School of Earth and Planetary Sciences

Revision and description of select Mesozoic actinopterygians from the Sydney, Great Artesian and Perth basins of Australia.

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Declaration

To the best of my knowledge and belief, this thesis contains no material previously published by any other person except where due acknowledgement has been made.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

This research is supported by an Australian Government Research Training Program (RTP) Scholarship.

Signature: [redacted] Date: 15.12.2023

Statement of Contribution by Others

Chapters 1 to 5 have been prepared as co-authored manuscripts for peer-reviewed publication in the scientific literature. These chapters are reproductions of submitted and published manuscripts, with the exception of formatting consistent with the thesis. Contributions below are formatted to the CRediT (Contributor Roles Taxonomy) author statement.

Signed author statements can be found in Appendix 1.

The study presented in Chapter 1 was published in the peer-reviewed journal '*Alcheringa'* on the 3rd of March 2020.

Berrell, R. W., Boisvert, C., Trinajstic, K., Siversson, M., Avarado-Ortega, J., Cavin, L., Salisbury, S., and Kemp, A. 2020. A review of Australia's Mesozoic fishes. *Alcheringa*.

Rodney Berrell: Conceptualization, methodology, and wrote the original draft and final manulscript. All authors contributed to the investigation, manuscript preparation, reviewing and editing; in addition, **Kate Trinijstic, Anne Kemp, Mikeal Siversson** assisted with methodology.

The study presented in Chapter 2 was published in the peer-reviewed journal '*Palaeogeography, Palaeoclimatology, Palaeoecology'* on the 10th of October 2014 and presented at the Society for Vertebrate Paleontology conference on the 5-8th November 2014.

Haig, David W., Martin, Sarah K., Mory, Arthur J., Mcloughlin, Stephen., Backhouse, John., **Berrell, Rodney W**., Kear, Benjamin P., Hall, Russell., Foster, Clinton B., Shi, Guang R., Bevan, Jennifer C. 2015. Early Triassic (early Olenekian) life in the interior of East Gondwana: mixed marine–terrestrial biota from the Kockatea Shale, Western Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Vol.417, pp.511-533.

and

Berrell, R., Haig, D., Kear, B. A rare early Olenekian (earliest Triassic) marine vertebrate assemblage from the Kockatea Shale of Western Australia. Journal of Vertebrate Paleontology, Program and Abstracts, 2014, page 90.

This paper investigated a complete vertebrate assemblage. My contribution was the description of three new taxa which were the first record of a coelacanth in WA for the Mesozoic and two additional basal actinopterygians. The other authors each wrote the section on their taxonomic specialization. All authors edited the manuscript.

Chapter 3 has been prepared in the style guide to be submitted to the peer-reviewed journal '*Gondwana Research'* however, it has only just been submitted at the time of submitting this thesis.

Berrell, R. W., and Trinajstic, K. 2023. A redescription of the basal halecomorph fish *Promecosomina formosa* Woodward 1908 from the early Triassic of the Sydney Basin, New South Wales, Australia.

Rodney Berrell: Conceptualization, Methodology, Writing-Original draft preparation, reviewing and editing. **Kate Trinajstic:** Writing-Original draft preparation, photography and visiting specimens in the museum along with secondary measurements recorded, reviewing and editing.

Chapter 4 was accepted to the peer-reviewed journal '*Cretaceous Research*' on the 16th March 2023.

Berrell, R.W., Cavin, L., Trinajstic, K., Boisvert, C., Smith, E. T. 2022. The first record of amiid fishes (Halecomorphi, Amiiformes, amiidae, Calamopleurini) from Eastern Gondwana. Cretaceous Research.

Rodney Berrell: Conceptualization, Methodology, Writing-Original draft preparation, reviewing and editing. **Lionel Cavin:** Writing-Original draft preparation, reviewing and editing. **Kate Trinajstic:** Writing-Original draft preparation, reviewing and editing. **Catherine Boisvert:** Writing-Original draft preparation, reviewing and editing. **Elizabeth Smith:** Methodology, Writing-Original draft preparation, reviewing and editing.

Part of the study presented in Chapter 5 was accepted in the peer-reviewed journal '*Journal of Vertebrate Paleontology*' on the 28th of May 2019 and presented at the Society for Vertebrate Paleontology conference on the 5-8th November 2014.

