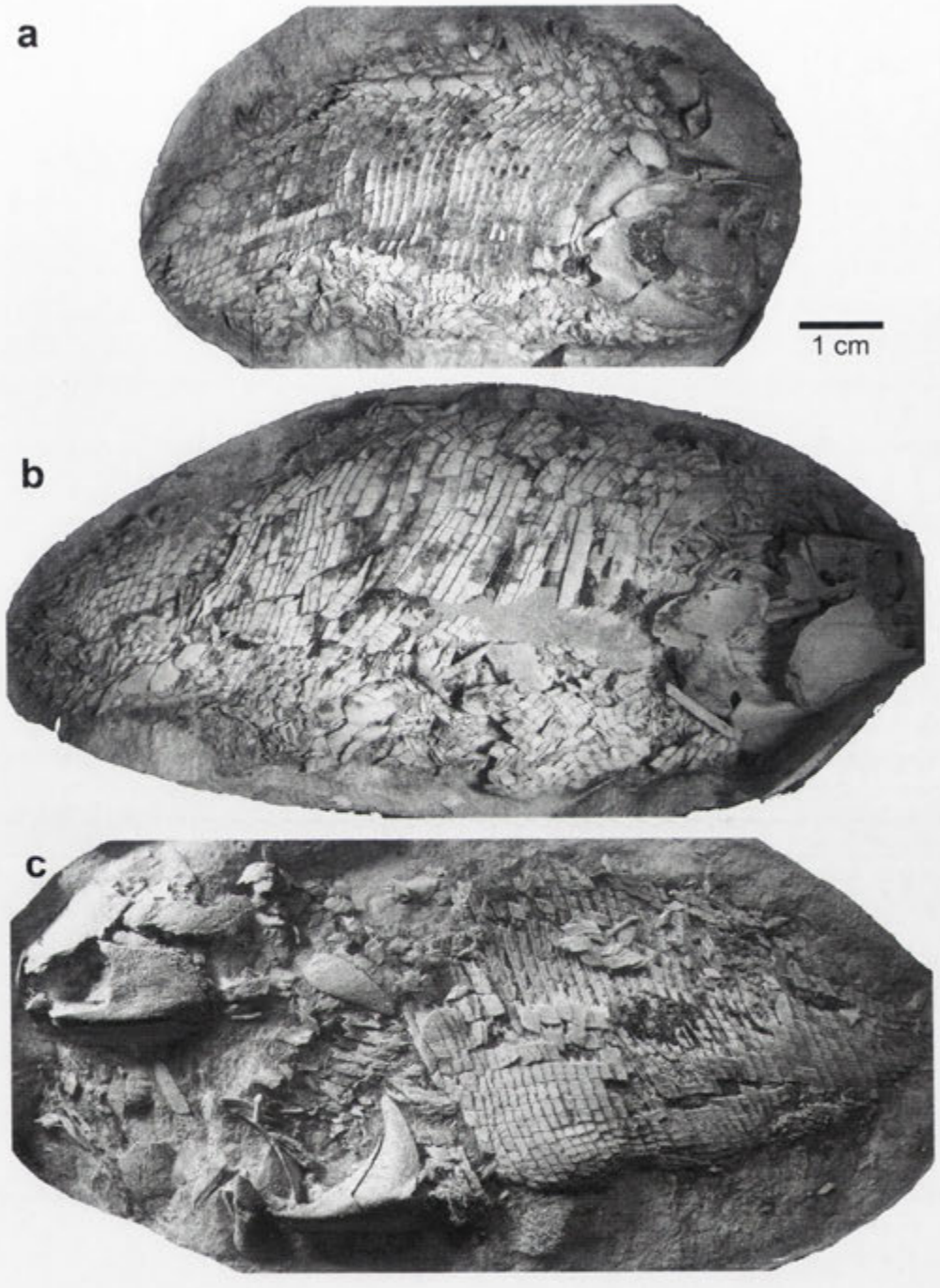


Figure 6.7
Moythomasia durgaringa Gardiner and Bartram. Photographs of **a.** MV P. 221799b, **b.** MV P.227029a and **c.** MV P.221790a.

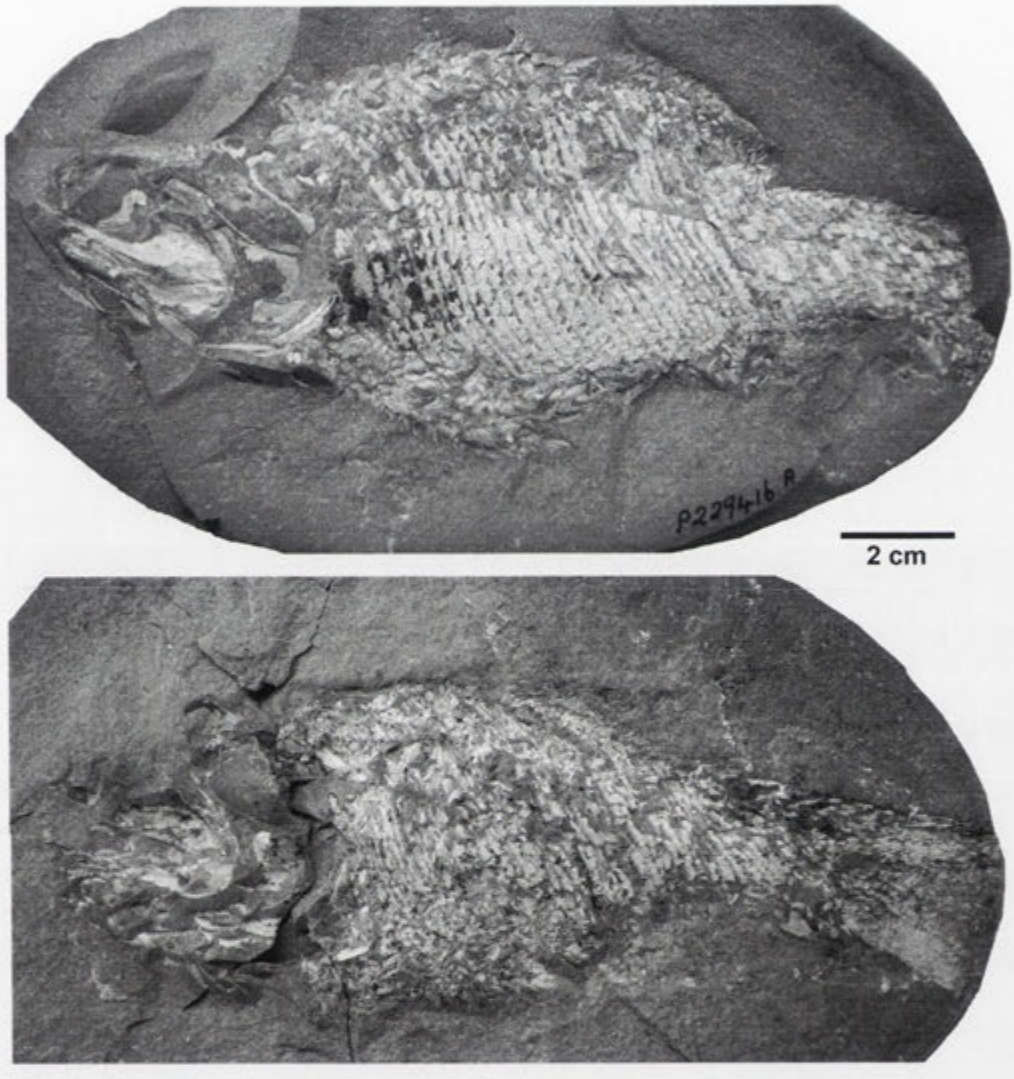


Figure 6.8
Moythomasia durgaringa Gardiner and Bartram. Photographs of unprepared specimens, still within calcareous concretions, collected at Paddy's Valley during the 2008 Museum Victoria expedition to the Gogo Formation. **a.** MV P. 229416a, **b.** MV P.229420b

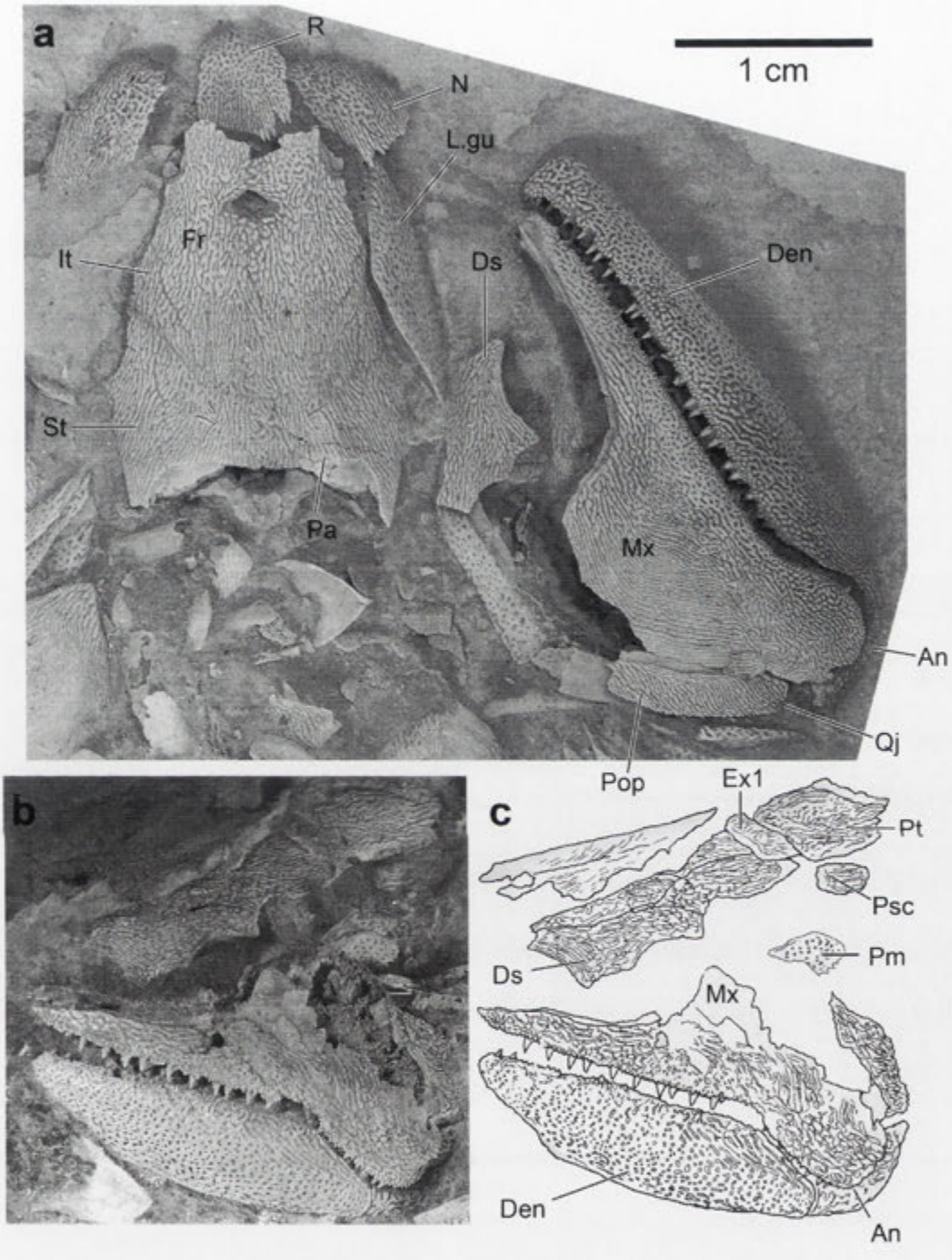


Figure 6.9
Moythomasia durgaringa Gardiner and Bartram. **a.** Photograph of the head region of MV P.221788a. **b.** Photograph and **c.** reconstruction of the head region of MV P.221789a.

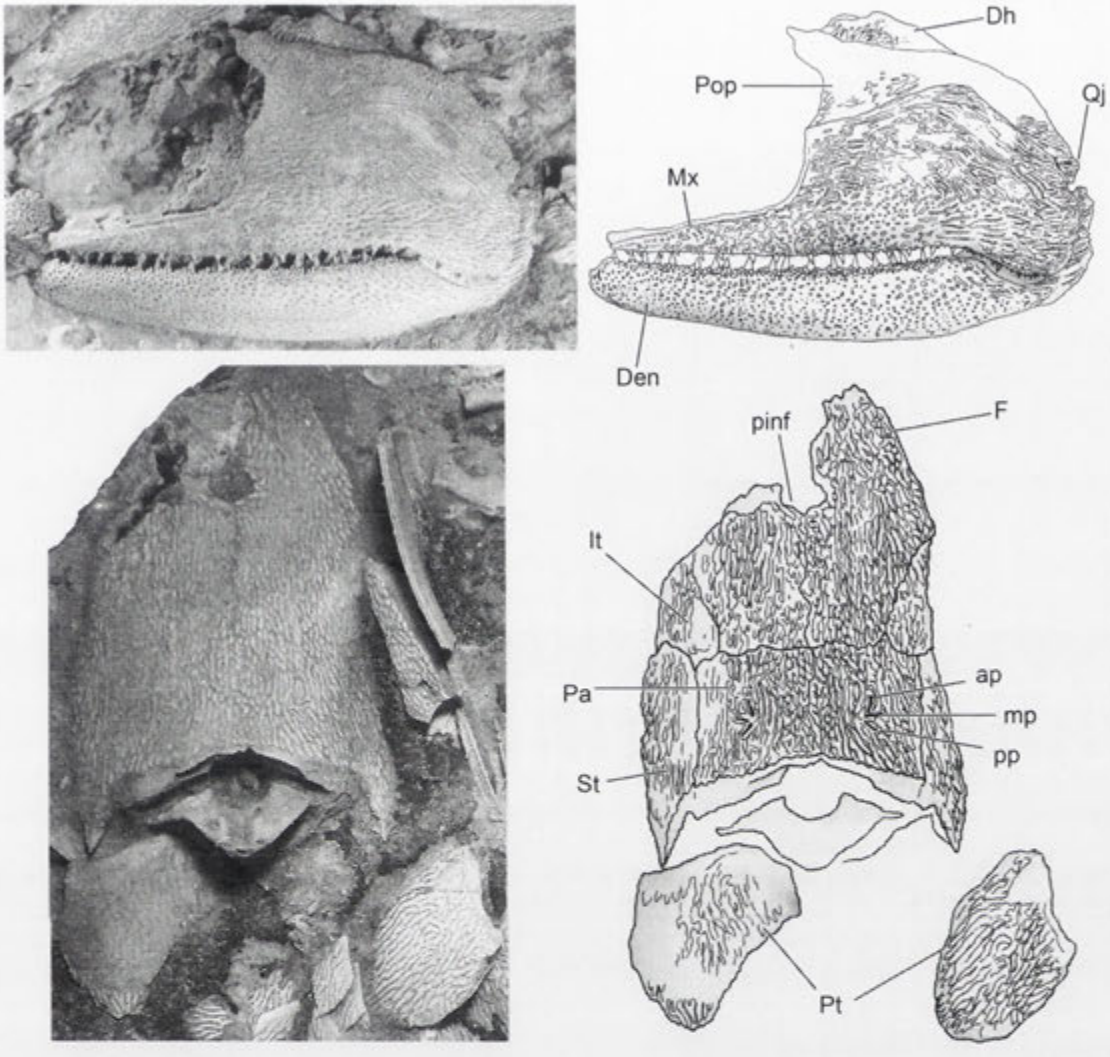


Figure 6.10
Moythomasia durgaringa Gardiner and Bartram. **a.** Photograph and **b.** reconstruction of the cheek and lower jaw of MV P. 221790a. **c.** Photograph and **d.** reconstruction of the skull roof of MV P. 221799b.

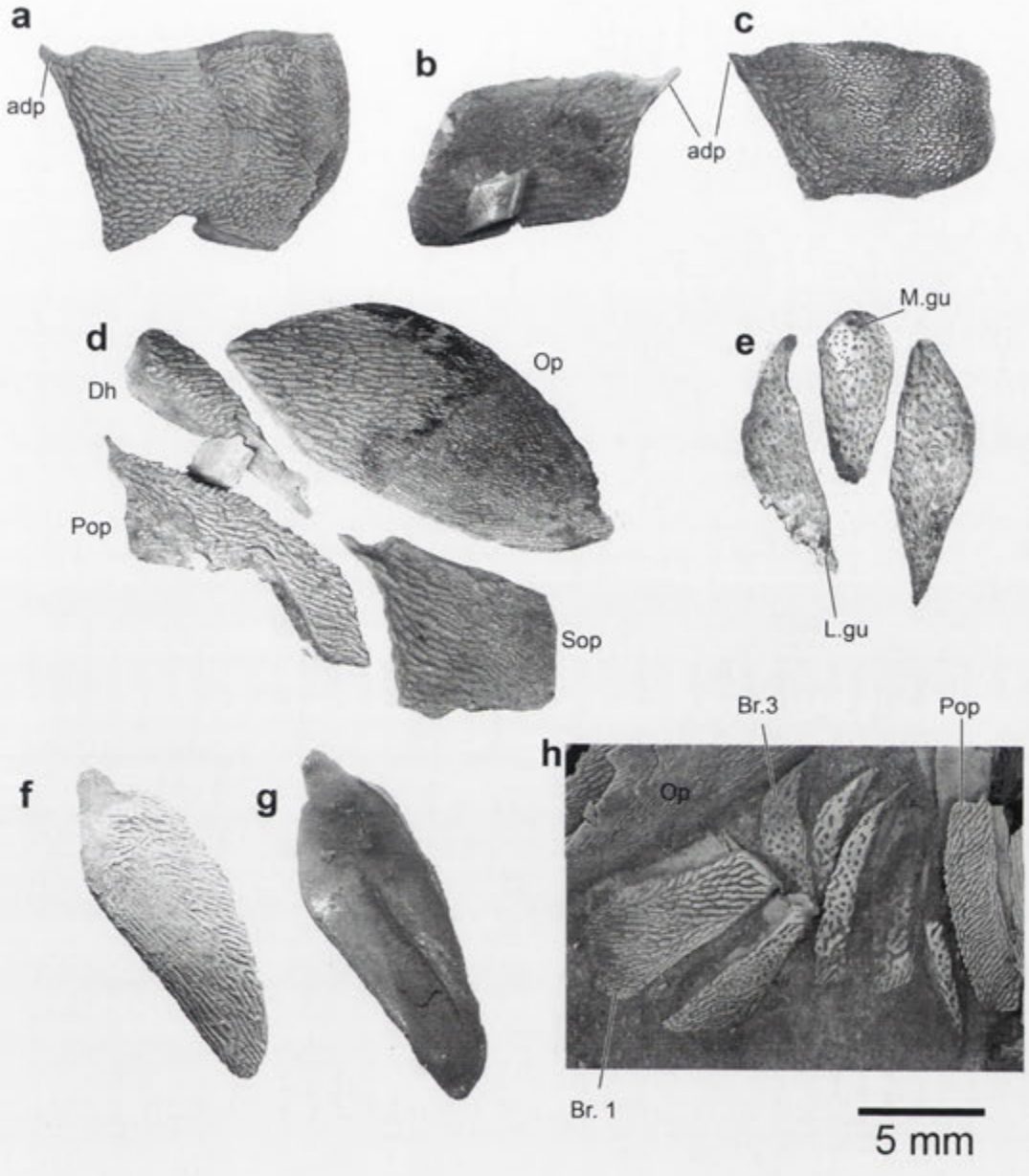


Figure 6.11
Moythomasia durgaringa Gardiner and Bartram. **a-c.** Photographs of suboperculae in lateral view. **a.** MV P.221788, left subopercular. **b.** BMNH P.53218b, right subopercular. **c.** MV P.221799, left subopercular. **d.** Left operculum, subopercular, dermohyal and preopercular from the right side of BMNH P.53218a. This is the same specimen as Fig.10b. **e.** Gular bones of BMNH P.53217 in ventral view. **f.** Left supracleithrum of MV P.221789 in lateral view. **g.** Right supracleithrum of BMNH P.53221 in visceral view. **h.** Branchiostegal rays of MV P.221788.

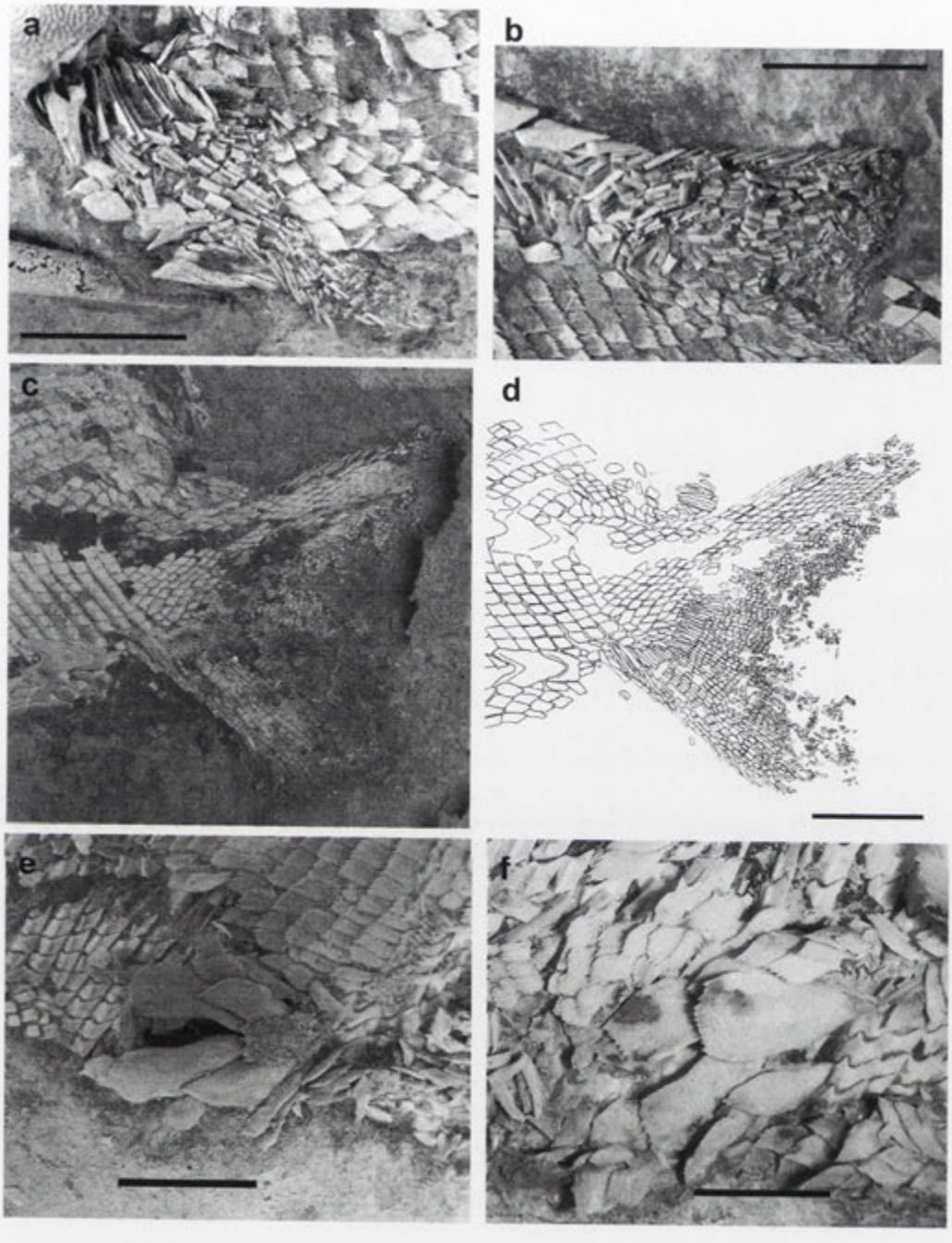


Figure 6.12
Moythomasia durgaringa Gardiner and Bartram. **a.** Left pectoral fin and **b.** dorsal fin of MV P.221789. **c.** Photograph and **b.** reconstruction of the caudal fin of BMNH P.56478. **e-f** Paired ventral scutes immediately anterior to the anal fin of **e.** MV P.221790 and **f.** MV P.227029. Scale bars = 1 cm.

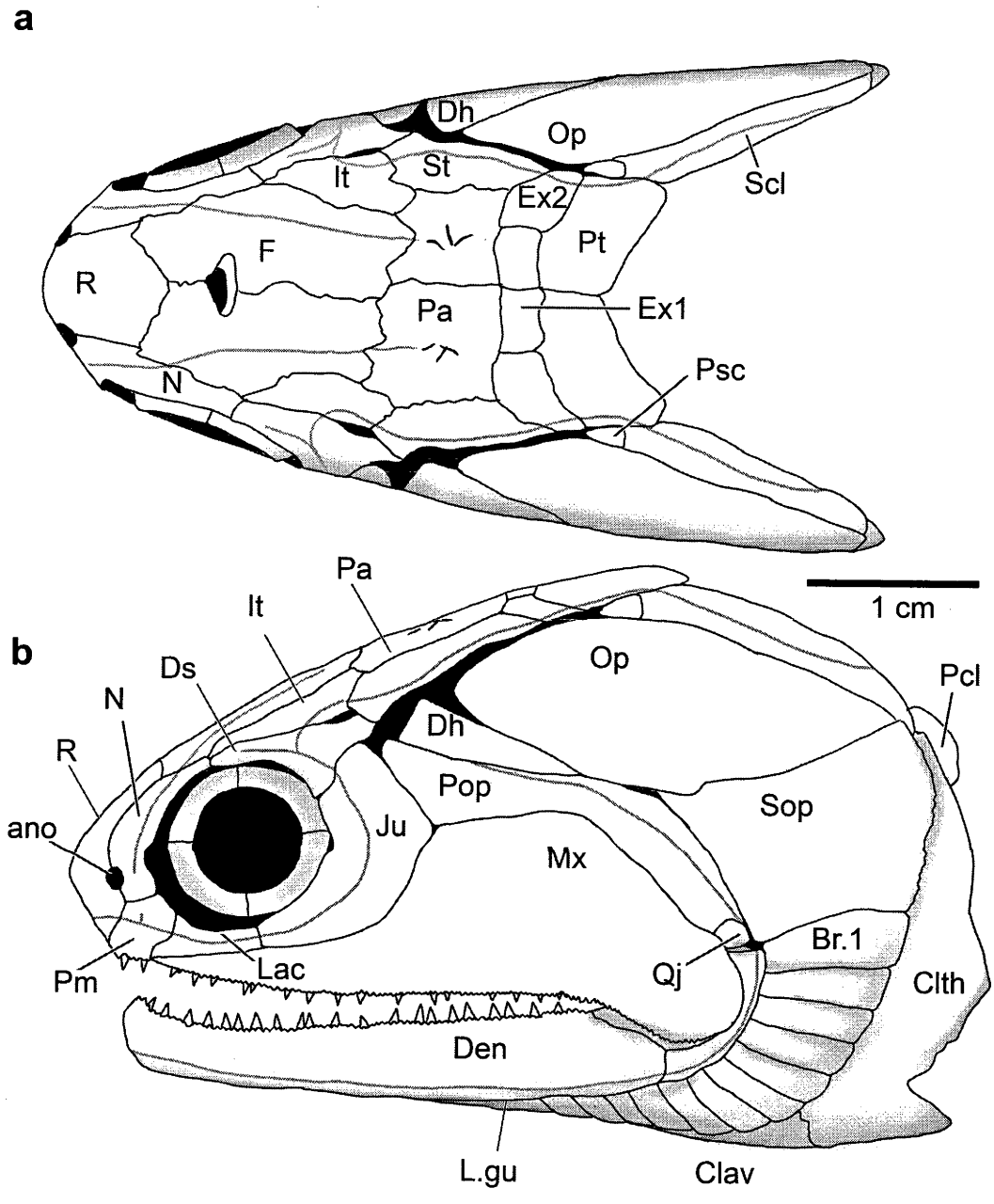


Figure 6.13
Moythomasia durgaringa Gardiner and Bartram. Reconstruction of the skull in **a.** dorsal and **b.** lateral views.

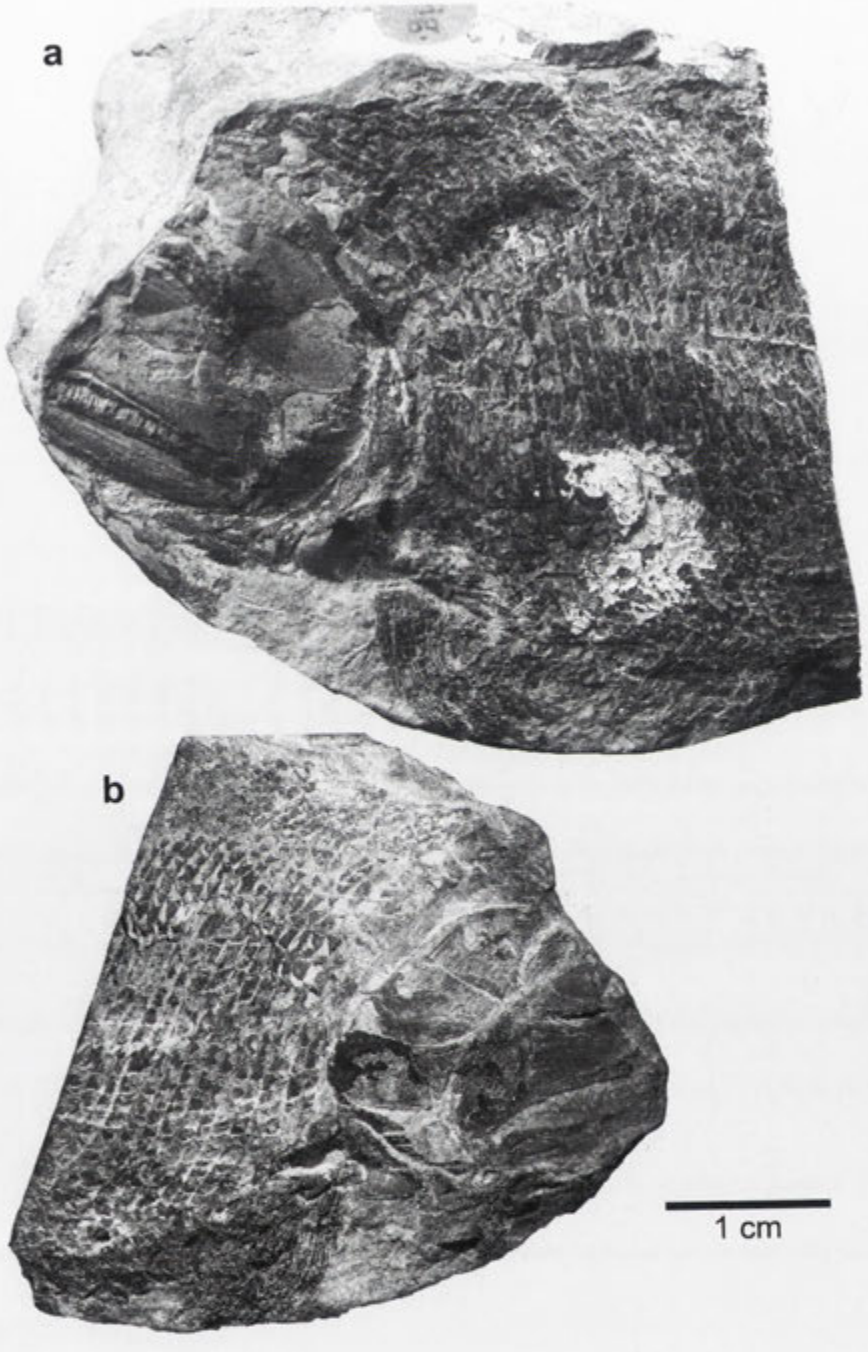


Figure 6.14
Moythomasia lineata sp. nov. Photographs of holotype specimen.**a.** NRM P 4848a and **b.** P 4848b.

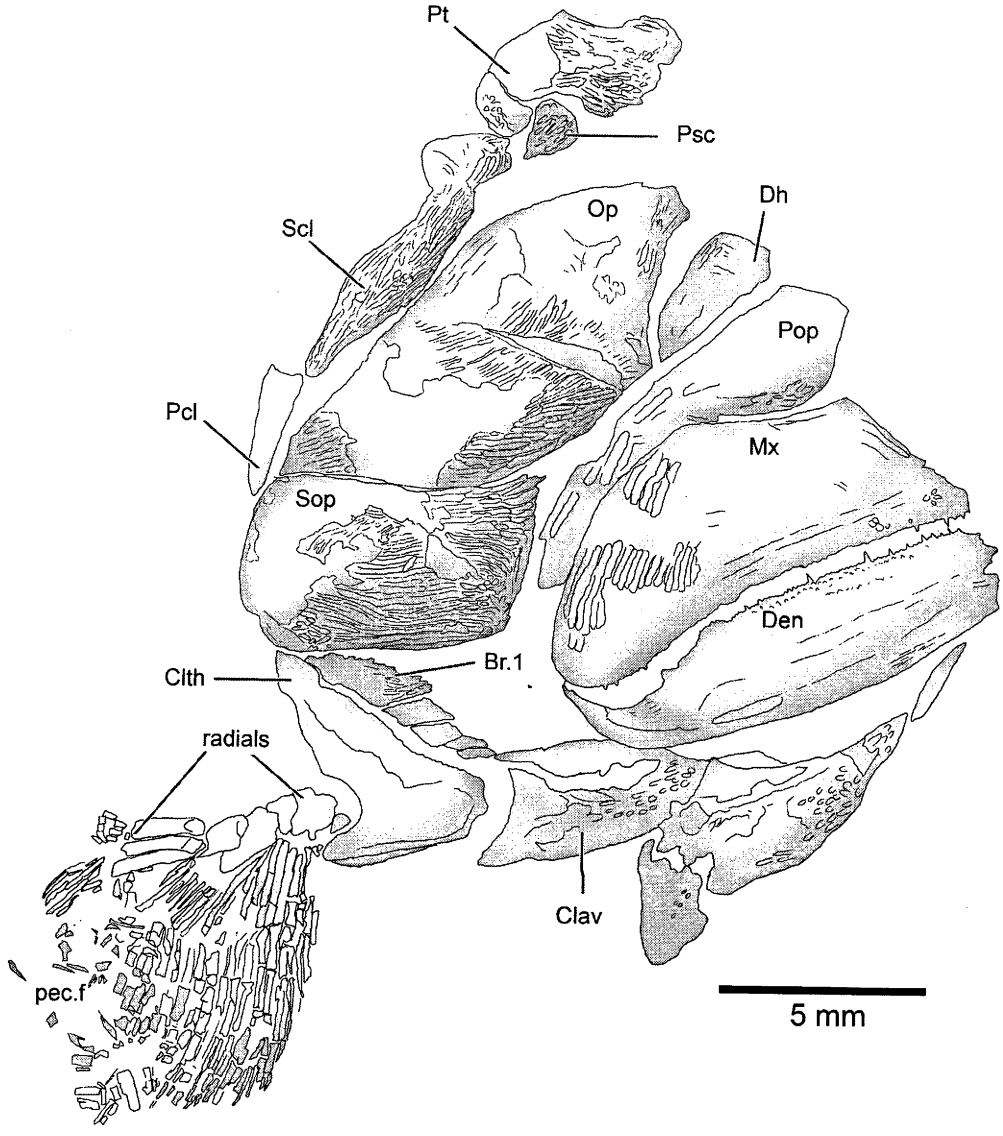


Figure 6.15
Moythomasia lineata sp. nov. Reconstruction of skull, pectoral girdle and pectoral fin of holotype (NRM P 4848b).

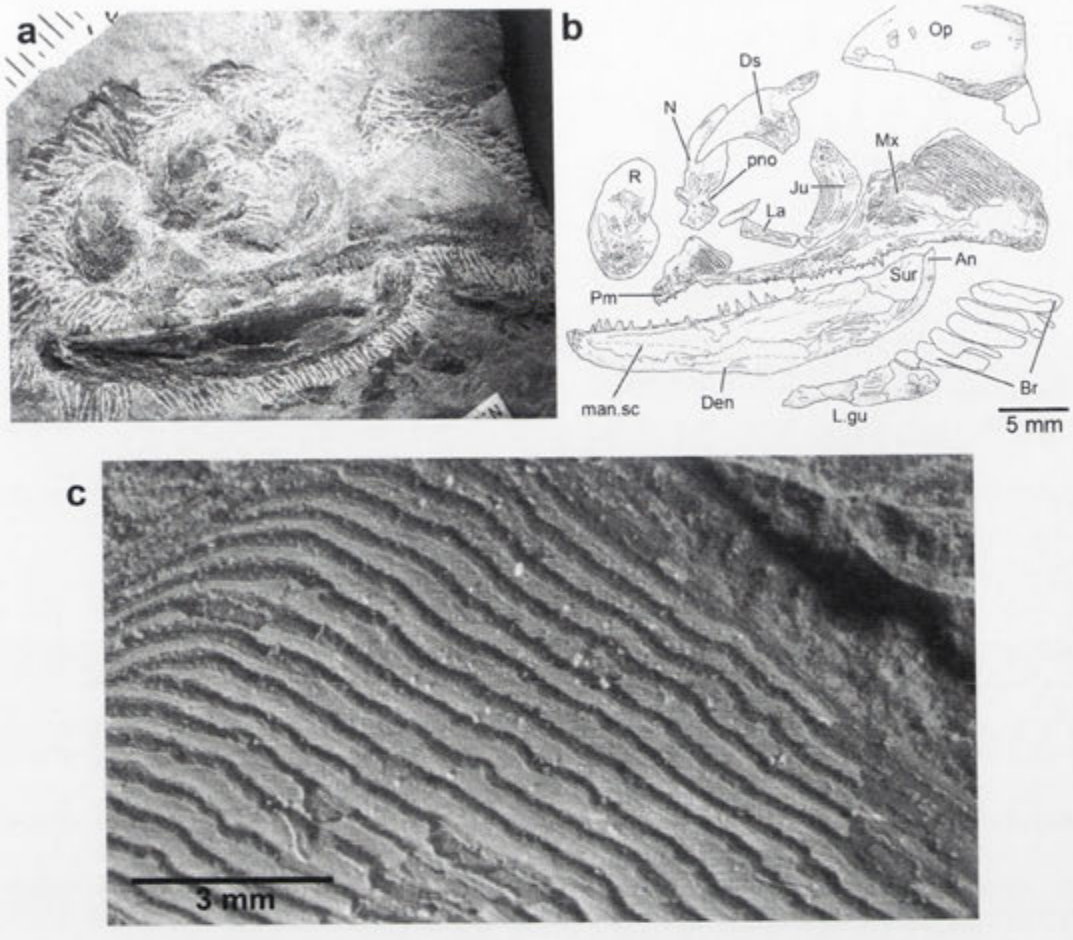


Figure 6.16
Moythomasia lineata sp. nov. **a.** Photograph and **b.** reconstruction of the partial skull and lower jaw of NRM P 4846. **c.** Detail of ornamentation on the maxilla.

