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# Polymorphism, variation and evolutionary change in early vertebrates from the Gogo Formation, Western Australia

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## Abstract

The imperfection of the fossil record was used by Charles Darwin to explain the lack of evidence for 'organs of extreme perfection and complication", which under his theory of natural selection must have evolved through a series of gradual transitions. In addition, a major premise in the theory of natural selection is that variation between organisms is required so selection for particular traits can occur. The fossil record has subsequently revealed a small number of sites comprising fossils of exceptional preservation including the Gogo Formation of Western Australia. Here a unique Late Devonian (Frasnian) reef fauna, with exceptional three-dimensional preservation of macrofossils combined with unprecedented soft-tissue preservation has preserved examples of the transitional forms and morphological variation Darwin predicted. The most significant discoveries have contributed: insights into reproductive biology, including the oldest known vertebrate embryos and evidence of sexual dimorphism with internal fertilization; the anatomy and variation present in the earliest gnathostomes, the placoderms, provides evidence of directional selection; some of the earliest morphological changes required in the transition from an aquatic to land environment are seen in the primitive tetrapodomorph, *Gogonasus*.

**Keywords:** Darwin, placoderm, reproduction, heterochrony, evolutionary trends; evolution

## Introduction

Today Charles Darwin is most closely associated with the biological sciences; however, he was first recognised as a scientist in the field of geology receiving the Wollaston Medal, the Geological Society of London's highest honour in 1859 (Darwin & Barlow 1958). After graduating from Cambridge University Darwin worked as a field assistant to the geologist Adam Sedgewick with whom he obtained valuable practical experience in the observation and interpretation of geological structures and fossils. During the early stages of the voyage of the Beagle he read the Principles of Geology by Charles Lyall and was greatly influenced by the theory of (Darwin & Barlow 1958). The study of stratigraphy was in its early phase but it had already being noted that the further back in the rock record you went the more dissimilar plants and animals appeared from extant forms (*e.g.* Cuvier 1821). Whilst on his voyage Darwin (1859) recognised many fossils in the rock record and posed the question " By what mechanism did new species replace old ones?" Unfortunately Darwin's account of the fossil record in Australia was not inspiring (Darwin 1859). However, he recognised that for his theory of evolution to be fully accepted evidence from the fossil record was paramount as it clearly showed changes in life through time.

Darwin acknowledged that there were many problems with the data obtained from the fossil record, which needed to be overcome prior to undertaking any evolutionary study with respect to fossils. The first is preservation bias – hard parts are preserved in greater detail and number then soft parts. This leads to the second problem that of missing data – this can be the absence of fossils themselves from time period or the absence of parts of the fossils themselves requiring interpretation and reconstruction on the part of the palaeontologist. Sites that yield fossils of exceptional preservation and in high quantities have in recent years alleviated these problems to a large extent. But we still must be careful not to place too much emphasis on: 1. The incompleteness of the fossil record thereby not recognising the wealth of information it can provide; 2. The large amount of data we have already obtained from the fossil record thereby not accepting the limitations and biases inherent in the geological record of our Earth.

Despite these problems, palaeontologists have made huge advances in the understanding of past life and evolutionary processes in recent years. The Devonian Reef, which crops out along the Lennard shelf in the Canning Basin (Figure 1A), has yielded many remarkable fossil sites (see Playford *et al.* 2009 for a full review), the Gogo Formation having the most diverse fauna with over 40 genera of fish preserved as original bone in addition to invertebrates and the reefal structures (see Long 2006, Long & Trinajstic 2010 for a full review). Recently new technologies, especially computerised tomography (CT), have opened up novel avenues of investigating fossils and this has led to the discovery of many morphological features, not all of them bone.

## Preservation and preparation of the fossils

The standard method of preparation was devised at the British Museum of Natural History by Harry Toombs and comprises sequential acetic acid (8–10%) baths where the carbonate is disaggregated to expose the bone (Rixon 1976). Unfortunately, recent discoveries of soft tissues structures have indicated that this method has also dissolved much muscle tissue over the years. New methods, using a lesser concentration of acid (5–8%), are preserving the soft tissue and bony structures in much greater detail (Long *et al*. 2008).

