

# A review of recent discoveries of exceptionally preserved fossil fishes from the Gogo sites (Late Devonian, Western Australia)

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**ABSTRACT:** Significant new material of Late Devonian Gogo Formation fish fossils is still surfacing. Collecting in the past decade has uncovered the first Gogo shark fossils (*Gogoselachus* plus another new undescribed taxon), the first acanthodian (*Halmacanthodes ahlbergi*), the first coelacanth, as well as the first placoderm embryos. Recent studies have elucidated the nature of placoderm claspers, pelvic girdles, synarcuals and embryos, the structure of their teeth, a description of well-preserved muscles in placoderms, and how muscles attach to bones. Molecular biomarkers have also been identified in Gogo fossils. There are now five basal ray-fin fishes in the fauna, including one undescribed new taxon. The lungfish fauna from Gogo is the most diverse known for any Devonian site, with 10 genera and 12 species. The dermal skeleton and endocast of the dipterid *Rhinodipterus kimberleyensis* have been described in detail from CT scans; and the ontogenetic stages of neurocranium formation in *Griphognathus*. New specimens of the tetrapodomorph fish *Gogonassus andrewsae* have shed further light on its endocranium, pectoral girdle and fin. Through their exceptional preservation of both hard and varied kinds of soft tissues, the Gogo fishes remain crucial for resolving key debates on the diversification, physiology, biomechanics and phylogenetic relationships of early gnathostomes.

**KEY WORDS:** diversity, Gogo Formation, ontogeny, osteichthyans, phylogeny, placoderms, preservation, vertebrates.

The Late Devonian (Frasnian) Gogo Formation fauna currently comprises some 50 species of fishes in addition to concavacarid crustaceans, making up approximately a quarter of the fauna, along with rare eurypterids, tentaculitids and other invertebrates (Briggs *et al.* 2011). The excellent 3-D preservation of the fish fossils makes them a standard reference for the study of anatomical features in early vertebrates. In this paper we discuss a number of new vertebrate discoveries from the Gogo Formation that have come to light or been featured in various research projects since our previous major review paper (Long & Trinajstić 2010). Most of the work on Gogo fishes published prior to 2010 can be found in that publication.

## 1. Geological setting

The Gogo Formation includes the oldest inter-reef deposits in the southern region of the Lennard Shelf within the Canning Basin. Details of its history of mapping and discovery can be found in Playford & Lowry (1966), Long & Trinajstić (2010) and Playford *et al.* (2009). The outcrops of the Gogo Formation occur over a large area (*c.* 200 km<sup>2</sup>) between prominent outcrops of the Devonian reef complex to the east of Fitzroy Crossing, on Gogo and Mt Pierre Stations. The Gogo Formation is about 700 m thick, measured from drill core, and is the basal lateral facies equivalent of the Sadler Limestone Formation (marginal-slope facies), Pillara Limestone (platform facies) and Windjana Formation (reef facies, Playford 1980). The Gogo Formation has been dated as early Frasnian



(*falsiovalis* to *punctata* conodont zones), based on revision of the conodont fauna and radiolarians from the upper part of the formation (Glenister & Klapper 1966; Druce 1976; Nazarov *et al.* 1982; Nazarov & Ormiston 1983). Three local hypoxic events suggesting sea level rises are recognised in the early Frasnian, indicative of oxygen depletion at the sea floor (Playford & Wallace 2001).

## 2. Preservation of Gogo fishes

The Gogo fish fossils are generally preserved as three-dimensional, undistorted or compressed bone and mineralised cartilage within limestone concretions that rapidly formed after death. Finer resolution preservation occurs of biomineralised soft tissues, which to date have included muscle fibres and bundles, nerve cells and umbilical structures (Trinajstić *et al.* 2007; Long *et al.* 2008, 2009), as well as mineralised muscle blocks in ptyctodonts (Trinajstić *et al.* 2007) and arthrodirans (Trinajstić *et al.* 2013). The extraordinary preservation of the fossils is the result of microbially-induced encapsulation of the fauna preventing full decomposition (Mendelez *et al.* 2013a, b).