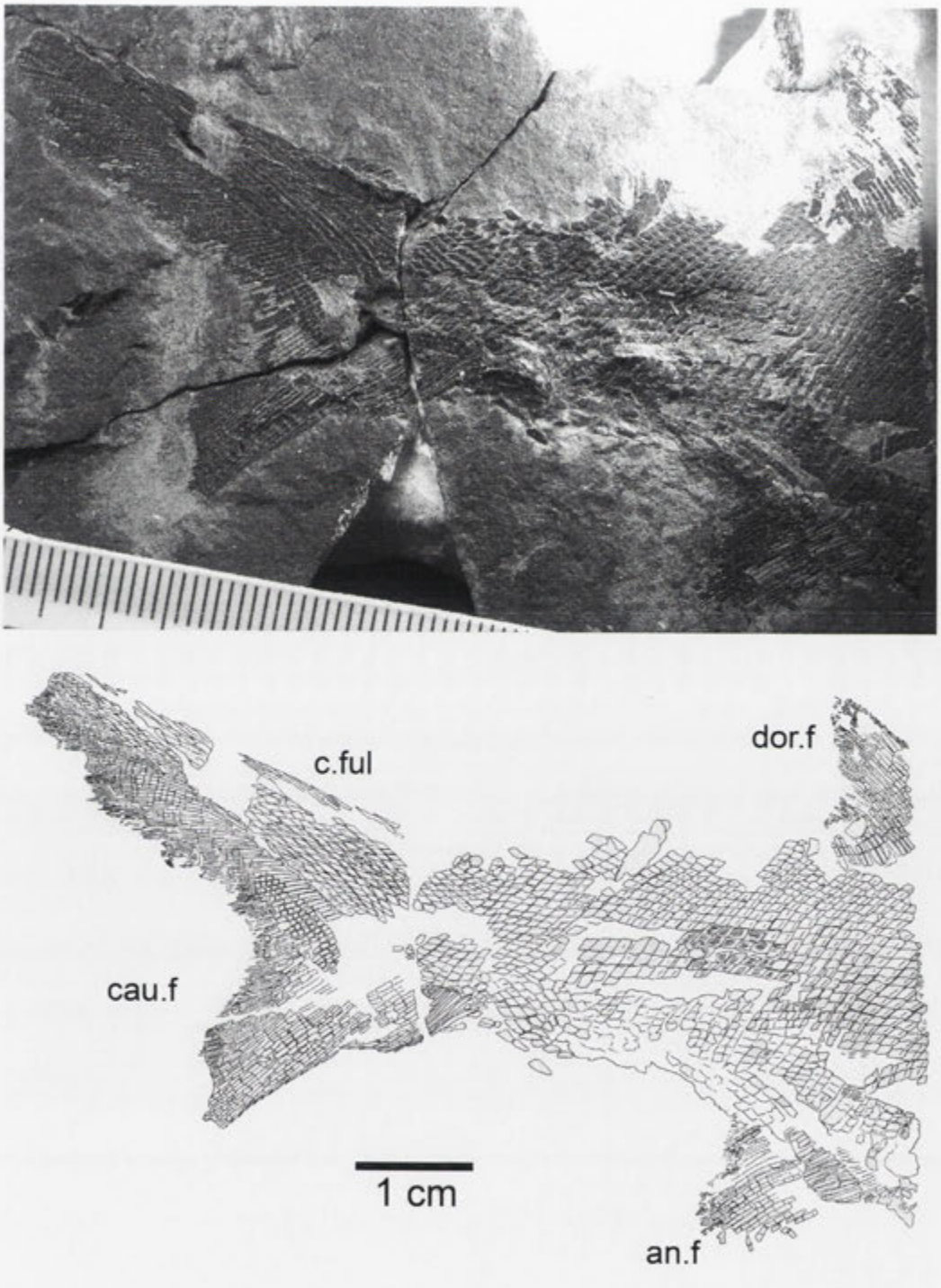


Figure 6.17
Moythomasia lineata sp. nov. **a.** Photograph and **b.** reconstruction of NRM P 5293, representing the posterior half of the fish.

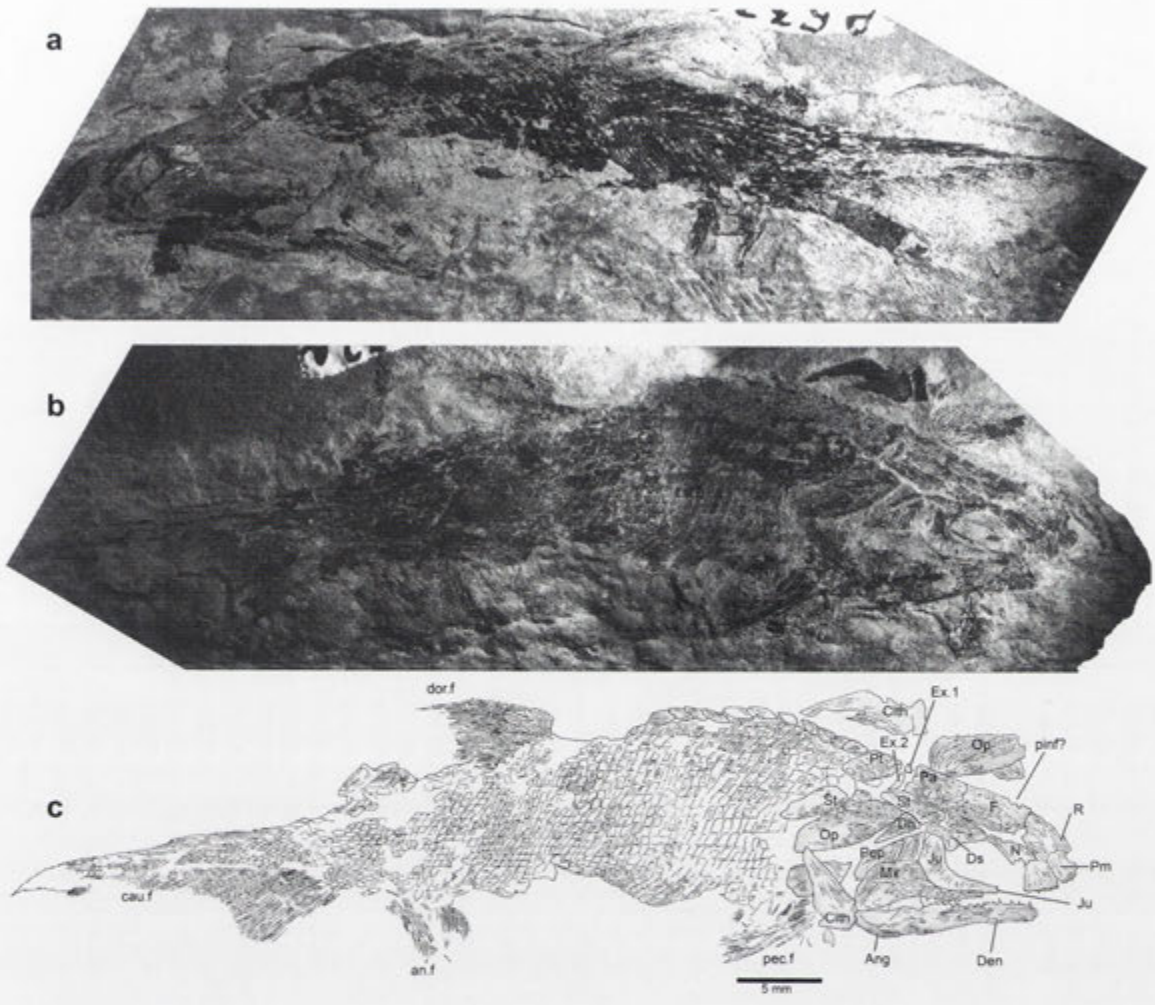


Figure 6.18
Moythomasia lineata sp. nov. Complete small specimen. **a.** Photograph of NRM P 5332b. **b.** Photograph and **c.** reconstruction of NRM P 5332a.

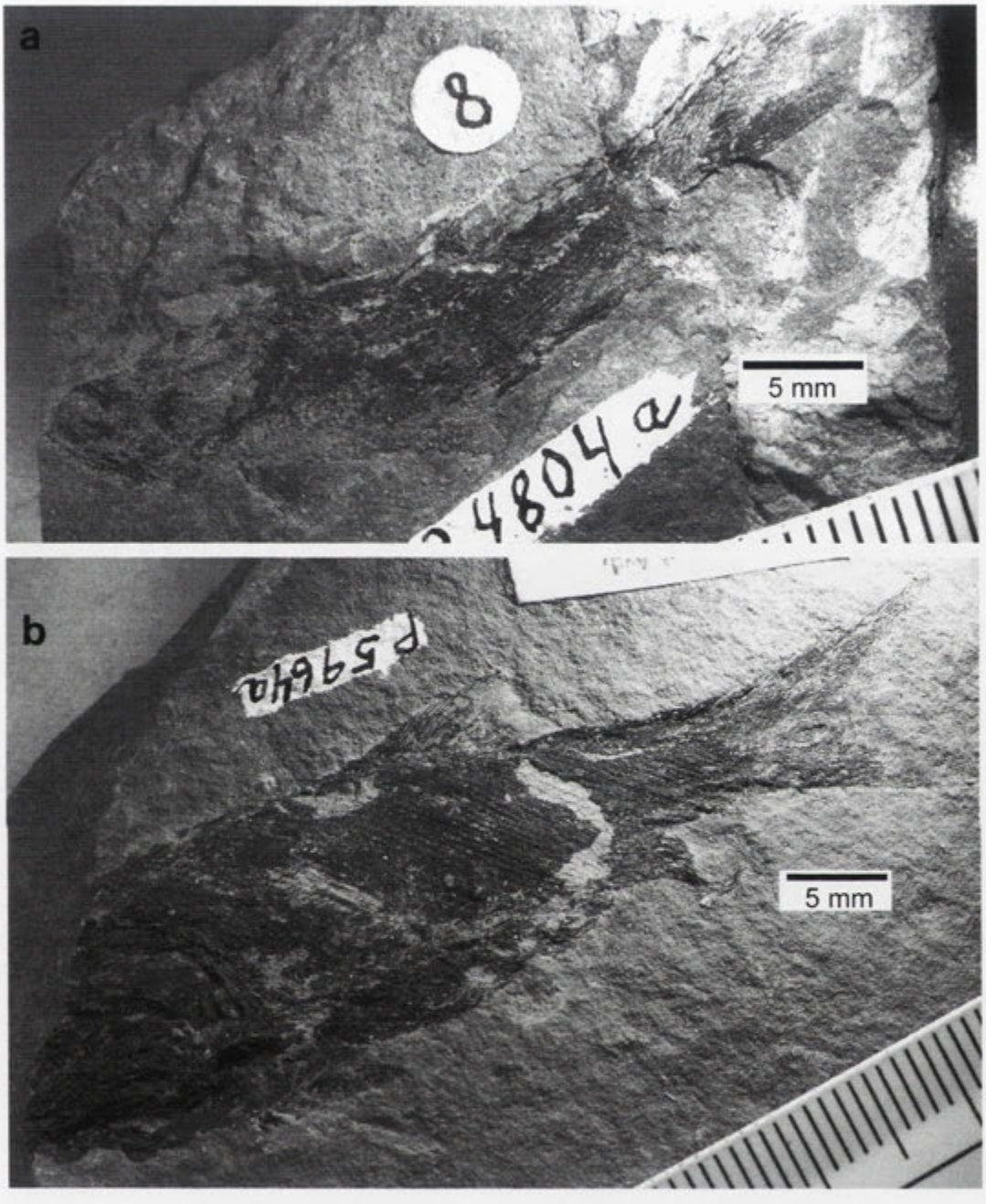


Figure 6.19
Moythomasia lineata sp. nov. Photographs of complete small specimens in left lateral view. **a.** NRM P 4804a and **b.** P 5964a. Note more gracile body form and more posterior position on the anal fin compared to *M. nitida* (Fig. 6.2).

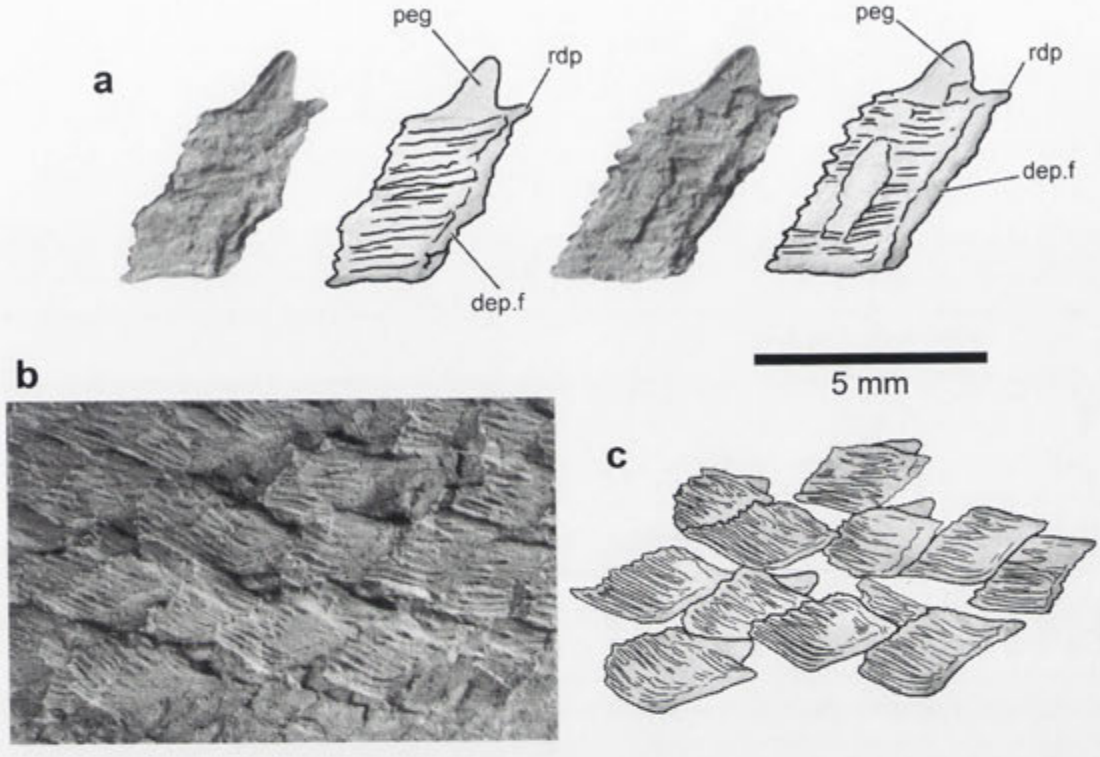


Figure 6.20
Moythomasia lineata sp. nov. **a.** Photographs alongside reconstructions of two separate anterior flank scales from the holotype. **b.** Photograph and **c.** reconstruction of mid-body flank scales at a level immediately anterior to the dorsal fin of NRM P 4085b.

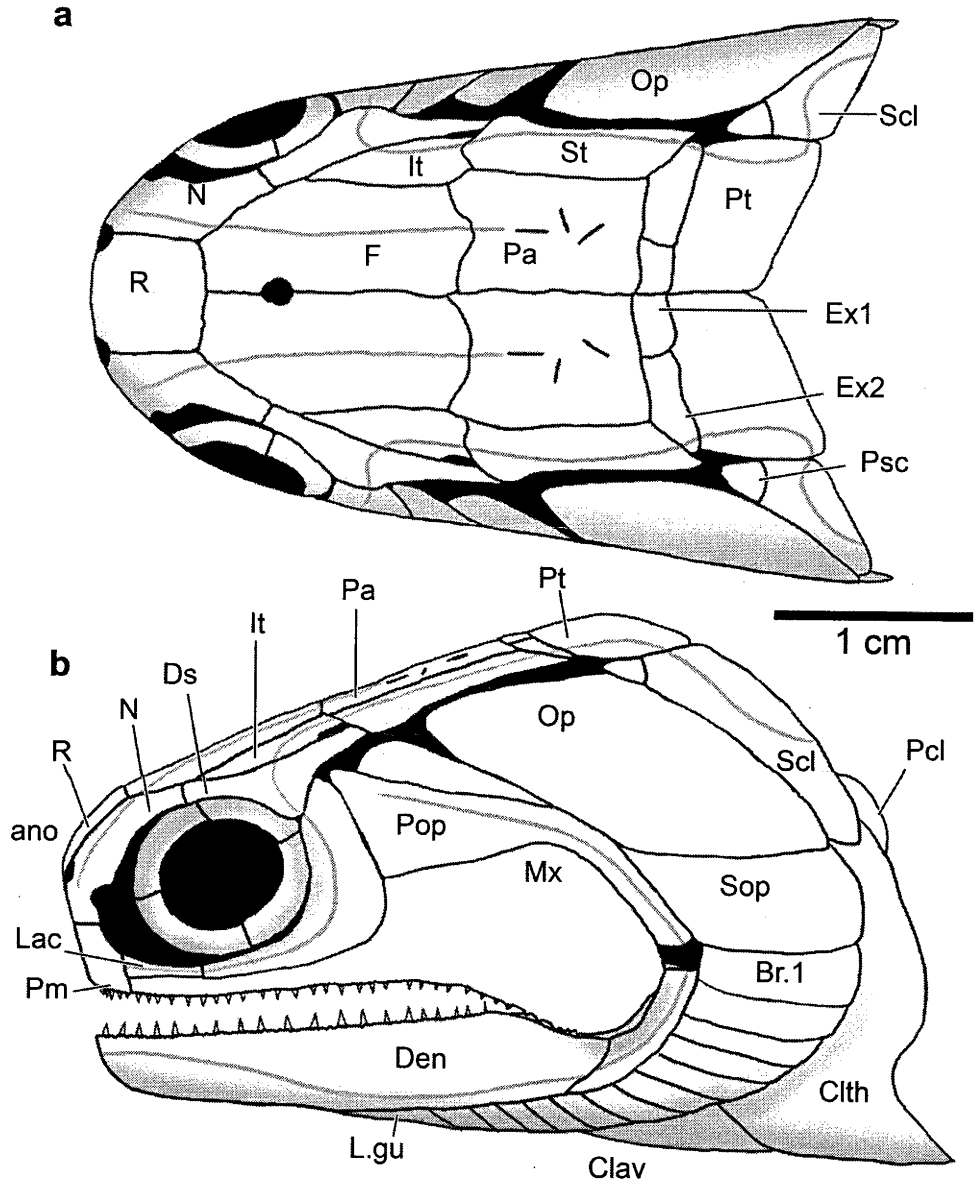


Figure 6.21
Moythomasia lineata sp. nov. Reconstruction of the head in **a.** dorsal and **b.** lateral view.

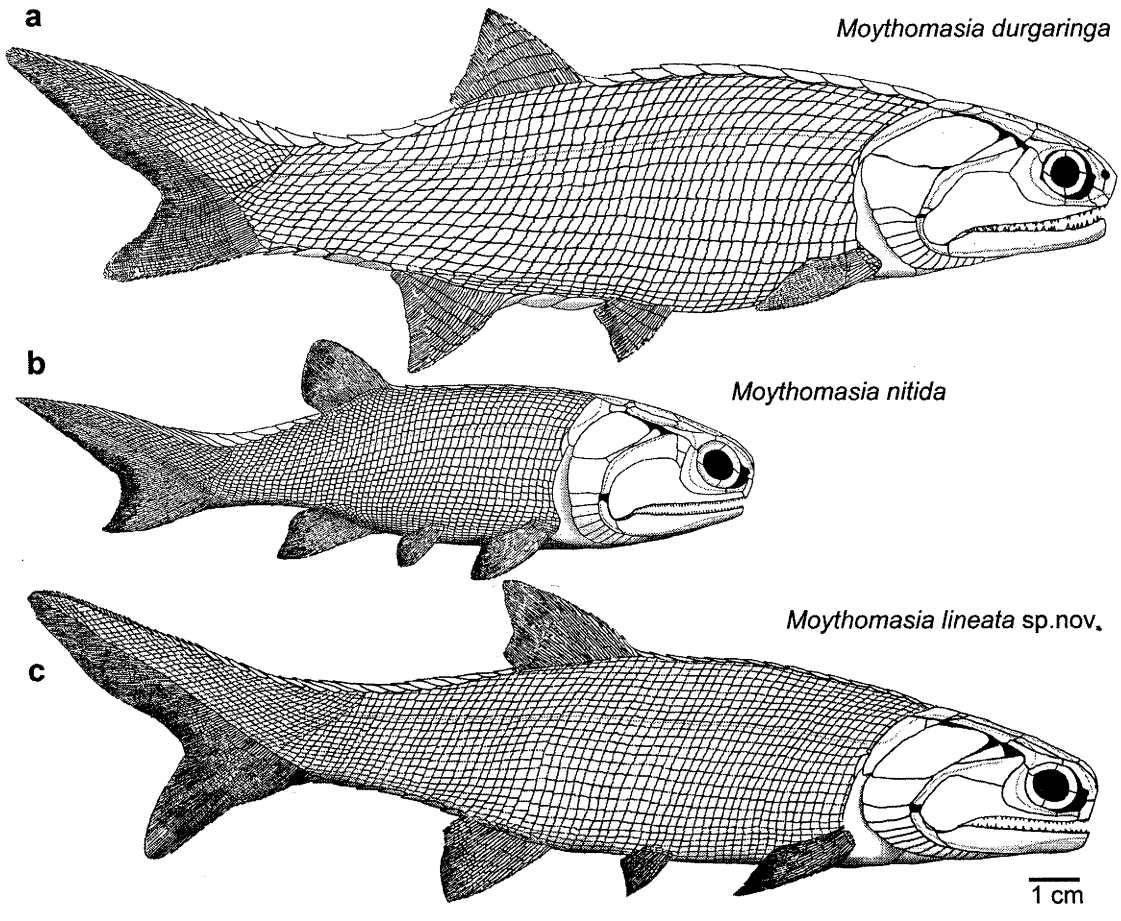


Figure 6.22
Lateral full-body reconstructions of all *Moythomasia* spp. known from complete remains. **a.** *M. durgaringa* Gardiner and Bartram. **b.** *M. nitida* Gross. **c.** *M. lineata* sp. nov.

Chapter 7. A preliminary description of a new genus and species of basal actinopterygian from the Late Devonian Gogo Formation of Western Australia.

7.0 Preamble

This chapter represents an as yet unsubmitted manuscript, with myself as sole author, of a new genus the basal actinopterygian from the Gogo Formation.

7.1 Abstract

This chapter presents a preliminary description of a new basal actinopterygian from the Gogo Formation of Western Australia. The new fish, *Pickeringia acanthophilus* gen. et. sp. nov., is tentatively placed in the Mimiidae based on the apparent lack of a surangular and the presence of an anterolateral flange on the supratemporal that contribute to the spiracular opening. *Pickeringia* gen. nov. differs from all other Devonian actinopterygians in the possession of extensive spinose ornamentation on the skull, pectoral girdle, scales and lepidotrichia. A partial neurocranium is similar to that of previously described actinopterygians from the Gogo, but differs in its possession of very large vestibular fontanelles and large paired openings on the floor of the aortic canal.

7.2 Introduction

Successive discoveries since the 1960s have revealed a greater diversity of ray-finned fishes in the Late Devonian (Frasnian) Gogo Formation that any other contemporaneous fauna (Gardiner and Bartram 1977, Gardiner 1984, Choo et al., 2009). In 1990, John Long collected a fossil actinopterygian (WAM 03.6.1) in counterpart from Paddy's Valley. Upon preparation of one-half (WAM 03.6.1a, henceforth referred to as "A-block") of this

specimen by Long at the WA museum in 2003, the fish was revealed to represent a hithero unknown genus and species, including a partial braincase. The specimen was transported to Museum Victoria in 2005 for further examination where the other half ("B-block") was prepared by David Pickering. A preliminary description of the osteology is presented herein. The specimen is sufficiently different from all other basal actinopterygians to require the erection of a new genus. It represents the fourth genus and fifth species of basal actinopterygian from the Gogo Formation.

7.3 Materials and methods

Western Australian Museum (WAM), 03.6.1 is the only representative of this taxon among the available material from the Gogo Formation. One half of the specimen (03.6.1a, Fig 7.3) was prepared by John Long at WAM, including the braincase. The other half (03.6.1b) was prepared by David Pickering at Museum Victoria. All photographs are by the author except for Fig 7.2a by Erich Fitzgerald and Fig.7. by Lucinda Gibson. CT images of the braincase were supplied by Tim Senden at The Australian National University, Canberra.

7.4 Systematic Palaeontology

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii Cope, 1887

Family Mimiidae Gardiner, 1993

Genus *Pickeringia*, gen. nov.

(Figs. 7.1-7.12 inclusive)

Etymology.

After David Pickering for his outstanding preparation of part of the holotype specimen along

with numerous other Gogo fossils.

Diagnosis.

As for type species (monotypic genus)

Type species

Pickeringia acanthophilus, sp.nov. (Figs 7.1-7.12)

Locality

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

Etymology.

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

Diagnosis

Basal actinopterygian with open pineal foramen and a spiracular slit bordered by the intertemporal, T-shaped dermosphenotic and supratemporal. Parietal in contact with the much smaller intertemporal via anterolateral margin. Supratemporals with anterolateral prongs that embrace the posterior of the spiracular opening. Surangular absent. Posterior corners of supratemporals extend beyond posterior margin of parietal. Ventral otic fissure passes into rear of orbit. Very large vestibular fontanelles that extend anteriorly to almost make contact with the ventral otic fissure. Single pair of large circular ventral openings on the aortic canal. Skull roof and pectoral girdle ornamented with raised, pointed denticles bearing small barb-like serrations. Macromeric ganoid scales ornamented with thick,

rostrocaudal teardrop shaped ridges with prominent raised striae. Lateral serrations on median scutes and caudal fulcra. Sharp barb-like lateral or posterolateral serrations on primary lepidotrichia of pectoral, pelvic, anal and caudal fins.

Holotype and only specimen.

WAM 03.6.1. A partially articulated fish preserved in counterpart with both halves (A+B) mounted in resin. Partial neurocranium, dermosphenotics, snout and post-temporals recovered as separate elements.

7.5 Description

The neurocranium of *Pickeringia* is of a very similar grade of organisation to that of *Mimipiscis* and *Moythomasia durgaringa* (Gardiner 1984, Gardiner and Bartram 1977). In this preliminary description, only points of contrast with these forms are mentioned.

The foramen magnum of *Pickeringia* (Fig. 7.6) is more than 70% the size of the opening for the notochordal canal and comparatively larger than in *Mimipiscis* (Gardiner 1984). There are two large paired openings on the floor aortic canal, immediately posterior of where the canal bifurcates (Fig 7.4, 7.7). These are visible as two circular holes on the ventral surface of the occipital region and were presumably for the exit of the second efferent arteries. The corresponding region in specimens of *Mimipiscis* and *Moythomasia durgaringa* is variable, but such large, discrete openings are never present. A similar configuration to that in *Pickeringia* is present in *Kansasiella* (Poplin 1974. Fig.14).

The enormous vestibular fontanelles (Fig. 7.5,7,7) are far broader and longer than in *Mimipiscis* and *Moythomasia durgaringa*. These extend anteriorly to underly the hyomandibular facet and are almost confluent with the ventral otic fissure.

Open vestibular fontanelles are widely distributed among fossil gnathostomes and are considered to be a primitive character by Gardiner (1984). Large fontanelles of a similarly size to that of *Pickeringia* are unusual in actinopterygians but are present in some fossil sarcopterygians, including *Youngolepis* (Chang and Yu 1981), *Eusthenopteron* (Jarvik 1996) and *Gogonasus* (Long et al. 1997). In some Carboniferous actinopterygians, the ventral otic fissure may be in close proximity or confluent with the vestibular fontanelle, but this is due to the posterior migration of the fissure in conjunction with the development of the posterior myodome (Gardiner and Bartram 1977). In contrast, the ventral otic fissure in *Pickeringia* is in the same relative position as the other Gogo taxa.

The ganoine ornamentation on the skull of *Pickeringa* is highly distinctive. The skull roof, pectoral girdle and most of the opercular-gular series are covered in denticles that taper posteriorly into sharp points. These and other ganoine structures bear small raised striae and serrations (Fig. 7.3), similar those present on the much longer linear ridges on the skull of *Moythomasia* (Chapter 7, Gardiner 1984). These extend into short, serrated ridges on the snout (Fig. 7.8), gulars, maxillae, lower jaw (Fig. 7.3), post-temporals (Fig. 7.10) and dermosphenotics (Fig. 7.9).

The snout (Fig. 7.8), comprising nasals, premaxillae and a median rostral, is similar to that of *Mimipiscis* except that the premaxillae are c.20% larger, with a long median suture excluding the rostral from contact with the occlusal margin. While closer in size and shape to

the premaxillae of *Moythomasia nitida* (Jessen 1968) and *M. lineata* (new species, Chapter 6), they meet the rostral in a V-shaped recess rather than a straight margin. The ethmoidal commissure is clearly visible as a raised furrow on the medial surface.

The maxilla (Fig. 7.1,7.2,7.3) is of similar shape to the other Gogo forms, consisting of a large postorbital blade and a narrow suborbital ramus. The preopercular is a long and acutely angled bone, conforming to the dorsal and posterodorsal margins of the maxillary blade. The T-shaped dermosphenotic (Fig. 7.9) is similar to that in the Bergisch-Gladbach *Moythomasia* spp. (Chapter 6), with a long posterior ramus that accounts for more than 1/3 the length of the bone and formed the ventral margin of the spiracular slit. None of the infraorbitals are preserved.

The skull roof (Fig. 7.4) comprises paired parietals, frontals, intertemporals and supratemporals. The parietals are large and rectangular, being only marginally shorter than the frontals and of a similar length to the narrow supratemporals, The frontals taper anteriorly, forming a V-shaped recess for the rostral and forming a large pineal foramen in the anterior half of their median contact. Intertemporals are small and triangular, the right example having medioposterior contact with the parietal as in *Moythomasia* whereas the left example barely meets the parietal. The supratemporals are similar to that of *Mimipiscis* with a small anterolateral prong that embraces the posterior spiracular opening. The extrascapulars are unknown.

The lower jaw (Fig. 7.1, 7.2, 7.3) comprises a large dentary and a crescentic posterior angular. The jaw is poorly preserved on the A-block, but no trace of a surangular is visible and what appears to be part of a zigzag suture between the dentary and angular is present, as

in *Mimipiscis* (Chapter 5) and *Gogosardina* (Chapter 4). The jaw is better preserved on the B-block but the maxilla is in articulation, covering the suture.

The operculum is of similar shape to that of *Mimipiscis.* The suboperculum is almost a square bone that is more than 50% the size of the operculum, and lacks the pointed anterodorsal process found in other Gogo actinopterygians. The first six branchiostegal rays are preserved, the 1st in the series being twice as dorsoventrally thick as the adjacent examples.

The cleithrum and clavicle are identical in shape to those in *Mimipiscis* and *Gogosardina.* It is distinguishable by its denticulate ornament (Fig 7.3).

The anterior pectoral fin is supported by a perforated propterygium, as is standard for the Actinopteri (Patterson 1982), to which at least two pairs of marginal rays attached (Fig. 7.3). Following this are four stout, hourglass-shaped radials as in *Moythomasia durgaringa* and unlike *Mimipiscis* where there are only three (Gardiner 1984). The metapterygium is not preserved.

The lepidotrichia of both pectoral fins are mostly out of articulation, making an accurate count of their number impossible. The proximal segments are more than twice as long as those in the remainder of the fin and are remarkable in possessing a single row of sharp, hook-like barbs along the lateral edge (Fig. 7.11). Smaller lepidotrichial segments, from closer to the distal edge of the fin, lack these serrations. Small paired fringing fulcra were present.

The small pelvic fins are situated midway between the pectoral and anal fins (Fig. 7.1). More than ten primary lepidotrichia are present in articulation on the preserved right fin (on B-block) with fragments of additional rays. The posteriormost five rays are smooth, the remainder of the primary segments in and out of articulation possess prominent lateral serrations. Numerous small disarticulated segments from the edge of the fins are smooth and without barbs.

The large triangular anal fin (Fig. 7.1) is made of more than 30 branched, segmented lepidotrichia. Sharp posterolaterally directed barbs are present on all visible primary lepidotrichia to at least the fourth segment from the fin base. The only preserved section of the dorsal fin are several smooth lepidotrichial segments from the extreme posterior of the fin (Fig. 7.2).

The heterocercal caudal fin (Fig. 7.1) is deeply cleft with a triangular lower hypochordal lobe. Only the base of the notochordal mass of the fin is preserved. More the More the 40 lepidotrichia are preserved, alternating with fringing fulcra on the ventral margin. As with the other fins, all primary fin-ray segments are barbed (Fig. 7.11), with the serrations sometimes extending to the second or third segment. The distal half of the lower lobe is free of serration.

From what is preserved (the dorsal surface from the occipit to the dorsal fin is missing), the body appears to have been fairly deep and fusiform, with similar proportions to *Moythomasia durgaringa*. The whole fish had a standard body length of c.10cm, the head accounting for ¼ of this.

The squamation of *Pickeringia* is highly distinctive, although disrupted on the holotype anterior of the anal fin. Based on their size, between 60-70 transverse scale rows were originally present.

The scales are ornamented with raised ridges that anastomose on the anterior half of the body and are separate at the tail and near the anal fin (Fig. 7.12). These ridges are broad at the anterior end and taper towards sharp posterior serrations that extend beyond the level of the free field, giving the ridges a teardrop shape. Each ridge is further ornamented with raised striae, creating a similar serrated pattern to the ganoine denticles on the skull roof. Peg-and-socket articulation is well-developed on anterior scales, becoming reduced towards the rear of the fish.

Anterior flank scales (Fig. 7.11a) are have between 3-7 ridges. Examples from the tail are almond shaped, with two ridges.The scales on the ventral surface anterior to the pelvic fins are unique among Devonian actinoptergians in being much larger and more strongly ornamented than the adjacent flank scales (Fig. 7.11b). The largest examples are more than 200% the size of the lower flank scales and may possess more than 10 ridges. The depressed field accounts for up to a third of the length while the peg is absent.

Median caudal fulcra or scutes are preserved on the dorsal margin of the caudal fin and in between the caudal and anal fin on the ventral surface. A single example from immediately behind the occipit on a-block suggests a complete dorsal series from head to dorsal fin. The upper caudal series narrows posteriorly with an increasing degree of overlap to form a rigid cutwater on the caudal fin. Once again, the ornamentation is unique with ganoine striations tapering into sharp lateral or posterolateral barbs that extend beyond the main body of the

scute (Fig. 7.11d). At least a single pair of wedge-shaped scutes were present anterior to the anal fin, about four times the size of the adjacent scales (Fig. 7.11c). Unlike the smoother examples on *Moythomasia* (Chapter 6), these are strongly ornamented with the same short, tapering ridges as on the rest of the squamation.

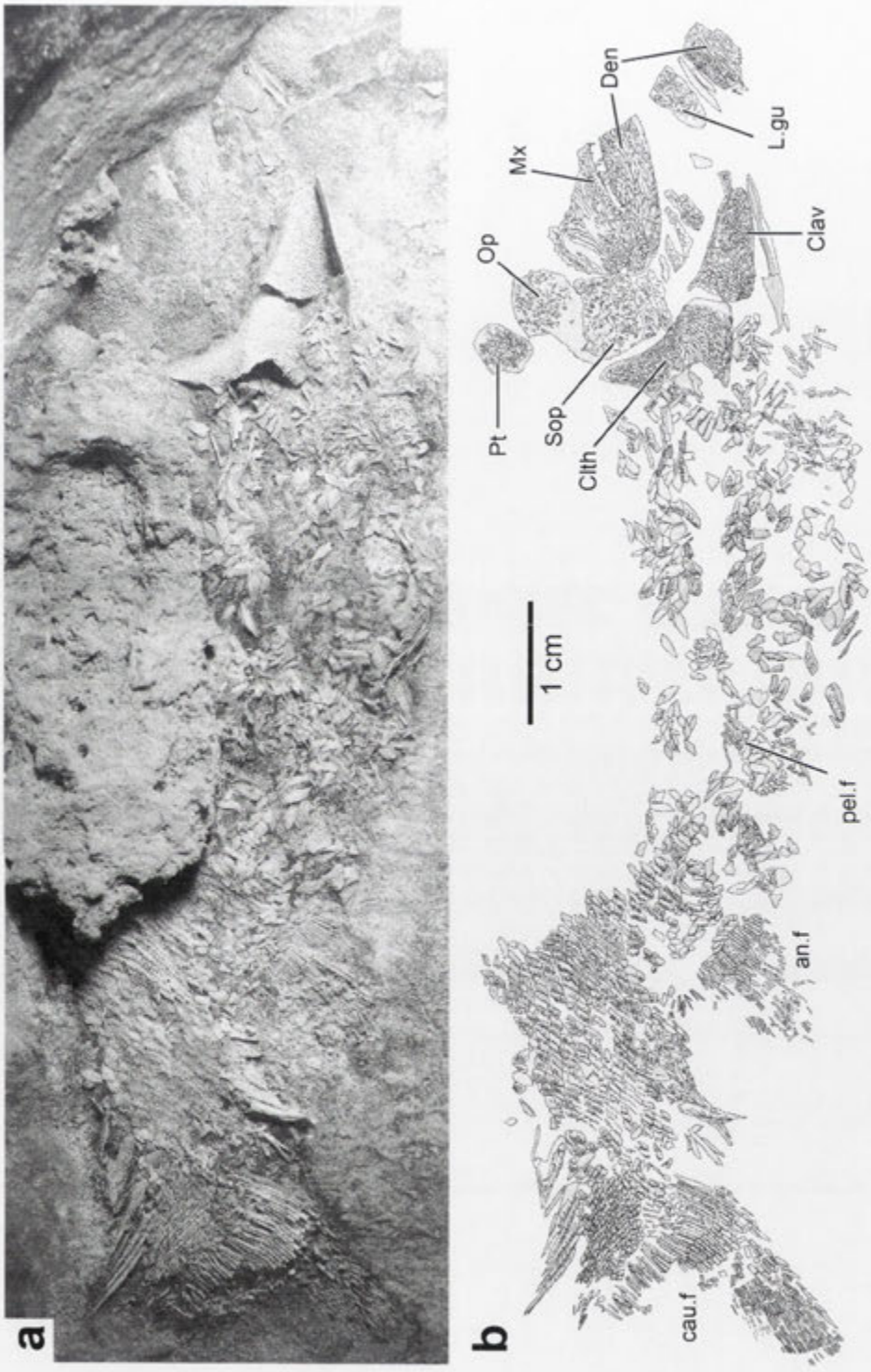


Figure 7.1
Pickeringia acanthophilus gen. et sp. nov., right lateral view of holotype WAM 03.6.1b.

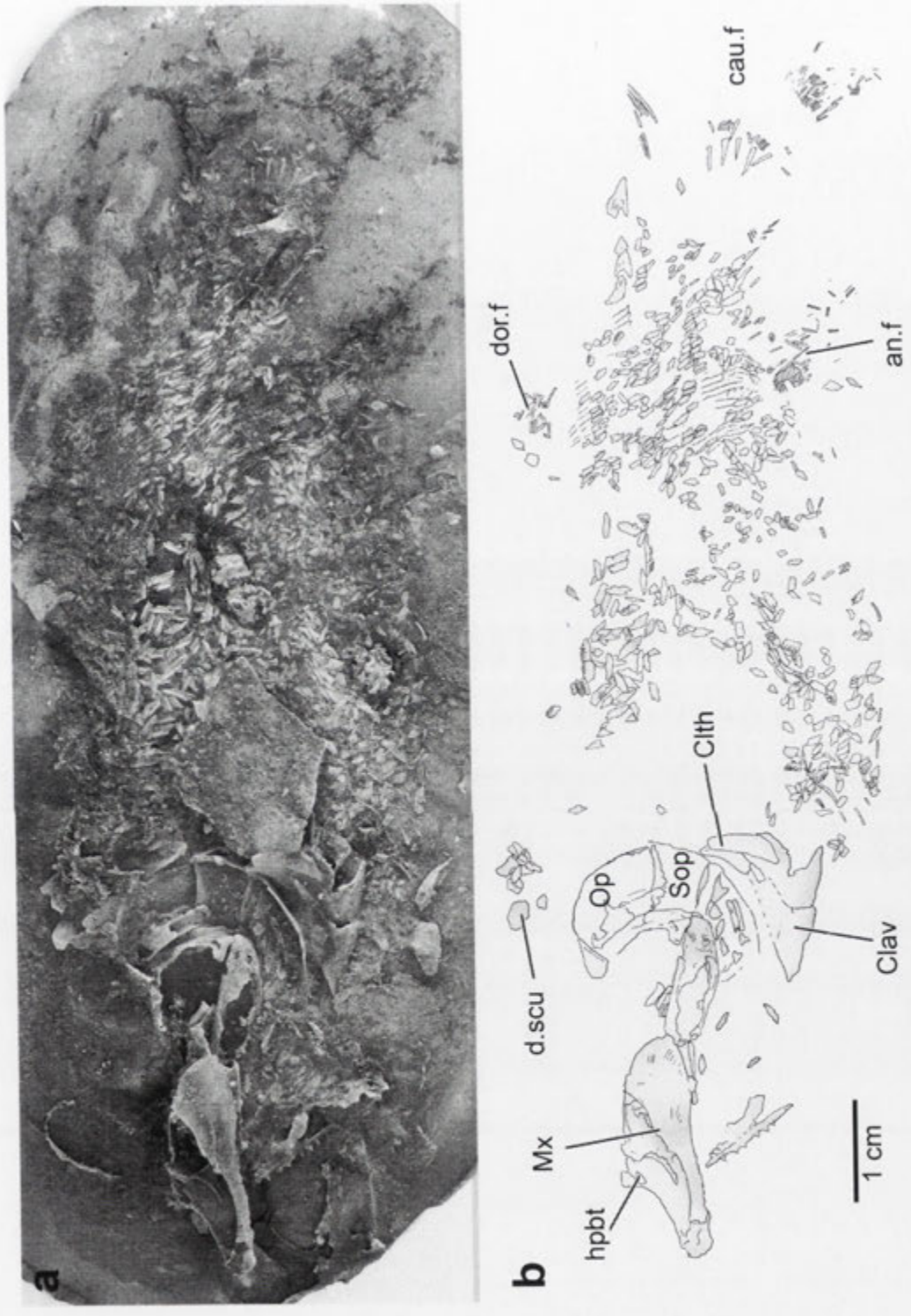


Figure 7.2
Pickeringia acanthophilus gen. et sp. nov., left lateral view of holotype WAM 03.6.1a.