The partial decomposition of the fish, prior to fossilisation, is thought to have aided their preservation. The breakdown of fats results in the formation of a compound called adipocere, a low density, water insoluble substance (Zangerl 1971; Berner 1981), which is the precursor for the calcium carbonate concretions, the fossil forming the nucleus (Figure 1B). The rapid formation of the nodule combined with the overall lack of high-level tectonic forces in the region after burial of the reef complexes (Playford *et al.* 2009) has resulted in the high level of preservation (Long & Trinajstic 2010). Recently the first soft tissues including muscle fibres (Figure 2A) and an umbilical cord (Figure 2A, C) have been recovered (Trinajstic *et al.* 2007; Long *et al.* 2008). In addition extensive musculature has now been recovered from a yet unpublished acanthodian ("spiny shark") and actinopterygians (ray fin fishes).

The muscle is mostly mineralised and in rare cases individual crystals of hydroxyapatite replace individual cells providing incredible structural detail (Trinajtic *et al.* 2007; Long & Trinajstic 2010). Scanning electron microscopy has shown incredible detail of the muscle structure in a number of fossil taxa including nerve tissue running between muscle fibres and blood capillaries (Figure 2D).

**Figure 1.** The Bugle Gap area of the Canning Basin. A. the Devonain reef outcrop at Bugle Gap with the inter-reef basins containing the fossil bearing nodules. B. A Gogo nodule containing a fossil actinopterygian (boney fish) with some soft tissue preserved.