Biomarkers from the fossil and carbonate nodules indicate the presence of a stratified water column with persistent euxinic conditions in the photic zone supporting the sulphur reducing bacteria which were important for the rapid formation of carbonate nodules that encapsulated the fauna (Mendelez *et al.* 2013a, b). These features facilitated the mineralisation of soft tissues, rarely preserved in fossils of this age (Trinajstić

*et al.* 2007, 2013). In addition, an overall lack of major tectonic forces in the region after burial of the reef complex sedimentary sequence enabled the fossil specimens to retain their 3-D shape without any sign of post-burial compaction (Playford *et al.* 2009).

Specimens figured herein are held in the collections of the following Australian museums and university collections: ANU, The Australian National University, Research School of Earth Sciences, Canberra; MV, Museum Victoria; SAM, South Australian Museum; WAM, Western Australian Museum.

### 3. The search for Gogo fish fossils

The history of Gogo fish expeditions and their outcomes from the initial discovery through to the 2005 Museum Victoria expedition has been summarised in Long (2006). The discovery of many new species resulting from the author's (JL) expeditions between 1986 and 2005 was due in part to careful re-examination of known sites mapped by the earlier joint expeditions (1963, 1967) and outlined in Miles (1971), but also due to searching those Gogo outcrops depicted on the geological maps, but not known to have yielded fishes previously. These include sites around Embayment Hill, south of Stromatoporoid Camp, first prospected successfully for fishes on the 2001 expedition, yielding the new actinopterygian *Gogosardina coatsi* (Choo *et al.* 2009), plus areas in between Stromatoporoid Camp and Long's Well, which produced the first Gogo acanthodian (Burrow *et al.* 2012), chondrichthyans (Long *et al.* 2015) and first coelacanth from the Gogo formation, all found on the 2008 Museum Victoria expedition. In 2011 a Curtin University expedition to Gogo recovered many significant new finds, including arthrodires with soft tissue preservation and a complete specimen of the tetrapodomorph fish *Gogonasus*.

### 4. The Gogo fish fauna

The Gogo fish fauna currently comprises some 50 species of placoderms, actinopterygians, dipnoans, acanthodians and single taxon representatives of chondrichthyan, onychodontiform, actinistian and osteolepiform fishes. Of these, some were newly discovered on the 2005 and 2008 Gogo expeditions, and have not yet been formally described (for example, a second chondrichthyan and an actinistian). The most abundant vertebrate group is the placoderms, with the highest diversity exhibited by the small eubranchyothoracid arthrodires. Notably absent from the fauna are the agnathans (jawless fish) and one osteichthyan group, the porolepiforms. However, slightly younger (mid-late Frasnian) sediments of the Virgin Hills Formation, representing distal forereef slope deposits that conformably overlay the Gogo Formation, have recently yielded numerous sharks teeth, acanthodian scales and thelodont scales (Trinajstic & George 2009; Trinajstic *et al.* 2014; Roelofs *et al.* 2015; Hairapetian *et al.* 2016).

Lately, major advances have been achieved in studying these fossils using micro-CT tomography from both synchrotron and micro-CT machines. At first, only prepared material was scanned, with great resolution at the 10–30-micron level using the ANU Vizlab facility (e.g., *Gogonasus*, Long *et al.* 2006). Recent work using the Grenoble synchrotron has been applied to specimens still embedded within limestone to resolve soft-tissue preservation (Trinajstic *et al.* 2013; Sanchez *et al.* 2013). Most recently, the neutron beam at ANSTO in Lucas heights, Sydney region, has been applied to image larger scale specimens within thick nodules (c. 10 cm) with good resolution.