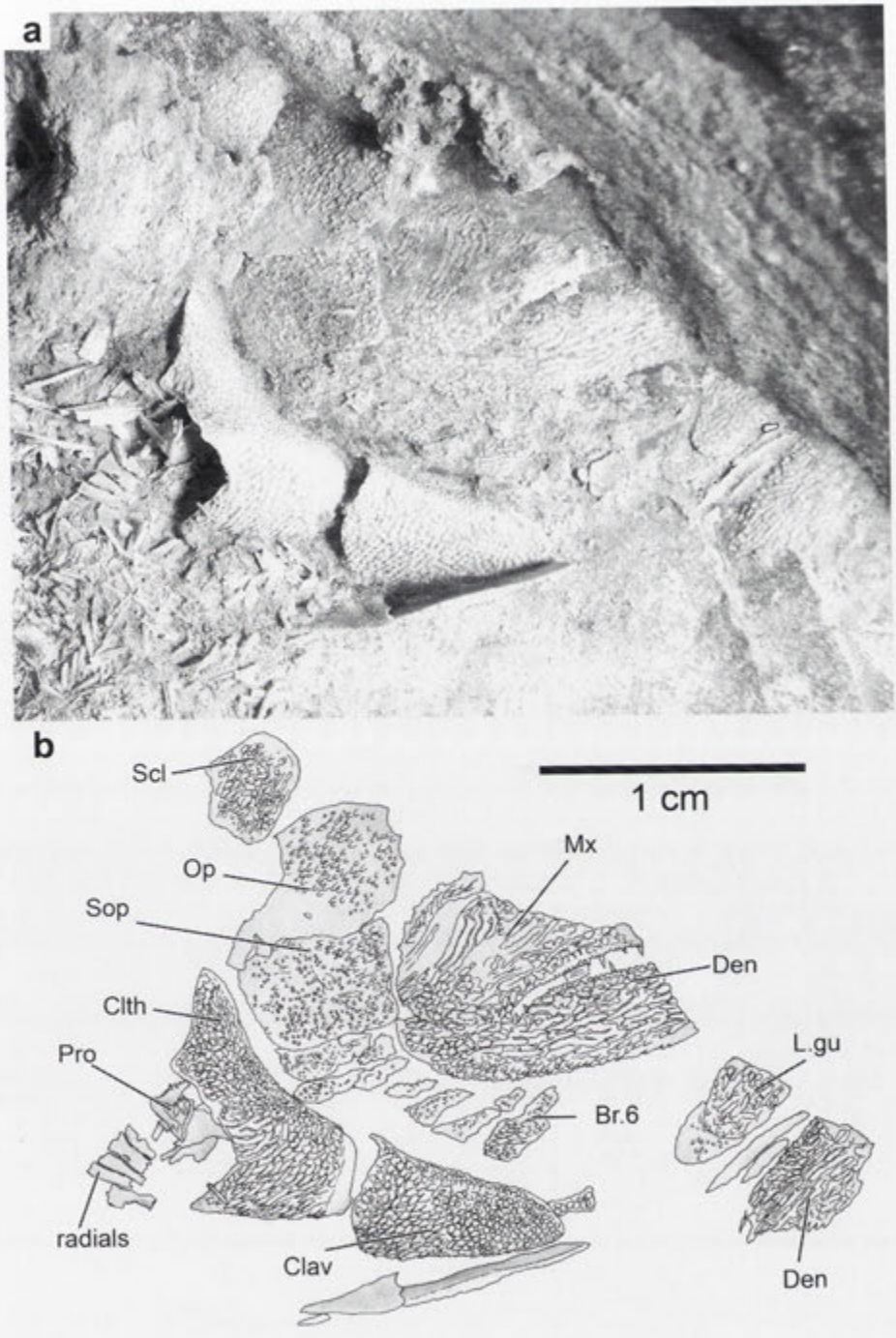


Figure 7.3
Pickeringia acanthophilus gen. et sp. nov., detail of head region of WAM 03.6.1b

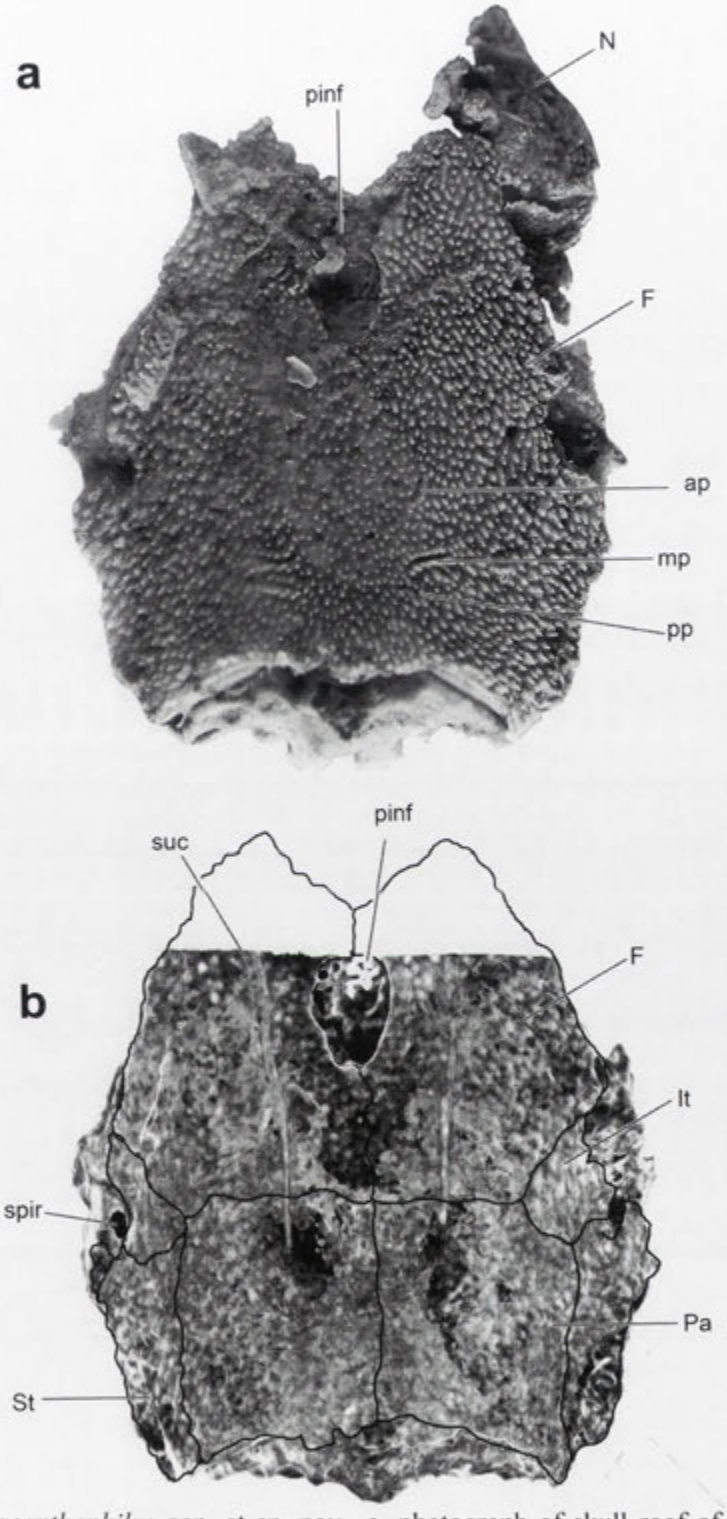


Figure 7.4
Pickeringia acanthophilus gen. et sp. nov., **a.** photograph of skull roof of holotype in dorsal view. **b.** CT tomograph of same specimen, with dermal surface rendered semi-transparent.

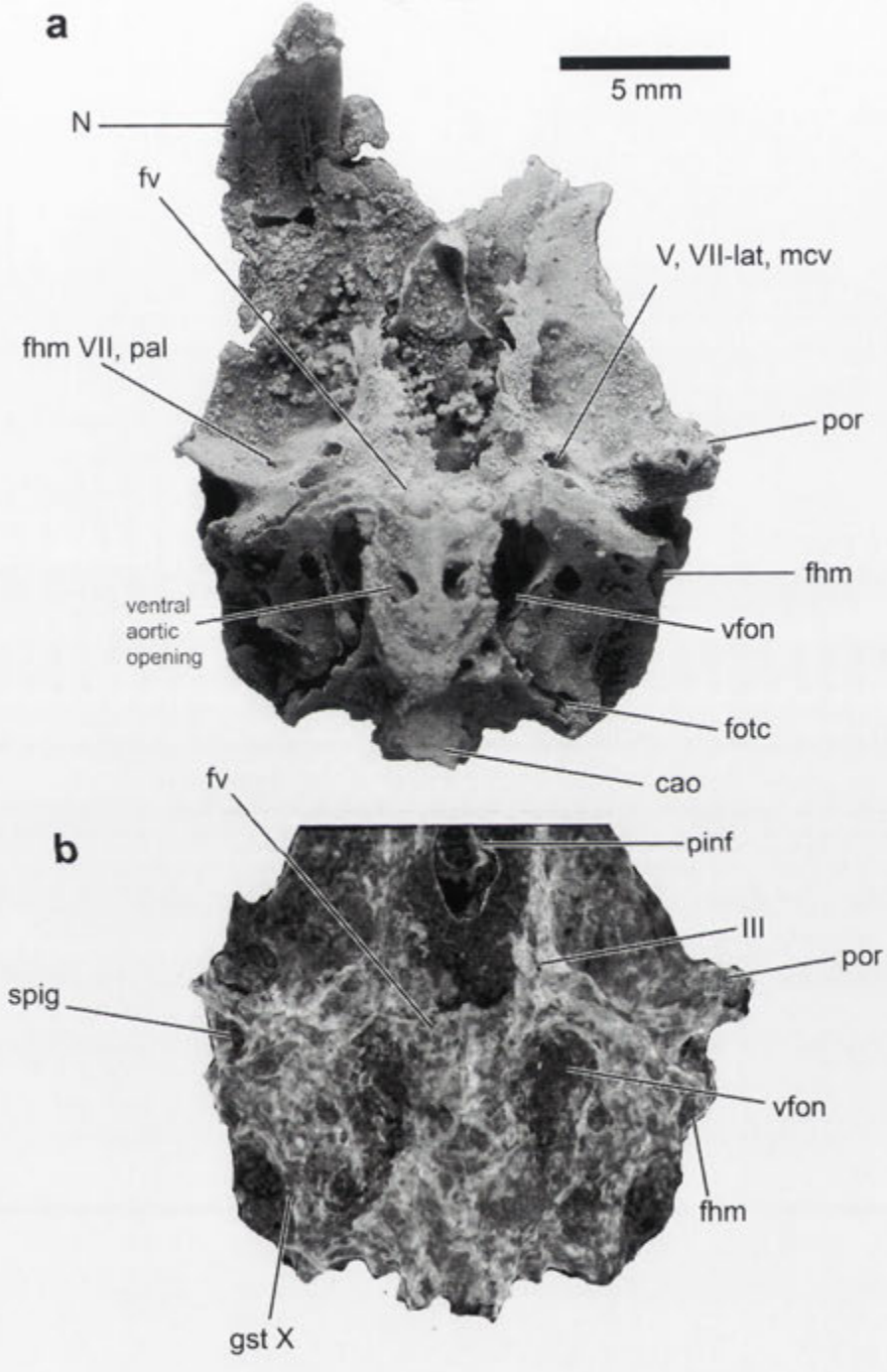


Figure 7.5.
Pickeringia acanthophilus gen. et sp. nov., neurocranium of holotype in ventral view. **a.** photograph and **b.** CT tomograph.

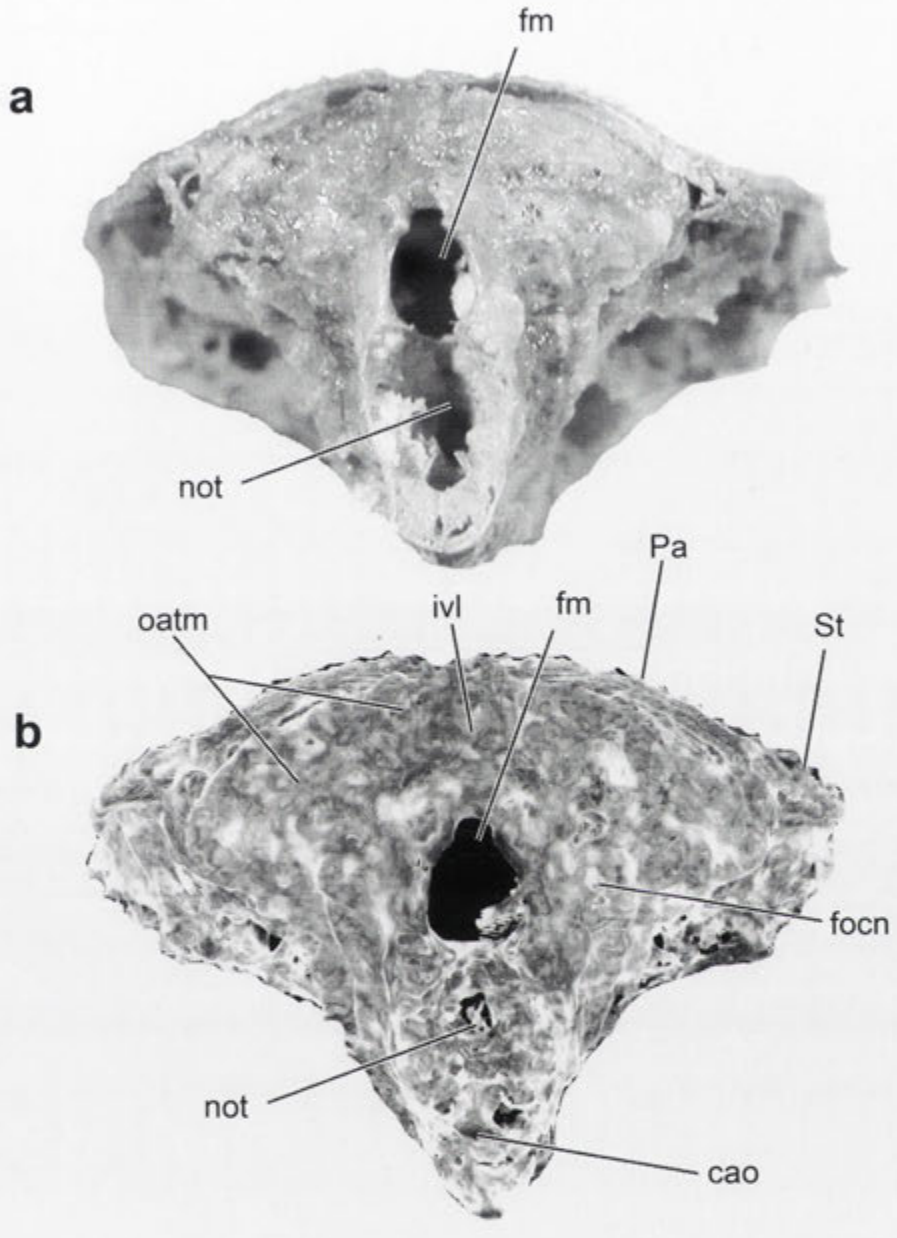


Figure 7.6
Pickeringia acanthophilus gen. et sp. nov., holotype specimen, occipital region of neurocranium of holotype in posterior view. **a.** photograph and **b.** CT tomograph.

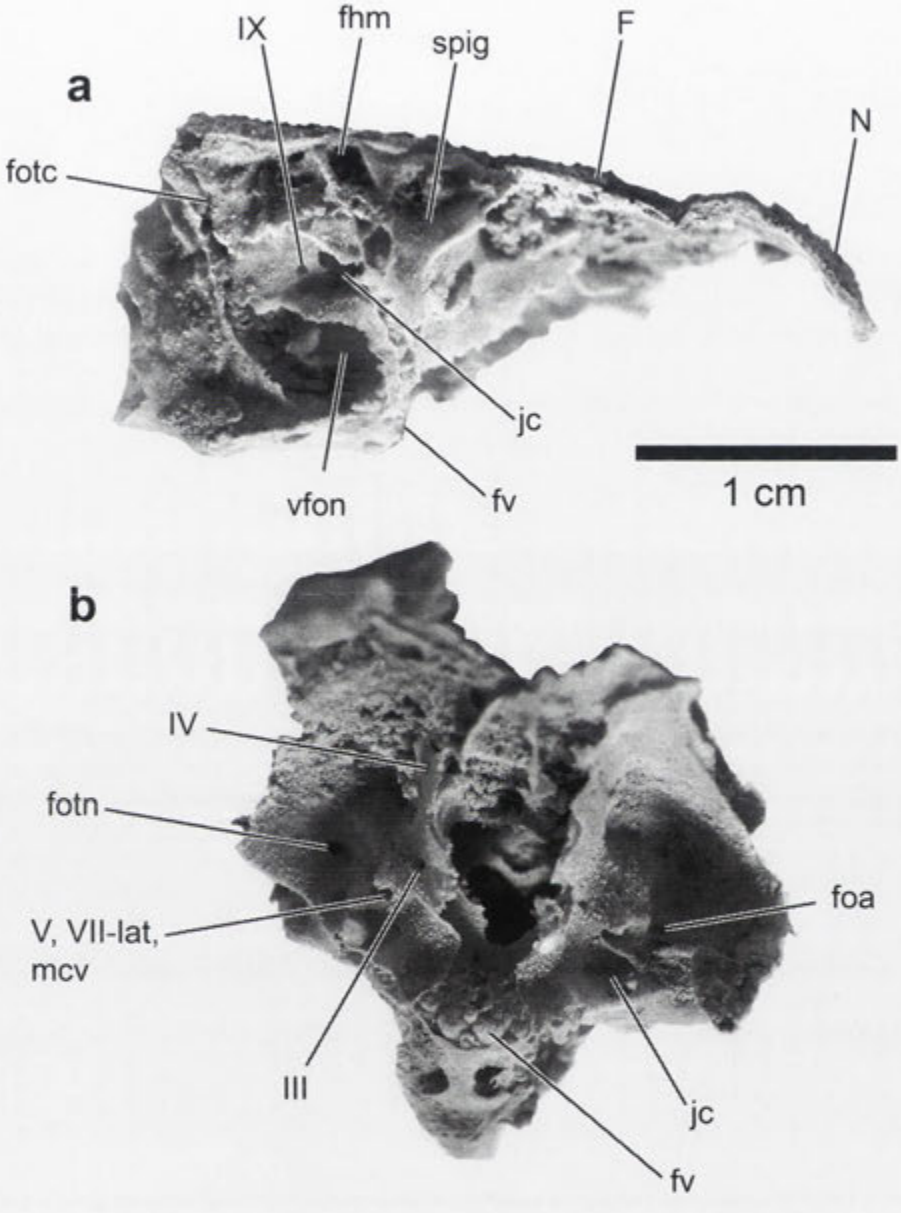


Figure 7.7
Pickeringia acanthophilus gen. et sp. nov., neurocranium of holotype in **a.** ventrolateral and **b.** ventroanterior view.

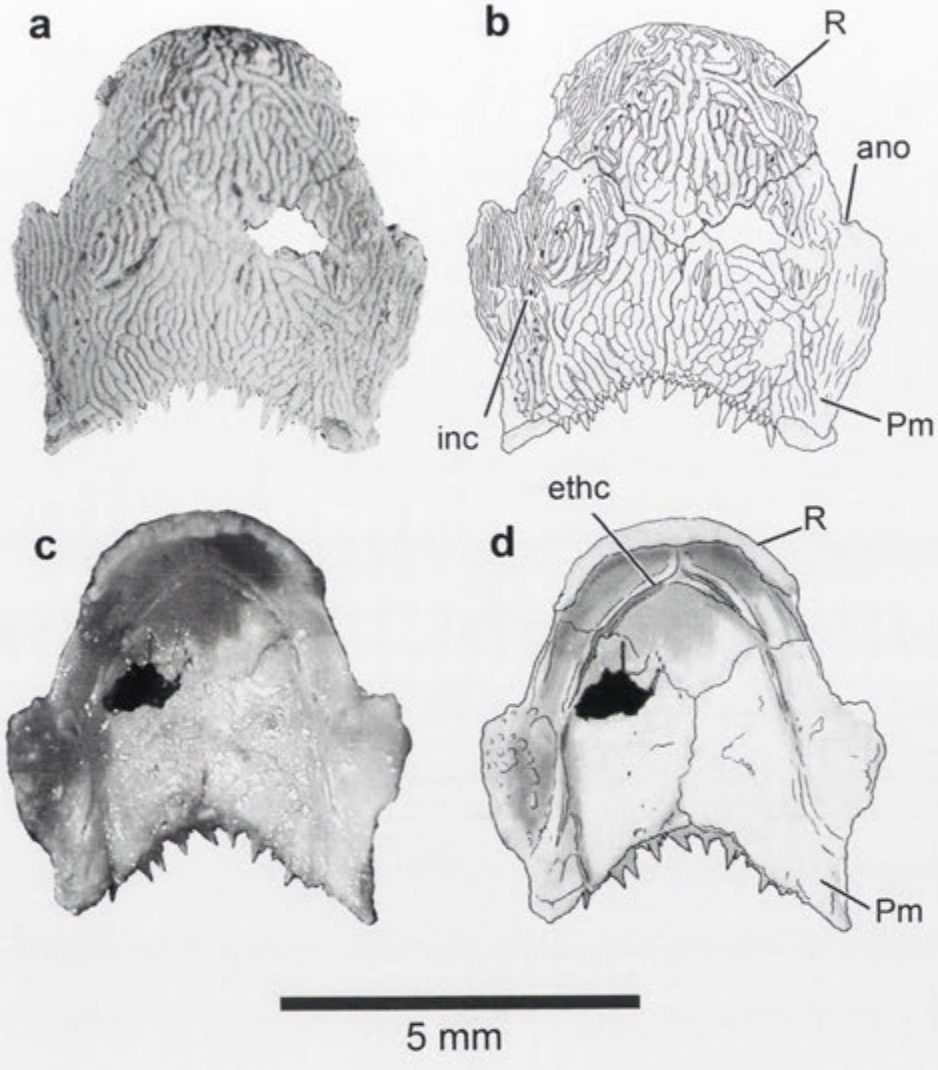


Figure 7.8
Pickeringia acanthophilus gen. et sp. nov., Holotype snout. **a.** photograph and **b.** reconstruction of snout in anterior view. Posterior view of same specimen as **c.** photograph and **d.** reconstruction.

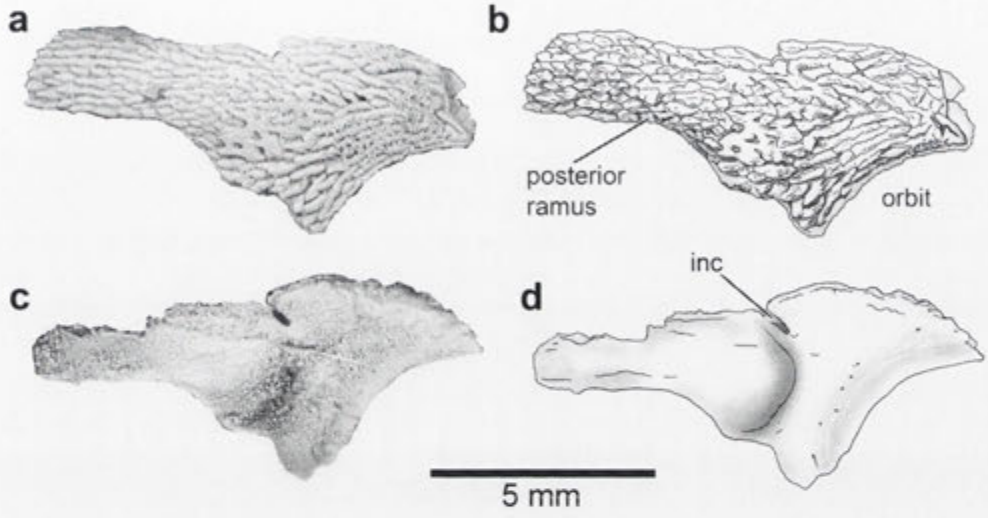


Figure 7.9
Pickeringia acanthophilus gen. et sp. nov., Photographs and reconstructions of the right dermosphenotic (**a,b**) in lateral view and the left dermosphenotic (**c,d**) in medial view.

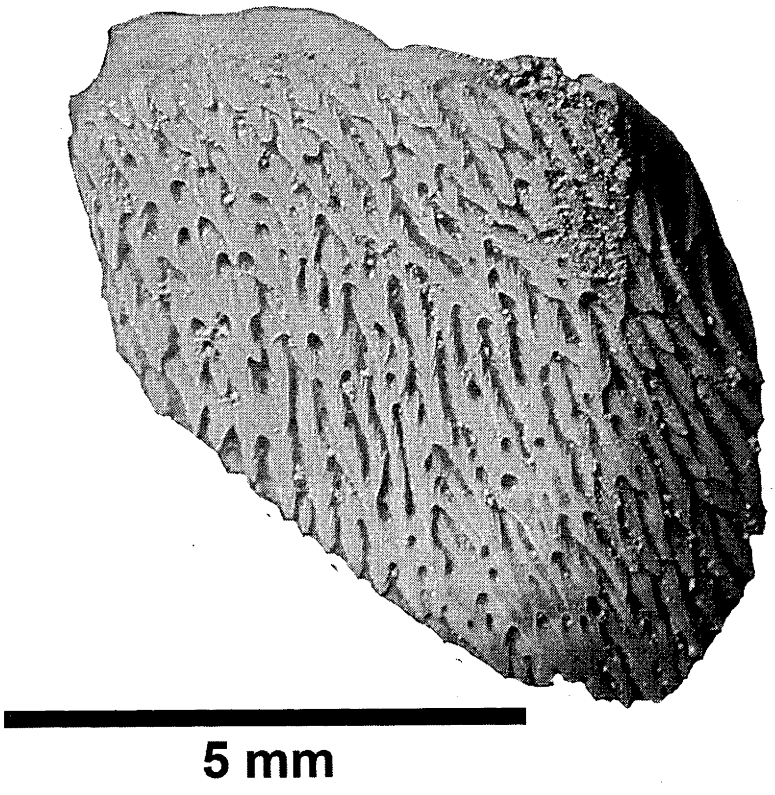


Figure 7.10
Pickeringia acanthophilus gen. et sp. nov., Holotype right post-temporal in dorsal view, showing distinctive dermal ornamentation.

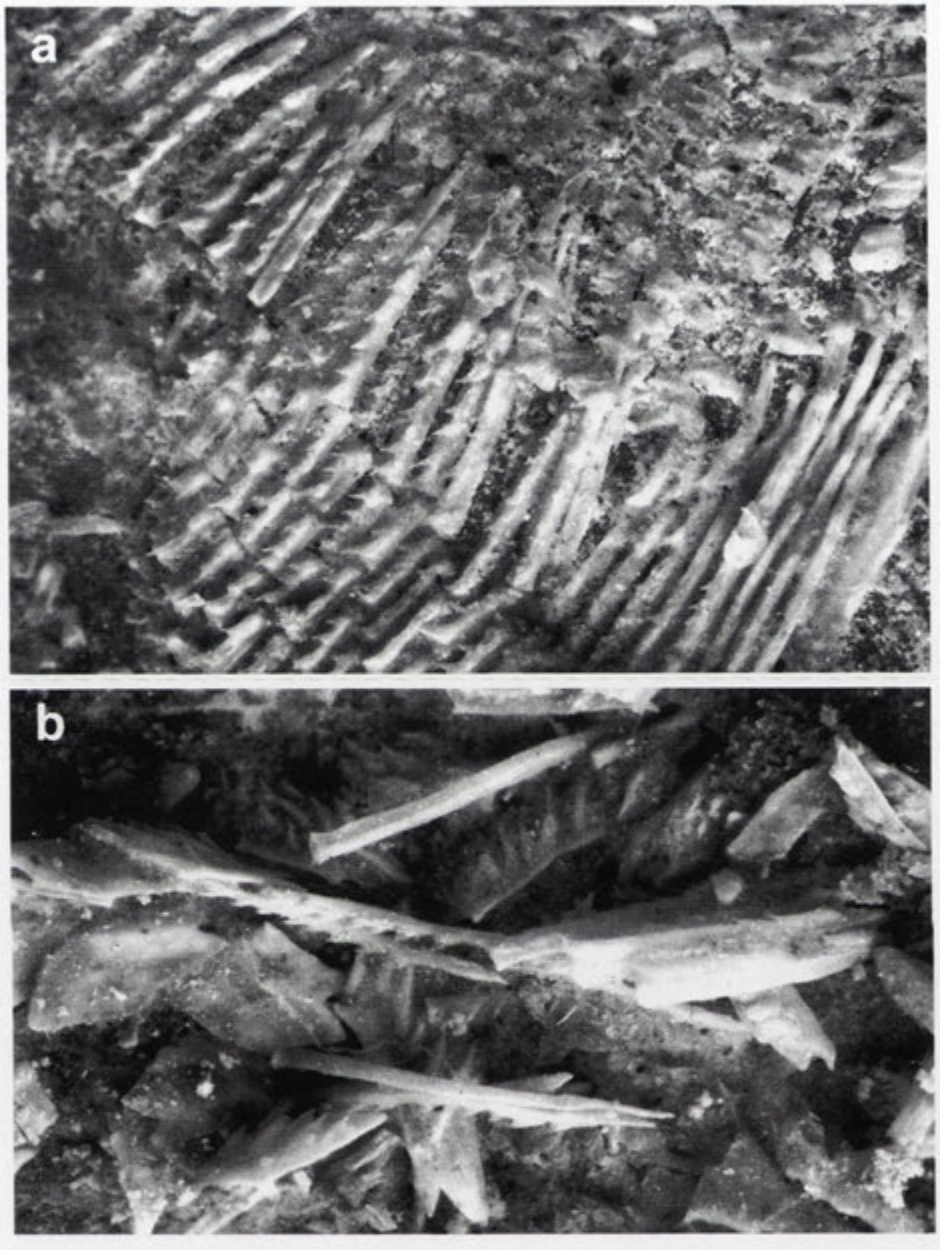


Figure 7.11
Pickeringia acanthophilus gen. et sp. nov., Fins of holotype specimen. **a**. detail of proximal caudal lepidotrichia in articulation. **b.** detail of disarticulated proximal lepidotrichia of right pectoral fin.

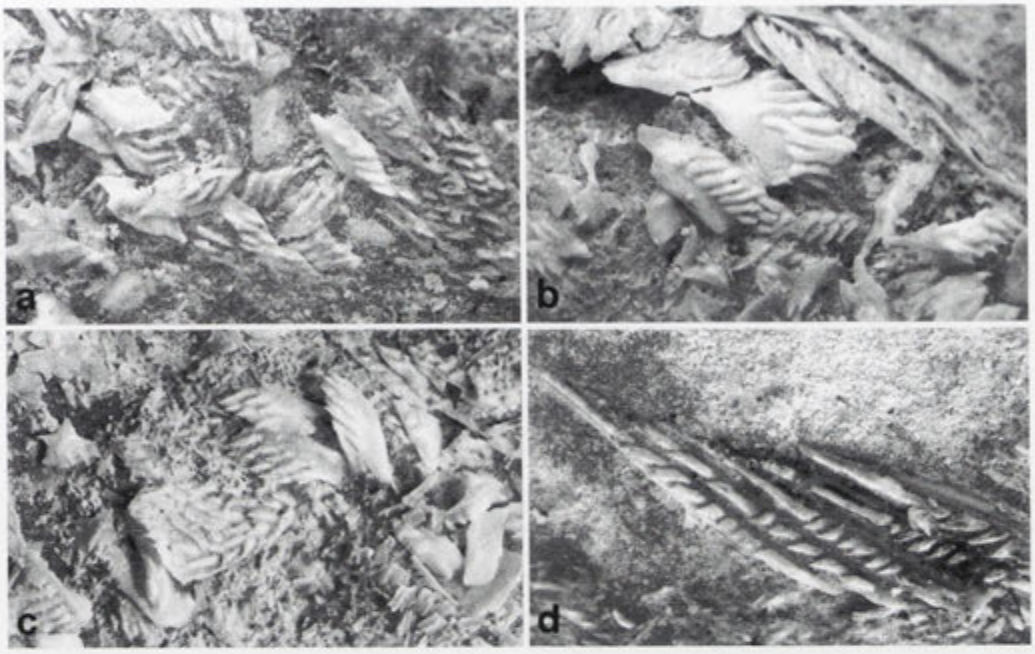


Figure 7.12
Pickeringia acanthophilus gen. et sp. nov., Squamation of holotype specimen. **a.** anterior lower-lateral scales. **b.** ventral scales, anterior to pelvic fins, **c.** ventral scales and paired scute immediately anterior to anal fin. **d.** fulcra on the dorsal surface of the caudal fin. Scale bar = 2mm.

Chapter 8. Discussion and Conclusion

8.1 The Howqualepididae and the inclusion of the Bunga Beds form

Long, Choo and Young (2008) erected the Howqualepididae, comprising *Howqualepis rostridens* from Mount Howitt, Victoria and *Donnrosenia schaefferi* from the Aztec Siltstone of Antarctica. ANU V2929 appears to represent a third taxon within this clade. All three fish have an elongate body form with macromeric squamation; long-based pelvic fins; small fringing fulcra without medial contact between the distal hemilepidotrichia, and extensive unsegmented primary lepidotrichia that comprise most of the length of the pectoral fin. Among the other Devonian actinopterygians, only *Tegeolepis clarki* (Dunkle and Schaeffer, 1973) possesses extensive unsegmented pectoral lepidotrichia but is distinguished from the Gondwanan forms in lacking a terminal segmented fringe on the pectoral fins, in possessing micromeric squamation and having small, short-based pelvic fins.

Assigning the Bunga Beds taxon to a genus is difficult owing to the lack of key skull characters that are used to characterise *Howqualepis rostridens* from the similar *Donnrosenia*. For example, *H. rostridens* possesses an extremely long maxillary blade, a dentigerous rostral and small, dorsoventrally compressed premaxillae (Long 1988). *Donnrosenia* displays a short, deep maxillary blade, dorsoventrally prominent premaxillae, a small accessory operculum and much smaller teeth than *Howqualepis* (Long, Choo and Young, 2008).

ANU V2929 is considered to be closer *H. rostridens* in having more extensive unsegmented pectoral lepidotrichia and relatively smaller scales than *Donnrosenia*. The pectoral fins of ANU V2929 are more similar to that of *H. rostridens* in that both forms

possess unsegmented lepidotrichia that account for over 75% of the maximum length of the fin. Those of *Donnrosenia* account for less than 70% of the maximum fin length (Long, Choo and Young, 2008. Fig.7).

Based on these anatomical similarities and pending the discovery of skull material for this taxon, ANU V2929 is tentatively assigned to *Howqualepis*. The Bunga Bed form is not conspecific with *H. rostridens* and is distinguished in having a larger anal fin with a greater number of primary lepidotrichia and in possessing porous dermal ornamentation of the pectoral girdle.

8.2 Gogo actinopterygians: Diversity and lifestyle

Until recently, the Gogo actinopterygians comprised only two taxa (*Mimipiscis toombsi* and *Moythomasia durgaringa*) which indicated a low diversity of ray-finned fish within that fauna. Recent research has revealed at least three additional taxa within the Gogo assemblage: *Mimipiscis bartrami* sp.nov., *Gogosardina coatesi* gen et. sp. nov. and *Pickeringa acanthophilus* gen et. sp. nov. This represents the greatest number of actinopterygian species within a Devonian vertebrate assemblage. Comparing the Gogo with roughly contemporaneous marine faunas, the famed Escuminac Formation of Miguasha, Canada contains a single ray-finned taxa (*Cheirolepis canadensis*, Arratia and Cloutier 1996) while the Oberer Plattenkalk at Bergisch-Gladbach, Germany, which contains a fauna broadly similar to that of the Gogo (Schultze and Cloutier 1996), has only two species (*Moythomasia nitida* and *M. lineata*, see Chapter 7).

The higher number of ray-finned taxa in the Gogo Formation could simply be a result of whatever environmental or preservational factors that contributed to the high ichthyofaunal

diversity in the local record. Comprising over forty described taxa (Long 2006), the Gogo Formation is by far the most speciose vertebrate fauna in the Late Devonian, with novel forms discovered on almost every field expedition. The Gogo ichthyofauna is unusual in the extreme rarity of several major groups of fish that elsewhere are well represented (Schultze and Clouter 1996, Anderson et al. 1999).

With their fusiform bodies and lacking the heavy extensive osteology of contemporary sarcopterygians and placoderms, the Gogo ray-finned fishes are likely to have been fast midwater predators. Other groups of Devonian fish with similar characteristics, the acanthodians and basal chondrichthyians, are each known from only a single undescribed speciman at Gogo (pers.obs. 2005 and 2008 Gogo field expeditions.) whereas such fish were more common and speciose in other ichthyofaunas (Schultze and Cloutier 1996). In a study of sharks of the Famennian Cleveland Shale, Ohio (Williams 1990), of 53 specimens of *Cladoselache* with identifiable stomach contents, 34 (about 64%) contained the remains of actinopterygians indicating that they were important predators of early ray-finned fishes.

The most numerous and speciose macropredators in the Gogo assemblage were various forms of arthrodire placoderms. It is certainly possible that some of these were predators of ray-finned fishes although evidence for this is lacking. Based on landmark-based morphological data Anderson (2008), some Gogo taxa, notably *Incisoscutum*, may have fed primarily on resilient prey items by either grazing on the reef or consuming armoured prey in the water column and were thus less likely to have targeted actinopterygians. Gut contents visible in as yet unprepared placoderm material collected in the 2008 Gogo expedition has revealed conodont elements, suggesting that soft-bodied prey was also taken. There is only a single record of actinopterygian remains associated with the gut contents of an arthrodire,

comprising indeterminate palaeoniscoid scales found within the arthrodire *Coccosteus* from the Middle Devonian of Scotland. (Davidson and Trewin 2005)

While the Gogo reefs may have been the earliest known center for diversification among the basal actinopterygians, it should however be noted that actinopterygians did not undergo large-scale diversification until after the Devonian. The Gogo total of five species, while impressive for the Devonian, is overshadowed when compared with actinopterygian diversity from a typical Carboniferous fauna with over 30 recorded from the Bear Gulch assemblage of Montana (Lund and Poplin 1999).

The conodont remains within MV P228849b (Chapter 4) represents the second described instance of such elements being present within a Gogo actinopterygian. Nicoll (1977) describes the presence of the apparatuses of two separate conodont animals found within the gut region of a "stegotrachelid palaeoniscoid fish" from the Gogo Formation. The fish (CPC 17220 – currently housed in the Australian National University, Canberra) is a representative of *Mimipiscis bartrami* sp.nov. (Chapter 5). Conodont elements within the gut cavity of this fish comprised a complete apparatus of *Hibbardella angulatus* (15 elements) and an incomplete apparatus of *Icriodus brevis* (13 elements).

In contrast to CPC 17220, the conodont elements within MV P228849b, which represent a single prioniodinid individual, are not within the gut cavity but instead situated among the branchial elements, indicating that the conodont animal was not fully ingested prior to the death of the fish. Aside from two isolated elements that have scattered from the main cluster, the structures of the conodont apparatus appear to be in anatomical position. The set of S elements, positioned in a dorsal position relative to the palaeoniscoid, are orientated with

their cusps rostral and their denticles directed obliquely dorsal as indicated for *Promissum* (Purnell et al. 2000). One M element is identified overlying the dorsal S elements and the position of the Sa element, anterolateral to it, indicates some postmortem movement. It would appear that the S and M elements lie together as a single anterior unit (Aldridge 1987). A pair of P1 elements, in functional opposition lie caudal to the S elements (Donoghue and Purnell 1999). Given the orientation of the apparatus, the conodont animal was consumed tail-first and, using *Clydagnathus* as a guide (Briggs et al. 1983), the complete animal was in excess of 10 cm in length.

Extant macropredatory actinopterygians are known to attempt the ingestion of prey objects of a size too large to be easily swallowed, leading to injury or death if the fish is unable to expel it (pers.obs of captive *Apteronotus, Echidna, Geophagus, Gymnothorax, Antennarius, Pterois* and *Epinephelus* sp.). It is probable that MV P228849 represents a *Gogosardina* that attempted to consume a conodont animal of a similar size to itself. The fish subsequently expired when it found itself unable to either fully ingest or spit out the food item.

