The Gogo Formation Lagerstätte: a view of Australia’s first great barrier reef

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Abstract: Discoveries from the Late Devonian Gogo Formation in the Canning Basin, Western Australia, have provided insights into the origin and evolution of many unique gnathostome features such as the origins of teeth, internal fertilization, air-breathing, transitional tissues between bone and cartilage, and insights into the fin-to-limb transition. Although vertebrate studies have dominated evolutionary work, invertebrate studies have added important insights into the palaeoecology of the site and demonstrated close faunal affinities along the margins of northern Gondwana and China. Geochemical analyses have broadened our understanding of the pathways involved in the exceptional preservation of this Devonian Konservat-Lagerstätte. Fossils from the Gogo Formation show extensive soft tissue preservation through phosphatization, recording anatomical details not normally obtained from fossil sites.

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The Late Devonian reef complexes of the Canning Basin in Western Australia (Fig. 1) are of immense significance in terms of their contribution to the study of ancient reef systems and their faunal compositions (Aitchison 1993; Wood 1999). The Gogo Formation Lagerstätte preserves the reef framework in addition to a diverse invertebrate and vertebrate fossil fauna that includes high-fidelity preservation of organs and soft tissues in three dimensions, as well as biomolecules. This exceptional preservation has allowed detailed anatomical study of both invertebrate and vertebrate taxa.

Although recent work has concentrated on the vertebrates, the fauna is dominated by arthropods and the first morphological descriptions were of ammonoids (Forod 1890). Bivalved arthropods, comprising phyllocarids (Crustacea, Malacostraca) and thyrodeocephalans (Concavicularia) make up c. 25% of all fossils found in the Gogo Formation (Briggs et al. 2011) and are also abundant in some other Devonian Lagerstätten (Frey et al. 2020). The vertebrate fauna is dominated by arthrodir placoderms and contains the highest diversity of ptyctodonts, early actinopterygians and lungfishes known from any site of similar age (Long 2016). Antiarach placoderms, acanthodians, chondrichthyan, coelacanths, onychododonts and a stem tetrapod are also present (Long and Trinajstic 2010, 2018).

The significance of the Gogo Formation was realized in the 1960s following the development of the acetic acid technique, first used at the British Museum (Natural History), now the Natural History Museum, to reveal the 3D preservation of the fossils. Concretions collected during 1963 and 1967 joint expeditions of the Western Australian Museum, British Museum (Natural History), London, and the Hunterian Museum, Glasgow, brought several tonnes of fossil-bearing rocks back to the UK. It was at the Natural History Museum that the first vertebrate fossils were acid prepared and the majority of the holotypes determined (Long 2006). Subsequent field collecting by one of us (JAL, 1986–2019) yielded many new taxa, including the first acanthodian, chondrichthyan, coelacanths and complete tetrapodomorphs (Long and Trinajstic 2018). However, the remoteness of the site, the difficulty transporting material and the large number of exceptionally preserved specimens has resulted in a collection bias towards complete or nearly complete specimens, particularly of vertebrates; concretions preserving isolated body parts are usually left in the field.

Age, geology and palaeoenvironmental setting

The Kimberley Region of Western Australia is home to an extensive Late Devonian reef system that developed as reef-fringed platforms extending 1400 km along the northern margin of east Gondwana (Playford 1980), making this one of the largest fossil reefs known to date. During the growth of these reef complexes, Western Australia was located c. 30° south of the equator in a subtropical zone facing the Paleotethys Ocean. Sea surface temperatures within the basin during the early Frasnian were 23–25°C (Joachimski et al. 2002).

Today the exhumed barrier reef crops out as discontinuous limestone ranges, 350 km long and 50 km wide along the Lennard Shelf (Fig. 1), between the Precambrian basement and a deep graben, the Fitzroy Trough, along the northern margin of the Canning Basin (Playford and Lowry 1966; Playford 1980). No single locality preserves a continuous record of the reef, which originated in the Givetian and terminated at the end of the Famennian (Playford et al. 2009). The reef framework comprises stomatopoid sponges and isolated rugose and tabulate corals that flourished along the margins of the subsiding Fitzroy Trough (Begg 1987). Depositional environments represent the basinal, marginal slope, fore-reef and reef platform facies of the Gogo, Sadler and Pillara limestones, respectively. The reef platform is thought to have reached sea level, ten to hundreds of metres above the sea floor, and there is some evidence of evaporites in the back-reef lagoonal facies, which suggests periods of local exposure. The reef platforms were flanked by strongly sloping marginal reef deposits that graded into the flat basin floor (Playford 1980). The basinal facies are estimated to have been deposited in waters several hundred metres deep (Playford and Hocking 1999; Copp 2000) and although the
upper water column was oxic, there is evidence of stratification with persistent euxinia within the photic zone (Melendez et al. 2013a).