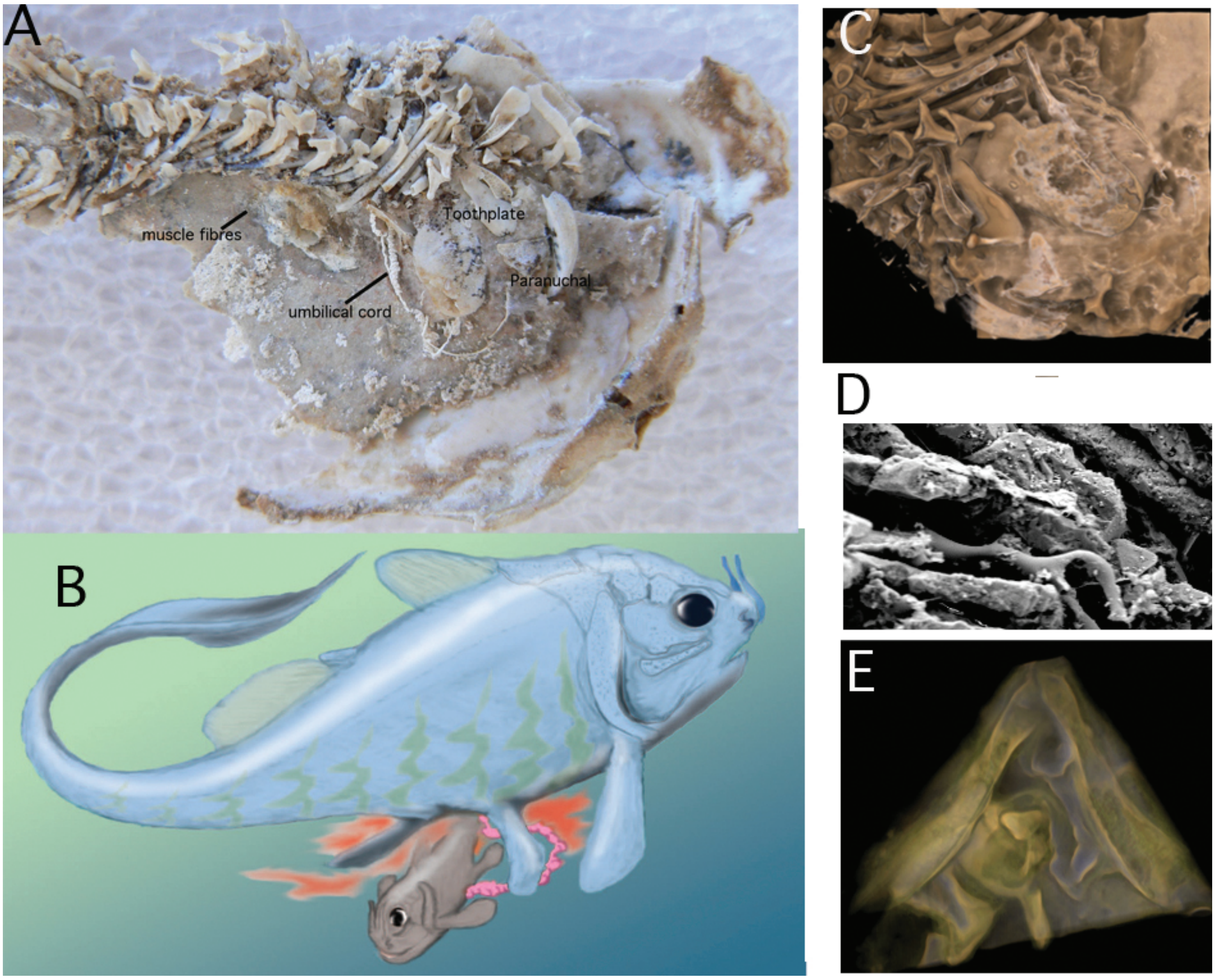

**Figure 2.** *Materpiscis* – the mother fish. A. post-cranial region of *Materpiscis* showing the umbilical cord and soft tissue. B. Reconstruction of the mother fish giving birth (with permission Dr John Long). C. CT scan showing the umbilical cord underneath a dermal plate. D. SEM of muscle fibres with capillary running between them from the arthrodire *Eastmanosteus.* E. CT scan of the tooth plates of *Materpiscis*. CT scans taken at ANU by Prof. Tim Senden.

## Reproduction in the fossil record

The premise of survival of the fittest is central to Darwin's evolutionary theory, and although this expression is often attributed to Darwin, it was actually coined by Mr Herbert Spencer and not used by Darwin until the later edition of "The Origin of Species" (1869). Survival in evolutionary terms is measured as reproductive success and different reproductive strategies have evolved in order to maximise the species chance at survival. The two main reproductive strategies can be summarised as:

1. Producing many offspring with little parental care in order that some will survive; or
2. Producing few offspring with large amounts of parental care increasing the chances that most will survive. These strategies represent the extremes of a continuum but are helpful in looking at different strategies animals and plants use. But how does one determine reproductive strategies within the fossil record?

Evidence of reproduction is very rare in the vertebrate fossil record. The recent discovery of embryos within ptyctodonts (Placodermi) from the Gogo Formation has provided the earliest evidence of internal fertilisation and live birth in the fossil record (Long *et al*. 2008, 2009; Ahlberg *et al.* 2009). Placoderms (fishes with the head and thorax covered by an armour of bony dermal plates) were the dominant members of the vertebrate marine community in the Devonian The presence of an umbilical cord attaching the embryo to the mother provides the earliest evidence for matrotrophy, where the mother provided nutrition to the embryo, in the fossil record (Figure 2A–C, E). Following this discovery a further three embryos were found in ptyctodonts (Long *et al.* 2008) and two embryos were discovered in arthrodires (Long *et al.* 2009), the dominant group of Late Devonian placoderms. In addition pelvic claspers were also identified within the arthrodires providing crucial evidence for internal fertilisation within the arthrodires (Ahlberg *et al*. 2009; Long *et al.* 2009).

The recent advance in three-dimensional imaging of bone means that fossils can be virtually dissected and histological information obtained non-destructively. Of the structures reveal through micro-CT perhaps the umbilical cord from *Materpiscis* (the mother fish) is the best known (Long *et al*. 2008). This tiny, coiled structure changed scientific thinking about reproduction in the earliest jawed fish, the placoderms. The structure was first recognised macroscopically, during preparation of the fish, sitting on the surface of the newly prepared area. However, there was an overlying body plate from the fossil embryo making examination of the earliest umbilical cord ever discovered difficult. In recent years collaboration with Drs Tim Senden and Arjay Limay from ANU has resulted in ultra-fine micro CT imagery of key Gogo material. Micro –CT scans of the specimen allowed us to trace to path of the umbilical cord, from a crystalline mass thought to be the yolk sac to the embryonic bones (Figure 2C). In addition, virtual thin sectioning was able to show the internal structure of the embryonic bones and teeth without having to destroy them (Figure 2E). The bone histology enabled us to determine that the small bones inside the adult fish were definitely an embryo and not its last supper (Figure 2C, E). The distinctive tooth structure (Figure 2E) confirmed this as we could confidently identify the embryo as the same species as the mother.