8.3 The status of scale-based taxa assigned to *Moythomasia* spp.

In addition to the four species of *Moythomasia* described in Chapter 6, there are additional taxa referred to this genus based on fragmentary material. While these forms possess features that may be diagnostic at species level, none can be confidently assigned as congeneric to the more completely known forms and will henceforth be referred to as *?Moythomasia* spp.

?Moythomasia striata is based on Frasnian-aged scales from Wildungen, Germany (Fig. 6.2). They were considered similar to the material now designated *M. lineata* sp.nov. Jessen (1968) and a comparison of these two forms is necessary. Both do indeed share a linear free-field ornament of straight, separate ridges in the absence of pores. However the scales of *?M. striata* differ from *M. lineata* sp.nov. in the configuration of the depressed field, rostro-dorsal process and dorsal peg. The depressed field of the Wildungen form is exceptionally broad, accounting for c.30-50% of the scale length compared with c.25% on *M. lineata* sp.nov. The rostro-dorsal process is much more prominent in *?M. striata*, with the apex often positioned at a level above the peg whereas the shorter process in *M. lineata* sp.nov. is always at an equal or lower vertical position to the peg-apex. The peg of *?M. striata* on presumed anterior flank-scales is taller and more anteriorly positioned than those of *M. lineata* sp.nov. The two forms are thus not considered to be conspecific.

The other Wildungen species, *?M. laevigata*, is based on large (over 1 cm long) rhomboidal scales, most of which are smooth and punctated with no ridging (Gross 1953: Fig. 7). Some anterior flank scales lack pores and possess fine vertical ridges against the leading edge of the free field, becoming deflected horizontally near the dorsal and ventral margins. Similar in form are the scales of *?M. antiqua* from New York (Gross 1953, Gardiner 1963), which again possess smooth free fields, punctuated with small pores. The isolated scales from Iowa referred to as *?Moythomasia* sp. by Storrs (1987) are unusual in possessing a very narrow depressed field and in having vertically aligned ridges on the leading edge of the free field, anterior to the more typical horizontal ornament on the remainder of the field. These features are also present on the unusual, short-bodied Famennian genera *Limnomis* (Daeschler 2000: Fig. 10) and *Cuneognathus* (Friedman and Blom 2006: Fig. 6), suggesting a possible kinship with these forms. The Iowa form differs

from the Famennian genera in possessing a well-developed dorsal peg.

?*M. devonica*, the second Portage taxon, does at least include some material of the skull and pectoral girdle. This form has been compared favourably with *M. nitida* (Gardiner 1963) and includes at least one partially articulated specimen that preserves a large section of squamation. Based on a cursory examination of material in the BMNH collections, I believe a case could be made for inclusion of this taxon within *Moythomasia*. However, pending a detailed re-examination of all the material assigned to this taxon (the scale figured for this species in Gross 1933: Fig. 20 looks strikingly different from the BMNH material), this form should be only questionably assigned to the genus.

There is no single shared feature on the individual scales of *Moythomasia* spp. that is unique for the genus, exclusive of all other stem-actinopterans. Anterior flank scales of the four valid species have a straight anterior margin, prominent rostro-dorsal process, a dorsal peg with a pointed-apex tapering from a broad base, prominent keel and socket, a narrow anterior depressed-field and a serrated posterior margin created by terminal points of ganoine ridges. Such a description also applies to the scales of '*Mimia*', *Gogosardina*, *Howqualepis* and *Donnrosenia*. The ganoine striations on the scales of *M. durgaringa* and *M. nitida* strongly anastomose as in the squamation of *Howqualepis* and '*Mimia*'. The corresponding structures for *M. perforata* and *M. lineata* sp. nov. are straight, separate ridges as in *Gogosardina*. The pores present on the scales of *M. perforata*, *M. nitida* and *M. durgaringa* (but absent on *M. lineata* sp.nov.) are also present in *Andreolepis* (Märss 2001), *Donnrosenia* (Long et al. 2008, small punctae visible on the central scale in Fig. 2.10), *Pseudogonatodus* and *Drydenius* (Gardiner 1967). The inability to isolate a shared derived feature on the squamation of *Moythomasia* renders all scale-based members of this genus as

dubious.

It can also be argued that isolated ganoid scales cannot even be confidently assigned to the Actinopterygii without the benefit of articulated conspecific remains for comparison. The newly discovered basal sarcopterygian *Guiyu* mentioned in Chapter 1 possesses all the scale-characteristics shared by all the species assigned to *Moythomasia* to the point that it would have likely been tentatively placed into that genus had it been known only from isolated squamation.

8.4 Phylogenetic analysis

While Devonian actinopterygians have been incorporated into numerous studies, (Patterson 1982, Gardiner 1984, Gardiner and Schaeffer 1989, Coates 1998, Coates 1999, Lund 2000, Lund and Poplin 2002), many of these are primarily concerned with the position of the early taxa relative to post-Palaeozoic forms. The interrelationships of the earliest actinopterygians are only superficially addressed in these studies. Several recent studies have examined the possible interrelationships among early actinopterygians with emphasis on Devonian taxa (Fig 8.1). These analyses have produced little consensus on the phylogenetic placement of taxa beyond the basal or near-basal position of *Cheirolepis.* Taverne (1997) presented a tree of Devonian actinopterygians, plus the extant bichirs, finding *Dialipina* to be the basal taxon of the Actinopterygii with the remainder of examined genera forming successive plesions of stem actinopterygians and actinopterans. Schultze and Cumbaa (2001) coded a selection of Devonian and Carboniferous fossil taxa along with *Polypterus* that produced 9 equally parsimonious trees, a strict consensus of which again found *Dialipina* to be the basal taxon of the Actinopterygii, followed by *Polypterus, Tegeolepis, Cheirolepis, Osorioichthys* with poor resolution further up the tree.

In a recent comprehensive study (Fig. 8.1C), Friedman and Blom (2006) presented a consensus of four trees (with the problematic *Dialipina* omitted from the primary analysis) placing *Cheirolepis* in the basal position followed by *Osorioichthys*. A novel clade containing *Tegeolepis* and *Howqualepis* was resolved above *Osorioichthys*, united by long, unsegmented pectoral lepidotrichia and enlarged parasymphysial teeth on the reflexed anterior dentary. Above this clade is a large assemblage with *Mimipiscis toombsi* resolved as the sister taxon of a large assemblage consisting of *Kentuckia*, two unusual short-bodied forms (*Cuneognathus* and *Limnomis*) and a variety of robust "*Stegotrachelus*-grade" taxa.

Cloutier and Arratia (2004) conducted a comprehensive phylogenetic study that incorporated a wide range of Devonian taxa but produced highly disparate results. Of the four trees incorporating extant taxa, three placed all Palaeozoic taxa outside the crown-group Actinopterygii, diverging strongly from previous analyses. With regards to Devonian actinopterygians, the only consistently resolved relationships were the monophyletic union of the three *Cheirolepis* spp. and a novel sister-taxon relationship between *Mimipiscis* and *Moythomasia* exclusive to all other Devonian forms.

The authors of that study attributed these conflictual results to the selection of outgroups and the large amount of missing data for many of the examined taxa. With regards to this study, the novel sister-relationship of *Mimipiscis* and *Moythomasia* deserves close scrutiny. Some characters are incorrectly coded in the Cloutier and Arratia (2004) analysis. The single *Moythomasia* used in the study appears to represent a combination of features taken from *M. durgaringa* and *M. nitida.* The taxon is referred to as *M. nitida* in their Appendix I and *M. durgaringa* in Appendix 2. Characters 1-8, 11, 84 and 107 are coded correctly with regards to *M. durgaringa* but are incorrect or unknown in *M. nitida.* Conversely, characters 39, 40,

56 and 155 are correctly coded with regards to *M. nitida* but are incorrect for *M. durgaringa.* Character 123 is unknown in *M. nitida* and scored incorrectly for *M. durgaringa.* The result is a construct that diverges from any previously coded version of *Moythomasia* or indeed any existing fossil taxon. Also problematic (as already pointed out by Friedman and Blom, 2006) are seemingly arbitrary assessments of structural homologies. Notable is the assumption in character 10 where the simple, slightly pointed apex of the premaxillae of *Mimipiscis* and *Moythomasia* is considered homologous to the complex nasal process of advanced actinopterygians.

Attempts to resolve the interrelationships between the basal Actinopterygii encounter numerous hindrances. The ray-finned fishes of the Gogo Formation represent the only Palaeozoic representatives of this group with complete dermal and endochondral preservation. Of the remainder, the vast majority are based on flattened dermal remains with little or no endochondral preservation. The researcher is left with three less than ideal choices when selecting characters: focus on a handful of well known forms and ignore the great majority of fossil taxa (e.g. Gardiner et al. 2005); rely primarily on dermal characters and omit potentially valuable braincase data (e.g. Friedman and Blom 2006); or accept a vast amount of missing data in constructing the character matrix (e.g. Cloutier and Arratia 2004). It is also likely that a large proportion of early actinopterygian diversity is currently missing from the fossil record. The ray-finned fishes must have diverged from the sarcopterygians at some point prior to the Late Silurian yet well preserved, undoubtable actinopterygian fossils do not appear prior to the mid-Devonian (see Chapter 1). Given that lobe-finned taxa are invariably included for outgroup comparison, of concern are major morphological gaps in determining dermal skull homologies of the Actinopterygii and Sarcopterygii although recent discoveries such as *Ligulalepis* (Basden et al. 2000, Basden and Young 2001) and *Psarolepis*

(Zhu et al. 1999) have gone a long way in addressing this.

Given the poor level of consensus among the limited number of well preserved Devonian taxa, the excellent preservation of *Mimipiscis bartrami* and *Gogosardina* can assist in addressing the interrelationships of the earliest actinopterygians. The following analysis expands on that presented by Friedman and Blom (2006) by the addition of newly described Devonian taxa and by the inclusion of a selection of Early Carboniferous forms.

The matrix comprises 82 characters of which the first 54 were used in the analysis of Friedman and Blom (2006). The majority of the remainder represent morphological features that were noted in the description of the taxa examined in this project (Characters 57, 60, 61, 62, 63, 65, 66) or characters used in other studies that only become applicable with the inclusion of Carboniferous taxa (Characters 56, 59, 67, 68, 69, 70, 71, 75, 76, 78, 79, 80, 81).

The list of included taxa is detailed as Table 2, including an outgroup of three Devonian sarcopterygians and *Guiyu oneiros*. The Devonian ingroup comprises seventeen taxa which represent the totality of undisputed Devonian actinopterygian taxa that have been well described. The Carboniferous ingroup comprises twelve selected taxa, representing completely known forms that have been fully described in the recent literature.

Omitted taxa include *Dialipina* and the Guildayichthyiformes from the Bear Gulch Limestone (Lund 2000), both of which possess complex facial osteologies that are difficult to directly compare with the other forms used in this study. ?*Howqualepis youngorum* sp. nov. (Chapter 3) and *Krasnoyarichthys* (Prokofiev 2002) were not included due to the

absence of cranial data in both taxa. *Pickeringia* gen. nov. is complete but not fully described and will be incorporated into future studies.

Tegeolepis clarki and *Kentuckia hlavini* from the Famennian of Ohio are included but are problematic as both forms are incompletely described and several characters featured in available reconstructions are suspect. For example, the reported presence of four infraorbitals in these taxa (Dunkle 1964) differs greatly from other Devonian taxa. *Stegotrachelus* was previously restored with a similar infraorbital arrangement (Gardiner 1963), but this has subsequently been reinterpreted as comprising two bones (jugal and lacrimal) as in the majority of Devonian actinopterygians (Swartz 2009). The congeneric status of *K. hlavini* with the type species, *K. deani* from the Early Carboniferous of Iowa (Eastman 1908), has been called into question (Friedman and Blom 2006).

The selection of Carboniferous taxa includes forms where either specimens were readily available or have had recent comprehensive descriptions with accompanying photographs of specimens. It should be noted that ray-finned Carboniferous diversity encompasses hundreds of species, many of which are poorly preserved or incompletely described. Personal observation of specimens of *Amblypterus, Cosmoptychius*, *Nematoptychius, Phanerosteon, Rhabdolepis* and *Watsonichthys* in the BMNH collections suggest that redescriptions are warranted for these Carboniferous genera.

PAUP 4.0b10 for Microsoft Windows was used to perform a branch-and-bound search, the results processed on Maclade 2.0 (see appendix). Any phylogenetic analysis of this nature is hampered by the imperfect preservation of Devonian actinopterygians from outside the Gogo Formation where specimens lack the combination of near-complete dermal and

endochondral preservation. Potentially important characters of the braincase must therefore be excluded from this restricted Devonian- Early Carboniferous dataset.

This analysis represents the first use of the new anatomical information of *Moythomasia durgaringa* detailed in Chapter 6. A complete pectoral fin of *Howqualepis rostridens* was not figured in the original description of that taxon (Long 1988) and fresh latex peels have revealed previously unrecognised posterior segmentation of the pectoral fin (Chapter 3), resulting in recoding from previous studies (Friedman and Blom 2006). A major revision of *Stegotrachelus finlayi* was forthcoming at the time of writing (Brian Swartz, personal communication) and subsequently published (Swartz 2009). The coding for *Stegotrachelus* was based on new photographs supplied by Brian Swartz.

OUTGROUP

TAXON	AGE	LOCALITY	DATA SOURCE
Guiyu oneiros	Ludlow	Kuanti Fm, China	Zhu Min, pers.com
Miguashaia bureaui	Frasnian	Escuminac Fm, Canada	Cloutier 1996
Onychodus jandemarrai	Frasnian	Gogo Fm, W.Australia	Andrews et al. 2006
Uranolophus wyomingensis	Pragian	Wyoming	Campbell and Barwick 1988

DEVONIAN ACTINOPTERYGII

TAXON	AGE	LOCALITY and HORIZON	DATA SOURCE
Cheirolepis canadensis	Frasnian	Escuminac Fm, Canada	Arratia and Cloutier 1996
Cheirolepis schultzei	Givetian-Frasnian	Denay Limestone, Nevada	Cloutier and Arratia, 2004
Cheirolepis trailli	Eifelian-Givetian	Old Red Sandstone,Scotland	Pearson and Westoll 1979
Cuneognathus gardineri	Famennian	Obrutschew Bjerg,Greenland	Friedman and Blom 2006
Donnrosennia schaefferi	Givetian	Aztec Siltstone, Antarctica	Chapter 2
Gogosardina coatesi	Frasnian	Gogo Fm, W.Australia	Chapter 4
Howqualepis rostridens	Givetian	Mt Howitt, Victoria	Long 1988, Chapter 3
Kentuckia hlavini	Famennian	Cleveland Shale,Ohio	Dunkle 1964
Limnomis delaneyi	Famennian	Catskill Fm, Pennsylvania	Daeschler 2000
Mimipiscis bartrami	Frasnian	Gogo Fm, Australia	Chapter 5
Mimipiscis toombsi	Frasnian	Gogo Fm, Australia	Chapter 5
Osorioichthys margini	Famennian	Famenne Fm, Belgium	Taverne 1997
Tegeolepis clarki	Famennian	Cleveland Shale, USA	Dunkle and Schaeffer 1974

CARBONIFEROUS ACTINOPTERYGII

TAXON	AGE	LOCALITY	DATA SOURCE
Aesopichthys erinaceus	Namurian	Bear Gulch, Montana	Poplin and Lund 2000
Cyanorhis bergeraci	Namurian	Bear Gulch, Montana	Lund and Poplin 1997
Kalops diophrys	Namurian	Bear Gulch, Montana	Poplin and Lund 2002
Kalops monophrys	Namurian	Bear Gulch, Montana	Poplin and Lund 2002
Mansfieldiscus sweeti	Lower Carb.	Mansfield, Victoria	Long 1988
Melanecta anneae	Namurian	Manse Burn Fm, Scotland	Coates 1998
Novagonatodus kasantsevae	Lower Carb.	Mansfield, Victoria	Holland et al. 2006
Paratarassius hibbardi	Namurian	Bear Gulch, Montana	Lund 2002
Proceramala montanensis	Namurian	Bear Gulch, Montana	Poplin and Lund 2000
Tarassius problematicus	Visean	Calciferous Sandstone, Scotland	Lund 2002
Wendichthys dicksoni	Namurian	Bear Gulch, Montana	Lund and Poplin 1997
Woodichthys bearsdeni	Namurian	Manse Burn Fm, Scotland	Coates 1998

TABLE 2. List of fossil taxa included in the analyses.

8.4.1 Character list

The following is the character list used in phylogenetic analysis. Multistate characters marked with an asterisk are ordered.

1. Rostral (or equivalent ethmoid bone) - contributes to biting margin.

0 = absent

1 = present

Source: Friedman and Blom (2006), Character 1

2. Premaxillae, shape of

0 = wider than deep

1 = depth approximately equal to width

Source: Friedman and Blom (2006), Character 2

3. Postrostrals *

0 = absent

1 = mosaic of small bones

2 = median postrostral with or without accessory bones.

Source: Lund (2000), Character 6; Zhu et al. (2009), Character 2; Cloutier and Arratia (2004), Characters 47-48; Friedman (2007), Character 6.

Notes: Friedman and Blom (2006) code simply for the presence or absence of postrostrals.

4. Single median rostral, contacting nasals laterally, frontals/postrostrals posteriorly.

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 4

5. Rostral (or equivalent ethmoid bone) with transverse ornamentation.

0 = false

1 = true

Source: Friedman and Blom 2006, Character 5

6. Posterior nostril in communication with orbital fenestra

0 = false

1 = true

Source: Friedman and Blom 2006, Character 6

7. Posterior nostril - contribution to margin by premaxillae

0 = false

1 = true

Source: Friedman and Blom 2006, Character 7

8. Nasal bone as single consolidated ossification

0 = false - multiple bones carry supraorbital canal.

1 = present

Source: Friedman and Blom 2006, Character 8

9. Pineal foramen

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 9

10. Parietals (= sarcopterygian postparietal) - shape

0 = rectangular - long axis parallel to midline

1 = subquadrate/square.

Source: Friedman and Blom 2006, Character 10

11. Frontals (=sarcopterygian parietals) - relative size

0 = frontal shorter than parietal

1 = frontal roughly equal to parietakl

2 = frontal longer than parietal

Source: Friedman and Blom 2006, Character 11

12. Intertemporal, relative length

0 = shorter than supratemporal

1 = of similar length to supratemporal

2 = of greater length to supratemporal

Source: Friedman and Blom 2006, Character 12

13. Intertemporal, contact with supratemporal anterior to that between frontal and parietal

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 13

14. Dermosphenotic, contact with frontals blocked by intertemporal or dermopterotic

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 14

15. Extrascapulae, number of paired examples.

0 = one pair

1 = two pair

Source: Friedman and Blom 2006, Character 15

16. Lacrimal, anterior expansion

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 16

17. Jugal - notch in anterior margin.

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 17

18. Suborbital bones - anamesic bones between jugal and preoperculum.

0 = absent

1 = present, single or single vertical row.

2 = present, multiple vertical rows.

Source: Friedman and Blom 2006, Character 18

19. Accessory operculum

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 19

20. Lateral gulars *

0 = large with rounded posterolateral profile

1 = equivalent in area to 3 branchiostegal rays, angular posterolateral profile.

2 = of similar size and shape to adjacent branchiostegal rays.

Source: Friedman and Blom 2006, Character 20

21. Mandibular canal - course of canal.

0 = traces ventral margin of jaw along entire length.

1 = arches dorsally in anterior half of jaw.

Source: Friedman and Blom 2006, Character 21

22. Dentary with conspicuously reflexed distal tip.

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 22

23. Infradentaries, number of. *

0 = more than two

1 = two (angular and surangular)

2 = one (angular only)

Source: Friedman and Blom 2006, Character 23

24. Enlarged parasymphysial teeth

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 24

25. Acrodin caps on teeth

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 25

26. Porous ganoine ornamentation on lower jaw

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 26

27. Mentomeckelian region ossified.

0 = true

1 = false

Source: Friedman and Blom 2006, Character 27

28. Parasphenoid - with ascending process.

0 = false

1 = true

Source: Friedman and Blom 2006, Character 28

29. Parasphenoid - anterior tripartite subdivision.

0 = false

1 = true

Source: Friedman and Blom 2006, Character 29

30. Ganoine

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 30 (in part)

Notes: The presence of prismatic or non-prismatic ganoine is not coded as in Friedman and Blom (2006) owing to the uncertainty of this state in the majority of examined taxa.

31. Scale rows, number of

0 = fewer than 60

1 = more than 60

Source: Friedman and Blom 2006, Character 31

32. Scales - Peg-and-socket articulation between scales with narrow based peg.

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 32

Notes: The presence of narrow-based dorsal pegs on the scales is considered here to be a primitive character, based on the presence of such structures on the basal sarcopterygians

Guiyu (Zhu et al. 2009) and *Psarolepis* (Zhu pers. comm.)

33. Scales - anterodorsal extension

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 33

34. Scales

0 = macromeric

1 = micromeric

Source: Friedman and Blom 2006, Character 34

35. Scales - well-developed pores/punctae on ganoine surface

0 = false

1 = true

Source: Friedman and Blom 2006, Character 35

36. Scales - curved ridges coursing along anterior margin of scale, truncating transverse ornament ridges.

0 = false

1 = true

Source: Friedman and Blom 2006, Character 36

37. Fringing fulcra

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 37 (in part)

Notes: States for character 37 regarding fringing fulcra have been simplified to "absent or present" due to a reappraisal of the diversity and form of fulcra in early actinopterygians by Gloria Arratia (Arratia 2009). According to that study, the dichotomy of such structures into "modified lepidotrichs" and "true fringing fulcra" as presented in Friedman and Blom (2006) is inaccurate. A closer examination of the spinose structures on the leading fin-edges of early actinopterygians is warranted (Arratia, pers. comm) .

38. Pelvic fins

0 = present

1 = absent or greatly reduced

Source: Friedman and Blom 2006, Character 38

39. Presupracleithrum

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 39

40. Scapulacoracoid with horizontal plate

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 40

41. Pectoral fin - anterior rays embrace propterygium

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 41

42. Pectoral fin - metapterygium enlarged relative to radials.

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 42

43. Pectoral fin insertion

0 = into basal fleshy lobe

1 = directly into lateral flank.

Source: Friedman and Blom 2006, Character 43

44. Pectoral fin segmentation

0 = roughly even segmentation to fin-base

1 = proximal segments account for up to 50% of length from base to fin-tip

2 = proximal segments account for over 50% of length from base to fin-tip.

Notes: Character states for character 44, regarding the segmentation of the pectoral fin, were expanded. A complete pectoral fin of *Howqualepis* was not figured in the original description (Long 1988) and fresh latex peels have revealed extensive posterior segmentation (Chapter 3). Both *Howqualepis* and *Donnrosenia* have unsegmented proximal anterior lepidotrichia on the pectoral fin that are longer than in most other examined forms, accounting for more than 60% the length of the fin. *Tegeolepis* is the only Devonian taxon in

which all pectoral lepidotrichia have long, unsegmented regions.

45. Pelvic fin insertion.

0 = short based

1 = long based

Source: Friedman and Blom 2006, Character 45

46. Caudal fin - epichordal lobe

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 46

47. Fulcra on median dorsal surface of caudal fin

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 47

48. Scutes anterior to dorsal fin.

0 = few - limited to region anterior to dorsal fin.

1 = complete series from occipit to dorsal fin

2 = no median dorsal scutes anterior to dorsal fin.

Source: Friedman and Blom 2006, Character 48

49. Ventral scutes between caudal and anal fins

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 49

50. Ventral scutes anterior to anal fin

0 = present

1 = absent

Source: Friedman and Blom 2006, Character 50

51. Anal fin - relative position to (2^{nd}) dorsal fin *

0 = shifted anterior to dorsal fin.

1 = opposite to dorsal fin

2 = shifted posterior to dorsal fin.

Source: Friedman and Blom 2006, Character 51

52. Dorsal fins, number of

0 = two

1 = one

Source: Friedman and Blom 2006, Character 52

53. Dermohyal

0 = absent

1 = present

Source: Friedman and Blom 2006, Character 53

54. Dermosphenotic *

0 = absent

1 = present - with distinct posterior ramus

2 = present - without distinct posterior ramus

Source: Friedman and Blom 2006, Character 54; Long et al. 2008, Character 54

55. Intertemporal - contact with parietal

0 = no contact

1 = contacts parietal laterally

2 = contacts parietal posterolaterally

56. Rostral - shape of

0 = widens anteriorly

1 = equal anteriorly and posteriorly

2 = narrows anteriorly

Source: Long et al. 2008, Character 58.

57. Quadratojugal as distinct ossification.

0 = present

1 = absent

Source: Lund et al. 1995, Character 47; Cloutier and Arratia 2004, Character 92.

Notes: None of the *Moythomasia* specimens from the Bergisch-Gladbach site possess a distinct quadratojugal.

58. Operculum - relative size.

0 = at least twice as high as suboperculum.

1 = less than twice as high as suboperculum.

Source: Lund and Poplin 2002, Character 43; Cloutier and Arratia 2004, Character 109.

59. Median extrascapular

0 = present

1 = absent

Source: Lund 2000, Character 20; Cloutier and Arratia 2004, Character 60 (in part)

60. Scales - anastomosing linear ornament

0 = absent

1 = present

Notes: New character. The presence of anastomosing ornament was used in the diagnosis of *Mimipiscis* (Chapter 4) and in separating *Moythomasia nitida* from *M. lineata* (Chapter 5).

61. Suboperculum - narrow, tapering anterodorsal process.

0 = absent

1 = present

Notes: New character. Elongate, tapering anterodorsal processes are prominent features on the subopercular of most Gondwanan Devonian actinopterygians and *Cheirolepis*. It is not considered homologous to the accessory operculae of some taxa as *Donnrosenia* possesses both accessory operculae and anterodorsal processes.

62. Supratemporal - narrow anterolateral flange forming ventral margin of spiracular opening.

0 = absent

1 = present

Notes: New character, unambiguously present only in the two *Mimipiscis* spp.

63. Extrascapulae - medially-directed branch of sensory canals.

0 = present

1 = absent

Note: New character. The three species of *Moythomasia* are unique among the examined taxa in lacking a medial branch of the sensory canals as they pass through the lateral extrascapulae.

64. Body form

0 = fusiform elongate

1 = fusiform robust

2 = deep bodied

3 = anguilliform

Source: Poplin and Lund 2002, Character 0 (in part); Long et al. 2009, Character 68

Notes: In this analysis, a fish is considered to be elongate when its standard length is at least 4 times greater than its height and robust when the standard length is less than 4 times greater than height.

65. Serrated linear ganoine ornament on skull roof

0 = absent

1 = present

Notes: New character. The three species of *Moythomasia* are unique among examined taxa in possessing elongate linear dermal ornament with "herring-bone" serrations along their length (Chapter 5).

66. Preoperculum - vertical linear ornament

0 = absent

1 = present

Notes: New character. Widely spaced vertical linear ridges on the anteriodorsal ramus of the preoperculum is a character restricted to the Bergisch-Gladbach species of *Moythomasia* (= *M. nitida* and *M.striata*).

67. Jaw suspension

0 = horizontal

1 = vertical

68. Rostral notch

0 = absent

1 = present

Source: Lund and Poplin 1997, Character 7.

Notes: A key synapomorphy of the Rhadinichthyidae in Lund and Poplin (1997). The rostral notch refers to the incomplete upper jaw margin in some taxa owing to the truncated ventral margin of the median rostral.

69. Antorbital bone

0 = absent

1 = present

Source: Cloutier and Arratia 2004, Character 78.

70. Dermopterotic

0 = absent

1 = present

Source: Gardiner and Schaeffer 1989, Character 1; Cloutier and Arratia, Character 70

Note: Here assumed to represent the fusion of the intertemporal and supratemporal.

71. Infraorbitals - number of.

0 = two (jugal and lacrimal)

1 = more than two.

Source: Gardiner and Schaeffer 1989, Character A9, Cloutier and Arratia (2004), Character 78

72. Mandibular canal

0 = not passing through dentary

1 = primarily carried by dentary.

Source: Patterson (1982), Character 7; Cloutier and Arratia (2004), Character 141.

73. Pectoral fin - perforated propterygium.

0 = absent

1 = present

Source: Gardiner et al. (2005), Character 39 (in part)

74. Dermal intracranial joint

0 = present

1 = absent

Source: Long et al. (2006), Character 3; Zhu et al. (2009), Character 21

75. Branchiostegal rays

0 = 12 or more

1 = fewer than 12

Source: Cloutier and Arratia (2004), Character 114

76. Branchiostegal rays - 1st ray ventral to suboperculum.

0 = of similar depth to adjacent branchiostegal ray.

1 = deeper than 2nd branchiostegal ray.

Source: Cloutier and Arratia (2004), Character 113

77. Jugal canal

0 = present

1 = absent

Source: Lund et al. (1995), Character 46; Cloutier and Arratia (2004), Character 136; Zhu et al. (2009), Character 117.

78. Dorsal fin - length of base *

0 = ends far from caudal fin

1 = ends close to caudal fin

2 = merged with caudal fin

Source: Lund (2000), Character 58; Cloutier and Arratia (2004), Character 161.

79. Anal fin - length of base *

0 = ends far from caudal fin

1 = ends close to caudal fin

2 = merged with caudal fin

Source: Lund (2000), Character 66; Cloutier and Arratia (2004), Character 167.

80. Pectoral fin rays

0 = fin rays adjacent to one another for their entire length.

1 = pectoral fin fan-shaped, with rays radiating distally.

81. Suborbital bones

0 = absent

1 = present

Source: Gardiner and Schaeffer (1989), Character 9; Cloutier and Arratia (2004), Character 84.

82. Maxilla, posteroventral overlap of lower jaw.

0 = none or minimal overlap.

1 = pronounced posteroventral overlap.

Source: Lund (2000), Character 31; Poplin and Lund (2000), Character 18; Cloutier and Arratia (2004), Character 18; Zhu et al. (2009), Character 79.

8.4.2 Results

The analysis produced 12 most parsimonious trees (L = 287, CI = 0.3554, RI = 0.6408, RC = 0.2277). A strict consensus of these trees is presented (Figure 8.2). The apomorphy list is presented as Appendix IV.

While this study is not primarily concerned with the affinities of this outgroup taxon, it is interesting to note that *Guiyu*, which combines sarcopterygian and classical stem-actinopterygian characters, keyed out in a polytomy with the Sarcopterygii and Actinopterygii. As indicated in the diagnosis, the monophyly of the Actinopterygii is well supported with 12 unambiguous characters: posterior nostril in communication with orbital fenestra; frontals equal or longer than parietals; loss of enlarged parasymphysial teeth (regained in *Tegeolepis* and *Howqualepis*); the presence of fringing fulcra, dermohyal, and tripartite dermosphenotic; loss of the median extrascapular (regained in some post-Devonian taxa); mandibular canal primarily carried by the dentary; absence of a dermal intracranial joint; 12 or more branchiostegal rays (reduced in some post-Devonian taxa); absence of a jugal canal and the absence of numerous small suborbital bones.

Cheirolepis occupies the basal position within the Actinopterygii, followed by *Osorioichthys*, agreeing with Friedman and Blom (2006) and Taverne (1997). Above this, the close phyletic proximity of *Tegeolepis* to *Howqualepis* presented by Friedman and Blom is reaffirmed, although *Donnrosenia* remains as sister-taxon to the the Victorian form within a monophyletic Howqualepididae. The sister-relationship between *Tegeolepis* and the Howqualepididae is poorly supported, based on an anterior expansion of the lacrimal and the absence of mentomeckelian ossification, both features unknown in *Donnrosenia.* The monophyly of the Howqualepididae (*Howqualepis* + *Donnrosenia*) is unambiguously

supported by an open pineal foramen, intertemporal-supertemporal contact anterior to frontal-parietal contact, long-based pelvic fins, anastomosing scale-ornament and a tapering subopercular process.

A sister-taxon relationship is maintained between *Limnomis* and *Cuneognathus* as in Friedman and Blom (2006) based on the absence of pelvic fins and the lack of dorsal pegs on the flank scales. One key synapomorphy that previously united the two taxa, the presence of curved ridges coursing along the anterior scale margin combined with transverse ridges along the remainder of the scale (character 36 in Friedman and Blom 2006) is not resolved in this study due to the presence of the feature in *Mansfieldiscus* and *Novagonatodus* (Long 1988), both of which were not included in the Devonian-only analysis of Friedman and Blom.

The remainder of taxa all fall within a large clade, supported by having subquadrate parietals; enlarged frontals; and a pronounced maxillary overlap of the lower jaw. Within this grouping, the majority of taxa fall within one of two large groupings. One contains all of the "*Stegotrachelus*-grade" (= small, generally robust stem-actinopterans with a full series of dorsal scutes) forms of the Late Devonian along with *Mansfieldiscus* and *Novagonatodus* of the Mansfield Group of Victoria. The other large clade contains the totality of examined Bear Gulch taxa, including the Tarassidae comprising the Scottish *Tarassius* along with the Bear Gulch *Paratarassius*. Forming an unresolved polytomy with these two major divisions are *Kentuckia hlavini* and a clade comprising *Melanecta* and *Woodichthys* from the Namurian of Bearsden, Scotland.

The "*Stegotrachelus*-grade" grouping is primarily united in having an open pineal foramen; robust body forms and a complete series of median scutes extending from the head to the dorsal fin. The two Mansfield taxa (*Mansfieldiscus* and *Novagonatodus*) are the only Carboniferous members to fall within this group, forming a small subclade whose members lack intertemporals and possess anamesic suborbital bones. Within the "*Stegotrachelus*-grade" grouping, the congeneric status of the three species of *Moythomasia* is unambiguously supported by their comparatively long intertemporals, having four extrascapulae with no median-branching of the occipital canal and in their distinctive serrated cranial ornamentation. The monophyly of the Mimiidae (*Mimipiscis* + *Gogosardina*) is supported by the lack of a surangular on the lower jaw, the absence of ascending processes on the parasphenoid and in their moderately enlarged proximal lepidotrichia. The sister-taxon relationship between *Mimipiscis* + *Moythomasia* resolved by Cloutier and Arratia (2004) is not supported by this analysis.

The "Bear Gulch" clade is unambiguously supported in having parietals that are wider than long; small lateral gulars and the presence of an antorbital bone. An extremely basal position for the tarrassids as the sister-group to all other actinopterygians, as presented by Lund (2002), is not supported. The two genera are positioned as derived members of the "Bear Gulch" clade as the sister group to *Kalops*.

The resulting cladogram presents a striking degree of regional unity among the Early Carboniferous forms, with all taxa grouping into three clades that appear to be divisible on geographic as well as anatomical grounds. The two Scottish Manse Burn taxa (*Melanecta* and *Woodichthys*) group together in a polytomy with *Kentuckia*, the "*Stegotrachelus*-grade" and the Bear Gulch clades. Both Victorian Mansfield taxa share a sister-group relationship

among the "*Stegotrachelus*-grade" forms. All the forms from Bear Gulch, Montana, group together along with the Scottish *Tarrasius*. Additionally the Rhadinichthyidae, to which *Cyanorhis* and *Wendichthys* belong, includes many British taxa (Moy-Thomas and Dyne 1938).

Given that the sarcopterygian record extends well into the Silurian, while undisputed complete actinopterygians do not appear until the Middle Devonian, it is clear that much of the early evolutionary history of the ray-finned fishes remains unknown. By the Middle-Late Devonian, the majority of forms represented in the fossil record appear to belong to a single widespread radiation (the "*Stegotrachelus*-grade" forms) with a lesser diversity from other lineages (*Cheirolepis*, *Osorioichthys, Tegeolepis,* and *Kentuckia*). Based on this analysis, it is hypothesized that the enormous diversity of the ray-finned fishes during the Early Carboniferous arose in from multiple Devonian lineages, with the majority of examined taxa falling within a large Euramerican grouping (the Bear Gulch clade). The "*Stegotrachelus*-grade" forms, which were more diverse in the Late Devonian, persist at Mansfield, Victoria (*Mansfieldiscus* and *Novagonatodus*), while a possible third group is represented in the Manse Burn Formation, Scotland (*Melanecta* and *Woodichthys*).

A preliminary analysis presented by Long, Choo and Young (2008) suggested the possibility of an exclusive, primarily Gondwanan radiation containing all the Gogo taxa, the Howqualepididae and (*Limnomis* + *Cuneognathus*). This concept is not supported in the current analysis. The monophyly of *Moythomasia* was questioned in the same study but is supported here as also it is in Friedman and Blom (2006). However, the analysis does still suggest a limited degree of regional endemism within Devonian Gondwana with the Mimiidae restricted to marine deposits of Frasnian Western Australia and the

Howqualepididae restricted to Givetian freshwater deposits of Eastern Gondwana. The Gogo *Moythomasia durgaringa* does however appear to be representative of a wide-ranging Late Devonian genus.

The presence of a surangular on *Moythomasia* and the Howqualepididae suggests that the absence of this feature is a derived state of the Mimiidae. Gardiner (1984) considered *Moythomasia durgaringa* to be more advanced than *Mimipiscis* due to the latter lacking ascending processes on the parasphenoid, a feature shared with *Cheirolepis trailli*. However, the presence of ascending processes in *Howqualepis* and *Tegeolepis* suggests that their absence in *Mimipiscis* is the result of a derived loss of these structures rather than a retained primitive feature.

Donnrosenia and *Howqualepis* are determined in Chapter 3 to represent sister taxa within a monophyletic Howqualepididae. The presence of a grade of Devonian actinopterygian so far found exclusively in Middle Devonian freshwater deposits of southeastern Australia and Victoria Land, Antarctica highlights the close biogeographical similarity between the fossil faunas of these two regions. The apparent absence of these ray-finned fishes in Devonian sites outside this area also adds to a growing body of fossil evidence that indicates a regionally endemic freshwater vertebrate fauna within Middle Devonian Eastern Gondwana. Similarities in key taxa of placoderms (Young 1988, Young and Long 2005), acanthodians (Long 1983, Young 1989b, Young and Burrow 2004), chondrichthyans (Young 1982, 2007; Long and Young 1995) and dipnoans (Long 1992, 2003) have been well documented.

8.4.3 Biogeographical implications

Global comparisons between Devonian actinopterygian faunas are made difficult owing

to the general paucity of articulated remains in Gondwana. Articulated pre-Carboniferous ray-fins are unknown from South America, Africa and Asia. The record of articulated remains is restricted to Middle Devonian freshwater settings in Antarctica and southeastern Australia and the Frasnian Gogo reef fauna.

In the Givetian, Easterrn Gondwana and Euramerica had disjunct freshwater actinopterygian faunas, represented by *Cheirolepis* and *Stegotrachelus* in the North and the Howqualepididae in the south. By the Frasnian, the genus *Moythomasia* had attained a pan-global marine distribution and was present in both Euramerica and Australia, living alongside several apparently regionally endemic taxa (Mimiidae, *Pickeringia*). The available record corresponds with changes in the palaeogeography of other East Gondwanan vertebrates (Young et al. 2000, Young et al. in press) with strong endemism prior to the Late Devonian with increased cosmopolitanism towards the end of the period.

Recent studies indicate a relationship between *Howqualepis* (from the Givetian of Australia) and *Tegeolepis* (from the Famennian of North America). The two genera were resolved as sister-taxa by Friedman and Blom (2006). The analysis presented above supports a close phyletic proximity between the two genera, with *Tegeolepis* as the sister of a Gondwanan Howqualepididae (*Howqualepis* + *Donnrosenia*). Swartz (2009) does not support a monophyletic Howqualepidae, with *Donnrosenia* resolved as a more basal form, but maintains a sister-relationship between *Howqualepis* and *Tegeolepis*.

If the proposed close relationship to the Howqualepididae (or at least *Howqualepis*) is correct, the presence of *Tegeolepis* in the Cleveland Shale may be the consequence of a northern dispersal in the Late Devonian of a Gondwanan actinopterygian clade. Such a

dispersal corresponds closely with the biogeographic record for other key groups of vertebrates, particularly placoderms, that appear in Late Devonian Laurussia after an extended pre-Frasnian record in Eastern Gondwana including asterolepids (Young 1983, Panteleyev 1994), phyllolepids (Young and Long 2005) and groenlandaspids. The biogeographic dispersal of Gondwanan vertebrates into the northern hemisphere during the Late Devonian is discussed in detail by Young et al. (in press).