The age of the Gogo Formation ranges from middle Givetian based on miospores (Grey 1992) to early Frasnian (Lower to Middle asymmetric zones) based on conodonts (Seddon 1970; Druce 1976). This makes the fossil sites c. 384–382 Myr old. The type section of the Gogo Formation is a c. 430-m-thick sequence of organic rich, grey to black fine-grained shales and siltstones with lenses of limestone that are interbedded with horizons of resistant, silty calcareous concretions ranging from 3 to 50 cm in dimension (Long 1988), but more commonly 5 to 20 cm (Fig. 2a and b) (Playford and Wallace 2001). The early Frasnian nodular layers interfinger with the marginal-slope facies of the Sadler Formation.

Geochemical analyses indicate that organic matter formed the nucleus of the Gogo concretions, although not all of them reveal an identifiable fossil; many contain just a smudge of organic matter and are considered barren (Lengger et al. 2017). The concretions formed sufficiently early to maintain the 3D nature of the fossils (Fig. 2c). Some fossils show fractures in the dermal armour or carapace (Briggs et al. 2011) and provide evidence that some compaction occurred (Lengger et al. 2017), but it was not extensive. In all cases concretion formation was rapid, as indicated by the isotopic values (Playford and Wallace 2001) (Box 1), soft tissue preservation (Box 2) and disruption of the sediment around the fossil, which occurred post entombment due to the release of decomposition gases and shows that bacterial activity persisted even after the first phase of concretion formation (Trinajstic et al. 2007).

The Gogo Formation biota: diversity and biogeography

Early work on the reef complexes concentrated on geological mapping, mineral exploration and biostratigraphy using cephalopods for correlation (Teichert 1947). Initial taxonomic work included descriptions of sponges (Rigby 1986), gastropods and ammonoids (Glenister 1958), conodonts (Glenister and Klapper 1966; Seddon 1970; Druce 1976; Nicoll 1980; Choo et al. 2009), tentaculites (Playford 1980; Farsan 1994), orthococonic cephalopods and pelagic bivalve genera such as Buchiola and Ontaria (Becker et al. 1993), for biostratigraphic and biogeographic correlation. The vertebrate fauna is very diverse, but many genera are monospecific and represented by only one or two specimens. Long and Trinajstic (2010, 2018) provided a full review of the vertebrates known to date. Here we focus on taxonomic groups that have been utilized in biogeographic studies or have contributed to a more detailed anatomical, evolutionary or ecological understanding of the fauna.

Protists

A diverse and well-preserved radiolarian fauna has been recovered from concretions SE of Menyous Gap (Aitchison 1993). Previous collecting from Longs Well (Fig. 1) yielded poorly preserved radiolarians from two groups, spherical Entactinidae and bilaterally symmetrical Palaeoscenidiidae (Nazarov et al. 1982; Nazarov and Ormiston 1983), which have a global distribution. Specimens collected more recently preserve exquisite internal structures, which allow diagnosis to species level. The Gogo radiolarian fauna is not only the best preserved but also the most diverse Frasnian assemblage known (Aitchison 1993; Won 1997a, b). Aitchison (1993) recognized 14 genera and 57 species, 41 of which are endemic; this number subsequently increased to 17 genera and over 100 species (Won 1997a). The excellent preservation has allowed the identification of a wide range of morphotypes and the clarification of the morphology of the structure of different skeletal elements, permitting better taxonomic resolution (Won 1997a).