## 5. New information on Gogo placoderms

### 5.1. Antiarchs

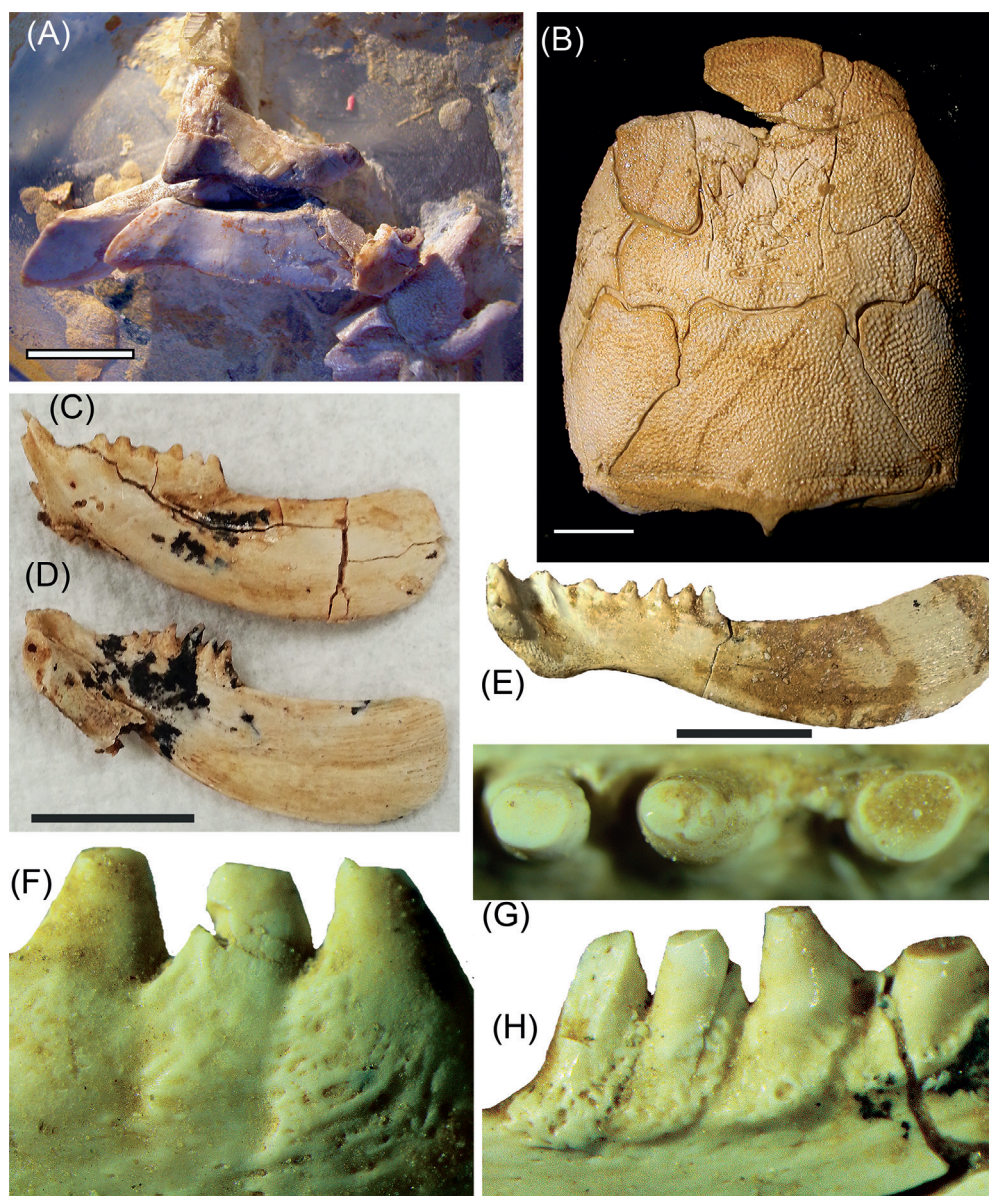
Only one antiarch is present at Gogo, the bothriolepidoid *Bothriolepis* sp., and although undescribed, research on the mouthparts (Young 1984) and pelvic region (Long *et al.* 2015b) has been undertaken. Most recently, the lower jaw bones (inferognathals) and spines of the pectoral fin dermal bone were analysed using synchrotron imaging by Rückelin *et al.* (2012) to determine if teeth were present. This study concluded that there was no difference in the microanatomy of the 'tooth-like' structures on the jaws and spines on the pectoral fins and bones. It was suggested that antiarchs might have not secondarily lost dentine (as was implied in the acceptance that they had teeth on their jaws), as dentine cannot be found anywhere in their dermal skeletons (Rückelin *et al.* 2012). Two specimens of Gogo *Bothriolepis* were figured in a paper on antiarch reproduction (Long *et al.* 2015a, supplementary information) and also in a book (Long 2011). One specimen from the MV collections displayed unusual morphological features on the dorsal surface of the subanal lamina of the posterior ventrolateral plate, and another specimen from the ANU collections showed the presence of small paired plates in this region. These were initially interpreted as female 'genital plates', following identification of similar structures in *Pterichthyodes* and *Microbrachius*, but we are now revising this interpretation in the light of new research with our collaborators at the University of Rimouski, Quebec. Further work on the well-preserved Escuminac Formation *Bothriolepis canadensis* specimens is critical to resolving the issue. Continuation of the description of Gogo *Bothriolepis* material is now dependent on a number of new finds awaiting to be fully prepared, with others to be synchrotron-scanned prior to acid preparation to search for soft tissues.