Cavin, L., and **R.W. Berrell**. 2019. Revision of *Dugaldia emmilta* (Teleostei, Ichthyodectiformes) from the Toolebuc Formation, Albian of Australia, with comments on the jaw mechanics. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2019.1576049.

and

Berrell, R. W., and Cavin, L. 2019. Revision of *Dugaldia emmilta* (Teleostei, Ichthyodectiformes) from the Early Cretaceous of Australia. Journal of Vertebrate Paleontology, Program and Abstracts, 2019, page 63.

Lionel Cavin: Conceptualization, Writing-Original draft preparation, reviewing and editing. **Rodney Berrell:** Methodology, Writing-Original draft preparation, reviewing and editing.

Abstract

The late Mesozoic (mid-Jurassic – Late Cretaceous ~150Ma-65Ma) is an important period for understanding the origins and evolutionary story of modern fish. This time period saw the diversification of the teleosts, which are today the most speciose extant vertebrate group. Freshwater ecosystems are particularly important to study, because geographic barriers restrict dispersal opportunities for fishes which has implications for their evolution, and today freshwater fish show higher diversity than marine. However, despite this global diversity the modern fish fauna of Australia is considered depauperate. The Mesozoic fish fauna of Australia is also considered depauperate when compared to other sites, although it is unknown if this reflects a lack of study on the Australian fossil fauna or a long history of lack of diversity.

The overall objective of this study was to determine if the current lack of diversity in the Australian fish fauna is a continuation of low diversity from the Mesozoic. To resolve this question new collections of fishes from Mesozoic sites across Australia were undertaken and described. The five studies outlined below resulted in a refinement of the stratigraphic record, the recognition of new species and juvenile and adult populations, and the construction of phylogenetic relationships that differed from previous analyses.

The diversity of fishes from the earliest Triassic Kockatea Shale – Perth Basin, WA was increased from a few isolated scattered actinopterygian scales to the recognition of the coelacanth genus, *Whiteia* and a neopterygian *Teffichthys*. It was also confirmed that isolated elements, previously unidentified, could be resolved to the genus level. In addition, it was determined that the fishes from the Kockatea Shale fauna are more

closely related to fossils from co-eval faunas of Madagascar than to similar-aged faunas of eastern Australia. The palynomorphs used to date the Kockatea Shale were utilised to revise the age of the Blina Shale, which shares the temnospondyl taxa *Deltasaurus*, from Induan to Olenekian.

Multiple fish of various size ranges recovered from the Sydney Basin were previously attributed to different species of the genus *Promecosomina.* It was confirmed that only one species (*P. formosa*) was present and that the various-sized fishes represent an ontogenetic series. Thus, specimens of *P. beaconensis* are now considered to be the juveniles of *Promecosomina formosa* and *P. beaconensis* the junior synonym of *P. formosa.*

Phylogenetic inferences around the fishes from the Gosford sandstone have previously been presented as a narrative scenario. Here we presented the first cladistic phylogenetic hypothesis which included an increased number of basal taxa resulting in an altered the hypothesis of relationships with the Parasemionotiformes. *Promecosomina* is resolved as a Parasemionotiformes within the Parasemionotidae whereas taxa (e.g., *Watsonulus)* traditionally used to represent Parasemionotidae are resolved outside the family. This has raised questions to the validity of several early phylogenetic relationships where *Watsonulus* was used as the sole representative of the Parasemionotidae. The family Promecosominidae, previously considered to contain *Promecosomina* is left with no members and therefore considered invalid.

Dugaldia was originally described from a single isolated specimen discovered from the Toolebuc Formation near Cloncurry in Queensland and assigned as a neoteleost based on several plesiomorphic characters and a tripartite occipital condyle. Additional specimens recovered from the Toolebuc Formation near Richmond, Queensland have allowed the description of further features, enabling a phylogenetic analysis which placed *Dugaldia* within the Ichthyodectiformes.

Isolated toothed elements from the Late Cretaceous Griman Creek Formation, Lightning Ridge, NSW have previously been referred to as teleosts. Further description of these elements refutes this assignment and instead, they are identified here as belonging to the genus *Calamopleurus* which, has its origin in the Early Cretaceous of Brazil. The discovery of a Brazilian and African genus in eastern Gondwana suggests that there was faunal interchange between east and west Gondwana for at least the Early-‘Mid’ Cretaceous.