Invertebrates

Goniatites were first collected from Paddys Valley by ET Hardman in 1883–1884 but studied by Foord (1890); however, Teichert (1941, 1949) undertook the first biostratigraphic studies and further taxonomic and biostratigraphic research was carried out by Glenister (1958); Glenister and Klapper (1966) and Becker et al. (1993). The Gogo Formation ammonoids occur as hematitic moulds or in concretions, which contain either multiple specimens of a single species or two or three different species, usually associated with styliolinids and radiolarians (Becker and House 2009 in Playford et al. 2009). In contrast to many other taxa found in the Gogo Formation the diversity of ammonoids is low and there are no endemic genera. The ammonoids from the Gogo Formation (Fig. 3f) have a wide biogeographic distribution with close faunal links to the Rhenish Massif, Ardennes, North Africa, North America and Timan with 32 common species present (Becker 2000). The
equatorial *Timanites* had a geographic range that spread from the Canning Basin to the Urals, Timan and into Western Canada (Becker 2000). This pattern of distribution demonstrated that there was no biogeographic barrier between the eastern and western Prototethys regions or within the Uralian Transarctic seaway (Becker 2000). The distribution of early Frasnian conodonts from the Canning Basin also supports this conclusion (Klapper 2007).

The most abundant arthropods recovered are phyllocarids and concavicarids (Fig. 3b, c and e): the initial 1963 collection yielded 400 specimens alone (Rolfe 1966), and this number has been increased through subsequent collecting (Briggs *et al.* 2011). An unusual fossil among those that have been referred to as ‘*Mushia*’ due to their squashed appearance (Fig. 3d) lacks evidence of a carapace but has been shown to be a crustacean through chemotaxonomy (see Box 1, Fig. 4) (Melendez *et al.* 2013a).

The Gogo Formation has yielded a specimen of the eurypterid *Adelophthalmus waterstoni*. Originally assigned to *Rhenopterus* (Tetlie *et al.* 2004) it was shown to belong to *Adelophthalmus* by Poschmann (2006) and redescribed by Bicknell *et al.* (2020). Late Devonian eurypterids mainly inhabited marginal marine or freshwater settings prompting Tetlie *et al.* (2004) to suggest that the specimen may have been transported. However, a second, undescribed eurypterid specimen was found in 2008 (Fig. 3a) and, as many of the arthrodire species are likewise represented by only one or two specimens, a low number of specimens does not provide evidence for a freshwater habitat.

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**Box 1. Biomarkers and chemotaxonomy**

Pioneering research on Gogo fossils and the carbonate concretions that preserve them has revealed a remarkable array of biomolecules (Grice *et al.* 2019). A common fossil from the Gogo Formation has been known as ‘*Mushia*’ since its discovery in 1967 because it lacks diagnostic morphological characters. It consists of a mass of soft tissue, including muscles bands and body segmentation, but lacks a distinct head or other defining features (Fig. 3d). Chemical analysis of a specimen revealed the earliest intact sterols and products of their diagenetic transformation, ranging from stenols to triaromatic steroids. The concentration of lipid biomarkers of cholestane, produced by diagenesis of cholesterol, indicates that this example of ‘*Mushia*’ represents a crustacean (Melendez *et al.* 2013a), resolving its identity with a chemotaxonomic approach.

This analysis of biomarkers in a Gogo concretion extended the occurrence of intact sterols in the fossil record by 250 Myr (Melendez *et al.* 2013b; Grice *et al.* 2019). It also enhanced our understanding of the environment of preservation. The fossils were rapidly entombed under anoxic conditions, preserving not only the macrofossils but also evidence of a consortium of associated microbes (Lengger *et al.* 2017). This includes biomarkers of Chlorobi, which provide evidence that photic zone euxinia played a role in the exceptional preservation of the fossils and formation of the Gogo Formation concretions (Melendez *et al.* 2013a).
Box 2. Muscle architecture in the Gogo fossils