### 5.2. Ptyctodontids

Recently published work on Gogo ptyctodontids has focused on the description of the dermal skeleton, jaws and embryos of *Materpiscis* and *Austroptyctodus* (Trinajstic *et al.* 2012; Johanson & Trinajstic 2014) and the redescription of the pelvic girdle in *Campbellodus* (Trinajstic *et al.* 2015). The recognition of dermal and perichondral ossifications within the pelvic skeleton of *Campbellodus* showed for the first time that, like the pectoral girdle, the pelvic girdle was a composite structure. This suggests that in early jawed vertebrates the formation of paired girdles was an interactive process along the body flank (Trinajstic *et al.* 2015). A new specimen of *Campbellodus* (WAM 11.9.1) shows the articulated upper and lower jaws in near occlusion, indicating the inferognathals protruded well forward anteriorly of the supragathals (Fig. 1A), a feature also present in *Materpiscis* (Trinajstic *et al.* 2012). The description of the synarcual in *Campbellodus*, with the inclusion of developmental data from chondrichthyans, provided evidence that the synarcual first forms as individual vertebrae and that bone is deposited between vertebrae in development (Johanson *et al.* 2013; Johanson & Trinajstic 2014). These studies show the utility of combining fossil and extant taxa to inform on the evolution of the vertebrate skeleton.

### 5.3. Arthrodires

Recent work by Rücklin *et al.* (2012) and Donoghue & Rücklin (2014) have confirmed the earlier hypothesis put forward by Smith & Johanson (2003) that placoderms do possess true teeth, characterised by having a true dentine structure that developed



**Figure 1** Gogo placoderms. (A) ptyctodontid *Campbellodus decipiens*, WAM 11.9.1, showing articulated upper and lower jaws. (B), (E) ?*Torosteus* sp.: (B) WAM 91.4.31, skull roof in dorsal view; (E) right inferognathal in mesial view. (C), (D) (F–H) Torosteid, sp. indeterminate, SAM P50606: inferognathals in (C) lateral and (D) mesial views; (F–H) close up views showing teeth with resorption pits at bases. Scale bars = 1 cm.