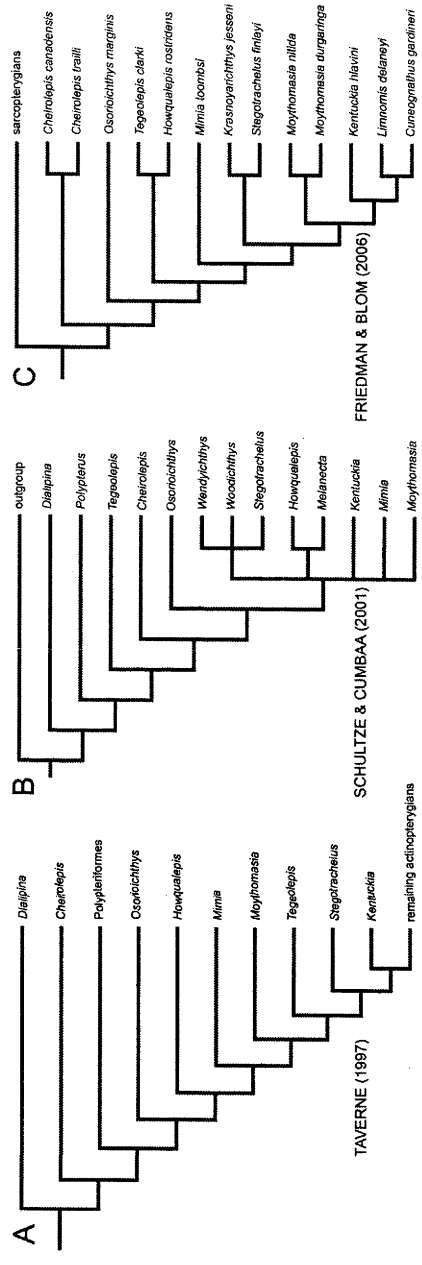


Figure 8.1
Cladograms produced from three recent phylogenetic analyses into the interrelationships of Devonian Actinopterygii.

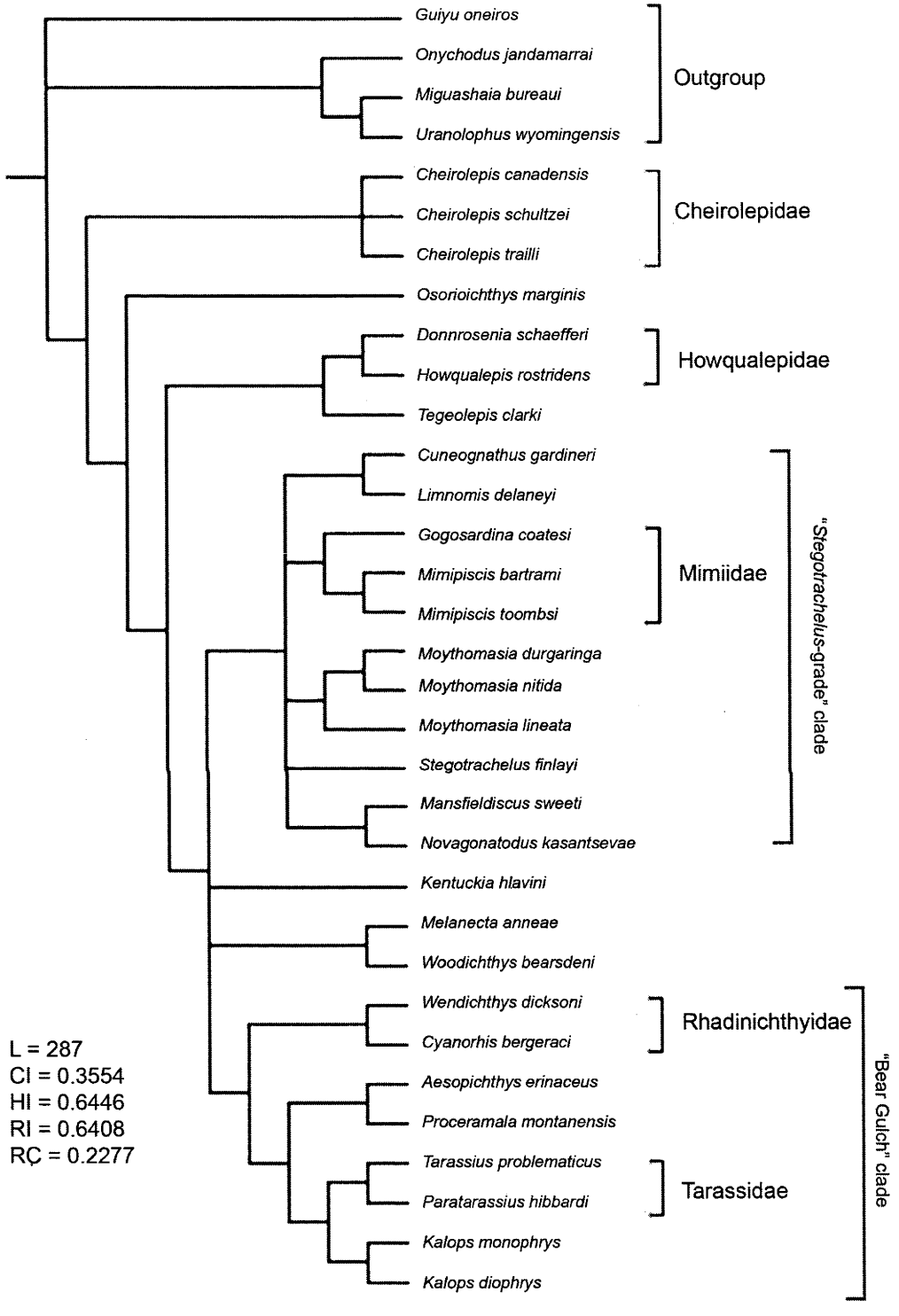


Figure 8.2
Strict consensus of 12 most parsimonious cladograms depicting relationships between Devonian and Early Carboniferous actinopterygians.

8.6 Conclusions

Based on the wealth of data collected during the last three years of research, the following conclusions are drawn:

1) The diversity of Middle-Late Devonian actinopterygians is greater than previously recognised. Newly described taxa in this thesis comprise *Donnrosenia schaefferi* from the Aztec Silstone, Antarctica; ?*Howqualepis youngorum* from the Bunga Beds, New South Wales; *Gogosardina coatesi*, *Mimipiscis bartrami* and *Pickeringia acanthophilus* from the Gogo Formation, Western Australia and *Moythomasia lineata* from Bergisch-Gladbach, Germany.

2) The Middle Devonian actinopterygians of the Bunga Beds, NSW; Mt Howitt, Victoria and the Aztec Siltstone, Antarctica represent a unique clade of elongate forms with extremely long proximal pectoral lepidotrichia: the Howqualepididae (*Howqualepis* and *Donnrosenia*). This contributes to a wider body of evidence indicating a regionally endemic freshwater ichthyofauna in eastern Gondwana during the Middle Devonian.

3) Material previously described as *Mimipiscis toombsi* (Gardiner 1984) comprises two distinct taxa, the true *M. toombsi* and *M. bartrami* sp.nov. The two species are separable on dermal skull proportions, the shape of the parasphenoid, body form and squamation.

4) A regionally endemic radiation of basal actinopterygians, the Mimiidae, was present in the Gogo Formation, comprising *Mimipiscis toombsi*, *M. bartrami*, *Gogosardina* and probably *Pickeringia*. These forms lacked ascending processes on the parasphenoid as well as a

surangular on the lower jaw. The phylogenetic analysis presented in Chapter 8 suggests that these are derived features for this group rather than retained archaic characters.

5) The genus *Moythomasia* represents the only Devonian ray-finned genus to have a distribution spanning both Gondwana and Euramerica. Four species (*M. perforata* from Latvia, *M. nitida* and *M. lineata* from Germany, and *M. durgaringa* from Gogo) are considered valid based on ornamentation, dermal-skull proportions and the absence of a medially-directed branch of the occipital canal on the extrascapulae. Scale-based taxa referred to this genus are considered *nomina dubia* due to the lack of unique derived features shared between the squamation of the four valid species.

6) The actinopterygian diversity of the Middle-Late Devonian comprised a diverse "*Stegotrachelus*-grade" radiation alongside additional aberrant genera. The immense diversification of the Actinopterygii in the Early Carboniferous involved several independent lineages.

8.7 Further research

Much additional work is possible from the Gogo Formation ray-finned fishes. Many new specimens were collected in the 2008 field season and await preparation, including a number of *Gogosardina*. Examination of these specimens is likely to reveal hithero unknown and diagnostically important details of the dermosphenotic, extrascapulae, infraorbitals and anterior parasphenoid. The braincase of *Gogosardina* is awaiting CT scanning and will undoubtedly reveal important information when compared with the neurocrania of other Gogo taxa. A fuller description of *Pickeringia* is also being prepared, hopefully augmented

by additional specimens.

Given the almost 30 million year gap in the fossil record between the earliest undoubted sarcopterygians and the earliest undoubted actinopterygian, it is likely that future fossil discoveries of indisputable ray-finned fishes from the Late Silurian-Early Devonian will clarify the origins of this extremely important group of vertebrates.

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APPENDIX 1

LONG, J. A.; CHOO, B. AND YOUNG, G.C. 2008. A new basal actinopterygian fish from the Middle Devonian Aztec Siltstone of Antarctica. Antarctic Science 20 : 393-412.

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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 subopercular, 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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Key words: Actinopterygii, Antarctica, *Donnrosenia*, Howqualepididae, new taxa

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 *Krasnoyarichthys 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

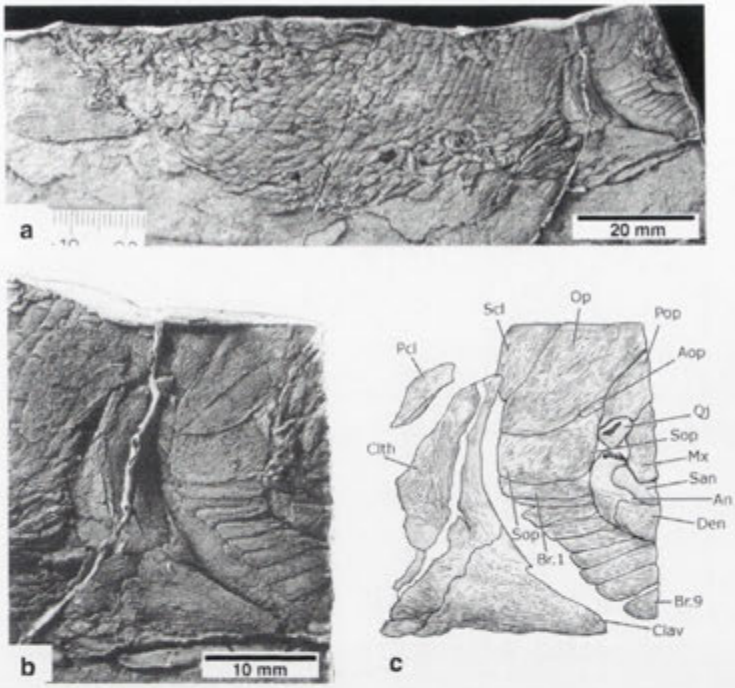


Fig. 1. *Donnrosenia schaefferi* gen. et sp. nov. Holotype (AM F54363) in right lateral view. Specimen is a latex cast whitened with ammonium chloride. **a.** photograph of entire specimen. **b.** Photograph. and **c.** drawing of the partial skull, opercular-gular series and pectoral girdle. Abbreviations: **An** = angular, **Aop** = accesory operculum, **Br.1** = 1st branchiostegal ray (counting from subopercular), **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** = subopercular.

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

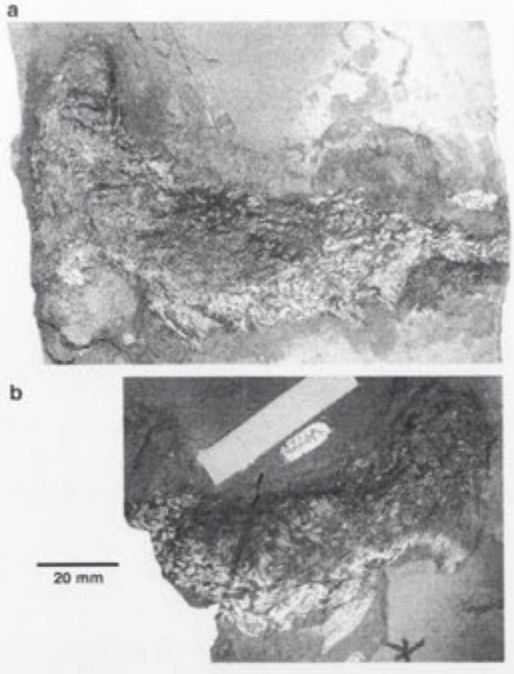


Fig. 2. *Donnrosenia schaefferi* gen. et sp. nov. Photographs of ANU V972. **a.** V972a in left lateral view, **b.** V972b/c in right lateral view. Specimens are bone remains and impressions in the rock.

(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 *Turinia 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).

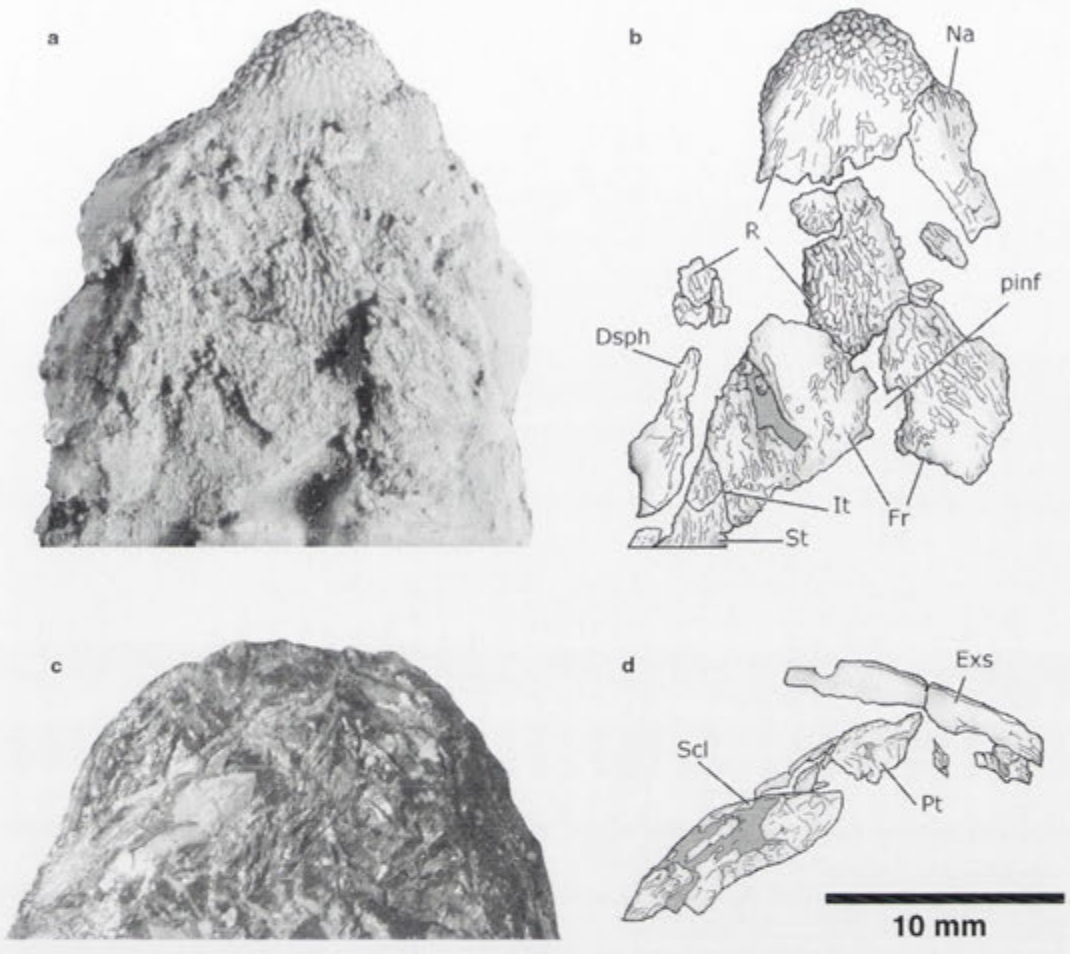


Fig. 3. *Donnrosenia schaefferi* gen. et sp. nov. Skull of ANU V972. **a.** Photograph, and **b.** line drawing of V972a showing anterior part of head in dorsal view. **c.** Photograph, and **d.** line drawing of V972b showing posterior part of head in ventral view. Abbreviations: Dsph = dermosphenotic, 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

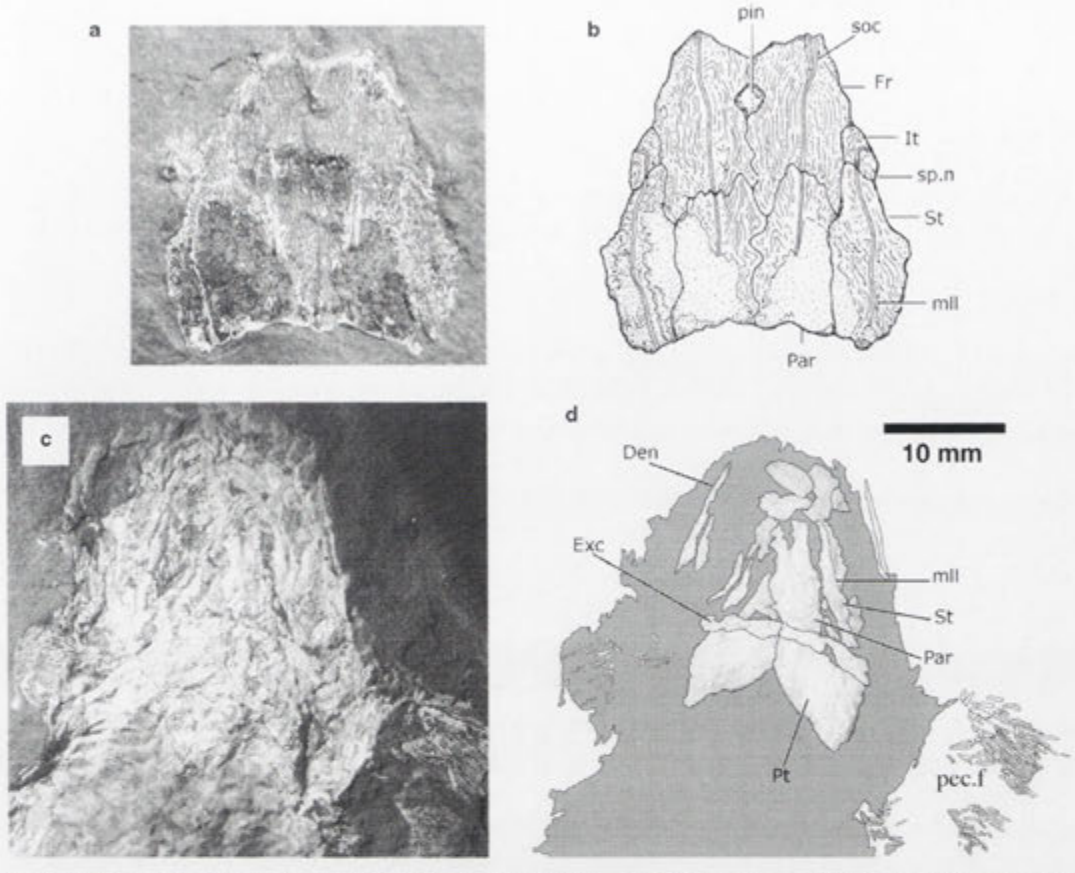


Fig. 4. *Donnrosenia schaefferi* gen. et sp. nov. Skulls in dorsal view. **a.** Photograph, and **b.** line drawing of ANU V2246. **c.** Photograph, and **d.** line drawing of AM F55938. Both specimens presented at the same scale. Abbreviations: Den = dentary, Exc = extrascapular, Fr = frontal, It = 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 *Krasnoyurichthys* 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.

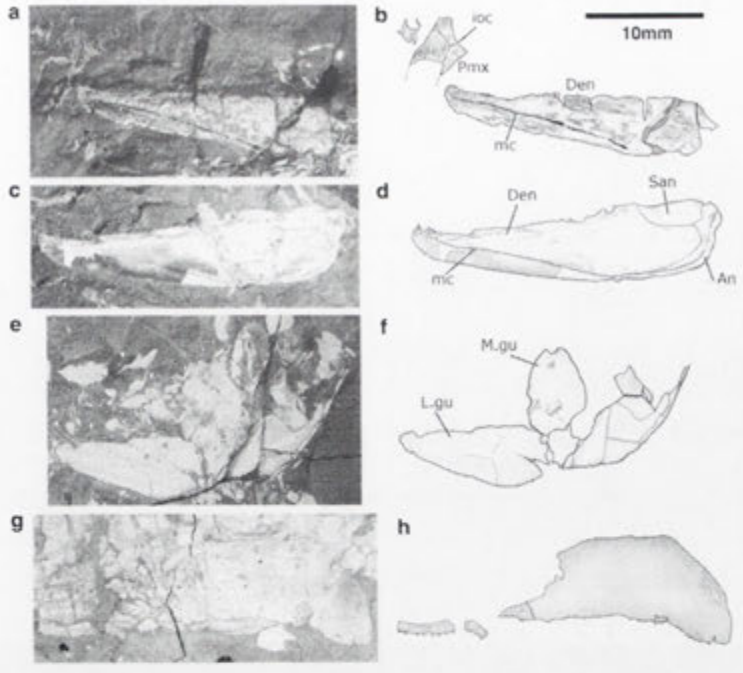


Fig. 5. *Donnrosenia schaefferi* gen. et sp. nov. Elements of the head as photographs and line drawings presented to scale. **a., b.** ANU V781a, partial left premaxilla and dentary in lateral view. **c., d.** ANU V815, left lower jaw in lateral view. **e., f.** ANU V781c, Lateral and median gular plates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

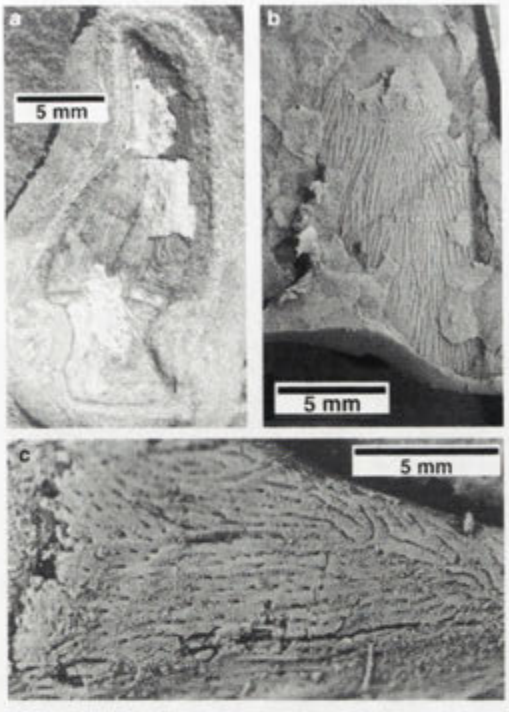


Fig. 6. *Donnrosenia schaefferi* gen. et sp. nov. **a.** ANU V763, left cleithrum in lateral view. **b.** ANU V886, left operculum in lateral view. **c.** AM F54363 (holotype), detail of right clavicle in lateral view showing porous ornamentation.

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

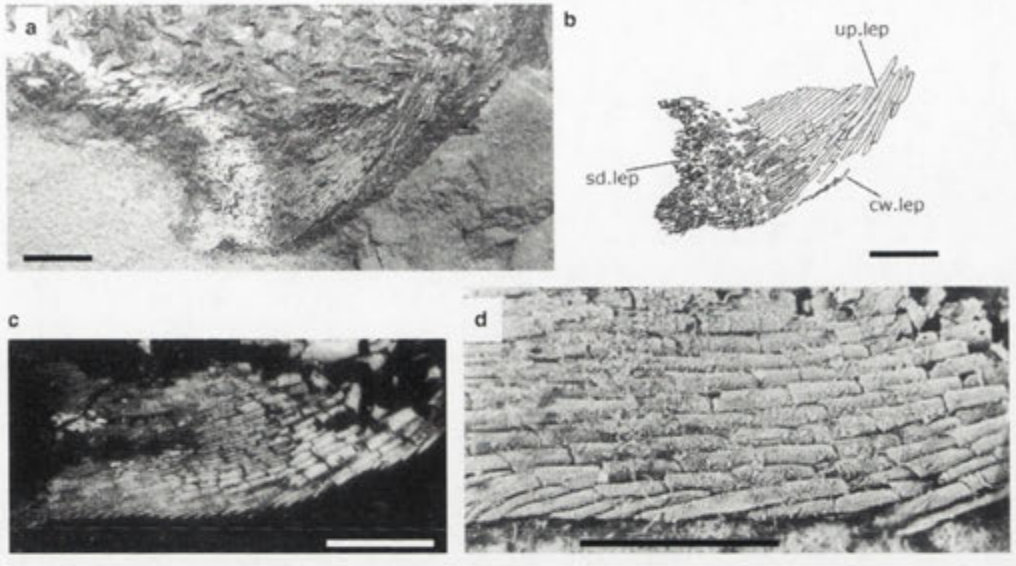


Fig. 7. *Donnrosenia schaefferi* gen. et sp. nov. Photographs of fins. **a.–c.** ANU V972b, **a.** right pectoral fin, **b.** right partial pelvic fin, **c.** anal fin. **d.** Holotype AM F54363, anal fin. (AM F54363), anal fin. Scale bar on each image = 5 mm. Abbreviations: cw.lep = cutwater lepidotrichia,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

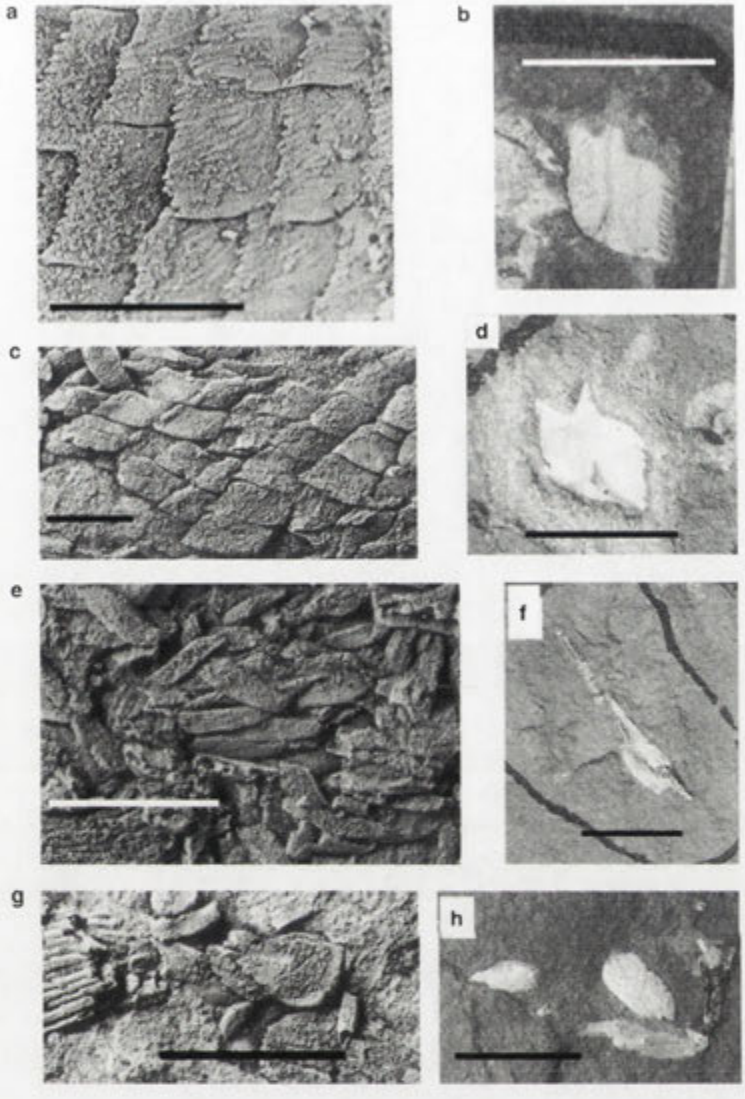


Fig. 8. *Donnrosenia schaefferi* gen. et sp. nov. Photographs of squamation. **a.** AM F54363 (holotype), Zone A scales in articulation. **b.** ANU 781b, single scale from Zone A. **c.** AM F54363 (holotype), Zone C scales. **d.** ANU 766, isolated scale from Zone B. **e.** AM F 54363 (holotype), Zone 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

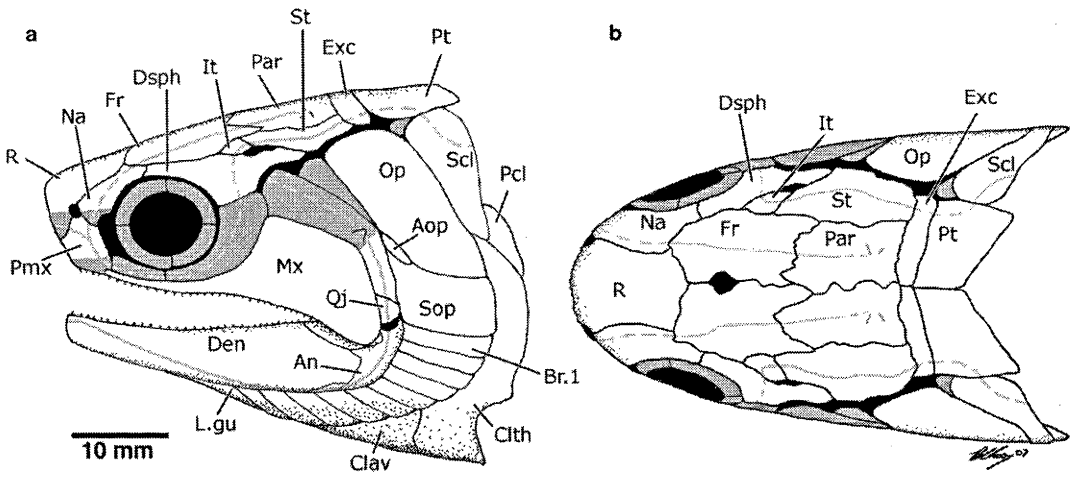


Fig. 9. *Donnrosenia schaefferi*, gen. et sp. nov. Restoration of the head in (**a**) lateral, and (**b**) dorsal views. Dark grey areas corresponds to missing sections of the skull. Light grey lines refer to the path of the sensory canal, continuous where observed on fossil specimens, broken where inferred 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

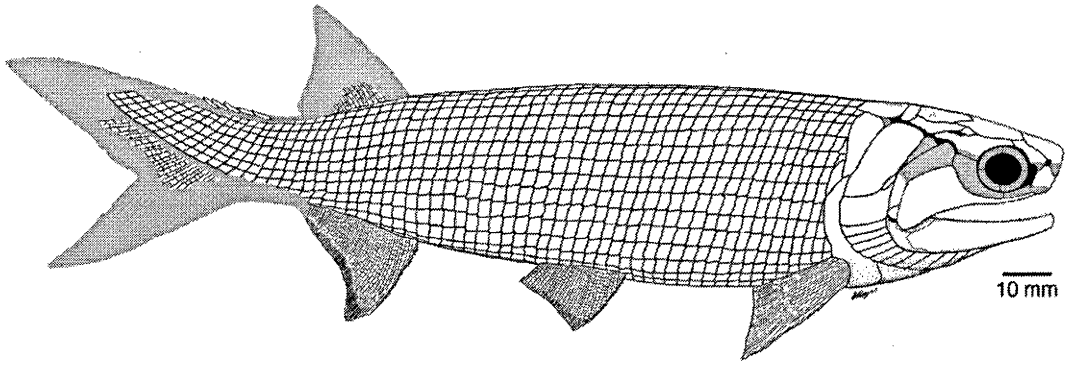


Fig. 10. *Donnrosenia schaefferi*, gen. et sp. nov. Restoration of the entire fish in lateral view. Grey blank areas refer to missing or poorly preserved sections of the animal.

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 it 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 sections 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 Trinajstic (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.

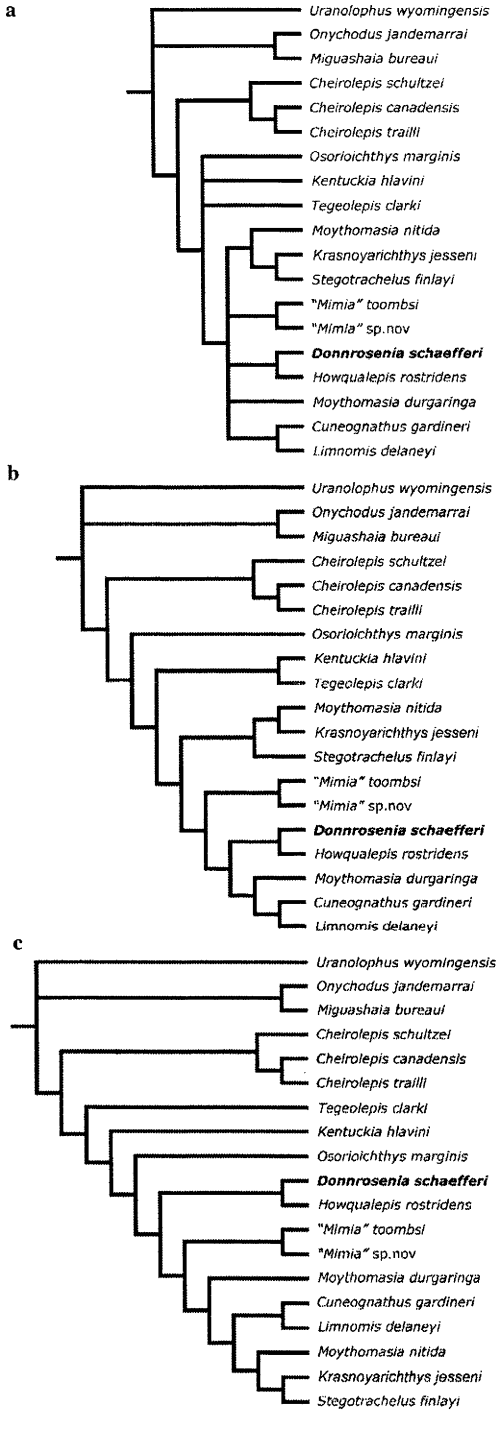
Zone E (dorsal scales, Fig. 2): Visible only as poorly preserved examples on ANU V972. Scales are rhomboidal, about twice as long as high.

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*, *Krasnoyarichthys* 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.

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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 nostrol 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 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
Cheirolepis canadensis	? 0 0 0 ? ? ? 0 1 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
Cheirolepis schultzei	0 0 0 0 ? ? 0 0 1 0	2 - - - 0 0 1 0 1 1	1 1 1 0 0 0 ? 0 ? /	? 0 0 1 0 0 1 ? 0 0
Cheirolepis trailli	0 0 0 0 ? 0 1 0 0 0	1 0 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
Cuneognathus gardineri	? ? 1 1 1 ? ? 1 0 1	2 0 1 0 0 ? ? ? 0 ?	? 0 ? 0 ? 0 ? ? ? /	1 0 0 1 0 1 2 1 1 ?
Donnrosenia schaefferi	? 1 1 1 0 ? ? 1 0 0	1 0 1 0 0 ? ? 0 1 1	1 1 1 0 ? 0 ? ? ? /	0 1 1 0 0 0 0 1 0 ? 1
Howqualepis rostridens	1 0 1 1 0 1 1 1 0 0	2 0 1 0 0 1 0 0 0 1	0 1 1 1 1 0 1 1 1 /	1 1 1 0 0 0 1 0 1 ?
Kentuckia hlavini	? ? 1 1 0 ? ? 1 1 1	2 1 0 1 0 ? 0 1 0 ?	0 0 ? 0 0 0 0 2 ? /	0 0 1 1 0 0 0 2 0 1
Krasnoyarichthys jesseni	? ? ? ? ? ? ? ? ? 1	2 0 0 ? 0 ? ? ? ? 1 ?	? ? ? ? ? ? ? ? ? /	0 1 1 0 0 0 0 2 0 0 ?
Limnomis delaneyi	1 1 1 1 1 1 0 1 0 1	2 0 0 0 0 ? 0 0 0 1	? 0 ? 0 1 0 ? ? ? /	0 0 1 0 0 1 2 1 1 ?
"Mimia" toombsi	0 1 1 1 0 1 1 1 0 0	2 0 0 0 0 0 0 0 0 1	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 0 0 1	0 0 2 0 1 0 ? 0 1 /	1 1 1 0 0 0 2 0 1 1
Moythomasia durgaringa	1 1 1 1 0 1 0 1 0 1	2 0 0 0 1 1 0 0 0 1	0 0 1 0 1 1 0 1 1 2	0 1 1 0 0 0 2 0 1 1
Moythomasia nitida	0 1 1 1 0 1 0 1 0 0	1 0 0 0 1 1 0 1 1 1	1 0 ? 0 ? 1 ? ? ? 2	0 1 1 0 1 0 2 0 1 1
Osorioichthys marginis	0 0 1 1 ? 0 1 1 1 0	1 0 0 0 1 0 0 1 0 0	1 0 1 0 ? 0 ? ? ? /	? 1 1 0 0 0 1 0 0 ?
Stegotrachelus finlayi	0 ? 1 1 0 1 0 1 0 1	2 ? ? ? 0 0 0 0 0 1	1 0 ? 0 ? 0 1 ? ? /	0 1 1 0 0 0 2 0 0 ?
Tegeolepis clarki	0 0 1 1 0 ? ? 1 1 0	1 0 0 0 ? 0 0 0 0 ?	0 1 1 1 0 0 1 2 1 /	1 1 1 1 0 0 0 0 ? ?
Onychodus jandemarrai	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
Miguashaia bureaui	0 0 ? ? ? ? ? 0 1 0	0 ? - ? 0 ? 0 ? 0 0	0 1 2 0 0 0 0 0 ? 0	0 0 0 0 - 0 0 0 0 ?
Uranolophus wyomingensis	? ? 0 0 - 0 ? ? 1 1	2 ? - ? ? ? ? ? 0 ?	0 0 0 0 0 ? 0 0 0 0	0 0 0 0 - 0 0 ? 0 0

	4 4 4 4 4 4 4 4 4 5	5 5 5 5 5 5 5 5 5 6	6 6 6 6 6 6 6 6 6 7	7
	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
Cheirolepis canadensis	0 ? 0 0 1 0 1 1 0 1	0 1 1 2 0 0 0 0 \ 0	1 0 0 0 ? 0 0 0 1 1	1
Cheirolepis schultzei	? ? 0 0 ? ? ? ? ? ?	? ? 1 2 0 0 0 ? - -	1 0 0 0 0 ? 0 ? 1 1	1
Cheirolepis trailli	0 0 0 0 1 0 1 1 1 1	0 1 1 2 0 0 0 0 0 0	1 0 0 0 1 0 0 0 1 1	1
Cuneognathus gardineri	? ? ? ? - 1 1 ? 1 ?	2 1 1 ? ? ? 1 1 0 0	0 0 0 0 1 0 0 1 1 1	1
Donnrosenia schaefferi	? ? 1 2 1 ? 1 1 1 1	1 1 ? 2 1 ? 1 2 0 0	0 0 1 0 0 ? 1 0 1 1	1
Howqualepis rostridens	1 0 1 2 1 0 1 1 1 1	1 1 1 2 1 0 1 2 1 0	0 0 0 0 0 1 1 0 1 1	1
Kentuckia hlavini	? ? ? 1 0 1 1 1 1 0	2 1 0 1 1 1 0 0 1 1	? 0 1 0 0 0 0 0 1 1	1
Krasnoyarichthys jesseni	? ? 1 0 0 ? 1 2 1 2	2 1 1 ? ? ? ? ? ? 1	1 1 1 1 1 ? 0 1 1 1	?
Limnomis delaneyi	? ? 1 / - 1 1 2 1 1	2 1 1 ? 0 2 1 1 1 0	0 0 0 0 0 0 1 1 1 1	1
"Mimia" toombsi	1 1 1 1 0 1 1 2 1 1	1 1 1 1 1 0 1 2 1 0	0 2 1 1 0 1 1 1 1 1	1
"Mimia" sp.nov	? ? 1 1 0 1 1 2 1 1	1 1 1 1 1 0 1 2 1 0	0 2 1 0 0 1 1 1 1 1	1
Moythomasia durgaringa	1 1 1 1 0 1 1 2 1 1	1 1 1 1 1 0 1 2 1 1	0 1 0 1 0 1 1 1 1 1	1
Moythomasia nitida	? 1 1 0 0 1 1 2 1 1	1 1 1 2 0 0 0 1 1 0	1 2 0 0 1 0 0 1 1 1	1
Osorioichthys marginis	1 ? 0 1 ? ? ? 1 ? ?	? ? 1 ? 1 1 0 2 1 0	0 2 0 1 1 ? 1 ? 1 1	1
Stegotrachelus finlayi	? ? 1 0 0 1 1 2 1 /	2 1 1 2 1 0 0 1 1 1	1 0 1 0 1 0 0 1 1 1	1
Tegeolepis clarki	? ? 1 2 0 ? 1 0 1 0	1 1 0 1 0 2 2 0 0 0	1 0 1 1 1 ? ? 0 1 1	1
Onychodus jandemarrai	- ? 0 0 0 0 0 0 0 0	1 0 0 0 0 0 0 2 0 -	1 0 0 1 0 ? 0 0 0 0	0
Miguashaia bureaui	- ? 0 0 0 0 0 0 0 0	1 0 0 0 0 ? 0 - 0 -	0 1 1 0 0 0 0 0 0 0	0
Uranolophus wyomingensis	- ? 0 ? ? ? 1 1 ? ?	? 0 0 0 ? ? 0 - 0 -	? 1 1 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 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 postions 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. Opeculum, 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).