Soft tissues, mineralized as spicule, are known in both invertebrate and vertebrate fossils from the Gogo Formation. The first mention of soft tissue preservation in a Gogo fossil was within the early actinopterygian Mystacolepis (Gardner and Bartman 1977); however, no description was provided. A small amount of mineralized tissue, identified as poorly preserved sarcomeral sheaths, was obtained between the carapace and opisthoca of the eurypterid Adelophthalmus waterstoni (Tetlie et al. 2004) and similar sarcomeral sheaths have been recovered from placoderms (Trinajstic et al. 2013). Mineralized muscle fibres, comprising myofibrils showing banding where fibres have ruptured along Z bands during decay, are evident in Montecaris gogoensis (Briggs et al. 2011) and in some vertebrate taxa (Fig. 4b–e) (Trinajstic et al. 2007; Long and Trinajstic 2010). The first detailed description of muscle tissue from the Gogo Formation was in the arthrodire placoderm Eastmanosteus (WAM 00.3.1), which preserves small portions of the gnathal muscles attached to the infrapharaglial plate (Trinajstic et al. 2007). Extraordinary details include the preservation of a nerve extending between muscle fibres and attached to them by a multipolar motor end plate (Trinajstic et al. 2007). More than one muscle fibre is innervated by the same axon, indicating that all of the muscle fibres contracted together as a motor unit. The most extensive soft tissue preservation has been reported from arthrodire placoderms, which reveal details of the neck (Fig. 4c–e), trunk (Fig. 4f) and caudal (Fig. 4b) musculature (Trinajstic et al. 2013). The musculature shows regionalization into discrete jaw, neck, abdominal and caudal units, which correspond to the regions of the vertebral column (Johnson et al. 2013, 2015; Trinajstic et al. 2013). The neck musculature comprises two sets of head elevators in contrast to the single set previously identified (Miles and Westoll 1960) on the basis of muscle scars on the dermal plates of the head and shoulder. The caudal musculature, which acts as a fin elevator and head depressor muscle in extant fishes, is also preserved. The function of this muscle in arthrodires, however, was limited to depression of the head (Trinajstic et al. 2013). The abdominal muscles comprise a set of specialized transverse and longitudinal muscles previously known only in tetrapods. The function of these muscles is unknown, but they may have enabled movement of the reproductive intromittent organs, which are unique in placoderms in being independent of the pelvic fins. Thus, this remarkable discovery overturned conventional ideas of the musculature of early fishes.

Vertebrates

Ninety species of conodont are known from the Gogo Formation and overlying Sadler Limestone in the Bugle Gap area, 56 of which are endemic (Seddon 1970). However, these figures are in need of revision as they predate multielement taxonomy (Nicoll 1977; Long and Trinajstic 2010). The discovery of embryos in arthrodires (Fig. 4a) and placoderms (Fig. 5) has revealed a number of morphological and histological textures as they grow upwards, creating multiple microhabitats that promote diversification of the fauna (Sheehan 1985; Wood 1999). Interpretaions of the palaeoecology of the Gogo fauna have been based on the gross morphology of fossils (Anderson 2008; Long and Trinajstic 2010, 2018; Briggs et al. 2011; King et al. 2018; Trinajstic and Roelofs 2019a, b), predation and stomach contents (Nicoll 1977; Long 1991; Choo et al. 2009; Trinajstic and Roelofs 2019b); they have also been inferred from facies analyses (Playford and Wallace 2001; Playford et al. 2009) and geochemistry (Melendez et al. 2013b). The stratified water column and anoxic bottom muds (Melendez et al. 2013a) resulted in a restricted benthic fauna and the majority of Gogo Formation taxa were pelagic (Briggs et al. 2011). Bothriolepis, with dorsally positioned eyes, a flat ventral armour and bottom-facing mouth, (Fig. 6a) is considered to have occupied a demersal habitat in more oxygenated waters along the reef margins (Trinajstic and Roelofs 2019b).

The large predatory placoderm Eastmanosteus calliaspis, which reached up to 1.5 m in length (Fig. 6b), is considered to have been nektonic (Long and Trinajstic 2010). Specimens of Eastmanosteus occur in locations 150 m from the reef margin (see Miles 1971), in association with the phyllocarid Schugorocaris wani and Dithyrocaris sp. indet., which are also considered to be nektonic on the basis of their streamlined shape (Briggs et al. 2011). The presence of gravel in the stomach, cambered shape and small eyes of Holonema westollii (Fig. 4d) were previously considered to indicate a nekto-benthic lifestyle, feeding in the bottom mud (Miles 1971). More recently, a planktivorous lifestyle has been postulated on the basis of the unusual jaw
and toothplate structure (Trinajstic 1999; Trinajstic and Roelofs 2019b). Concretions containing just the anterior section of the tail and posterior ventrolateral plate of Holonema indicate that the carcass floated and fragmented before fossilization (Trinajstic 1999; Fig. 4d). However, as the tail maintains the scale cover and alignment of the vertebrae, and the toothplates remain articulated in concretions containing the head armour, such carcasses could not have floated far (Allison and Briggs 1991).