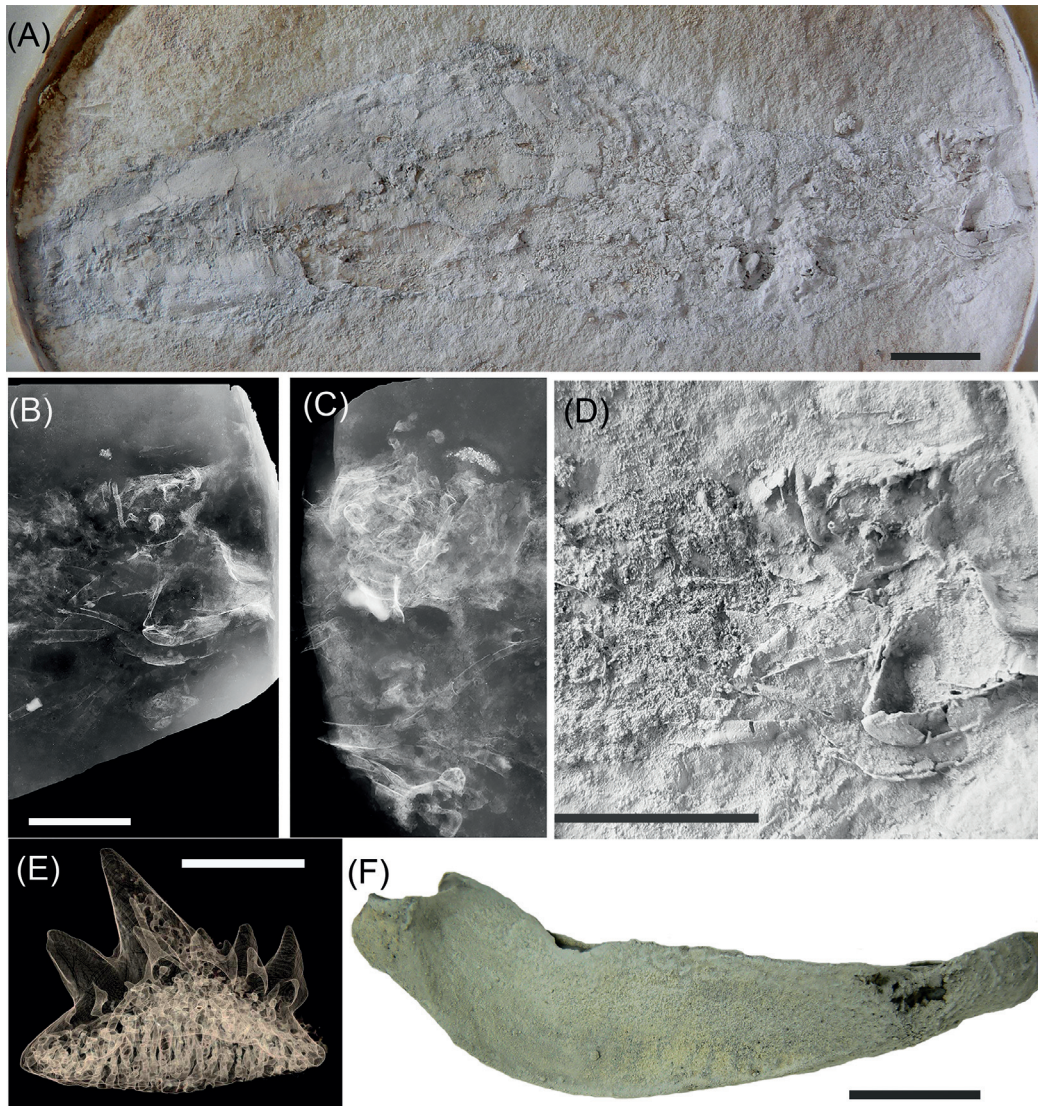
in association with a looped vasculature and pulp cavity. The teeth developed successively ahead of their biting function, with the pulp canals of older teeth becoming infilled with bone; however, both upper and lower teeth lack a hypermineralised capping layer such as the acrodin or enameloid common to the teeth of higher vertebrates.