APPENDIX II

CHOO, B. 2009. A basal actinopterygian fish from the Middle Devonian Bunga Beds of New South Wales, Australia. Proceedings of the Linnean Society of New South Wales (130), 37-46.

A Basal Actinopterygian Fish from the Middle Devonian Bunga Beds of New South Wales, Australia.

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Choo, B. (2009). A basal actinopterygian fish from the Middle Devonian Bunga Beds of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* **130**, 37-46.

A partial articulated skeleton of a basal actinopterygian fish is described from the Middle Devonian Bunga Beds of New South Wales. The specimen represents a new species and is questionably assigned as a congener of *Howqualepis rostridens* from the Middle Devonian of central Victoria. This represents the first record of an articulated postcranium of a Devonian ray-finned fish from New South Wales. The pectoral fin of *Howqualepis* is also redescribed based on a re-examination of Victorian material. The fin is broader in shape and less extensively unsegmented than previously recognised. The close similarity of the new form with contemporaneous taxa from Victoria and the Aztec Siltstone of Antarctica adds to an already wide body of evidence supporting a regionally endemic freshwater vertebrate fauna in the Middle Devonian of Eastern Gondwana.

Manuscript received 7 Feb 2008, accepted for publication 22 October 2008.

KEYWORDS = Actinopterygians, Bunga Beds, Devonian, fish, *Howqualepis*, New South Wales

INTRODUCTION

In stark contrast to their modern abundance and diversity, actinopterygians are a sparse component of most Devonian vertebrate assemblages. Australia is notable in producing some of the finest fossils of Devonian actinopterygians, the best known of which are exceptionally preserved specimens from the Frasnian Gogo Formation of northern Western Australia. Included within the assemblage are *Moythomasia durgaringa* (Gardiner & Bartram 1977, Gardiner 1984), the currently preoccupied *"Mimia" toombsi* (ibid), *Gogosardina coatesi* (Choo et. al, in press) and at least two additional forms (Choo, in prep).

Southeastern Australian fossil sites have also produced a substantial amount of early ray-finned fishes. The first record of Australian Devonian actinopterygians consisted of the isolated scales of *Ligulalepis toombsi* from the Lower Devonian Taemas-Wee Jasper Limestones of New South Wales (Schultze 1968). A subsequently discovered braincase and skull-roof was assigned to this genus (Basden *et al.* 2000, Basden & Young 2001). Long (1988) described *Howqualepis rostridens* based on numerous specimens from the Givetian Mt Howitt fauna of central Victoria (age revised in Young, 1999).

Adding to this Eastern Australian record is an incomplete but articulated fossil that was recently discovered by Gavin Young from the Middle Devonian Bunga Beds, near the shoreline at Bunga Beach in south coastal New South Wales. This represents the first discovery of an articulated Devonian actinopterygian postcranium from New South Wales. Subsequent repeated searches failed to recover additional material of this form (Gavin Young, pers. com.).

GEOLOGICAL SETTING

The Bunga Beds represent a thinly bedded sequence of carbonaceous shale and sandstone that comprises the lowest section of an extensively fossiliferous Devonian sequence (Fergusson et al. 1979, Young 2007). Young (2007, figs 1, 2) provides and up to date account of the lithology, fossil assemblage and possible age of the Bunga Beds. The age of the unit is poorly constrained and probably older than the Late Devonian age stated in recent

literature (Cas et al. 2000, Giordano and Cas 2001, Rickard and Love 2000).

The dark shales of the Bunga Beds are highly fossiliferous with abundant plant material and uncommon vertebrate remains (Young 2007, fig. 3), possibly representing a deepwater lacustrine depositional environment. The fossil fish fauna includes ischnacanthid acanthodians (Burrow 1996), several taxa of chondrichthyans including *Antarctilamna prisca* (Young 1982), originally described from the Givetian Aztec Silstone of Antarctica, and a possible tetrapodomorph sarcopterygian (Young 2007, table 1). The fossil ichthyofauna of the Bunga Beds seems impoverished due to the apparent absence of placoderms and dipnoans that are abundant in other southeastern Australian sites of a similar age.

MATERIALS AND METHODS

The fossil was recovered as a natural mould set within a matrix of dark shale. After collection, the specimen was split into part and counterpart and bone remnants removed. Bone margins were exposed with mechanical preparation and the impressions of the fish were examined using a latex rubber cast whitened with ammonium chloride. For comparison, fresh latex casts were made from the following specimens of *Howqualepis rostridens* in Museum Victoria (MV) = P.160745A, P.160782A, P.160788, P.160792B, P.160811, P.160822A, P.160851B, P.160857.

Abbreviations for actinpterygian dermal bones and other structures used in the text and figures are as follows: **an.f**, anal fin; **Br. 1**, 1st branchiostegal ray; **Br. 7**, 7th branchiostegal ray; **c.ful**, caudal (basal) fulcra; **Clav**, clavicle; **Clth**, cleithrum; **cw.lep**, cutwater of short lepidotrichial segments; **d.lep**, probable dorsal lepidotrichia; **f.ful**, fringing fulcra; **nm**, notochordal mass of caudal fin; **Op**, operculum; **Sop**, suboperculum; **pec.f**, pectoral fin; **pel.f**, pelvic fin; **pseg**, segmented posterior lepidotrichia on pectoral fin; **tfr**, terminal fringe of fine branching segments on pectoral fin; **vhl**, ventral hypochordal lobe of caudal fin; **useg**. unsegmented proximal lepidotrichia on pectoral fin.

SYSTEMATIC PALAEONTOLOGY

CLASS OSTEICHTHYES Huxley, 1880
SUBCLASS ACTINOPTERYGII, Cope, 1887
Family Howqualepididae Long, Choo and Young, 2008

Diagnosis (revised)

Basal actinopterygians with an open spiracular slit bordered by the intertemporal, dermosphenotic and supratemporal. Intertemporal is very small (less than 1/3 the size of parietals). Pineal foramen present on anterior half of the median frontal contact. Dermosphenotic is elongate and tripartite. Suboperculum has a prominent anterodorsal process. Body form is elongate and fusiform. Squamation macromeric; scales are rhombic with linear ganoine ornamentation. Fringing fulcra are spine-like terminal sections of the anterior fin rays, lacking median contact between the hemilepidotrichia. Longest anterior pectoral fin rays are proximally unsegmented for over 60% of their length. Median scute series on dorsal and ventral surface do not extend anteriorly to reach the head.

Remarks

Diagnosis slightly modified from Long et. al (2008) to incorporate the revised description of the pectoral fin and fringing fulcra of *Howqualepis* presented below.

Genus *?Howqualepis* Long, 1988
?Howqualepis youngorum sp. nov.

Etymology

After Professor Gavin Young (ANU) who discovered the holotype specimen and Mr Ben Young for conducting both the preparatory work as well as the key photography of the specimen.

Repository

The type and only known specimen is lodged in the collections of the Department of Earth & Marine Sciences, Australian National University, Canberra, represented in the text by the prefix **ANU V**.

Holotype.

ANU V2929a, b, an incomplete, partially articulated fish preserved laterally in part and counterpart. Consists of an incomplete opercular-gular series, cleithrum, clavicle, scales and all fins except the dorsal fin (Figs. 1-4). Collected by Gavin Young (ANU) from the Bunga Beds at Bunga Beach, south of Bermagui, New South Wales.

Diagnosis

A *Howqualepis* with more than 54 primary lepidotrichia on the anal fin and porous ornamentation on the cleithrum and clavicle.

Remarks

Tentatively assigned to the genus *Howqualepis*. The extensive unsegmented pectoral lepidotrichia of *?Howqualepis youngorum* sp.nov separates this taxon from all other Devonian actinopterygians except *Howqualepis rostridens* Long, 1988, *Donnrosenia schaefferi* Long, Choo and Young, 2008, and *Tegeolepis clarki* Newberry, 1888. *?H. youngorum* differs from *Donnrosenia* in that the unsegmented fin-rays account for more than 75% of the total length of the pectoral fin. *?H. youngorum* differs from *Tegeolepis* in possessing macromeric squamation, long-based pelvic fins and a segmented terminal fringe on the pectoral fin. Separable from *H. rostridens* in having porous (as opposed to entirely linear) ornament on the pectoral girdle and in having a larger anal fin (54+ vs 45 primary lepidotrichia).

DESCRIPTION

Overall body form

ANU V2929 is preserved in lateral aspect (Fig. 1). The anterior part of the specimen terminates at an oblique breakage margin, with elements of the opercular-gular series and pectoral girdle preserved along with the pectoral fin (Fig. 2). 2.5 cm behind this is an incomplete pelvic fin with patches of squamation present above and to the rear of the fin (Fig. 3). The largest preserved segment comprises the rear section of the fish, including well preserved anal and caudal fins along with extensive squamation (Fig. 4). The preserved sections suggest a highly elongate, fusiform body form similar to that of *Howqualepis rostridens* (Long 1988) and quite unlike the more compact and robust form of "*Mimia*" or *Moythomasia* (Jessen 1968, Gardiner 1984).

As preserved, the fossil measures slightly less than 12 cm from the anterior preserved edge of the clavicle to the posteriormost caudal scales. Assuming that the missing portions of the fish were of similarly proportions to that of *Howqualepis rostridens*, the complete fish would have measured about 14 cm from snout to caudal peduncle.

Opercular-gular series

A section of the dermal operculo-gular series of ANU V2929 is preserved in articulation and comprises

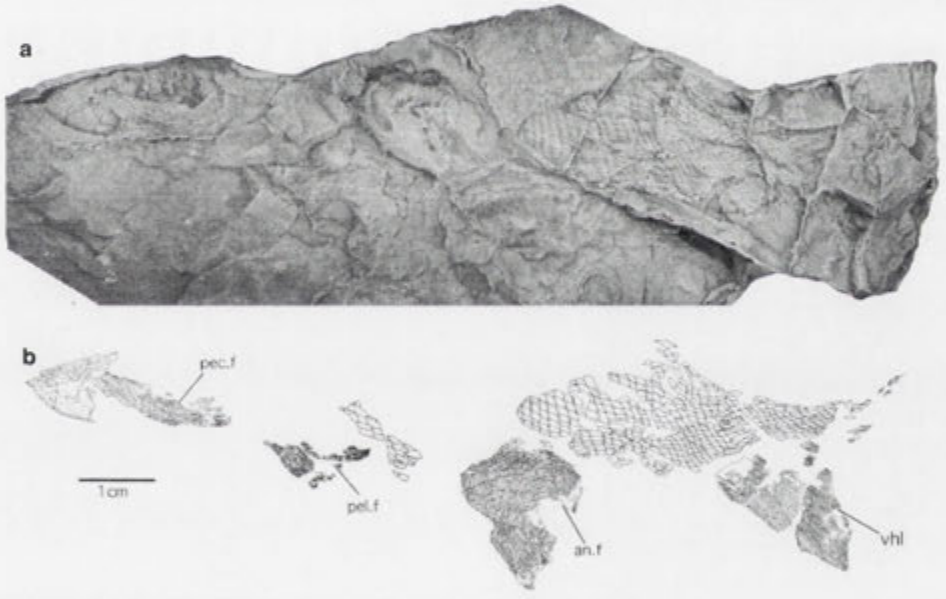


Figure 1. *?Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of holotype (ANU V2929A) showing the entire preserved fossil in lateral view. The specimen is a latex cast whitened with ammonium chloride.

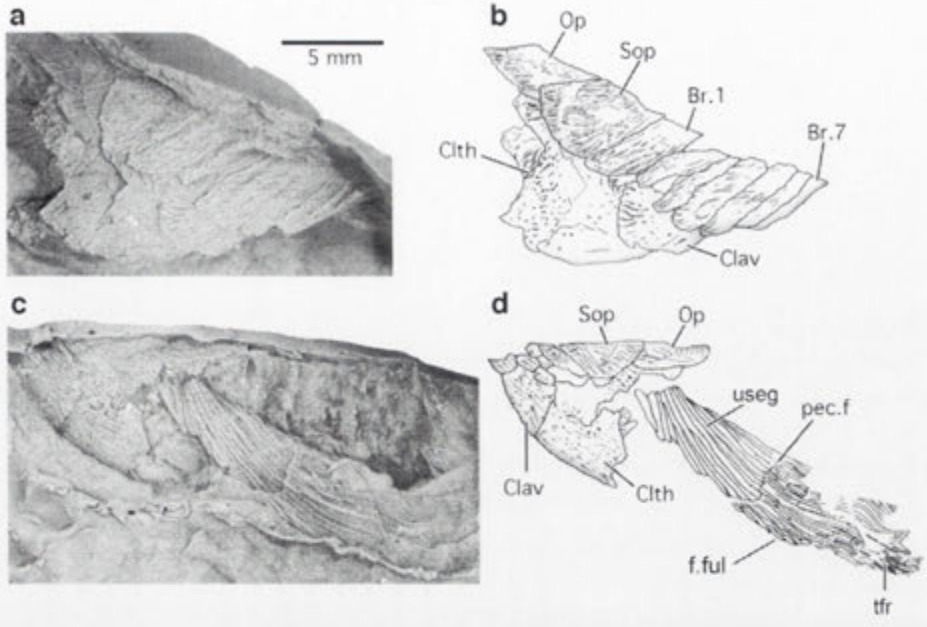


Figure 2. ?*Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the pectoral girdle and opercular-gular series of the holotype counterpart (ANU V2929B), c. photograph and d. line drawing of pectoral girdle, opercular-gular series and pectoral fin of the holotype (ANU V2929A).

a posteroventral fragment of the operculum, a partial suboperculum, and at least seven branchiostegal rays (Fig.2). The anterior portions of most of these elements are missing, the preserved sections terminating at a margin of clean breakage, suggesting that a substantial portion of the fossil, possibly including the skull, was lost prior to collection due to weathering.

The posterodorsal-most bone in the series is tentatively identified as the posteroventral fragment of an operculum. It is an oblong bone bone, missing the dorsal and anterior margins. The bone surface is ornamented with short, posterolaterally directed linear ridges. The suboperculum is rectangular with a convex posterior margin. Ornament consists of short linear ridges that extend to near the posterior bone margin.

At least seven branchiostegal rays are visible on ANU V2929b (Fig. 2). The first branchiostegal ray, whose dorsal margin is overlapped by the suboperculum, is more than twice as thick dorsoventrally as the other bones in the series. The 2nd ray is poorly preserved while the 3rd is narrower than the following two rays. Rays 6 and 7 are very narrow. Ornament on all bones in this series consists of short rostrocaudally directed ridges with little evidence of the tubercular ornament present on the laterally facing branchiostegals of *Howqualepis rostridens* (Long 1988).

Pectoral girdle

A partial cleithrum and clavicle (Fig. 2) have a similar overall shape to those of most early actinopterygians. The cleithrum consists of an expanded ventral region with a slender vertically directed blade although the dorsal portion of this structure is missing. The bone is convex postiorly with a moderately deep embayment on the posterior margin for the insertion of the pectoral fin, similar to that of *H. rostridens* (Long 1988. Fig.27). The clavicle is triangular and overlaps the cleithrum posteriorly and is itself dorsally overlapped by the branchiostegal rays.

Preserved sections of ornament on both the cleithrum and clavicle consists of limited areas of short ridges, particularly around the posterior margin of the clavicle and the vertical blade of the cleithrum, that are largely replaced by rostrocaudally oriented

rows of small pores over most of the remainder of the bone surface. This differs from the condition in *Howqualepis rostridens* where the dermal surface of the corresponding area is covered in a mixture of ridges and raised tubercles with no porous ornamentation (Long, 1988. Fig.15). *Donnrosenia* has very similar ornamentation on the clavicle but has entirely linear ornamentation on the cleithrum (Long, Choo & Young, 2008. Fig.6). *Moythomasia durgaringa* and *M. nitida* also have porous ornamentation on the pectoral girdle, but restricted to the ventral faces of the cleithrum and clavicle (Choo, in prep) whereas pores are also present on the lateral surface in ?*H. youngorum*.

Fins

The pectoral fin (Fig. 2) is incomplete with no traces of the endoskeletal radial although the visible lepidotrichia are well preserved. The fin is elongate and triangular with more than 14 primary lepidotrichia present. As with *H. rostridens* and *Donnrosenia*, the anterior lepidotrichia are unsegmented for most of their length with secondary division restricted to the region near the fin margin. The trailing edge of the fin is not preserved and it is unclear if the posterior fin rays were fully segmented as in *H. rostridens* (see below). The fin reaches its maximum length at about the seventh primary ray, which is unsegmented for more than 75% of its length as in *H. rostridens*, longer than the c.65% unsegmented region in the fin of *Donnrosenia* (Long et.al, 2008). A short section of the leading edge is preserved with spine-like fringing fulcra formed by terminal branching of the leading fin rays. As with *H. rostridens* and *Donnrosenia* (see below) there is no medial contact visible between the distal hemilepidotrichia of each fringing fulcra on any of the fins.

The pelvic fin (Fig. 3) is long-based and triangular. Its preserved lateral aspect and does not appear to be as elongate as in *H. rostridens* although it is unclear if a section of the posterior margin is missing. The fins are located approximately midway along the body between the pectoral and anal fins. Primary lepidotrichia are only preserved for the anterior half of the fin, comprising more than 22 rays suggesting more the 40 primary rays on the entire preserved section. These rays are evenly segmented along their preserved length. Slender spine-like fringing fulcra are present on the leading edge.

The anal fin (Fig. 4a, b) is large and triangular in shape. At least 54 primary segmented lepidotrichia are present as opposed to c.45 fin rays on the anal fin of *H. rostridens*. It is unclear if the fin originally had a short posterior fringe trailing behind the main

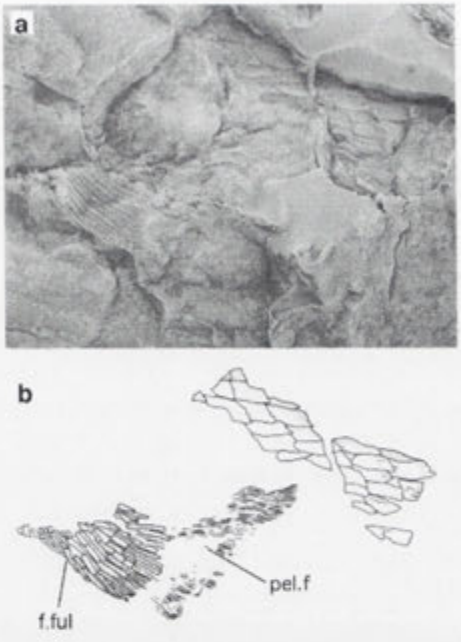


Figure 3. ?*Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the pelvic fin and associated squamation on ANU V2929A.

triangular area of the fin as in *H. rostridens*. If this was the case then the complete fin would have probably had over 60 primary lepidotrichia. As in the other fins, shortened spine-like lepidotrichial segments form a serrated cutwater of fringing fulcra on the leading edge.

As was the case in other known Devonian actinopterygians, the caudal fin (Fig. 4) was heterocercal in structure with a distinct posterior cleft separating the dorsal lobe (notochordal mass of the fin plus the dorsal hypochordal lobe) from the ventral hypochordal lobe. While little of its dorsal counterpart has been preserved, the ventral hypochordal lobe is elongate and triangular with c.40 primary lepidotrichia preserved. Spine-like fringing fulcra are present on the leading edge.

The dorsal fin is not preserved in the holotype although a pair or large, isolated lepidotrichs preserved near the counterpart tail may have originated from that fin (Fig. 4d).

Scales and squamation

Articulated macromeric scales, scutes and basal fulcra are preserved from the caudal fin, extending

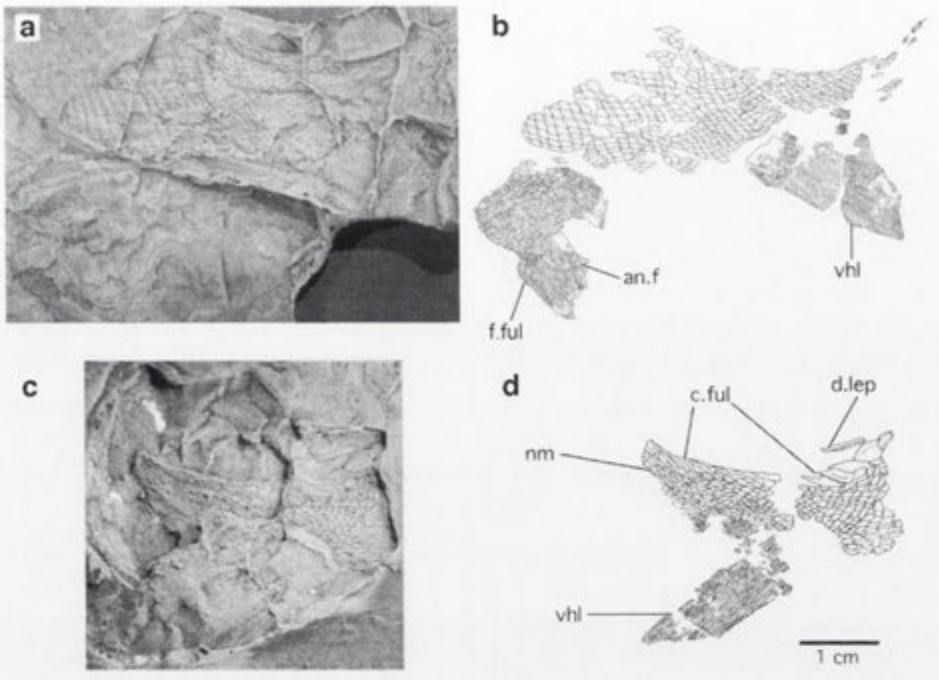


Figure 4. ?*Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the anal and caudal fins of ANU V2929A, c. photograph and d. line drawing of the caudal fin of the holotype counterpart (ANU V2929B).

forwards to above the anal fin (Fig. 4c, d). There are also isolated patches of scales preserved above and to the rear of the pelvic fins (Fig. 3). Very little of the scale ornamentation has been preserved. The visible scale types are described in accordance with the zonation terminology as proposed in in Esin (1990) and employed in Trinajastic (1999).

Area C = flank scales extending from above the pelvic fins to above the anal fin. Scales are elongate and rectangular, with rostrocaudal length being at least twice the height of the scale. Ventral margin is gently convex. The disposition of the peg and socket articulation is unknown in the scales close to the pelvic fins and absent in the scales near the anal fin. Free field ornamentation is poorly preserved but individual scales show remnants of longitudinal furrows. Scales from near the front and rear of the field seem to have two or three serrations protruding along the caudal edge suggesting little or no rostrocaudal decrease in the number of serrations.

Area D = scales anterior to the caudal fin and on the notochordal mass of the caudal fin. Scales anterior to the caudal fin are rhombic in form, becoming smaller and increasingly elongate on the notochordal mass of the fin. Scales near area C have a gently convex ventral margin, becoming less prominent towards the caudal fin until the margin is completely straight at those scales near the caudal inversion. Peg and socket articulation is absent. The free field is smooth with no preserved traces of raised ornamentation. Posterior serrations range from two in scales near area C to none on those scales on the caudal fin.

Area H = scales adjacent to the base of the anal fin. These scales are small, elongate rhomboids. Peg and socket articulation is not visible and probably absent. There is no evidence of ornamentation or posterior ridges.

The only dermal scutes that have been preserved are an articulated series visible anterior to the dorsal caudal lobe and extending over the dorsal margin of the caudal fin (Fig 3b, c). Anterior to the caudal fin, the scutes are triangular plates with a caudally-

directed apex and are about three times longer than the adjacent flank scales. As the series progresses posteriorly over the notochordal mass of the caudal fin, the scutes narrow and spine-like with extensive overlap between the individual scutes.

Redescription of the pectoral fin of *Howqualepis rostridens*

Long (1988) described the pectoral fin of *Howqualepis rostridens* as consisting of 25 primary lepidotrichia that are unsegmented for most of their extent, save for some secondary division near the fin margin. A complete pectoral fin was not figured and re-examination of this form has revealed the fin to be more extensive than previously recognised (Fig. 5). Additionally, the leading edge of the pectoral and other fins was described as having short, parallel rays similar to fringing fulcra, but not paired (ibid). A similar condition in *Donnrosenia* led to Long et. al (2008) to diagnose the Howqualepididae as possessing short spine-like lepidotrichia in lieu of true fringing fulcra.

The anterior two-thirds of the fin consist of c.25 lepidotrichia that possess extensive proximally unsegmented sections that in some specimens display distal bifurcation. At the lateral margins, these primary rays branch into a fringe of narrow, segments. The relative length of the proximal rays to the segmented fringe is variable, with the unsegmented region accounting for between 75-90% of the length of the fin. There appears to be no correlation between the degree of distal segmentation and the size of the specimen.

Posterior of the unsegmented rays are at more than 10 additional primary lepidotrichia that are segmented from base to margin, again displaying a variable degree of distal branching. The pectoral fin of *H. rostridens* was thus broader in shape and less-extensively unsegmented than has previously been described. In the majority of specimens, the delicate elements of the posterior rays and terminal fringe are scattered or missing, leaving only the thick unsegmented proximal sections in articulation. This configuration of the pectoral fin-rays is similar to that of a number of Carboniferous taxa including *Rhadinichthys* (Moy-Thomas & Bradley Dyne, 1938).

On the leading edge of the pectoral fins of *Howqualepis rostridens*, *?H. youngorum* sp.nov and *Donnrosenia*, the terminal sections of the otherwise unsegmented marginal fin rays branch at least twice, to forming narrow spine-like elements that are not obviously paired. These elements are called "terminal lepidotrichia" in *Cheirolepis* (Pearson and Westoll, 1979) and *Melanecta* (Coates, 1998) or "cutwater lepidotrichia" in the Howqualepididae

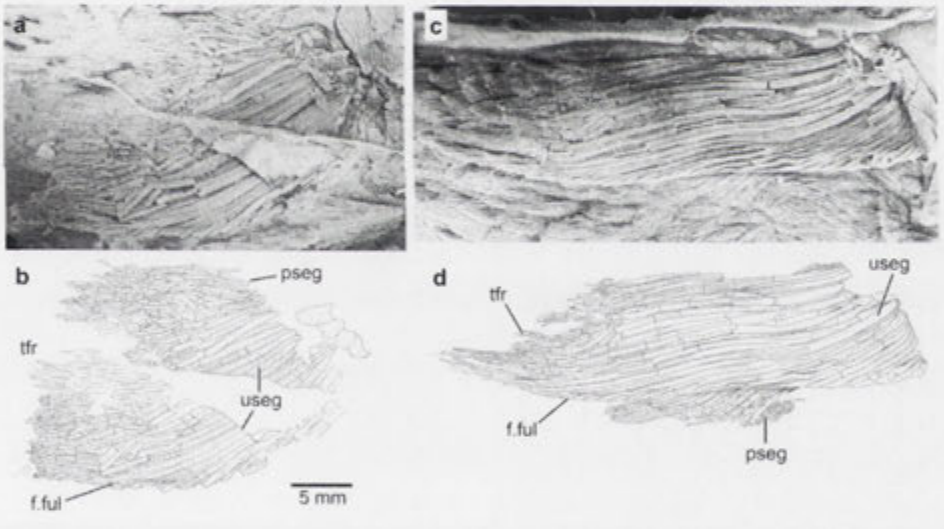


Figure 5. Pectoral fin of *Howqualepis rostridens*. a. photograph and b. line drawing of the fin of MV P.160857. c. photograph and d. line drawing of the fin of MV P.160851B. In this specimen, the posterior section has partially torn off and folded to be visible ventral of the anterior edge of the fin.

(Long, Choo and Young, 2008). In a recent study, such structures fall into Arratia's "Pattern A" class of fringing fulcra, formed from overlapping branched projections of the anteriormost lepidotrichia (Arratia, in press), a condition found in all undisputed Devonian actinopterygians with the exception of *Tegeolepis* which appears to lack any sort of spiny cutwater (Dunkle and Schaeffer, 1973). The fulcra of *Cheirolepis*, which are of similar form to those of the Howqualepididae, comprise distally enlarged hemilepidotrichia that partially enclose their paired counterparts (Arratia, in press). The more obviously paired structures present in *Moythomasia* and "*Mimia*" (also falling within "Pattern A") are the result of the terminal segments being of equal length and in medial contact. Given that the scheme proposed by Arratia (and adopted here) means that all Devonian fringing fulcra are in fact modified spine-like lepidotrichia (merely differing in the nature of contact between the hemilepidotrichia), the diagnosis of Howqualepidiae has been adjusted accordingly in the systematic description.

DISCUSSION

Long, Choo and Young (2008) erected the Howqualepididae, comprising *Howqualepis rostridens* from Mount Howitt, Victoria and *Donnrosenia schaefferi* from the Aztec Siltstone of Antarctica. ANU V2929 appears to represent a third taxon within this clade (Fig. 6). All three fish have an elongate body form with macromeric squamation; long-based pelvic fins; small fringing fulcra without medial contact between the distal hemilepidotrichia, and extensive unsegmented primary lepidotrichia that comprise most of the length of the pectoral fin. Among the other Devonian actinopterygians, only *Tegeolepis clarki* (Dunkle and Schaeffer, 1973) possesses extensive unsegmented pectoral lepidotrichia but is distinguished from the Gondwanan forms in lacking a terminal segmented fringe on the pectoral fins, in possessing micromeric squamation and having small, short-based pelvic fins.

Assigning the Bunga Bed taxon to a genus is rendered difficult owing to the lack of key skull characters that are used to characterise *Howqualepis rostridens* from the similar *Donnrosenia*. For example, *H. rostridens* possesses an extremely long maxillary blade, a dentigerous rostral and small, dorsoventrally compressed premaxillae (Long 1988). *Donnrosenia* displays a short, deep maxillary blade, dorsoventrally prominent premaxillae, a small accessory operculum and much smaller teeth than *Howqualepis* (Long, Choo and Young, 2008).

ANU V2929 is considered to be closer *H.rostridens* in having more extensive unsegmented pectoral lepidotrichia and relatively smaller scales than *Donnrosenia*. The pectoral fins of ANU V2929 are more similar to that of *H. rostridens* in that both forms possess unsegmented lepidotrichia that account for over 75% of the maximum length of the fin. Those of *Donnrosenia* account for less than 70% of the maximum fin length (Long, Choo and Young, 2008. Fig.7).

Based on these anatomical similarities and pending the discovery of skull material for this taxon, ANU V2929 is tentatively assigned to *Howqualepis*. The Bunga Bed form is not conspecific with *H. rostridens* and is distinguished in having a larger anal fin with a greater number of primary lepidotrichia and in possessing porous dermal ornamentation of the pectoral girdle.

The presence of a grade of Devonian actinopterygian so far found exclusively in Middle Devonian freshwater deposits of southeastern Australia and Victoria Land, Antarctica highlights the close biogeographical similarity between the fossil faunas of these two regions. The apparent absence of these ray-finned fishes in Devonian sites outside this area also adds to a growing body of fossil evidence that indicates a regionally endemic freshwater vertebrate fauna within Middle Devonian Eastern Gondwana. Similarities in key taxa of placoderms (Young 1988, Young and Long 2005), acanthodians (Long 1983, Young 1989, Young & Burrow 2004), chondrichthyans (Young 1982, 2007; Long & Young 1995) and dipnoans (Long 1992, 2003) have been well documented.

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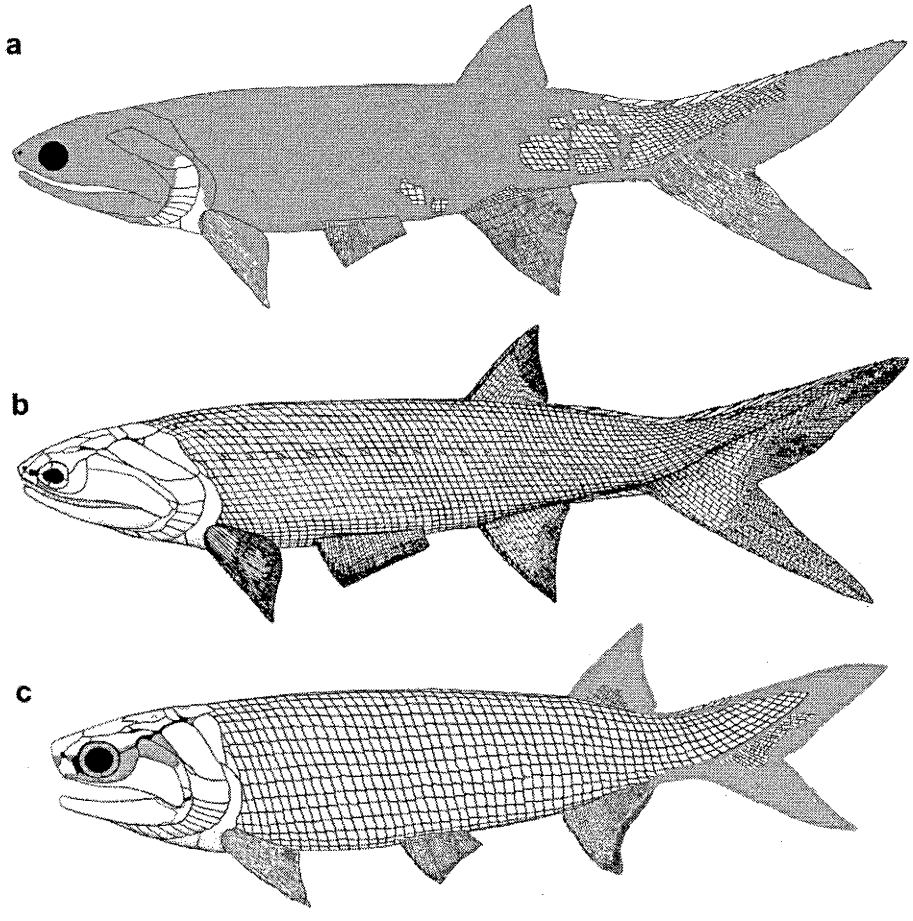


Figure 6. Comparison of the three known species of the Howqualepididae. Reconstructions presented in lateral view and are not to scale. Unknown parts of the anatomy are represented by dark grey areas. a. ?*Howqualepis youngorum* sp.nov., based on the preserved extent of the holotype with outline based on *H. rostridens*, c.14cm long. b. *Howqualepis rostridens* from Mount Howitt, Victoria (modified after Long, 1988). Size of specimens range from 20-50cm. c. *Donnrosenia schaefferi* from the Aztec Siltstone, Southern Victoria Land, Antarctica (from Long et.al, 2008), c. 14cm long.

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APPENDIX III

CHOO, B., LONG, J.A., and TRINAJSTIC, K. 2009. A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia. Acta Zoologica (Stockholm) 90 (Supplement 1): 194-210.

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A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia

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actinopterygian, Devonian, fossil, Gogo Formation

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Abstract

Choo, B., Long, J.A. and Trinajstic, K. 2009. A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia. — *Acta Zoologica* (Stockholm) **90** (Suppl. 1): 194–210

A new basal actinopterygian, *Gogosardina coatesi* gen. et sp. nov., is described from the Upper Devonian Gogo Formation of the Canning Basin, Western Australia. The new taxon is known from four prepared specimens that display the typical exceptional preservation of fossil vertebrates from the region. *Gogosardina*, gen. nov. possesses a series of four small postrostrals, no surangular and a highly gracile body covered with over 140 vertical rows of very small scales, all ornamented with separate horizontal ganoine ridges. One specimen contains conodont elements lodged among the branchial arches, indicating dietary habits and a possible cause of death.

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Introduction

Research into the Late Devonian (Frasnian) Gogo fish fauna of the Canning Basin, Western Australia has greatly contributed to our understanding of the anatomy and interrelationships of early vertebrates owing to an extraordinary level of fossil preservation. Exceptional specimens are recovered as three-dimensional articulated skeletons with exquisite dermal, perichondral and, in rare cases, soft tissue preservation (Trinajstic *et al.* 2007). To date, over 40 species of placoderms, actinopterygians and sarcopterygians have been described in the assemblage (Long 2006). In contrast to the diverse placoderm and dipnoan fauna, recorded actinopterygian diversity has, to date, been low. This work partly redresses this by providing the first comprehensive description of *Gogosardina* gen. nov., the first new actinopterygian described from the Gogo Formation in over 30 years. Moreover, these remains have considerable significance in providing the identification of isolated scales from a previously unknown palaeoniscoid found throughout the Canning Basin (Trinajstic and George, in press).

Complete specimens of early actinopterygians are a sparse component of most pre-Carboniferous vertebrate assemblages and are currently known from only a dozen described Devonian genera. In Australia, articulated Devonian actinopterygians are rare with the only complete specimens consisting of the Gogo material, plus *Howqualepis* from the Givetian Mt Howitt locality in central Victoria (Long 1988). The actinopterygian fauna of the Gogo Formation has, to date, been represented by only two taxa: *Moythomasia durgaringa* Gardiner and Bartram 1977 and *Mimia toombsi* Gardiner and Bartram 1977. Additional anatomical information was presented by Gardiner (1984) and their squamation described in detail by Trinajstic (1999a,b). *Mimia* is a preoccupied genus that will shortly be renamed, the fish will henceforth be referred to as '*Mimia*'.

The presence of at least three additional taxa of Gogo actinopterygians has become apparent based on superb material recovered by Western Australian Museum expeditions to the region from 1986 to 2003 as well as the 2005 Museum Victoria expedition. The material described herein represents one of these, initially recognized as a novel form based on a specimen collected by J.A. Long in 2001. In addition, a well-preserved conodont apparatus was recovered in the branchial regions of one specimen, giving a rare insight into the lifestyle and diet of these animals.

The Gogo material has been of exceptional importance in being the most complete Palaeozoic examples of ray-finned fishes, with three-dimensional preservation of the full dermal skeleton combined with rarely recovered fine details of the neurocranium. Both of the previously described taxa have featured in the majority of recent phylogenetic analyses of early ray-finned fish (Long 1988; Gardiner and Schaeffer 1989; Taverne 1997; Coates 1999; Schultze and Cumbaa

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2001; Cloutier and Arratia 2004; Friedman and Blom 2006). Given the typically imperfect preservation of forms from outside the Gogo, the interrelationships of early actinopterygians remain poorly resolved (Cloutier and Arratia 2004). The material described herein will be incorporated into future phylogenetic studies of early actinopterygians (Choo, in prep.).

Geological setting

The Gogo Formation, of the Canning Basin (Fig. 1), preserves the basinal facies of an ancient barrier reef complex which is exposed for a strike length of *c.* 350 km making them arguably one of the best examples of Palaeozoic reefs anywhere (Playford and Lowry 1966). The Gogo Formation consists of a sequence of inter-reef siltstone and thin beds of limestone. The latter contain the fossil-bearing nodules, which are usually bedded and range in size from around 2.5 to 36 cm in diameter. The concretions are composed of silty micritic limestone and are commonly found to have developed around a fossil fish or phyllocarid crustacean. Other nuclei include bivalves, gastropods, cephalopods, bryozoans, tentaculitids and corals. The formation is well dated on palaeontological and sedimentological grounds as Frasnian (Druce 1975; Wales and Forman 1981).

Materials and methods

All prepared specimens of this taxon were recovered as part and counterpart when the encasing nodule was broken in the field. Due to the delicate nature of the bones, each side of the specimen was placed face down into a slab of clear epoxy resin and prepared from the unexposed side. Specimens were given repeated baths in a dilute acetic acid solution followed by a session of washing under slow-running water. The protruding bones reinforced with an ethanol-diluted solution of either Mowital B30 or Paraloid. The holotype specimen suffered extensive damage during preparation due to the failure of the resin base to properly bond with the fossil bone. It currently consists of isolated scales, dermal elements of the skull, pectoral girdle along with impressions of the articulated fish with bone remnants set within the resin base. A fragmentary neurocranium survives with attached parasphenoid, right lower jaw and right maxilla.