The abundance of complete examples, and diverse size range of the actinopterygians Moythomasia durgarina (Fig. 5b) and Mimipiscis toombsi (Choo 2012), suggest that they were schooling fishes (Long and Trinajstic 2018). The presence of conodont elements in the stomach of M. toombsi (Nicoll 1977) and the branchial regions of G. coatesi (Choo et al. 2009) indicates that these fishes inhabited the reef slope close to the inter-reef basins and were able to swim across the basin.
Fig. 4. Vertebrate fossils from the Gogo Formation (a) embryo and preserved umbilical cord in the ptycotodont *Materpiscis attenborouigh* (Holotype, WAM 826 17.12.1); (b) embryos in the arthrodire *Incisoscutum ritchiei* (NHM P50934); (c) *Incisoscutum ritchiei* showing clasper and pelvic girdle (WAM 03.3.28); (d) arthrodire *Holonema westolli* showing articulated 3D preservation (above) and tail showing articulated squamation, vertebrae and clasper (below, MV P230241); (e) lower jaw of shark *Gogoselachus lynbeazleyae* (WAM 09.6.145); (f) tetrapodomorph *Gogonasus andrewsae* showing skull (left) and articulated pectoral girdle bones (right, both MV P221807); (g) Holotype skull of sarcopterygian *Onychodus jandemarrai* (WAM 92.8.2).
Smaller arthrodires such as the laterally compressed camuropiscids _Latocamurus_ (Fig. 5c), _Rolfosteus_ and _Tubonasus_ are interpreted as pelagic pursuit predators on the basis of their streamlined body shape, elongated rostra (Long 1990) and ability to open and close the jaws rapidly – attributes useful for prey capture (Anderson 2008, 2010). The narrow gnathal plates with flat, toothless anterior margins suggest that they swallowed their prey whole (Anderson 2010). Coccosteomorph taxa such as _Compagopiscis_ (Fig. 5j), _Torosteus_ and _Incisoscutum_ are found in numbers indicative of a schooling lifestyle (Long and Trinajstic 2010). Analyses of bite forces indicate that _Compagopiscis_ (Fig. 6f) was a generalist feeder (Anderson 2010) and _Torosteus_ was an active predator (Anderson 2010), whereas the dentition of _Incisoscutum_ shows it to have been durophagous (Dennis and Miles 1980), possibly feeding on pelagic bivalves such as _Buchiola_ and _Ontaria_, which often occur in the same concretions. All three fishes are similar in body size and morphology so probably shared a pelagic life style but occupied different trophic niches. They all

Fig. 5. Gogo fish preservation (a) antarch _Bothriolepis_ sp. (WAM 90.12.136); (b) actinopterygian _Moythomasia durgaringa_ (South Australian Museum specimen, yet to be registered); (c) arthrodire _Latocamurus coulthardi_ (WAM 86.9.699); (d) chirodipterid lungfish _Chirodipterus australis_ showing body and head in lateral view (left, NHM P56035) and palatal dentition (right, WAM 90.10.8); (e) long-snouted lungfish _Grippognathus whitei_: juvenile head in lateral view (left, Western Australian Museum specimen) and palatal dentition (right, ANU 49219).
Fig. 6. Muscle tissue preservation in Gogo fossils (a) crustacean ‘Mushia,’ (Western Australian Museum specimen); (b–e) arthrodire *Eastmanosteus calliaspis* showing articulated armour in dorsal view (b) and close up showing neck musculature (c) and (d) are SEM photographs of individual muscle fibres (WAM 00. 3.1); (e), both ANU V2582), (f) *Incisoscutum ritchiei* showing longitudinal and lateral muscle fibres (WAM 03.3.24) (g) field shot of actinopterygian with white muscle fibres present; (h) *Compagopiscis croucheri* tail showing skin and tendons with raised dimples near where a drill hole has penetrated (WAM 03.3.24).
occur in close proximity to the limestone ranges (Long and Trinajstic 2010), indicating that they were part of the nektion of the slope facies. The pyctodont placoderm Austropterygus gardineri has been recovered with ostracods in the abdominal region related to nocturnal forms, suggesting that it was a nocturnal feeder (Trinajstic and Roelofs 2019b). The phylcocarid Montecaris gogoensis, which is often found associated with these arthrodires, has a streamlined shape indicative of a nektonic lifestyle (Briggs et al. 2011), although it occupied a shallower habitat closer to the reef margin than Schugurocaris wangi. Other durophagous fishes recovered from this area include the lungfishes Chirodipnus (6e), Adololopus, Asthenorhynchus, Xenadipnus, Rhinodipnus and Holodipnus (Miles 1971; Campbell and Barwick 1988; Pridmore and Barwick 1993; Clement and Long 2010; Long 2010; Clement 2012; Clement and Ahlberg 2014). A specimen of the predatory juvenile Asthenorhynchus, although it occupied a shallower habitat closer to the reef margin, has been recovered with ostracods in the abdominal region related to its throat (Long 1991). Grippognathus (Fig. 6f), a lungfish with a duck-billed snout and an extensive electroreceptive network, is considered to have stirred up the bottom sediments (Campbell and Barwick 1988) to feed, requiring a well-oxygenated environment. Grippognathus lacks morphological features for air breathing (Campbell and Barwick 1988; Clement and Long 2010), consistent with an oxygenated habitat.