We conclude that the Australian fossil fauna is diverse, distinctive, and not depauperate; although it is understudied when compared to other continents such as Europe and North America.

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My sincere appreciation and thanks go to my supervisors and people who I consider great friends and mentors; Professor Kate Trinajstic, Dr. Catherine Boisvert, and Dr. Alison Blyth, Curtin University, Western Australia, firstly for allowing me to commence and continue my studies part time, whilst working full time and providing support, encouragement, and nudges in the right direction, when needed. I am very grateful to Kate who recognised that I had potential and backed me to complete a doctorate by PhD research.

I have had a very long introduction into palaeontology, at the age of five, I met the then collection manager Robert Jones from the Australian Museum, I am grateful for their time to a kid who had so many fossil-related questions.

I am thankful to the lecturers and mentors who taught me so much about geology and palaeontology: Prof. Ruth Mawson, Prof. John Talent, Prof. Glenn Brock, Prof. Steve Salisbury, Kerry Geddes, Dr. Anne Kemp, Dr. Carole Burrow, Dr. Ian Percival, Dr. Elizabeth and Robert Smith, among many more, great Australian Palaeontologists.

I am thankful to my employer and to the people I work with for their support during the time of writing my PhD, and glad to see that me following a scientific path in palaeontology did not make me any less of a hard-rock geologist.

My parents have always supported my interest in the natural world, from weekend bushwalks around the Blue Mountains to fossil-collecting trips around Australia.

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Chapter 3:

Fig. 3.1. Fossil localities where specimens of *Promecosomina formosa* were collected. **A,** Map of Australia indicating the position of the Sydney Basin (in purple), in New South Wales (NSW). Grid in latitude and longitude. Red rectangle denotes map area in B. **B,** Fossil bearing sites within the Sydney Basin (indicated by stars). **C,** Stratigraphic chart of the Sydney Basin indicating *Promecosomina*-bearing strata as fish silhouettes. Abbreviations for map: States of Australia: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria; WA, Western Australia. Abbreviations for stratigraphic chart: CM, Coal Measure; Gp, Group; O/I, Olenekian / Induan; Sst, Sandstone; ~, unconformity. Figure 1C redrawn from Herbert (1979).

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Psp, parasphenoid; Q, quadrate; R, rib; Ra, radial; sb, sclerotic bone; Sc, scale; Sca, scapula; Scl, supracleithrum; So, supraorbital; Sop, subopercle; Sy, symplectic; V, vomer.

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ethmoid; Mpt, metapterygoid; m.s.c, mandibular sensory canal; Mx, maxilla; Op, opercle; Pa, parietal; Phy, parhypural; Pmx, premaxilla; Pop, preopercle; Psp, parasphenoid; Pu, preural centrum (numbered); Q, quadrate; (r), right; Smx, supramaxilla (numbered); So, supraorbital; Soc, supraoccipital; Sop, subopercle; s.o.s.c, supraorbital sensory canal; sym, symphysis; Un, uroneural (numbered).

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Introduction

The Osteichthyes comprise the Sarcopterygii (lobe-finned fishes) which today are reduced to only 8 species and the Actinopterygii (ray-finned fishes) which are the most abundant vertebrate group with around 30,000 species (Nelson 2006). The evolutionary history of the Osteichthyes is complicated, partly because the currently known earliest forms are largely represented by partial fossils that exhibit a mosaic of plesiomorphic and derived characters common to actinopterygians, sarcopterygians and non-osteichthyans (e.g., placoderms), and because molecular data suggest the presence of long ghost lineages for most groups (Zhu et al. 2009). The earliest articulated macrofossil, which can be attributed to the osteichthyans is the stem sarcopterygian (Cui et al. 2019) *Guiyu oneiros* (Zhu et al. 2009), which was recovered from Ludlovian age (~425 MYA), marine strata dated from Yunnan China. The discovery (Zhu et al. 2009) and phylogenetic position of *Guiyu* (Cui et al. 2019) indicates an earlier divergence of the Osteichthyes than previously considered from the fossil record (Janvier 1996) and more in line with molecular data which suggested the presence of long ghost lineages for most groups (Zhu et al. 2009). The combination of both molecular and morphological data supports a divergence age for the Osteichthyes as early Silurian 430.5 MYA (King et al. 2020; Zhao et al. 2021).