## Natural selection and variation within the fossil record

Darwin recognised that populations comprise individuals that vary from one another and that selection of one variant over another could lead to evolutionary change. The recognition of variation in the fossil record is dependent on the preservation of the specimen, the number of specimens available and the ontogeny of the specimens available (McKinney & McNamara 1990). Many of the fish fossils from the Gogo Formation are mono specific genera, meaning that studies of variation are impossible, but amongst the arthrodires, there are several genera that comprise multiple specimens at various growth stages (Trinajstic & McNamara 1999; Trinajstic & Hazelton 2007; Trinajstic & Dennis Bryan 2009).

Several studies have now been undertaken on polymorphism within the arthrodires and its evolutionary significance. The first study on Australian fossil fishes was on the lateral line system in the arthrodire *Incisoscutum ritchiei* (Dennis & Miles 1981). Differences were noted not just between individuals, but also on the left and right sides of the fish (Trinajstic & Dennis Bryan 2009). The rostral plate (Figure 3A–C), which is the most anterior median plate of the head shield, was also found to be highly variable. In ancestral forms such as *Compagopiscis* and *Incisoscutum* (Figure 3C) the rostral plate has three forms, T-shaped, triangular and anteriorly protruding trinangular. The fossil record from Gogo indicates that there was selection for one morph – the triangular morph, and in descendents the rostral plate is always triangular (Trinajstic & Dennis Bryan 2009). In addition, there is also selection for an increase in the length of the rostral plate within the Camuropiscidae (Miles & Dennis 1979) with descendent species having a longer rostral plate then ancestor species (Figure 3C), an example of directional selection (Trinajstic & McNamara 1999; Trinajstic & Dennis Bryan 2009). The mechanism of this elongation has been determined to be peramorphic – or an increase in the time of growth compared to other dermal plates (Trinajstic & McNamara 1999). These evolutionary mechanisms are further explained below.

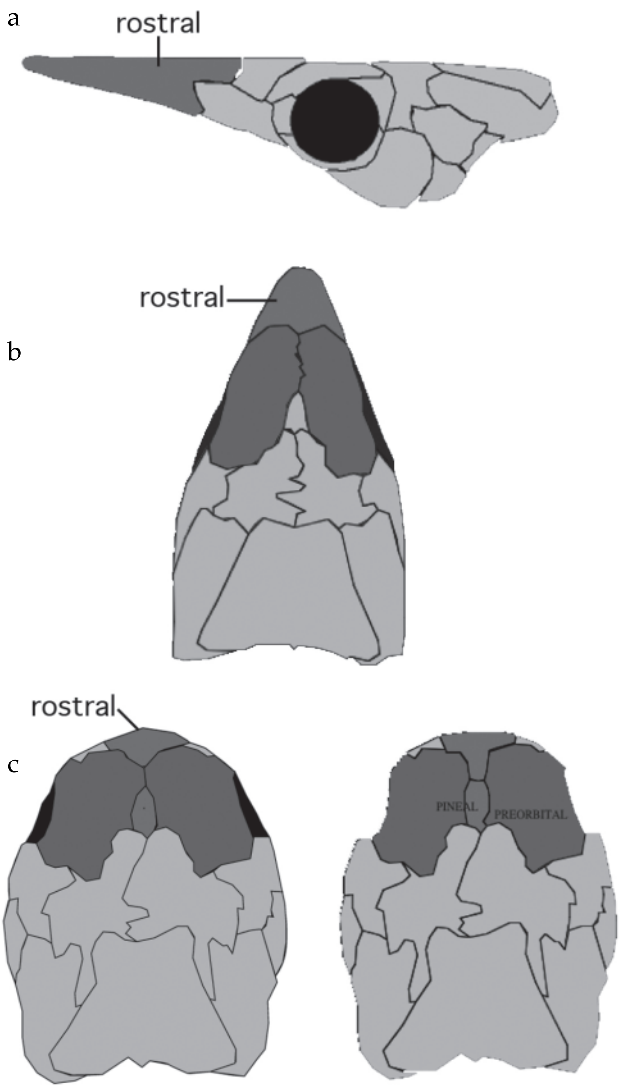

**Figure 3.** Directional selection for the triangular morph of the rostral plate. A. Lateral view of *Rolfosteus* showing the elongation of the rostral plate. B. *Camuropiscis* showing selection for the triangular morph of the rostral plate. C. *Incisoscutum* showing the two morphs (T-shaped and triangular) of the rostral plate.