Preservation

The taphonomy of the Gogo fossils has received little attention, and studies have largely focused on the soft tissue preservation of the vertebrates (Box 2). The fossils show some evidence of post-mortem transportation, probably as a result of flotation (Elder and Smith 1988; Carr 2010; Long and Trinajstic 2010). The antiarch (Fig. 5a) and arthrodire placoderm (Figs 4d, 5c, 6b and f) consist mainly of head and trunk shields but the dermal plates (including dentary elements) remain articulated and, in some cases, the scapulocoracoid and pelvic girdles with fin radials (Fig. 6f) are in life position (Trinajstic 2009). In specimens preserving the anterior part of the tail (no Gogo specimens preserve the tail posterior to the anal plate), the vertebral elements remain articulated (Fig. 5b–d), indicating that the carcasses were not transported far. The sarcopterygians are likewise represented by a large number of heads, whereas complete specimens with articulated postcranial skeletons and intact scale cover are very rare (Fig. 5f and g), as are isolated scale-covered tails. The actinopterygians, however, are mostly complete (Figs 2d and 5b) although sometimes the maxillary elements are missing, as are the lobes of the tail. The phyllocarids consist mostly of carapaces and in some instances only the massive mandibles are preserved (Fig. 3f) (Briggs et al. 2011).

The majority of the fossils from the Gogo Formation are preserved with the skeleton or cuticle composed of calcite, with some apatite and fluorapatite, and the soft tissues (see Box 2) phosphatized, consisting mainly of apatite with some calcite (Trinajstic et al. 2013; Long and Trinajstic 2010, 2018; Briggs et al. 2011). The phosphatization process is bacterially mediated (Briggs et al. 1993; Briggs and Wilby 1996; Trinajstic et al. 2007, 2013; Trinajstic 2009; Trinajstic et al. 2014), and the evidence suggests that this mechanism was essentially similar in both invertebrates and vertebrates (Briggs et al. 2011; Melendez et al. 2013a).

The first stage of the fossilization sequence occurred in the water column: photic zone euxinia prevented aerobic degradation (Melendez et al. 2013a). These conditions, supported by an elevated consortium of sulfate-reducing bacteria including Chlorobi, combined with abiotic sulfurredation and hydrogenation (Lengger et al. 2017), limited the decomposition of labile soft tissues and promoted their preservation, including molecular components such as sterols (Box 1). Soft tissues are best preserved where they were enclosed by cuticle (arthropods) (Telfie et al. 2004) or dermal bone (placoderms) (Trinajstic et al. 2007) or were under scales (osteichthyes) in a localized anoxic microenvironment favourable to rapid phosphatization (Long and Trinajstic 2010). The anoxic environment, coupled with a build-up of CO2 and volatile fatty acids from the decomposing carcass, resulted in a decrease in pH, which favoured the precipitation of calcium phosphate over calcium carbonate (Briggs et al. 1993; Briggs and Kear 1993; Wilby 1993). In some specimens a steep geochemical gradient is evident from different mineral species, ranging from the formation of carbonate dumbbells to cellular replication within muscle fibres by apatite (Fig. 2) (Briggs et al. 1993; Trinajstic et al. 2014).