All articulated specimens were whitened with ammonium chloride prior to principle photography with the exception of MV P228849b, which was left unwhitened in the interest of preserving the delicate conodont apparatus present within the fish's body. Scanning electron micrographs were produced of scales removed from the holotype specimen.

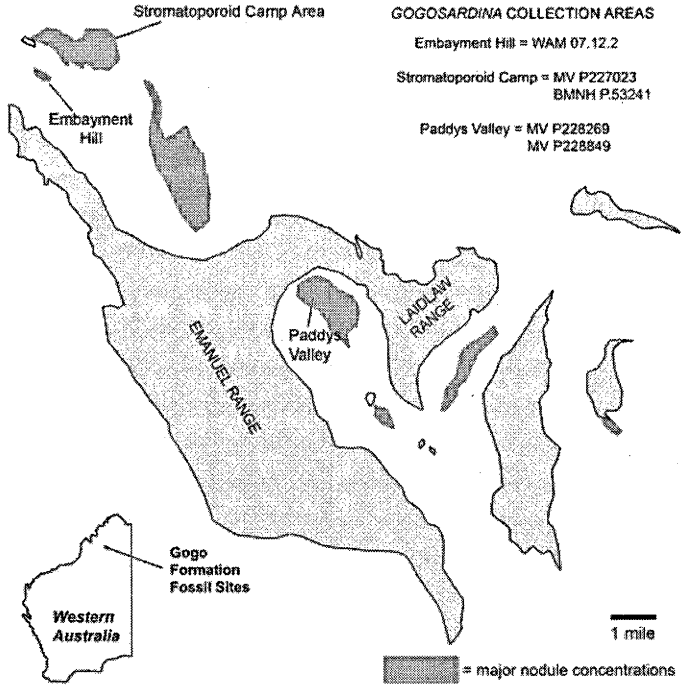


Fig. 1—Simplified map of the Gogo Formation, Western Australia, showing the collection areas which have produced specimens of *Gogosardina* gen. nov.

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Anatomical Abbreviations

Terminology herein follows that of Gardiner *et al.* (2005), Gardiner and Schaeffer (1989), and for the description of skull roofing bones we use actinopterygian terminology, following recent work such as Friedman and Blom (2006), rather than employing tetrapod skull roof homologies (as used in Schultze and Cumbaa 2001).

Anatomical abbreviations: **an.f**, anal fin; **Ang**, angular; **ap**, anterior pit-line; **ano**, anterior nasal opening; **anpl**, angular pit-line; **Ar**, articular; **binc**, dorsal branch of infraorbital sensory canal in premaxilla; **Bpt**, basipterygoid process; **Br**, branchiostegal rays; **cao**, aortic canal; **cau.f**, caudal fin; **c.ful**, caudal fulcra; **Cb**, ceratobranchials; **Ch**, ceratohyal; **Clav**, clavicle; **Clth**, cleithrum; **cono**, conodont elements; **Den**, dentary; **d.ful**, dorsal fulcra; **Dh**, dermohyal; **dor.f**, dorsal fin; **ethc**, tube for ethmoidal commissural sensory canal; **fepsa**, foramen for efferent pseudobranchial artery; **fos**, otico-sphenoid fissure; **Fr**, frontal; **ha**; haemal arches; **hb**, hypobranchial; **Hh**; hypohyal; **hpbt**, hole for basipterygoid process; **hpl**, horizontal pit-line; **Hy**, hyomandibular; **inc**, infraorbital sensory canal; **It**, intertemporal; **Ju**, jugal; **L.gu**, lateral gular; **lpr**, lateral postrostral; **mc**, mandibular canal; **mp**, middle pit-line; **mpr**, median postrostral; **man.tp**, mandibular toothplate series; **Men**, mentomeckelian; **Mk**, ossified Meckelian cartilage; **Mx**, Maxilla; **N**, nasal; **na**, neural arches; **npl**, nasal pit line; **Op**, operculum; **pec.f**, pectoral fin; **pel.f**, pelvic fin; **pal.tp**, toothplate series of the palatoquadrate; **Par**, parasphenoid; **Pcl**, postcleithrum; **pinf**, pineal foramen; **Pm**, premaxilla; **Pno**, posterior nasal opening; **Pop**, preoperculum; **pp**, posterior pit-line; **Ppr**, posterior postrostral; **Pt**, post-temporal; **Qj**, quadratojugal; **qjpl**, quadratojugal pit-line, **R**, rostral; **rpl**, radial plate; **Scl**, supracleithrum; **Sop**, suboperculum; **spig**, spiracular groove; **spip**, spiracular toothplate; **St**, supratemporal; **spir**, spiracular notch; **suc**, tube for supraorbital sensory canal; **v.ful**, ventral fulcra; **vhl**, ventral hypochordal lobe of caudal fin, **vpl**, vertical pit-line.

Institutional abbreviations: BMNH, Natural History Museum, London; MV, Museum Victoria; WAM, Western Australian Museum.

Systematic palaeontology

Class Osteichthyes Huxley (1880)
Subclass Actinopterygii Cope (1887)
Genus *Gogosardina* nov.

Diagnosis

As for type species (monotypic genus).

Type species

Gogosardina coatesi, sp. nov.

Locality and horizon

Gogo Formation, Western Australia, lower Frasnian, Upper Devonian.

Etymology

'Gogo sardine'; referring to the Gogo Formation and the highly gracile body form of the fish which superficially resembles that of some extant clupeid teleosts.

Gogosardina coatesi sp. nov. (Figs 2–14).

Diagnosis

Stem actinopterygian with skull roof having parietals, frontals and supratemporals of roughly equal rostrocaudal length; triangular intertemporals forming dorsal margin of spiracular slit; four small postrostral units (3 anterior and 1 posterior); posterior postrostral forms anterior margin of the pineal foramen; rostral stout and tapers anteriorly. Lower jaw comprises large dentary and small angular which meet in the smooth maxillary overlap area with a zig-zag suture; surangular absent. Parasphenoid with diamond-shaped posterior shelf that underlies the ventral otic fissure; ascending processes absent. Opercular elongate and four sided; subopercular with a well-developed anterodorsal process; first three branchiostegal rays of uniform height. Body elongate and fusiform; fringing fulcra present on at least the pectoral, pelvic and anal fins; pectoral fin-rays proximally unsegmented;

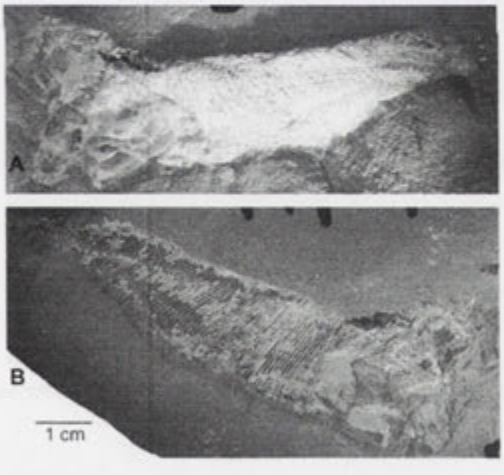


Fig. 2—*Gogosardina coatesi* gen. et sp. nov. Holotype (WAM 07.12.2) prior to preparation. —**A**. Main specimen in lateral view. —**B**. Counterpart in lateral view.

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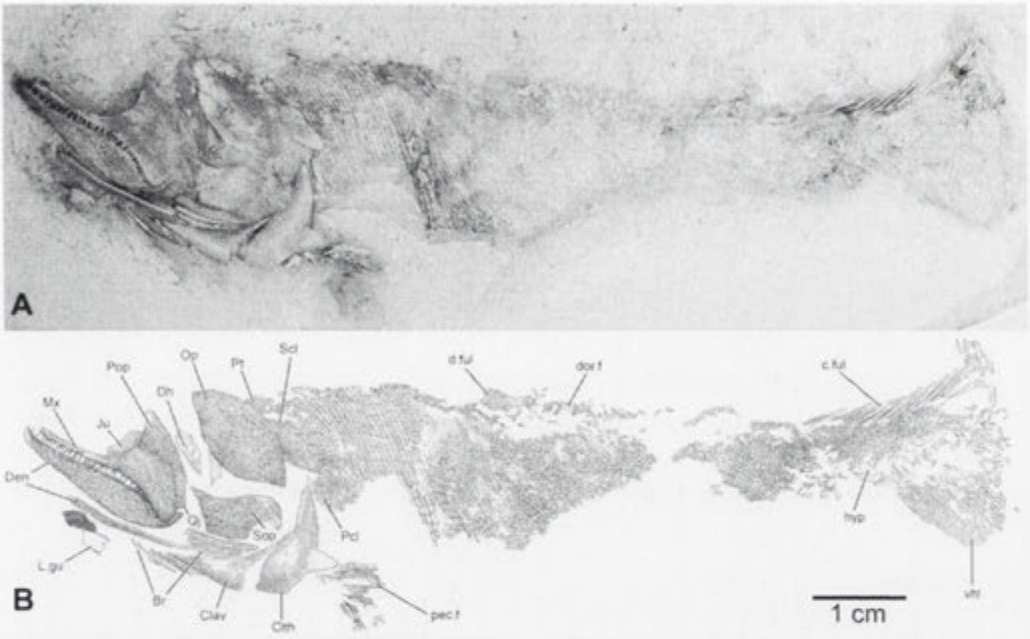


Fig. 3—*Gogosardina coatesi* gen. et sp. nov. MV P228849a in lateral view. —**A**. Photograph of specimen. —**B**. Interpretive drawing of specimen.

pelvic fins short-based; dorsal and anal fins large and long-based. Scales small and barely macromeric with *c.* 145 scale rows from occipit to caudal inversion; all scales have a free field ornament of separate horizontal ganoine ridges.

Etymology

For Mike Coates in recognition of his many contributions to palaeoichthyology.

Holotype

WAM 07.12.2. Originally an entire fossil fish, now consisting of a partial neurocranium with attached partial parasphenoid, right maxillary and lower jaw; dermal elements of the skull, left lower jaw, opercular–gular system, pectoral girdle and numerous scales along with a partially articulated counterpart mounted in resin, consisting of scales, skull roof and resin impressions of other bones. Collected in 2001 by John A. Long near Embayment Hill.

Referred specimens

MV P227023 (a + b): Articulated fish resin-mounted as separate part and counterpart; almost complete fish including that, in one half-mount, contains a well-preserved neurocranium that is not fully prepared at the time of writing. Collected by John A. Long at Stromatoporoid Camp in 1986.

MV P228269: Partial articulated postcranium resin-mounted as separate part and counterpart. Skull lacking skull-roof and neurocranium recovered as disarticulated pieces. Collected by Gavin Young at Paddy's Valley in 1972.

MV P228849 (a + b): Articulated fish resin-mounted as separate part and counterpart. Almost complete, lacking only the snout, skull-roof, neurocranium, most of the dorsal fin and much of the ventral body area including the pelvic and anal fins. Collected by John A. Long in Paddy's Valley in 2001.

BMNH P.53241: Unprepared specimen comprising the anterior half of a fish. Collected in 1967 near Stromatoporoid Camp, Gogo Station (H.A.T. 67/47, see Miles 1971: fig. 1)

Description

MV P228849 represents the most complete, fully prepared specimen and has a standard length of *c.* 11 cm with a lower jaw that is 1.8 cm long. MV P227023 and P228849 are of a similar size. MV P.228269 represents the largest known specimen with a jaw length of 2.35 cm.

The neurocranial anatomy of *Gogosardina* is not presented in this description as it requires further preparation of one

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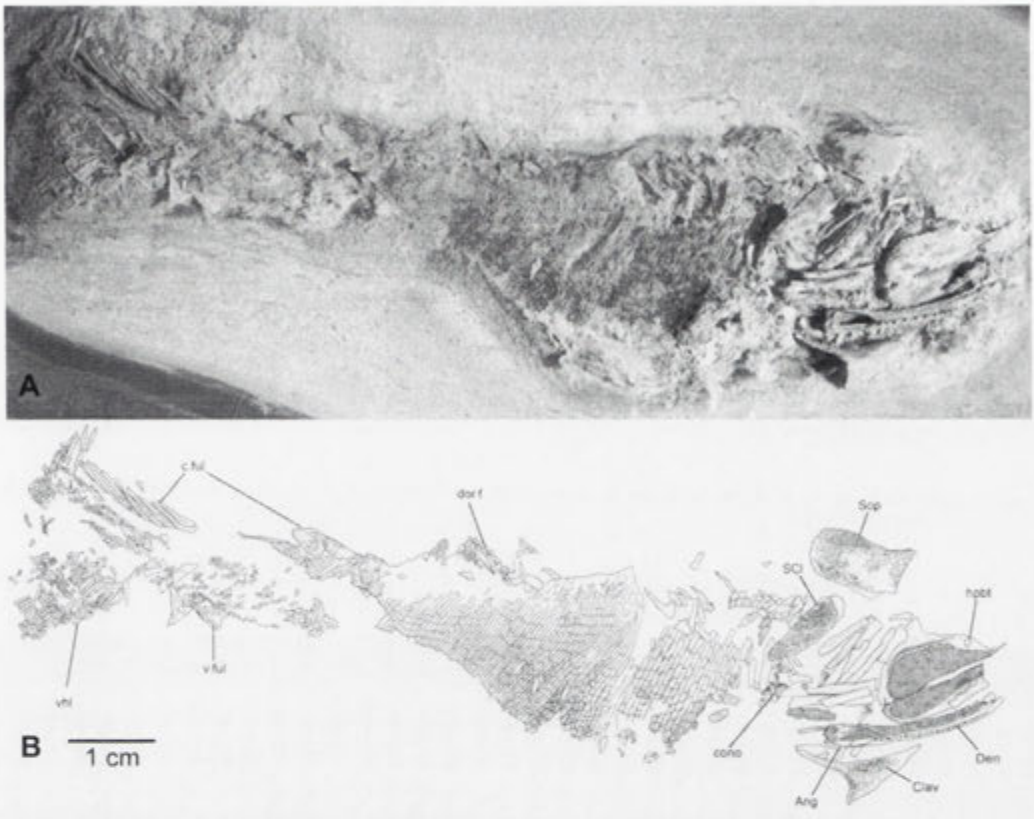


Fig. 4—*Gogosardina coatesi* gen. et sp. nov. MV P228849b in lateral view, counterpart of the specimen presented in Fig. 2. —**A**. Photograph. —**B**. Interpretive drawing of specimen.

specimen (MV P227023a) and high-resolution CT scanning before it can be fully studied; but will form a separate work in conjunction with other braincase material from an additional new taxon from the Gogo Formation.

Skull roof

The holotype is the only specimen that has a complete skull roof with the postrostrals in place. The skull roof (Figs 7 and 13) is comprised of the following paired elements: frontals, parietals, dermosphenotics (now destroyed), intertemporals and supratemporals. There are also a series of anamesic postrostral elements and an unknown number of extrascapulars.

Postrostrals (Fig. 7). The postrostral series is only preserved on the type specimen. It consists of a laterally arranged trio of small anterior bones that narrow to a single, posterior unit. The combined postrostral series sutures anteriorly to the rostral, anterolaterally to the nasals and laterally to the frontals. The posterior margin of the posterior unit forms the anterior margin of the pineal foramen. The (anterior) median unit is rectangular, flanked on each side by rhombic lateral postrostrals. The posterior postrostral is hexagonal and more than twice the size of the anterior units. Dermal surfaces are ornamented with linear rostrocaudal ridges.

Frontals (Fig. 7). Narrow bones of similar length to the parietals. The paired bones meet for the posterior 40% of their length in a smooth median suture, with a large central embayment for the pineal foramen. Anterior to the foramen, the medial margin is deflected anterolaterally, suturing with the posterior postrostral and a lateral postrostral. Overlapped anteriorly by the nasal and posteriorly by the parietal. The supraorbital canal enters the bone from the middle of the

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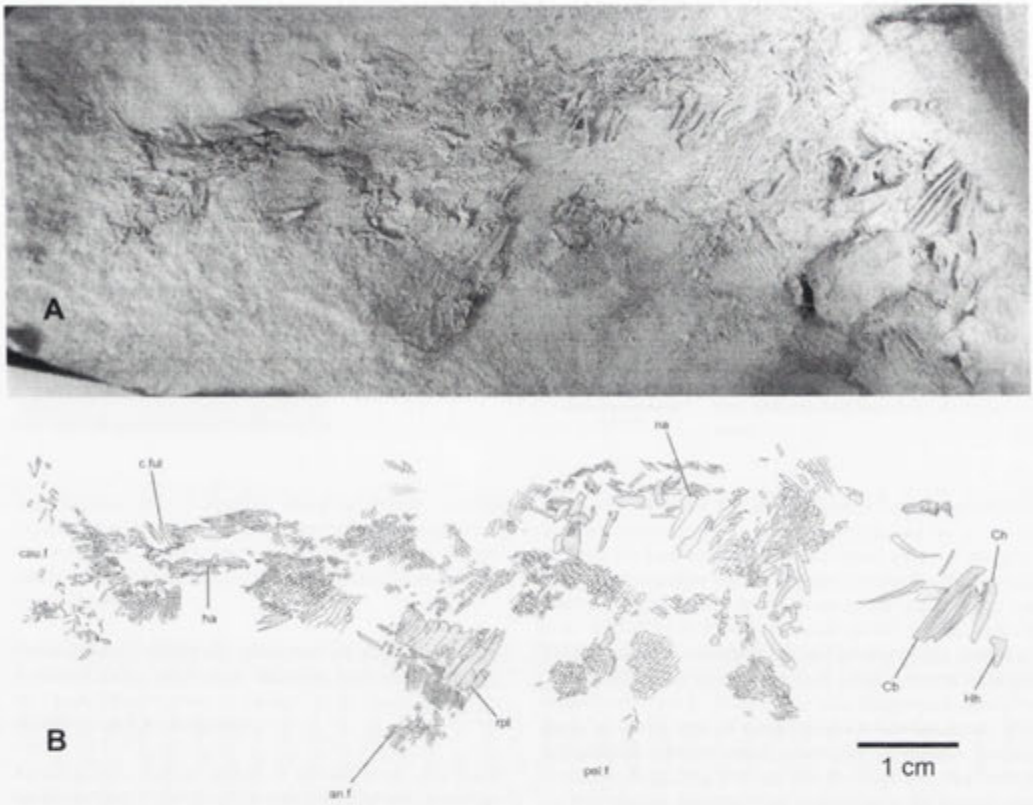


Fig. 5—*Gogosardina coatesi* gen. et sp. nov. MV P227023b in lateral view. —**A**. Photograph. —**B**. Interpretive drawing of specimen.

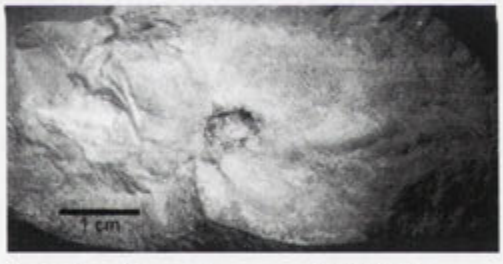


Fig. 6—*Gogosardina coatesi* gen. et sp. nov. BMNH P.53241, unprepared specimen in lateral view.

posterior margin and is deflected anterolaterally at the level of the pineal foramen. Ornament consists of fine rostrocaudally directed linear ridges, becoming shorter and more radial near the anterolateral margins.

Parietals (Fig. 7). Bones of roughly equal rostrocaudal length to the frontals and supratemporals. Dorsally convex and about 1.4 times longer than broad. Smooth marginal contact with neighbouring parietal, intertemporal and supratemporal, zig-zag anterior suture with the frontal. Rostrocaudally orientated anterior pit-line continuous with the supraorbital canal which exits the bone anteriorly. The middle pit-line sits close to the anterior pit-line and is directed towards the anterolateral suture with the intertemporal. The posterior pit-line is widely separated from the other two and is directed posteromedially. Dermal ornament consists of linear rostrocaudal ridges.

Supratemporals (Fig. 7). Narrow bones which sutures medially with the parietal and anteriorly to the intertemporal. Dermal surface is poorly preserved on the type specimen and the path of the path of the infraorbital sensory canal is not visible.

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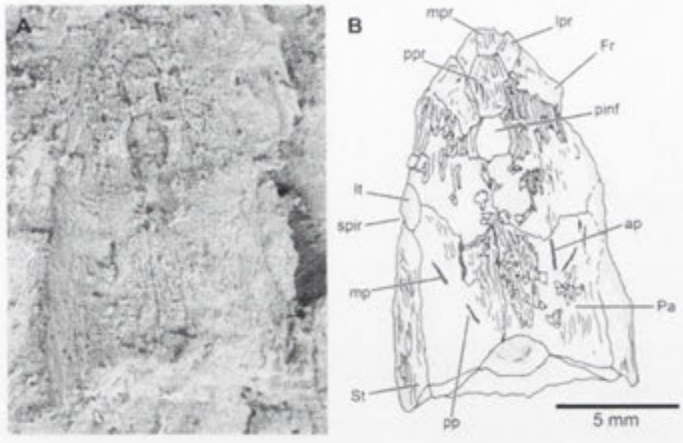


Fig. 7—*Gogosardina coatesi* gen. et sp. nov. Skull roof of the holotype (WAM 07.12.2) in dorsal view. —**A**. Photograph. —**B**. Interpretive drawing. Specimen represents bone impressions set in a resin base with attached fragments of dermal bone.

Intertemporals (Fig. 7). Narrow, triangular bones, one-fifth the length of the parietals. Ornament not preserved. Slight embayments on their lateral surfaces in dorsal view suggest that they formed at least part of the dorsal margin for an open spiracular slit.

Dermosphenotic. Originally preserved on the holotype but destroyed during preparation. Based on preliminary sketches, they were tripartite structures similar to the dermosphenotics of '*Mimia*' and *M. dargaringa*.

Extrascapulars. Broken pieces of dermal bone with linear ornamentation from the type specimen probably represent fragments of the extrascapulars. Their original size, shape and number cannot be determined.

Snout

The anterior section of the skull has been preserved on the holotype and MV P.228269 (Fig. 8). It comprises paired, medially abutting dentigerous premaxillae, nasals and a single median rostral.

Rostral (Fig. 8A–D). Small median bone of a similar size to the premaxillae. Short dorsal lamina folds downwards and abruptly narrows anteriorly to a tip set against the median premaxillary suture. Distinct posteroventral kinks where the ethmoid canal exits the bone. Dorsoposterior margin is convex, forming an embayment for the anterior postrostrals. Lateral margins straight, suturing with the nasals except for circular emarginations for the anterior nostrils. External surface consists of linear ridges along the dorsal surface, grading into an irregular, vermiculate pattern of short ridges and tubercles on the anterior face. Ethmoidal commisure is visible externally as an arc of pores and internally as an open groove.

Premaxilla (Fig. 8A–D). Flat, anterior facing bones with a small lateral aspect. Meets counterpart in a short, straight median suture. Inward sloping anterior margins of both premaxillae form a V-shaped recess for the median rostral. Posterior face forms anteroventral margin of the orbit and there is a small unornamented overlap surface for the anterior maxillary tip and probably the lacrymal. The dentigerous margin for each bone consists of large, conical teeth set in rounded sockets. Sharpened tubercles form an outer row of variably sized smaller teeth. The infraorbital sensory canal enters the premaxilla posteroventrally, branching 80% up into the bone with one branch exiting via the anterodorsal margin into the rostral, the other via the posterodorsal margin into the nasal. Complex ornamentation consists of posteroventrally directed linear ridges along the lateral face which grade into a vermiculation of short, irregular ridges and tubercles on the anterior aspect. Small tubercles close to the biting margin. The smooth internal surface is slightly concave with the infraorbital canal represented by a sharply defined tube.

Nasal (Fig. 8E–H). Narrow bones positioned dorsal and anterior to the premaxillae and lateral to the median rostral. Sutures with both these bones are straight, broken only by the notch on the dorsal margin for the posterior border of the incurrent naris. Lateral margin is gently concave, forming the anterodorsal margin of the orbit. The bone narrows at a slender dorsal lamina which sutures with the dermosphenotic. The external surface is covered in short-to medium length longitudinal ridges. The course of the supraorbital sensory canal is visible externally as a longitudinal row of widely spaced small pores with a short anterior pit-line and viscerally as an open groove.

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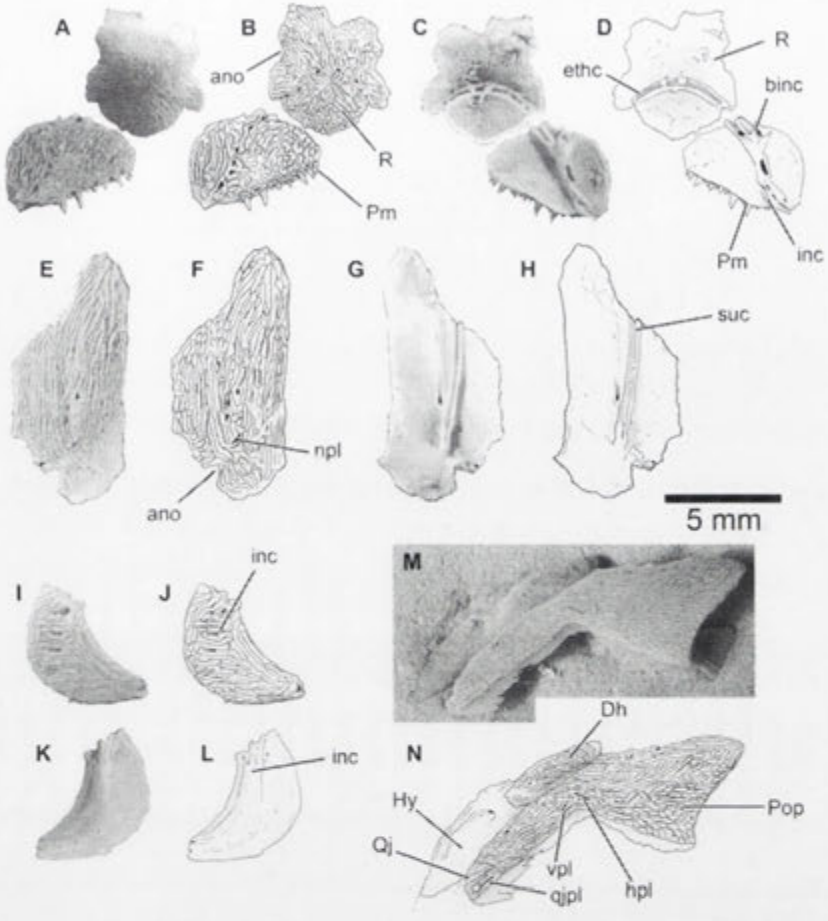


Fig. 8—*Gogosardina coatesi* gen. et sp. nov. MV P.228269. —**A**. Photograph. —**B**. Drawing of the rostral and right premaxilla in anterior view, presented as if flattened out in one plane. —**C**. Photograph. —**D**. Drawing of the same bones in medial view. Left nasal. —**E**. Photograph. —**F**. Drawing in lateral view. —**G**. Photograph. —**H**. Drawing in medial view. Right jugal presented in lateral view as a (**I**), photograph and (**J**), line drawing. —**K**. Photograph. —**L**. Drawing of jugal in medial view. —**M**. Photograph. —**N**. Drawing of preoperculum, quadratojugal, dermohyal and partially exposed hyomandibular.

Cheek and infraorbitals

The cheek comprises a large maxilla, preoperculum and small quadratojugal. The jugal represents the only infraorbital unit among the available material. There is space for a slender lachrymal between the jugal and premaxilla, but such a bone has not been identified.

Jugal (Figs 3 and 8I–L). Crescentic bone with a concave anterodorsal surface that forms posteroventral border of the orbit. Narrow at anteroventral suborbital extremity, broad posterodorsal surface. The infraorbital canal changes from a horizontal suborbital orientation to a vertical postorbital aspect as it passes through the bone. Dermal ornament consists of short linear ridges.

Maxilla (Figs 3 and 9). The maxilla is of the usual type found in Devonian actinopterygians with a narrow suborbital ramus and an expanded postorbital blade. The suborbital portion is long and low, expanding to meet the postorbital blade in a shallow curve. The postorbital region is rectangular, with a pronounced posteroventral extension that overlaps the

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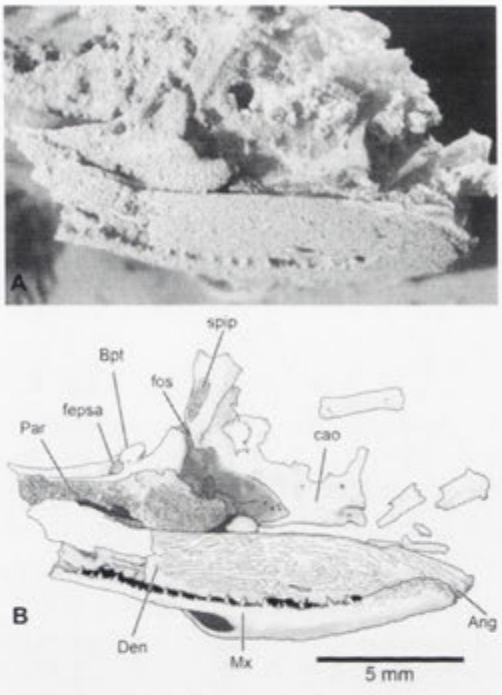


Fig. 9—*Gogosardina coatesi* gen. et sp. nov. Fragmentary neurocranium with parasphenoid of holotype specimen (WAM 07.12.2). —**A**. Photograph. —**B**. Drawing of the specimen in ventral view.

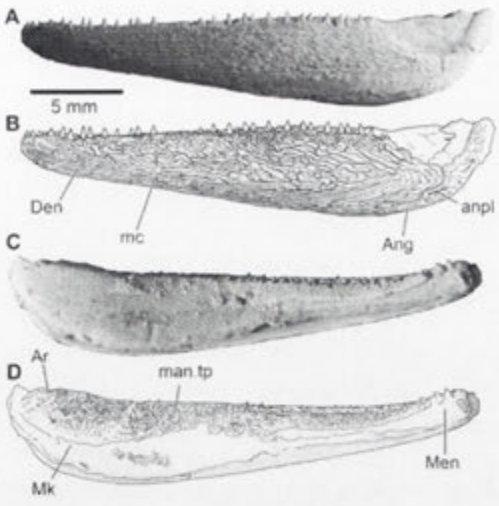


Fig. 10—*Gogosardina coatesi* gen. et sp. nov. MV P.228269. —**A**. Photograph. —**B**. Drawing of left lower jaw in lateral view. —**C**. Photograph. —**D**. Drawing of left lower jaw in medial view.

lower jaw in articulation. The occlusal margin is dentigerous along the entire length, consisting of an inner row of more than 25 large, acrodin-capped conical teeth and an outer row of numerous small teeth. Ornament consists of long ridges on the dorsal two-thirds of the maxillary blade and short, irregular ridges on the ventral one-third of the blade and on the suborbital ramus.

Preoperculum (Figs 3 and 8M–N). An acutely angled bone, overlapped on its ventral margin by the postorbital section of the maxilla. Robust anterodorsal horizontal ramus tapers towards the junction with the narrow, near-vertical posterior ramus. Anterior head is straight and meets the jugal. The posterior extremity is pointed and overlaps the quadratojugal. The preopercular canal runs close to the posterodorsal margin of the posterior 75% of the bone, exiting dorsally. Short vertical and horizontal pit-lines are present at the junction between the horizontal and posterior rami. Ornament of short linear ridges with scattered tubercles.

Quadratojugal (Fig. 8M–N). A small subrectangular bone overlapped anteriorly by the posteroventral corner of the maxilla and dorsally by the preoperculum. The quadratojugal pit-line is visible as a short, slanting surficial groove, orientated parallel to the posteroventral margin of the maxilla. Ornament restricted to a small portion of the surface and consists of very short linear ridges.

Parasphenoid and palatoquadrate

Parasphenoid (Fig. 9). Only the posterior half of the parasphenoid is preserved in the holotype. This tooth-covered bone is elongate with a broad posterior shelf extending to the level of the ventral otic fissure, similar to the configuration in *M. durgaringa* (Gardiner 1984, fig. 51). As with '*Mimia*' *toombsi* (ibid, fig. 50) there are no ascending processes.

Palatoquadrate (Figs 4 and 11). A long structure fused into a single unit with no trace of separate ossification centres in available specimens. It is very similar to the palatoquadrate in large specimens of '*Mimia*' *toombsi*, being roughly triangular with a circular hole for the basipterygoid process near the anterodorsal margin. Behind a narrow, suborbital ramus there is a tall postorbital plate whose posterior margin is fixed to the mesial surfaces of the preopercular and quadratojugal. The spiracular groove runs backwards from just posterior to the hole for the basipterygoid process and follows the contours of the ventral margin of the preoperculum. An extensive dentigerous dermal plate covers more than

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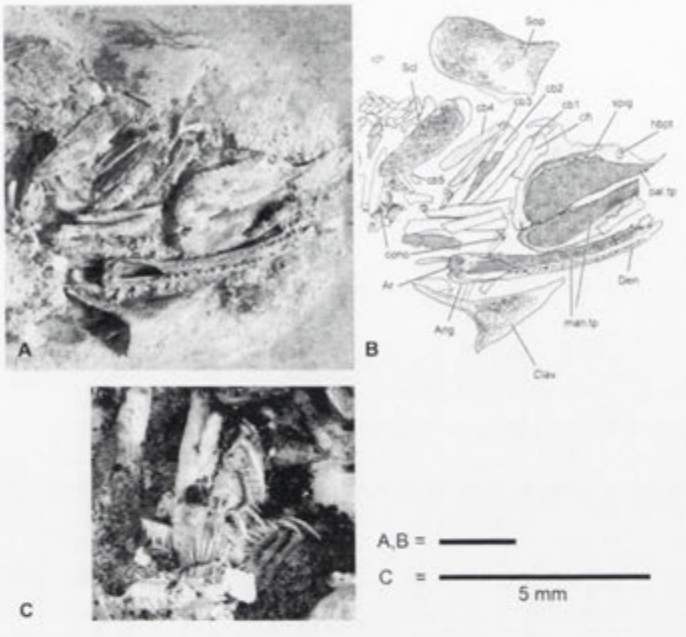


Fig. 11—*Gogosardina coatesi* gen. et sp. nov. Detailed of the head, branchial arches and pectoral girdle of MV P228849b, with various bones visible in mesial (left palatoquadrate and lower jaw), dorsal (right lower jaw) or lateral aspect. —**A**. Photograph. —**B**. Interpretive drawing of the specimen. —**C**. Enlargement of branchial region showing embedded conodont elements.

two-thirds of the medial surface, completely fused into a single ossification. It is of similar form to that of *'Mimia'* (Gardiner 1984: figs 54 and 56) except that the dorsal margin of the dermopalatines, which is straight in *'Mimia'*, forms a strongly undulating outline.

Operculo-gular system

Dermohyal (Figs 3 and 8M–N). Small, roughly triangular bone consisting of a rounded anteroproximal section tapering to a narrow posterior apex. Ornament consists of small tubercles and short posteroventrally orientated ridges.

Operculum (Fig. 3). Large, near-symmetrically lenticular bone with convex anterior and posterior margins meeting at narrow anterodorsal and posteroventral corners. Entire ventral margin overlaps the dorsal margin of the suboperculum. Lower 30% of the anterior margin overlaps the suboperculum, followed further upwards by a small area of contact with the dermohyal. The left operculum of MV P228849 possesses two circular pits on the dermal surface close to the middle of the bone that might represent sensory pits. These pits are however, not present on other examples of this taxon. Ornament consists of short to medium-length linear ridges arranged posterolaterally. The visceral is surface smooth except for small round depression near anterodorsal corner, corresponding to the presumed opercular cartilage housing in *'Mimia' toombsi* (Gardiner 1984).

Suboperculum (Figs 3 and 11). Rectangular bone about 70% the size of the operculum. Although shape varies among specimens, the length of the bone is always more than double the height. Has a prominent, prong-shaped anterodorsal process that functionally replaces the accessory operculum of certain other early actinopterygians (e.g. *Cheirolepis* and *M. nitida*) and gives the bone a strongly convex dorsal margin. Isolated circular depressions close to the anterior margin probably represent laterosensory pits. Ornament consists of horizontal, posterolateral linear ridges that flex into a posterodorsal orientation at the anterodorsal process.

Branchiostegal rays (Fig. 3). A complete branchiostegal series has not been preserved but at least eight are visible on MV P228849a. The first branchiostegal ray is a slender and elongate bone, its concave shape conforming to the ventral contours of the suboperculum. The next two rays are marginally shorter than the first, but show no variation in height. The branchiostegal rays possess only a slight overlap with their neighbours and there is no evidence of extensive unornamented hyoid processes or overlap surfaces as present in *'Mimia'* (Gardiner 1984: fig. 97) and *Cheirolepis* (Pearson and Westoll 1979: 363).

Gulars (Fig. 3). An incomplete lateral gular is viscerally exposed in MV P228849a as an angular unit below the left dentary.

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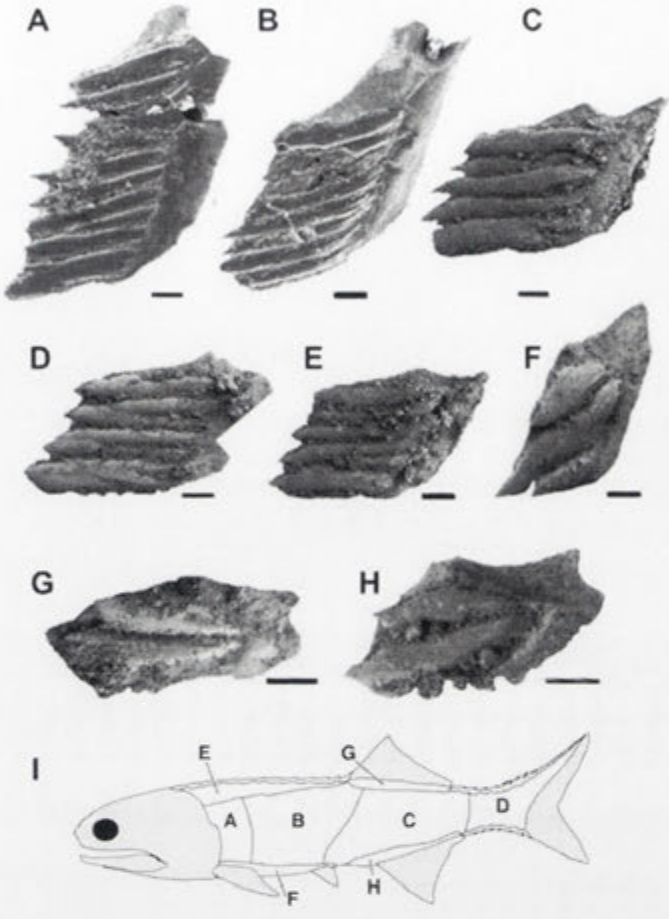


Fig. 12—*Gogosardina coatesi* gen. et sp. nov. Representative scales removed from the right side of the holotype (WAM 07.12.2) in lateral view. —**A**. Zone A scale from the anterior flank. —**B**. Zone B scale from the mid-flank. —**C**. Zone C scale from the rear flank. —**D**. Zone D scale from near the base of the caudal fin. —**E**. Zone E scale from the anterior dorsal surface. —**F**. Zone F scale from the anterior ventral surface. —**G**. Zone G scale from near the base of the dorsal fin. —**H**. Zone H scale from near the base of the anal fin. —**I**. Simplified diagrammatic outline of *Gogosardina* showing the distribution of the major areas with morphologically distinct scale types after Esin (1990). Scale bars for A–F = 100 ugs. Scale bars for G–H = 200 ugs.

Lower jaw

The lower jaw is effectively indistinguishable to that of '*Mimia*' (Gardiner 1984, fig. 90), consisting of a long dentary, angular, prearticular and coronoids. There is no surangular.

Dentary (Figs 3, 4 and 9–11). The largest bone on the lower jaw, consituting more than 85% of the dermal surface. Dentition consists of more than 20 large, conical, laniary teeth with an outer row of much smaller, numerous tubercle-like teeth. The posterodorsal section is unornamented, part of a smooth semicircular excavation that is overlapped by the posteroventral corner of the maxilla. The dentary meets the angular in this excavation with a zig-zag shaped suture. The pores of the mandibular sensory canal run close to the ventral margin of the bone throughout its length, with a slight dorsal deflection into the middle of the bone close to the anterior tip. Dermal ornament of long ridges near the ventral margin, becoming increasingly short and irregular dorsally and grading into tubercles near the biting margin.