Detailed synchrotron imaging of Gogo arthrodire bones has revealed Sharpey's fibres, which indicate the position of tendinous attachments of muscles to bone (Sanchez *et al.* 2013). A key finding of this study was that Sharpey's fibres were identified in some bones that lacked muscle scars, the traditional method for identifying where muscles were present, suggesting that previous muscle reconstructions did not capture the full complement of arthrodire muscles. This was shown in *Eastmanosteus*, where preservation of the neck muscles showed the presence of *levator capitis* major and minor, where previously only the *levator capitis* major had been predicted, as well as where *transversus abdominis* muscles had not been previously predicted (Trinajstić *et al.* 2013). Such studies will pave

the way for more accurate restoration of major muscle systems in these early vertebrates.

Further work on the pelvic region has advanced knowledge on reproduction in arthrodires. Intromittent organs were first recognised in a single adult male specimen of *Incisoscutum* (Ahlberg *et al.* 2009) and later were also found to be present within embryos (Johanson & Trinajstić 2014). The discovery of additional specimens with intromittent organs demonstrated that these paired elements were separate from the pelvic fins, which differs from chondrichthyans where they form part of the pelvic fin (Trinajstić *et al.* 2015). Females have also now been found with embryos of differing sizes, suggestive of different developmental stages occurring (Johanson & Trinajstić 2014).

Current work on Gogo arthrodires is focusing on the form and function of their sensory line pits and redescription of poorly known taxa, based on more complete new specimens. A possible new species of torosteid arthrodire, represented by two new specimens, is shown in Figure 1B–H, characterised by its short, deep inferognathals (Fig. 1C, D). The dentition



**Figure 2** Gogo chondrichthyans. (A–D) Chondrichthyan indet, WAM 08.7.1: (A) in right lateral view; (B), (C) radiographs of the head region of both sides; (D) close-up of head shown in (A), whitened with ammonium chloride. (E), (F) chondrichthyan, *Gogoselachus lynnbeazleyae*, WAM 09.6.145: (E) tooth shown as micro-CT tomogram; (F) right Meckel's cartilage in lateral view (from Long *et al.* 2015b). Scale bars = 1 cm.

is particularly interesting in showing inferognathal teeth cleanly worn down on the cusps (Fig. 1G–H) and with resorption pits at the coalescing tooth bases (Fig. 1F, G).

## 6. New information on Gogo acanthodians

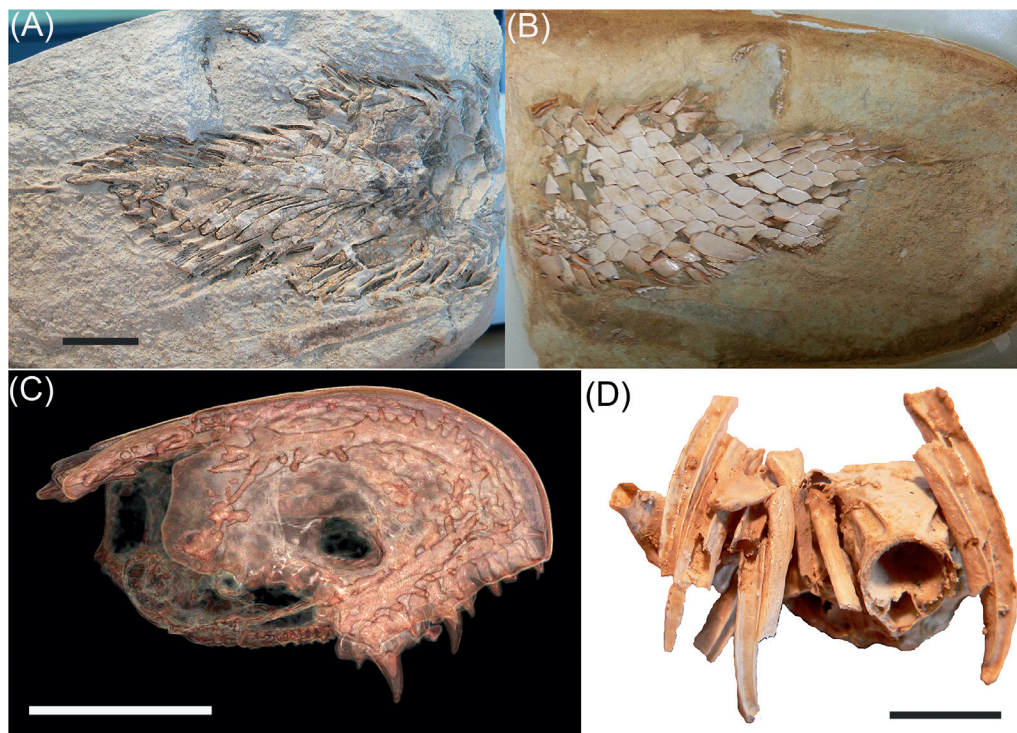
The first Gogo acanthodian was recently described, based on a single specimen found on the 2008 expedition. It is a small mesacanthid, named as *Halmacanthodes ahlbergi* by Burrow *et al.* (2012). Although 3-D-preserved, the delicate nature of the perichondral shell enveloping the bones prevented the braincase remaining intact; but the jaws and shoulder girdles were well preserved, as well as the body and head scales and small areas of mineralised tissue, which permitted the body shape to be determined (Burrow *et al.* 2012, fig. 1c, h).