Smooth structures c. 3 μm thick, which are often recovered between muscle blocks or wrapped around muscle fibres, have been identified as remnants of bacterial biofilm (Fig. 6a). This microbial

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Box 3. Outstanding questions

A number of taxa are either absent or lower in abundance and diversity than expected. Trilobites have not been recovered, despite the occurrence of benthic and pelagic examples at other Devonian sites in the Canning Basin (Becker et al. 1991; Feist and Becker 1997; Feist et al. 2009). Jawless fishes are also absent, although scales of Australolestes seddoni are found in the younger Virgin Hills Formation in the Canning Basin (Hairapetian et al. 2016), south of the Canning Basin (Trinajstic 2001) and in the coeval Gneudna Formation from the Carnarvon Basin, Western Australia (Trinajstic et al. 2014). The single acanthodian specimen recovered from the Gogo Formation (Burrow et al. 2012), Halicancanthodes ahlbergi, is the same species as that in the Gneudna Formation (Trinajstic et al. 2014). The rarity of acanthodian fossils in the Gogo Formation may be the result of preservation bias – the scales are not strongly imbricated and have poor preservation potential (Chevinas et al. 2017). No isolated scales and/or fin spines have been recovered, although they are common in the Virgin Hills Formation (Trinajstic and George 2009).

Only two chondrichthyan specimens, both endemic, have been recovered from the Gogo Formation. One of these, Gogoselache, is represented only by jaw cartilages, teeth and gill arches (Long et al. 2015) and the other, which is complete, has yet to be described. Chondrichthyan remains are common along the margins of Gondwana during the Frasnian, including panglobal species such as phoebodonts, protacrodonts and ctenacanthids (Ginter et al. 2002), which are also present in the Gneudna Formation (Trinajstic and George 2009). The absence of protacrodont sharks from strata of a similar age in Morocco has been attributed to the presence of anoxic bottom waters (Frey et al. 2020), but this does not explain the absence of other common nektonic taxa such as Phoebodus, which does occur in the Gneudna Formation.

Other taxa common to the Gogo and Gneudna formations include Bothriolepis sp., Holonema westolli, Myxothamnus dargarina, M. toombia, Gogosardina coatesi, Chirodipnus australis, Adololopus sp. and Gogonatus sp. (Long and Trinajstic 2010; Trinajstic et al. 2014), indicating the movement of taxa between the basins in spite of the differences in depositional environment among the isolated patch reefs. Eastmanosteus calliaspis and Holonema westolli are the only arthrodires from the Gogo Formation that also occur along the margins of northern Gondwana, indicating that they were capable swimmers (Carr 2010; Rücklin 2010). Other Gogo fish also occur along the margins of northern Gondwana, including the antiarch Bothriolepis, the early actinopterygian Myxothamnus and the sarcopterygian Onychodus. The absence of some taxa at Gogo cannot be attributed to a biogeographic barrier (Trinajstic et al. 2014); they simply may not have been found yet. Each collecting trip has yielded new species, including most recently the first coelacanths (Long and Trinajstic 2010), and over 40 years elapsed between the discovery of the first and second Bullrichshy species. This indicates that more taxa will probably be added to this already diverse assemblage.
film consisted of extracellular polymeric substances, which act as sites for phosphate reduction, as well as trapping cations such as Ca^{2+} that provided nucleation sites for carbonate precipitation (Grice et al. 2019). Extant biofilms contain the enzyme phosphatase, which is important for calcium phosphate aggregation and soft-tissue mineralization (Wilby and Martill 1992), and similar processes presumably played a role in the Gogo specimens. The biofilm, in addition to holding the carcass together, promoted the precipitation of calcium carbonate needed for rapid concretion formation (Grice et al. 2019). The distribution of methylthymoquin in the basinal muds, and its absence in concretions, provides additional evidence for their rapid formation (Lengger et al. 2017). There are still many unanswered questions about the Gogo fossil assemblage and its preservation (Box 3).

Summary

The Gogo Formation Lagerstätte provides critical information on the nature, evolution and biogeography of Late Devonian reef faunas. The fauna lived in the oxic zone of a stratified water column, which over laid a euxinic photic zone and anoxic bottom water. Sulfate-reducing organisms facilitated the fossilization process, particularly the mineralization of soft tissues. The exceptional preservation of the reefal assemblage has increased our understanding of key steps in evolution.

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Author contributions

KT: conceptualization (equal), investigation (equal), visualization (supporting), writing – original draft (lead), writing – review & editing (supporting); DEGB: investigation (supporting), visualization (supporting), writing – review & editing (supporting); JAL: conceptualization (equal), investigation (equal), visualization (lead), writing – original draft (supporting), writing – review & editing (equal)

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Data availability

Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

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