Angular (Figs 4, 9 and 10A–B). A short, crescent-shaped bone that forms the posterior and posteroventral dermal surface of the lower jaw. The mandibular canal follows the outer margin and there is a prominent angular pit-line close to the crescentic, ornamented suture with the dentary. Aside from the smooth section beneath the maxillary-overlap, the ornamentation consists of short ridges and tubercles.

Meckelian ossifications and mesial dermal bones (Figs 4, 10C–D and 11). The Meckelian cartialage is ossified into a single unit in the holotype and MV P228849. The endochondral

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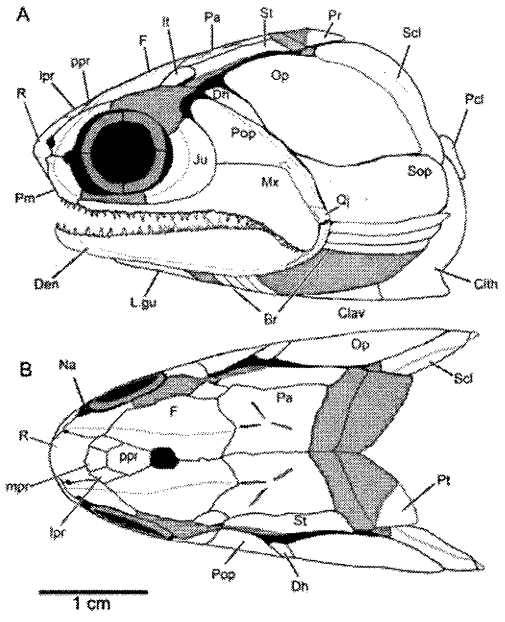


Fig. 13—*Gogosardina coatesi* gen. et sp. nov. Restoration of the head in —**A**. Lateral. —**B**. Dorsal view. Light grey lines correspond to preserved sections of the sensory canals. Dark grey corresponds to areas that have not been preserved.

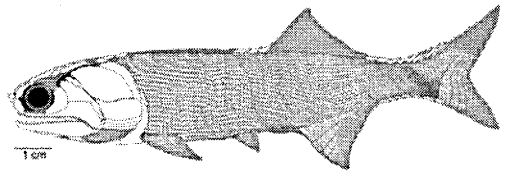


Fig. 14—*Gogosardina coatesi* gen. et sp. nov. Restoration of the entire fish in lateral view. Dark grey corresponds to missing parts of the anatomy.

articular region is free of dermal bone with two circular depressions for the insertion of the quadrate condyles. The coronoids and prearticular are completely fused in all prepared specimens. The combined series forms a flat and elongated denticulated surface that covers about half of the mesial surface of the lower jaw, excluding the articular region and the ventromedial surface. The anterior coronoids bear a row of pointed, conical teeth.

Hyoid and branchial arches

The hyomandibula (Fig. 8M–N) is a large, gently curved element of solid endochondral bone onto which the dermohyal is firmly attached along the anterodorsal flank. A perichondrally lined canal for the hyomandibular trunk of the facial nerve runs obliquely through the bone. Delicate tubular sections of perichondral bone, sometimes with attached toothplates, represent broken segments of the ceratohyal, interhyal and hypohyal. Four branchial arches are present (Figs 4, 5 and 11). Each bone is a perichondral structure with minimal endochondral ossification. The first four ceratobranchials are elongate, rod-like units of similar size with deep ventral longitudinal grooves. The anterior two have extensive toothplates. The fifth ceratobranchial is more slender and lacks a longitudinal groove, probably comprising the sole unit in the fifth arch as in *'Mimia'* (Gardiner 1984: fig. 108). Scattered hypobranchials are elongate bones bearing an expanded proximal end for attachment to the basibranchial.

There are 12 of a possible 15 elements that comprise a complete apparatus of a prioniodinid conodont animal within the branchial cavity of MV P228849 (Figs 4 and 11).

Pectoral girdle

Comprises the post-temporals, supracleithra, postcleithra, cleithra and clavicles. Presupracleithra and a ventral median clavicle are expected to have been present, as in the other Gogo actinopterygians, but have not been identified.

Post-temporal (Fig. 3). The only identified example consists of a partial left post-temporal on MV P228849, comprising the posterolateral corner of the bone. Ornament consist of a linear short-to-medium length rostrocaudally orientated ridges.

Supracleithrum (Figs 3, 4 and 11). A long and narrow element with a broad, rounded dorsal end with a smooth overlap surface for the post-temporal. The bone gently tapers towards the ventral tip which overlays the dorsal tip of the cleithrum. The main lateral line canal enters dorsally at the middle of the dorsal margin and exits approximately three-quarters down the posterior margin. Ornament consists of linear ridges with short, irregular or circular ridges near the anterior margin.

Cleithrum (Figs 3, 4 and 11). Large, tall bone with an expanded, convex ventral region and a slender, crescentic vertical blade. The anterior apex is almost completely ornamented with only a very narrow overlap surface for the supracleithrum, unlike the more extensive overlap surfaces in *'Mimia'* (Gardiner 1984) or *Howqualepis* (Long 1988). Convex posterior margin with a deep posteroventral notch for the insertion of the pectoral fin. The entire anterior margin below the level of the vertical blade is a smooth overlap surface for the clavicle. Dermal ornamentation comprises short ridges on the vertical blade, longer ridges at the pectoral swelling and a mixture of long ridges interspaced with elongated tubercles on the ventral face.

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Clavicle (Figs 3, 4 and 11). A long, semiconical bone with a tall, convex posterior which rigidly overlaps the cleithrum and narrows towards the anterior apex. Bends sharply inwards to a large flat ventral sheet that presumably contacts its counterpart. Dermal ornament of short ridges, becoming longer at rear of the ventral surface and on the posteroventral lateral surface.

Postcleithrum (Fig. 3). The postcleithrum is comparatively large with the ornamented surface of the bone being four times larger than the ornamented free fields of the adjacent flank scales. Unlike the postcleithrum of '*Mimia*' (Gardiner 1984: fig. 127), the ornamented surface comprises the majority of the unit with minimal overlap surfaces.

Body and fins

The head of *Gogosardina* occupies roughly 25% of the body length from the snout to the base of the caudal peduncle, the body being about five times as long as it is deep. This gives an elongate, streamlined appearance akin to *Howqualepis* (Long 1988) and *Donnrosenia* (Long *et al.* 2008), unlike the more robust, shorter bodies of contemporary Gogo forms.

Axial skeleton (Fig. 5). The axial ossifications are delicate structures comprised of perichondral bone. The anterior vertebral column comprises separate paired dorsal neural arch elements though anterior ventral haemal arch elements have not been positively identified. Each neural arch comprises a long distal neural spine, expanding ventrally to a medial face devoid of perichondral-lining and a spatulate epineural process on the lateral face. Articulated haemal arches are present near the caudal fin of MV P.227023b as unpaired, semicylindrical structures.

The dorsal lobe of the caudal fin of MV P228849a (Fig. 3) contains more than 18 hypurals. They are broad, spatulate structures, decreasing in size caudally, that protrude below the scale covering to be embraced by the lepidotrichia. They are broader and more robust than the hypurals of '*Mimia*' (Gardiner 1984: fig. 124) and appear to be the only significant difference in axial anatomy between these two genera.

Pectoral fins (Figs 3 and 6). The endoskeletal radials have not been preserved. About 27 primary lepidotrichia (visible on BMNH P.53241, fig. 6) were present. The longest fin rays have unsegmented proximal sections that accounted for close to half of their length, with the rays becoming distally articulated. Posterior fin rays appear to have been fully segmented to the base. Disarticulated spine-like structures appear to be fringing fulcra similar to those present on '*Mimia*'.

Pelvic fins (Fig. 5). The pelvic fin is poorly known, the only examples being impressions in MV P.227023a. The pelvic fin is small and short-based, situated marginally closer to the anal fin than the pectoral fins.

Anal fin (Fig. 5). A large triangular fin, supported by at least 14 long, closely packed radials, more than twice the number present in '*Mimia*'. More than 41 primary lepidotrichia were present. Fringing fulcra are present on the leading edge.

Dorsal fin (Fig. 3). Poorly preserved and of uncertain shape, based on broken proximal lepidotrichia. Based on the distribution of the dorsal scutes on MV P228849, the fin was of similar length to the anal fin. The leading edge of the dorsal fin appears to have been slightly anterior to the level of the leading edge of the anal fin.

Caudal fin (Figs 3–5). Large heterocercal tail with long, slender dorsal and ventral hypochordal lobes. The maximum extent of both lobes has not been preserved. About 30 lepidotrichia are present on the ventral hypochordal lobe while the dorsal lobe is too incompletely known for an accurate count. Fringing fulcra are present on the leading edge of the ventral lobe.

Scales and squamation

The scales of *Gogosardina* are very small but still macromeric. At least 145 rows are present on MV P228849 (Fig. 3). The scales undergo a marked decrease in size (with a corresponding increase in numbers) about halfway down the length of the fish, with flank scales at the level of the dorsal fin being about a third of the size of more anterior example. Scale size continues to decrease caudally to a size less than one-sixth of the anterior scales. As a result of this, the squamation of *Gogosardina* is not arranged in continuous horizontal rows that extend down the entire length of the fish.

The squamation of *Gogosardina* is divided into the nine areas designated by Esin (1990) (fig. 12I). Esin's method provides a uniform reference for the identification of palaeoniscoid scales and has been successfully used by Burrow (1994) to attribute various forms of *Ligulalepis* scales to particular body areas and by Trinajstic (1999a,b) to refer isolated scales from the Gneudna Formation to *M. durgaringa* and *Mi. toombsi*.

Area A (Fig. 12A). Scales are rectangular with the dorsal-ventral height greater than the rosto-caual length. The anterior margin is straight with the rostro-dorsal process high although unlike *M. durgaringa* it does not extend above peg. The peg is high with a rounded apex and a wide peg base, which is one-third the width of the scale. The keel is well-developed and the socket is deep and long forming a strong interlocking mechanism between scales. The anterior margin of the free field consists of narrow, discrete ganoine ridges, which terminate in up to nine acutely pointed serrations that overhang the posterior margin. The ridges slope in a dorsal to ventral–caudal direction at *c.* 20°. The ridges are plain when compared to *M. durgaringa* (Trinajstic 1999a) and '*Mimia*' (Trinajstic 1999b) with only fine, raised stria along

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the dorsal and ventral margins of each ridge. There is a decrease in the scale depth, and in the number of terminal serrations from area A to area B, and from the median line of area A to the dorsal and ventral margins.

Area B (Fig. 12B). Similar to area A scales, these scales are also higher then long with the free field ornamented with up to eight separate ganoine ridges which terminate in acutely pointed serrations beyond the body of the scale. The anterior portion of each ridge is ornamented withn arrow, raised striae. The keel, peg and socket are well-developed, indicating the scales are closely articulating making the anterior portion of the palaeoniscoid body relatively inflexible. There are pores along the depressed field of the scales and smaller pores between the ganoine ridges that make up the free field.

Area C (Fig. 12C). Through the transitional region from area B to area C a change in scale-shape is observed with the rostro-caudal length exceeding the dorsal–ventral height. The free field ornament remains similar to area B scales, the main difference being in the reduced number of ridges with no greater then six ridges present. Anteriorly, the ridges slope in a dorsal to ventral–caudal direction at *c.* 10° but caudally the ridges appear to be almost straight. The ventral margin of each scale is gently convex. The rostro-dorsal process is high extending above the peg. The peg and socket are reduced, and located midway along the dorsal margin of those scales close to area B and further reduced or absent in scales close to area D. Where the peg is present it has a wide base, extending across the dorsal margin of the free field.

Area D (Fig. 12D). Scales in area D are rhombic in form and become more elongate towards the caudal fin. The ridges are reduced in number to four in scales near area C and one, in scales close to the caudal fin. The ridges terminate in acute serrations that extend beyond the body of the scale. These scales have very poorly defined, low ridges instead of distinct pegs providing weak articulation between scales and permitting greater flexibility in the caudal region of the fish.

Area E (Fig. 12E). These scales are taller than long with a high, wide-based peg, extending the length of the free field, and no rostro-dorsal process. The free field ornament consists of three separate, parallel ganoine ridges that terminate in acute points, which do not extend beyond the body of the scale. The ornament on the ganoine ridges is most pronounced on scales from this body area. The keel and socket are well-developed and these scales were closely articulated making the anterior-dorsal region of the fish relatively rigid.

Area F (Fig. 12F). The scales are elongated with a low peg and the corresponding socket is shallow. The rostro-dorsal process is high with a rounded apex in scales closest to the fin margins and high with an acutely pointed apex in scales closer to areas B and C. The ornament on the free field consists of separate ridges running slightly downward in the direction of the rear corner of the scale. Posteriorly the ridges extend beyond the body of the scale and terminate in acute points.

Areas G (Fig. 12G). The scales in this area are almond-shaped. The free field is slightly raised above the wide depressed field. Scales from area G have an ornament of separate ridges with fine striae on the dorsal and ventral margins of each ridge. The ridges do not extend beyond the margin of the scale. There is no peg or socket visible on this scale type, however, there is a small anterior notch.

Area H (Fig. 12H). Scales are elongated, their length exceeding their height two to three times. The peg is low and extends along the dorsal margin of the scale with the corresponding socket being shallow and the keel is reduced when compare to area A–C scales. There is no rostro-dorsal process. The depressed field is wide, providing a secure attachment in the skin around the mobile fins (Burrow 1994). The ornament is consistent with that present on other scales.

Remarks. The scale types described for *Gogosardinus* can be attributed to the specific body areas designated by Esin (1990). There is a transition from high, narrow scales to low, wide scales from anterior to posterior, and from the midline to the dorsal and ventral margins of the fish. This scale morphology is consistent with those described for other palaeoniscoids (Long 1988; Esin 1990; Burrow 1994; Trinajstic 1999a,b). There are certain characteristics of scale morphology that remain consistent on scales from different parts of the fish's body (Esin 1990). The scales from *Gogosardina* all have a free field ornament of separate ganoine ridges, making isolates scales easy to identify. This pattern is different from the two other Gogo palaoniscoids, *M. durgaringa* and *Mi. toombsi*, in which the free field ornament became less ornate from the anterior to the posterior of the fish, with caudal scales only having fine striations around the anterior of the free field (Trinajstic 1999a,b).

Body scutes (Figs 3–5). Only a few dorsal scutes anterior to the dorsal fin on MV P228849 are preserved. Three are present in articulation, immediately anterior to the remnants of the fin on MV P228849a (Fig. 3), each slightly overlapping the one behind it. They are large plate-like structures with the anteriormost being over 20 times larger than the adjacent flank scales. Each scute has a pointed posterior margin that becomes a short spine on the scute at the anterior dorsal base. Broken plate-like fragments near the skull suggest that the dorsal fulcral series extended anteriorly to the occipit. Each scute in the dorsal series is ornamented with up to 17 longitudinal ridges. Posterior of the dorsal fin, the scutes are narrower and more triangular (Figs 3–5). As the series

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progresses posteriorly, the scutes become increasingly narrow and with a greater degree of overlap. Over the notochordal mass of the caudal fin, the scutes are spine-like and almost completely overlap one another.

Ventral scutes are poorly preserved. Two disarticulated examples in between the caudal and anal fin of MV P228849b (Fig. 4) are triangular in shape and similar to the anterior elements in the upper caudal series. No scutes have been preserved anterior of the anal fin.

Discussion

Comparisons with other early actinopterygians

Based on preliminary observations, *Gogosardina* appears most similar to *'Mimia'*, also from the Gogo Formation. Both represent the only genera of stem-actinopteran known to lack ascending processes on the parasphenoid. Both lack a surangular and possess a zig-zag suture of the angular and dentary in the maxillary overlap area. At present, two distinct species are present in material currently designated as *'Mimia' toombsi*. The relationship of *Gogosardina* to *'Mimia'* will be examined with the description of the second species of the latter genus (Choo, in prep.). The new genus is distinguishable from both species of *'Mimia'* in having a more elongate body form, smaller scale-size, in lacking anastomosing ridges on the anterior flank scales and in the contribution of the postrostral series to the margin of the pineal foramen.

Gogosardina is distinguishable from all other actinopterygians due to the unique arrangement of postrostrals wedged between the frontals, with the posterior unit forming the anterior margin of the pineal foramen. Among other Devonian forms, it differs from *Cheirolepis* in the absence of fleshy basal-lobes on the pectoral fin and possessing macromeric squamation (Pearson and Westoll 1979; Arratia and Cloutier 1996). It differs from *Osorioichthys* in the absence of fleshy pectoral lobes, suborbitals and surangulars, along with the presence of postrostrals and a pineal foramen (Taverne 1997). It differs from *Kentuckia* in the absence of accessory operculae, having parietals of a similar length to the frontals and a pineal foramen (Dunkle 1964). It differs from *Tegeolepis* in having macromeric squamation, large lateral gulars and lacking greatly enlarged teeth on the anterior dentary (Dunkle and Schaeffer 1973). It differs from *Donnrosenia* and *Howqualepis* in having a dorsal scute series that extends to the occipital region, short-based pelvic fins, in lacking a surangular and having more extensive distal segmentation on the pectoral fin (Long 1988; Long *et al.* 2008). It differs from *M. durgaringa* and *M. nitida* in its elongate body form, lacking any porous ornamentation and in possessing postrostrals (Jessen 1968; Gardiner 1984). It differs from *Krasnoyarichthys* in lacking an accessory operculum, in having a less extensive series of ventral scutes and having longer, narrower branchiostegal rays (Prokofiev 2002). It differs from *Stegotrachelus* in its more gracile body form, possessing postrostrals and having a prominent anterodorsal process on the suboperculum (Gardiner 1963). It differs from *Limnomis* and *Cuneognathus* in possessing pelvic fins and postrostrals, while lacking curved anterior ridges on the flank scales (Daeschler 2000; Friedman and Blom 2006). *Gogosardina* is distinguishable from the majority of post-Devonian actinopterygians in having a large pineal foramen and the absence of a dermopterotic.

Postrostral units in early actinopterygians

In contrast to the sarcopterygians where such bones are primitively present, the presence of distinct postrostrals (anamesic bones posterior to the rostral and anterior to the frontals) is an unusual feature within the actinopterygians and is restricted to a handful of fossil genera. The postrostral configuration *Gogosardina* as presented in the description (three laterally arrayed anterior bones followed by a single posterior unit which forms the anterior margin of the pineal foramen) is highly distinctive and thus of diagnostic importance.

The postrostral series of *Cheirolepis canadensis* is superficially similar to that of *Gogosardina* in overall configuration, consisting of a median postrostral flanked by lateral units, followed by a variable number (0–3) of median posterior postrostrals (Arratia and Cloutier 1996). The postrostral series of *Gogosardina* differs from *C. canadensis* in that the lateral units suture with the frontals laterally rather than posteriorly and in that the posterior bone is the largest in the series. Conversely, *C. trailli* has a single postrostral ossification (Pearson and Westoll 1979), but its shape and positioning more closely matches the extent of the entire postrostral series of *Gogosardina* with the bone nestled in a V-shaped anterior recess between the frontals. No species of *Cheirolepis* possesses such a large, open pineal foramen as *Gogosardina*, the structure being either absent, much smaller or covered by a pineal plate.

A single large postrostral is present in an undescribed second species of *'Mimia'* from the Gogo Formation. It conforms to the dorsal lamina of the larger rostral of *'Mimia' toombsi* and sutures posteriorly with the frontals (Choo, in prep.).

Postrostrals are present in a number of Carboniferous forms. The guildayichthyids (*Guildayichthys* and *Discoserra*) have a pair of anterior postrostrals that contribute to the anterior nasal openings along with a single, large posterior postrostral (Lund 2000). The tarassiids (*Tarrasius* and *Paratarrasius*) have a single median postrostral that does not contact the frontals (Lund and Poplin 2002). *Kalops* has an extremely large single postrostral that contributes to the anterior nasal openings and excludes the small rostral from the dorsal surface of the skull (Poplin and Lund 2002).

That the postrostral series of *Gogosardina* is only preserved in a single damaged individual invites scrutiny regarding the validity of our reconstruction. In the skull roof of the majority of Devonian actinopterygians, the pineal foramen is fully enclosed by the paired frontals. This configuration is

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impossible in *Gogosardina* as there is no trace of a median suture anterior to the pineal foramen in the type specimen and the frontals of MV P.227023a do not meet anteriorly, indicating that one or more ossifications were nestled between the frontals. However, the possibility that the four structures identified as separate postrostrals actually represent the fragments of a lesser number of bones cannot be ruled out without further specimens.

Conodont elements within the body of MV P228849

The conodont remains within MV P228849b represent the second described instance of such elements being present within a Gogo actinopterygian. Nicoll (1977) describes the presence of the apparatuses of two separate conodont animals found within the gut region of a 'stegotrachelid palaeoniscoid fish' from the Gogo Formation. The fish (CPC 17220 – currently housed in the Australian National University, Canberra) is a representative of the undescribed second species of *'Mimia'*. Conodont elements within the gut cavity of this fish comprised a complete apparatus of *Hibbardella angulatus* (15 elements) and an incomplete apparatus of *Icriodus brevis* (13 elements).

In contrast to CPC 17220, the conodont elements within MV P228849b, which represent a single prioniodinid individual, are not within the gut cavity but instead situated among the branchial elements, indicating that the conodont animal was not fully ingested prior to the death of the fish. Aside from two isolated elements that have scattered from the main cluster, the structures of the conodont apparatus appear to be in anatomical position. The set of S elements, positioned in a dorsal position relative to the palaeoniscoid, are orientated with their cusps rostral and their denticles directed obliquely dorsal as indicated for *Promissum* (Purnell *et al.* 2000). One M element is identified overlying the dorsal S elements and the position of the Sa element, anterolateral to it, indicates some post-mortem movement. It would appear that the S and M elements lie together as a single anterior unit (Aldridge 1987). A pair of P1 elements, in functional opposition lie caudal to the S elements (Donoghue and Purnell 1999). Given the orientation of the apparatus, the conodont animal was consumed tail-first and, using *Clydagnathus* as a guide (Briggs *et al.* 1983), the complete animal was in excess of 10 cm in length.

Extant macropredatory actinopterygians are known to sometimes attempt to injest prey objects of a size too large to be easily swallowed, leading to serious injury or death if the fish is unable to expel it (Choo, pers. obs. of captive *Echidna, Gymnothorax, Antennarius, Pterois* and *Epinephelus* sp.). It is probable that MV P228849 represents a *Gogosardina* that attempted to consume a conodont animal of a similar size to itself. The fish subsequently expired when it found itself unable to either fully injest or spit out the food item.

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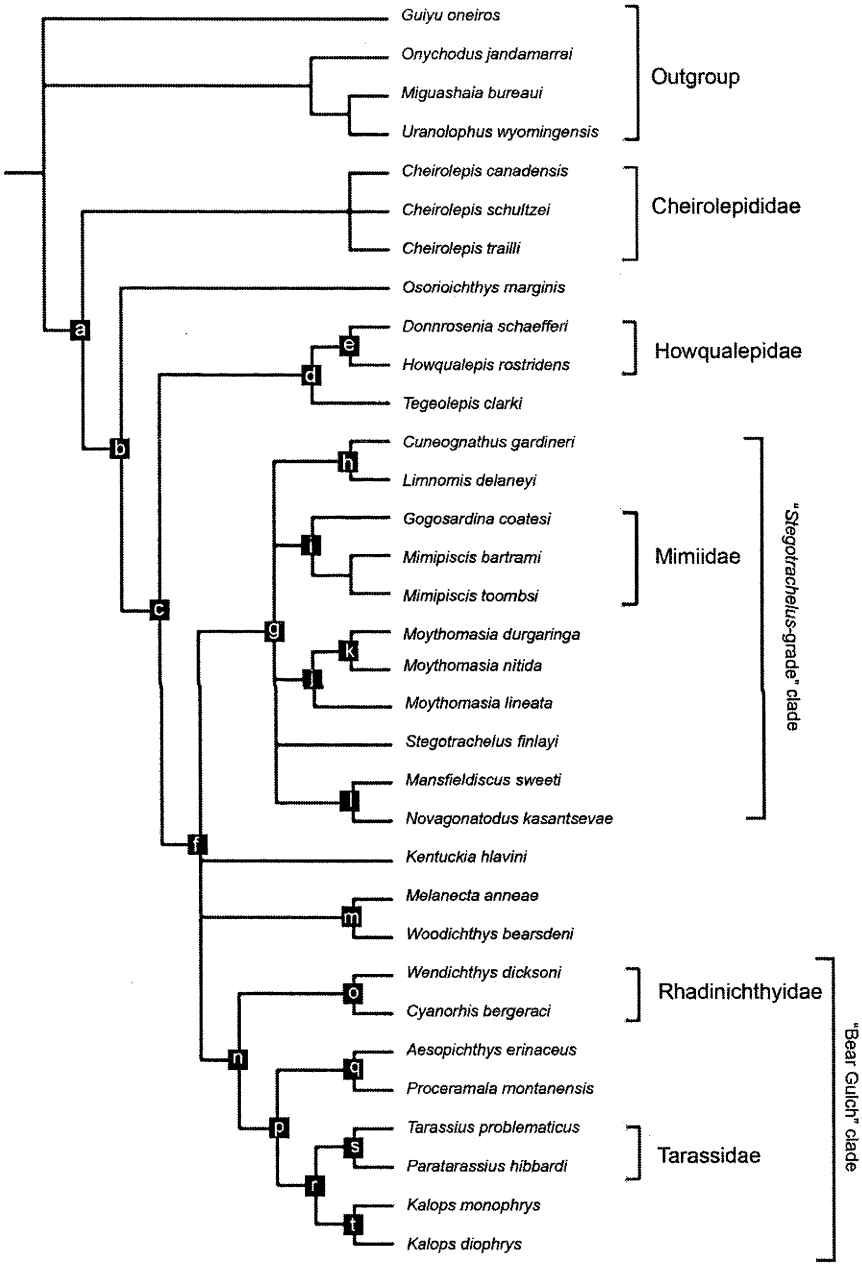
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APPENDIX IV

Apomorphy list



(preceding page) - the cladogram presented as Figure 8.2 with the addition of letters at nodes keyed to the apomorphy list presented below.

Apomorphy list for the analysis presented in chapter 8.4. Thickened arrows (==>) represent state changes in unambiguous characters whilst the remainder (-->) are ambiguous. Emboldened characters have a consistency index of 1.00 while the remainder are homoplastic. Where unresolved polytomies are present, only characters relevent to all trees are retained.

stem-a (Actinopterygii)

CHARACTER	
6 (Posterior nostril)	0 ==> 1
11 (Frontals, relative size)	0 ==> 1
21 (Mandibular canal - course of)	0 --> 1
22 (Dentary reflexure)	0 --> 1
23 (Infradentaries, number of)	0 --> 1
24 (Enlarged parasymphysial teeth)	1 ==> 0
31 (Scale rows - number of)	0 --> 1
37 (Fringing fulcra)	0 ==> 1
47 (Fulcra on dorsal ridge of caudal fin)	0 --> 1
53 (Dermohyal)	0 ==> 1
54 (Dermosphenotic)	0 ==> 1
59 (Median extrascapular)	0 ==> 1
72 (Mandibular canal)	**0 ==> 1**
74 (Dermal intracranial joint)	**0 ==> 1**
75 (Branchiostegal rays)	0 ==> 1
81 (Suborbital bones)	1 ==> 0

a-*Cheirolepis* spp.

3 (Postrostrals)	1 ==> 2
17 (Jugal - notch in anterior margin.)	0 ==> 1
19 (Accessory operculum)	0 ==> 1
32 (Scales - Peg-and-socket articulation)	0 --> 1
34 (Scales)	0 ==> 1
45 (Pelvic fin insertion)	0 --> 1
51 (Anal fin, anterior margin)	1 --> 0

a-b

3 (Postrostrals)	1 ==> 0
4 (Single median rostral)	0 ==> 1
8 (Single nasal)	0 ==> 1
28 (Parasphenoid - ascending process)	0 --> 1
39 (Presupracleithrum)	0 ==> 1
40 (Scapulacoracoid with horizontal plate)	**0 --> 1**
41 (Pectoral fin rays embrace propterygium)	**0 ==> 1**
56 (Rostral - shape of)	1 --> 2
73 (Perforated propterygium)	**0 --> 1**

b-*Osorioichthys*

7 (Posterior nostril - margin contributed to)	0 ==> 1
15 (Number of paired extrascapulae)	0 ==> 1
18 (Anamesic suborbital bones)	0 ==> 1
57 (Quadratojugal)	1 ==> 0
58 (Operculum, relative size)	0 ==> 1
76 (Branchiostegal rays - 1st ray ventral to)	0 ==> 1

b-c

20 (Lateral gulars)	**0 ==> 1**
21 (Mandibular canal - course of)	1 --> 0
33 (Scales - anterodorsal extension)	1 ==> 0
43 (Pectoral fin insertion)	0 ==> 1
55 (Intertemporal - contact with parietal)	1 --> 0

c-d (d = *Tegeolepis* + Howqualepididae)

16 (Lacrimal - anterior expansion)	0 ==> 1
22 (Dentary with distal reflexure)	1 --> 0
24 (Enlarged parasymphysial teeth.)	0 --> 1
27 (Mentomeckelian region is ossified)	0 ==> 1

44 (Pectoral fin segmentation) 0 --> 2

d-*Tegeolepis*
6 (Posterior nostril) 1 ==> 0
34 (Scales) 0 ==> 1
37 (Fringing fulcra) 1 ==> 0
44 (Pectoral fin segmentation) 2 --> 3
48 (Dorsal scutes) 0 ==> 1
49 (Ventral scutes) 1 ==> 0
53 (Dermohyal) 1 ==> 0
54 (Dermosphenotic) 1 ==> 2
56 (Rostral - shape of) 2 --> 0
58 (Operculum, relative size) 0 ==> 1
71 (Infraorbitals - number of) 0 ==> 1

d-e (e = Howqualepididae)
1 (Rostral contributes to biting margin) 0 --> 1
9 (Pineal foramen) 1 ==> 0
13 (Intertemporal, contact with supratemporal) 0 ==> 1
29 (Parasphenoid - anterior tripartite) 0 --> 1
45 (Pelvic fin insertion) 0 ==> 1
57 (Quadratojugal) 1 ==> 0
60 (Scales - anastomosing linear ornament) 0 ==> 1
61 (Suboperculum anterodorsal process) 0 ==> 1

e-*Donnrosenia*
2 (Premaxillae - shape of) 0 ==> 1
19 (Accessory operculum) 0 ==> 1
21 (Mandibular canal - course of) 0 ==> 1
22 (Dentary, distal reflexure) 0 --> 1
24 (Enlarged parasymphysial teeth) 1 --> 0
35 (Scales - well-developed pores/punctae) 0 ==> 1
82 (Maxilla, posteroventral overlap) 0 ==> 1

e-*Howqualepis*
10 (Parietals - shape of) 0 ==> 1
11 (Frontals - relative size) 1 ==> 2
76 (Branchiostegal rays - 1st ray) 0 ==> 1

c - f
10 (Parietals - shape of) 0 ==> 1
11 (Frontals - relative size) 1 ==> 2
31 (Scale rows - number of) 1 --> 0
42 (Pectoral fin - metapterygium enlarged rel) 0 --> 1
46 (Caudal fin - epichordal lobe) 0 ==> 1
51 (Anal fin, anterior margin) 1 ==> 2
56 (Rostral - shape of) 2 --> 1
82 (Maxilla, posteroventral overlap) 0 ==> 1

f - *Kentuckia*
19 (Accessory operculum) 0 ==> 1
23 (Infradentaries, number of) 1 ==> 0
44 (Pectoral fin segmentation) 0 ==> 1
55 (Intertemporal - contact with parietal) 0 ==> 1
71 (Infraorbitals - number of) 0 ==> 1

f - g (g = *Stegotrachelus*-grade clade)
9 (Pineal foramen) 1 ==> 0
29 (Parasphenoid - anterior tripartite) 0 --> 1
48 (Dorsal scutes) 0 ==> 1
49 (Ventral scutes between caudal and anal) 1 --> 0
55 (Intertemporal - contact with parietal) 0 --> 2

g - h
5 (Rostral) 0 ==> 1
32 (Scales - Peg-and-socket articulation) 0 ==> 1
38 (Pelvic fins) 0 ==> 1

g - *Cuneognathus*

13 (Intertemporal, contact with supratemporal)	0 ==> 1
55 (Intertemporal - contact with parietal)	2 --> 0

g - *Limnomis*

61 (Suboperculum - narrow, tapering anterodor)	0 ==> 1

g - i (i = Mimiidae)

23 (Infradentaries, number of)	1 ==> 2
28 (Parasphenoid - ascending process)	1 ==> 0
44 (Pectoral fin segmentation)	0 ==> 1
56 (Rostral - shape of)	1 ==> 2
57 (Quadratojugal)	1 ==> 0
62 (Supratemporal - narrow anterolateral flan)	**0 --> 1**

i - *Gogosardina*

2 (Premaxillae - shape of)	1 ==> 0
64 (Body form)	1 ==> 0

i - *Mimipiscis* spp.

55 (Intertemporal - contact with parietal)	2 ==> 1
60 (Scales - anastomosing linear ornament)	0 ==> 1

Mimipiscis* spp. - *M.toombsi

7 (Posterior nostril)	0 ==> 1
51 (Anal fin, anterior margin)	2 ==> 1

Mimipiscis* spp. - *M.bartrami

no inferred apomorphies

g - j (j = *Moythomasia* spp.)

12 (Intertemporal - relative length)	0 ==> 1
15 (Number of paired extrascapulae)	0 ==> 1
16 (Lacrimal - anterior expansion)	0 ==> 1
21 (Mandibular canal - course of)	0 --> 1
63 (Extrascapulae - median branching of canal)	**0 ==> 1**
65 (Serrated linear ganoine ornament on skull)	**0 ==> 1**
66 (Preoperculum - vertical linear ornament)	0 --> 1
76 (Branchiostegal rays - 1st ray)	0 ==> 1

j = *M.lineata*

58 (Operculum, relative size)	1 --> 0
64 (Body form)	1 ==> 0

j-k (k = M. durgaringa + M. nitida)

26 (Porous ganoine ornamentation on lower jaw)	**0 ==> 1**
31 (Scale rows - number of)	1 --> 0
35 (Scales - well-developed pores/punctae)	0 ==> 1
60 (Scales - anastomosing linear ornament)	0 ==> 1

k - *M.durgaringa*

1 (Rostral contributes to biting margin)	0 ==> 1
10 (Parietals - shape of (= sarcopterygian po)	0 ==> 1
11 (Frontals)	1 ==> 2
21 (Mandibular canal - course of)	1 --> 0
44 (Pectoral fin segmentation)	0 ==> 1
66 (Preoperculum - vertical linear ornament)	1 --> 0

k - *M.nitida*

18 (Anamesic suborbital bones)	0 ==> 1
19 (Accessory operculum)	0 ==> 1
51 (Anal fin, anterior margin)	2 ==> 1
61 (Suboperculum anterodorsal process)	1 ==> 0

g - *Stegotrachelus*

14 (Dermosphenotic, contact with frontals)	0 ==> 1
19 (Accessory operculum)	0 ==> 1
27 (Mentomeckelian region is ossified.)	0 ==> 1
51 (Anal fin, anterior margin)	2 ==> 1

g - l

16 (Lacrimal - anterior expansion)	0 --> 1
18 (Anamesic suborbital bones)	0 ==> 1
49 (Ventral scutes between caudal and anal)	0 --> 1
70 (Dermopterotic)	0 ==> 1

l - *Mansfieldiscus*

9 (Pineal foramen)	0 ==> 1
19 (Accessory operculum)	0 ==> 1
44 (Pectoral fin segmentation)	0 ==> 3
48 (Dorsal scutes)	1 ==> 0
69 (Antorbital bone)	0 ==> 1

l - *Novagonatodus*

17 (Jugal - notch in anterior margin.)	0 ==> 1
39 (Presupracleithrum)	1 ==> 0
45 (Pelvic fin insertion)	0 ==> 1
59 (Median extrascapular)	1 ==> 0

f - m

39 (Presupracleithrum)	1 ==> 0
44 (Pectoral fin segmentation)	0 ==> 2

m - *Melanecta*

1 (Rostral contributes to biting margin)	0 ==> 1
31 (Scale rows - number of)	0 ==> 1
45 (Pelvic fin insertion)	0 ==> 1
58 (Operculum, relative size)	0 ==> 1

m - *Woodichthys*

35 (Scales - well-developed pores/punctae)	0 ==> 1
56 (Rostral - shape of)	1 ==> 2

f - n (n = Bear Gulch clade)

10 (Parietals - shape of)	1 ==> 2
14 (Dermosphenotic, contact with frontals)	0 --> 1
18 (Anamesic suborbital bones)	0 --> 1
20 (Lateral gulars)	**1 ==> 2**
69 (Antorbital bone)	0 ==> 1
76 (Branchiostegal rays - 1st ray)	0 ==> 1

n - o (o = Rhadinichthyidae)

2 (Premaxillae - shape of)	0 ==> 2
68 (Rostral notch)	**0 ==> 1**

o - *Wendichthys*

17 (Jugal - notch in anterior margin)	0 ==> 1
39 (Presupracleithrum)	1 ==> 0

o - *Cyanorhis*

21 (Mandibular canal - course of)	0 ==> 1
57 (Quadratojugal)	1 ==> 0

n - p

15 (Number of paired extrascapulae)	1 --> 2
18 (Anamesic suborbital bones)	1 --> 2
43 (Pectoral fin insertion)	1 ==> 0
48 (Dorsal scutes)	0 ==> 1
49 (Ventral scutes between caudal and anal fi)	1 --> 0
56 (Rostral - shape of)	1 --> 0
79 (Anal fin - length of base)	0 --> 1
80 (Pectoral fin rays)	0 --> 1

p - q

2 (Premaxillae - shape of)	0 --> 1
5 (Rostral)	0 --> 1
64 (Body form)	0 ==> 2
67 (Jaw suspension)	0 ==> 1
75 (Branchiostegal rays)	0 ==> 1

q - *Aesopichthys*

15 (Number of paired extrascapulae)	2 --> 1
18 (Anamesic suborbital bones)	2 --> 1
58 (Operculum, relative size)	0 ==> 1

q- *Proceramala*

12 (Intertemporal - relative length)	0 ==> 1
71 (Infraorbitals - number of)	0 ==> 1
78 (Dorsal fin - length)	0 ==> 1

p - r

3 (Postrostrals)	0 ==> 2
4 (Single median rostral)	1 ==> 0
14 (Dermosphenotic, contact with frontals)	1 --> 0
31 (Scale rows - number of)	0 ==> 1
32 (Scales - Peg-and-socket articulation)	0 --> 1
33 (Scales - anterodorsal extension)	0 --> 1
45 (Pelvic fin insertion)	0 --> 1
81 (Suborbital bones)	0 ==> 1

r - s (s = Tarassidae)

6 (Posterior nostril)	1 --> 0
8 (Single nasal)	1 ==> 0
34 (Scale size)	0 ==> 1
37 (Fringing fulcra)	1 ==> 0
38 (Pelvic fins)	0 ==> 1
47 (Fulcra on dorsal ridge of caudal fin)	1 ==> 0
48 (Dorsal scutes)	1 ==> 2
49 (Ventral scutes between caudal and anal)	0 --> 1
50 (Ventral scutes anterior to anal fin)	**0 ==> 1**
56 (Rostral - shape of)	0 --> 1
58 (Operculum, relative size)	0 ==> 1
64 (Body form)	0 ==> 3
78 (Dorsal fin - length)	0 ==> 2
79 (Anal fin - length of base)	1 ==> 2
80 (Pectoral fin rays)	1 --> 0

s - *Tarassius*

10 (Parietals - shape of)	2 ==> 1
15 (Number of paired extrascapulae)	2 --> 0
18 (Anamesic suborbital bones)	2 ==> 0
43 (Pectoral fin insertion)	0 ==> 1
67 (Jaw suspension)	0 ==> 1
76 (Branchiostegal rays - 1st ray)	1 ==> 0
19 (Accessory operculum)	0 ==> 1
21 (Mandibular canal - course of)	0 ==> 1
54 (Dermosphenotic)	2 ==> 1
75 (Branchiostegal rays)	0 ==> 1
77 (Jugal canal)	1 ==> 0
82 (Maxilla, posteroventral overlap)	1 ==> 0

r - t (t = *Kalops* spp)

59 (Median extrascapular)	1 ==> 0
70 (Dermopterotic)	0 ==> 1
71 (Infraorbitals - number of)	0 ==> 1
79 (Anal fin - length of base)	1 --> 0

t = *Kalops monophrys*

15 (Number of paired extrascapulae)	2 --> 0

t = *Kalops diophrys*

21 (Mandibular canal - course of)	0 ==> 1