## Ontogeny and heterochrony

Recent studies of growth and development have been possible in four genera of arthrodiran placoderms: *Incisoscutum* (Dennis & Miles 1981), *Eastmanosteus* (Dennis-Bryan 1987) *Tubonasus* (Long 1988) and *Camuropiscis* (Trinajstic & Dennis-Bryan 2009). Trinajstic & McNamara (1999) recognised considerable variation in body form within *Compagopiscis croucheri*, which they attributed to allometry—*i.e.*, differences between size and shape during growth. It was determined that lengthwise growth occurred prior to breadth-wise growth indicating

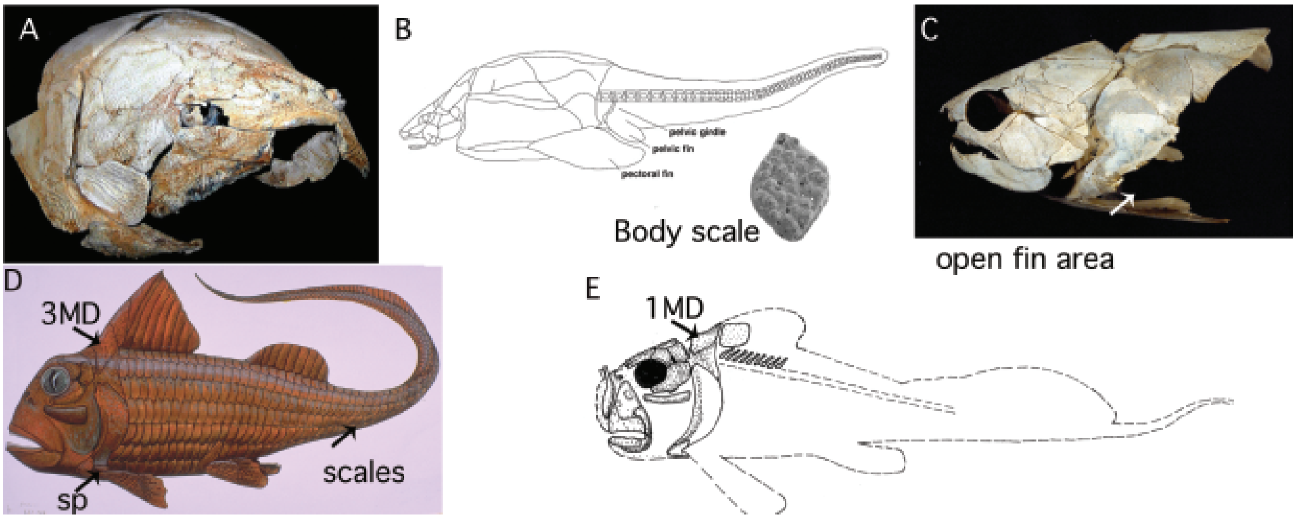

**Figure 4.** Evolutionary trends within the placoderms. A. *Holonema* dermal plates. B. Reconstruction of *Holonema* showing long armour, enclosed pectoral fin and body scales. C. *Mcnamaraspis* showing reduced body armour, open pectoral fin and no tail scales. D. *Campbellodus* showing 3 spinal plates (sp), three median dorsal plated (MD) and body scales. E. Reconstruction of *Materpiscis* showing a reduction to one median dorsal plate, loss of spinal plate and loss of body scales.

that juveniles had a more gracile appearance then adults (Trinajstic & McNamara 1999). This discovery led to the synonomy of two genera *Compagopiscis* and *Gogosteus* (Trinajstic & Hazelton 2007).

Within the diversification of the placoderms there were a number of homeomorphic trends, and many of these parallel changes seem to involve morphological aspects of locomotion (Carr 1995). Many of these changes can be attributed to heterochrony – changes in the rate and timing of development (McKinney & McNamara 1990). The presence of a long trunk shield, more than one median dorsal plate and scales covering the body behind the shoulder girdle are considered primitive characters for placoderms (Miles & Young 1977; Goujet 1984; Goujet & Young 2004). Within the ptyctodonts there is a trend for reduction in the body armour, including the loss of the spinal plate, posterior ventral plates and median dorsal plate elements, and the loss of post thoracic scales (Figure 4). A similar trend is seen in the arthrodires with more primitive forms such as *Holonema* having a tail covered in scales and an enclosed pectoral fin, and more derived forms such as *Mcnamaraspis* having a naked tail and an open pectoral fin (Figure 4). Carr (1995) suggested that the loss of body scales increased flexibility in arthrodires and similar selective pressures on ptyctodonts have resulted in a similar solution for increased swimming ability (Figure 4). In addition, the loss of the spinal plate and posterior lateral plate opened up the area for the pectoral fin allowing greater manoeuvrability of the fin. Information obtained from the study of placoderm embryos (Long *et al.* 2008, 2009) showed that not all bones ossified at the same time, the bones associated with respiration and feeding ossifying first and the dermal bones of the trunk armour ossify later. This suggests that the trend for the reduction in the number of dermal plates, evident through placoderm evolution, is the result of paedomorphosis. The combination of having greater pectoral fin movement and more streamlined body shape would result in an increased swimming ability. At the end of the Famennian arthrodires represented the top order predators in the Devonian seas.