## 7. New information on Gogo Chondrichthyans

Two Gogo sharks were found on the 2005 expedition (Fig. 2), and the first of these has now been formally described as *Gogoselachus lynnbeazleyae* (Long *et al.* 2015b), based on isolated

lower jaws, scapulocoracoids, parts of the visceral skeleton (gill-arches), scales and teeth (Fig. 2E, F). The mineralised cartilage was acid prepared from the limestone intact, and detailed investigation of its microstructure revealed that it retained bony cell spaces within the matrix binding the tesserae. This equates to an almost intermediate condition between modern sharks and stem gnathostomes like placoderms. Modern chondrichthyans have skeletons are made entirely of tessera with a non-cellular matrix (Maisey 2013).

A second, more complete shark-like vertebrate has been identified from the Gogo sites, collected on the 2005 expedition and is here shown in detail for the first time (Fig. 2A–D). It represents most of the body of the animal including its head (Fig. 2A, D), and is characterised by the body covered by numerous muscle fibres without scales present. The jaws and braincase are shark-like, but no teeth have been recovered. Radiographs show the gill-arches and some features of the neurocranium clearly (Fig. 2B, C). Long (2007) originally presented the specimen as a possible acanthodiform acanthodian. Trinajstic *et al.* (2011) referred to it as a chondrichthyan based on the jaw articulation, naked skin and pelvic girdle, which had previously not been visible due to extensive soft tissue



**Figure 3** Gogo tetrapodomorph, *Gogonasmus andrewsae*, MV P221807. (A, B) caudal fin region: (A) as found; (B) acid-prepared. (C), (D) Micro-CT tomograms: (C) showing ethmosphenoid division of the head, highlighting the laterosensory system of the dermal bones; (D) showing some of the gill-arches in association with the oticco-occipital region of the braincase. Scale bars = 1 cm.

overlying the skeleton. Although the jaws and visceral skeleton are displaced ventrally from the braincase, the articulated position of the hyomandibular against the palatoquadrate indicates chondrichthyan affinities, because it terminates well before the anterior margin of the postorbital blade of the palatoquadrate, as in *Acanthodes* and chondrichthyans (Brazeau & De Winter 2015).

## 8. New information on Gogo osteichthyans

### 8.1. Actinopterygians

There has been a series of recent papers focusing on the taxonomy of Gogo actinopterygians, first described in detail by Gardiner (1984), as well as elucidating their internal anatomy. Choo (2011) formally renamed 'Mimia' (preoccupied by a moth) as *Mimipiscis* and described the new species *M. bartrami* from complete Gogo specimens, one of which swallowed a conodont animal as its last meal (Choo 2011, fig. 10a). The ubiquitous genus *Moythomasia* was also revised by Choo (2015), who presented new reconstructions of the Gogo species *M. durgaringa*. Giles & Friedman (2014) recently described the endocast of *Mimipiscis toombsi*, noting its morphology as closer to basal osteichthyans than to the well-known Early Carboniferous form *Kentuckia*. Other recent papers describing new Devonian actinopterygians, or discussing Devonian vertebrate diversity data, routinely cross reference the Gogo specimens (Swartz 2012; Giles *et al.* 2015a; Sallan 2014).