### The completeness of the fossil record

Darwin recognised that many of the morphological transitions required for speciation by natural selection were missing from the fossil record. *"I remember well the time when the thought of the [structure of the] eye made me cold all over."* He attributed the lack of transitional forms to the imperfection of the geological record (Darwin 1859). However, since Darwin's time, knowledge of transitional species within the fossil record has greatly increased with one of the better-known transitions being the transition of the fin into the limb. One significant tetrapodomorph, *Gogonasus* is known from the Gogo Formation. The exact phylogenetic position of *Gogonasus* remains unresolved (Long *et al.* 1997, 2006; Ahlberg et *al.* 2007; Clack 2009; Holland & Long 2009; Long & Trinajstic 2010); however, its position as a tetrapodamorph is undisputed. The transition of fins to limbs requires strong muscles in the upper arm to support locomotion of land.

One anomaly in this transition seemed to be *Panderichthys* a fish that had a tetrapod – like braincase and teeth and no dorsal or anal fin; however, it appeared to have retained fin rays whilst also having bones homologous to the proximal part of the tetrapod limb skeleton. CT scanning of the specimen from Talinn in Estonian confirmed the presence of four distal radials indicating that fingers were not an evolutionary novelty of tetrapods but instead evolved from pre-existing distal radials common to all sarcopteyygians (Boisvert *et al.* 2008). *Gogonausus* is significant due to the exceptional preservation found at Gogo indicating not just the articulated fin skeleton but also the position of the cartilage filled spaces between the ossification (Long *et al.* 2006). Additional morphological information has been obtained through micro-CT scanning at ANU showing the path of sensory line canals, the internal structure of the ear and nose and details of the fore-fin skeletal structures.

### Future work in fossil imaging

To understand evolutionary sequences, what features are ancestral and what are derived, the first appearance of each novel morphological feature needs to be determined. A current controversy in vertebrate evolution is the presence or absence of teeth in early vertebrates. The presence of morphological structures, which determine the presence of true teeth, have been determined in the infragnathals (= lower jaw bone) of placoderms. This data suggests that teeth evolved only once in vertebrates, contra to Smith & Johanson (2003) and that the gnathostome tooth condition was established within arthrodires (Rücklin *et al.* 2009). Synchrotron scanning shows histological features at a subcellular detail in three dimensions. The placoderms from the Gogo Formation have been important to these studies with the dental elements showing the patterns common to tooth replacement (Figure 5A–B). CT scans done at ANU have shown the internal structure of the tooth suggesting the presence of immature teeth forming within (Figure 5C). The latest imaging technology, synchrotron scanning, is being used to aid in the resolution of this problem

## Summary

Deposits of exceptional preservation such as the Gogo Formation demonstrate many morphological features not apparent in less well-preserved faunas. From this a better understanding of the morphology of extinct faunas can be ascertained. In addition, it has been possible to study variation within and between species, ontogenetic variation and evolutionary trends within the fossil record. The fossil record is far more complete then in Darwin's time giving evidence for the stepwise acquisition of characters. One of the best known transitions is that of fin to limb and tetrapodomorph taxa from the Gogo Formation have provided much morphological data important in this current study.

**Figure 5.** Arthrodire infragnathals (lower toothplates). A. Infragnathals of *Compagopiscis* showing tooth rows (arrow) B. Infragnathal of *Bullerichthyes* showing change to a crushing dentition. C. CT scan of the infragnathal of *Compagopiscis* showing replacement teeth (arrow).

Increasingly computerized tomography is being used in the study of fossils with exceptional preservation providing increased resolution and understanding of histological features non-destructively.

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