### 8.2. Onychodontids

Since the description of the Gogo *Onychodus* by Andrews *et al.* (2006), there have been numerous phylogenetic analyses of lower vertebrates that utilise the character information derived from this taxon (e.g., Davis *et al.* 2012; Zhu *et al.* 2013; Dupret *et al.* 2014), but no new primary work on the

Gogo material has been performed. In their description of new Chinese specimens and review of onychodontid functional morphology, Lu & Zhu (2010) have reconstructed the possible braincase kinematics of the Gogo *Onychodus*.

### 8.3. Dipnomorphans

The lungfish fauna from Gogo is now the most diverse known for any Devonian vertebrate site, with ten genera and 12 species described. Recent additions to knowledge of Gogo dipnoans includes a detailed study of the dermal skeleton of the dipterid *Rhinodipterus kimberleyensis* by Clement (2012) and an account of the anatomy of the cranial endocast in that species (Clement & Ahlberg 2014), and how the buccal pump mechanism functioned in *Rhinodipterus* (Clement *et al.* 2016). Challands (2015) revised the phylogeny of early lungfishes and his work supports earlier suggestion that the Gogo *Chirodipterus* is not congeneric with the type material from Germany, or with the Chinese species (Friedman 2007a). This work supports the suggestion that *Griphognathus whitei* from Gogo could be the plesiomorphic sister taxon to all other rhynchodipterids as first suggested by Friedman (2007b) and Long (2010). A description of the ontogenetic stages of the posterior neurocranium formation in the rhynchodipterid *Griphognathus whitei* has also been published (Campbell *et al.* 2012).

A new kind of osteichthyan, *Cainocara* (Campbell & Barwick 2011), is the most recent new family to be described from the Gogo formation; however, we suggest an alternative interpretation, that the specimen described represents a poorly preserved incomplete dipnoan braincase (*cf.* *Griphognathus* sp.).

### 8.4. Tetrapodomorphans

The MV specimen of the tetrapodomorph fish *Gogonasmus andrewsae* (Long *et al.* 2006, Holland & Long 2009) has been further studied, shedding additional light on its endocranium (Holland 2014), pectoral girdle and fin (Holland 2013). An

unusual median cavity was identified within the endocranial walls of *Gogonasmus* that was suggested as a possible homologue of the rostral cavity in actinistians (Holland 2014, p. 13). Ongoing work is describing the gill-arches, pelvic girdle and caudal fin structure based on the MV specimen (Fig. 3A–D), along with a new specimen found on the 2011 Curtin University expedition.

The large spiracular openings on the dorsal surface of the head of *Gogonasmus* were recently confirmed as likely used for accessory breathing, based on observations of the spiracles for air-breathing in the most primitive living osteichthyan, *Polypterus*, by Graham *et al.* (2014).

## 9. Future directions

There are still large numbers of unprepared Gogo fishes held in collections of the Western Australian Museum, Museum Victoria, Curtin University and Flinders University, based on collecting expeditions spanning the past 30 years. As new imaging techniques are developed and employed (e.g., synchrotrons, micro-CT units), and trialled with unprepared Gogo specimens (e.g., ANSTO neutron beam Dingo facility), so will significant new anatomical features be described. It is increasingly important not to prepare all specimens in acid baths, unless certain significant new specimens clearly show discrete anatomical features necessary for advancing scientific knowledge (i.e., visible in split specimens). There is great potential to await future technological advances for analysing specimens, so storing unprepared specimens is a strategic conservation plan for these collections.

Finally, a study of the significance of the Gogo fossil site has been recently published that proposes a new method, based on various academic and other performance metrics, to assess the scientific significance of a fossil site (Long 2016).

## 10. Acknowledgements

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