Sarcopterygii

The crown Sarcopterygii comprise the Dipnotetrapodomorpha, the clade uniting lungfishes and tetrapods and their sister-group, the coelacanths (Müller and Reisz 2005; Benton et al. 2009; 2015). Current fossils suggest that the origin of the Sarcopterygii was in southern China (Zhu et al. 2009; Wang et al. 2020) and that diversification was rapid throughout the Late Silurian and Early Devonian. The earliest representatives of the crown-group sarcopterygians are *Youngolepis, Diabolepis, Kenichthys, and Styloichthys* (Zhu & Ahlberg

2004; Friedman 2007; Cui et al. 2022) and appear in the Early Devonian of China. *Youngolepis* and *Diabolepis* are resolved as crown-group Dipnoi (lungfishes) and their distinctive body plan and tooth plates indicate that their evolution occurred in a short 7-million-year timeframe (Cui et al. 2022). Following the initial divergence, lungfishes diversified throughout the Devonian, occupying the full range of aquatic environments across marine and terrestrial environments making them the most diverse of the Devonian sarcopterygians (Cui et al. 2022). The end-Famennian extinction severely impacted the diversity of sarcopterygians, although the genera of Dipnoi were not as affected as others and continued across the Devonian – Carboniferous boundary; however, they underwent a habitat shift becoming almost exclusively freshwater by the Late Carboniferous (Smithson et al. 2016; Kemp et al. 2017). The transition from fully marine to freshwater habitats has been suggested to have taken place to escape predation from placoderms (Long 2011). Although there was an early Carboniferous post extinction recovery diversity was low (Kemp 2017) and they remained constrained to freshwater and brackish environments (Challands et al. 2019).

The late Carboniferous early Permian saw a radiation event which is linked to the origin of the crown group lungfishes which is supported by both the fossil record and molecular data (Brownstein et al. 2023). Diversification of lungfish continued through the Permian to the Cretaceous when, with the exception of the origin of modern taxa in the lower Cretaceous, and a pulse of diversity in the Triassic lungfish diversity continued to decrease (Kemp 2017). Despite a previous global distribution (early Devonian-Cretaceous), with the decrease in diversity of lungfishes throughout the Mesozoic there was an accompanying constriction of their geographic range (Kemp 2023). Palaeontological research on Mesozoic lungfishes in

Australia has been extensive and has encompassed both macro and microfossils: an overview of this research is presented in Chapter 1 (Berrell et al. 2020).

Coelacanths diverged from other sarcopterygians in the Silurian and are resolved as the sister group to all other sarcopterygians (Amemiya et al. 2013). Fossils of coelacanths have been found in both freshwater and marine depositional settings since the Devonian; they represent a depauperate group of sarcopterygian fishes with only three radiation events, Late Devonian, Early Carboniferous, and Middle Triassic, documented (Cavin et al. 2021). Although Coelacanths have shown low taxonomic diversity since the Devonian with only 68 taxa recorded (Cavin et al. 2021) they have shown a large range of body sizes (Brownstein et al. 2022). Coelacanths are rare components of the Australian Mesozoic fauna, currently only recognised from Triassic-aged strata (Berrell et al. 2020), although Coelacanths are known from earlier strata (Jurassic and Cretaceous-aged) the number of species have greatly reduced towards the end of the Mesozoic with only two extant deep marine species remaining (Nelson 2006; Holder et al. 1999).

Actinopterygii

The crown group Actinopterygii comprise the Neopterygii, which are made up of the Holostei and the Teleostei, along with the more basal forms, the Cladistia and Chondrostei (Long 2011). Current phylogenetic analyses indicate a Ludlovian (~425 MYA, Late Silurian) origin for the Actinopterygii constrained by the divergence of the Sarcopterygii (Zhu et al. 2009) rather than the presence of actinopterygian fossils which remains and comprise mostly micro-remains (Friedman 2015). The earliest undisputed actinopterygian is *Cheirolepis* from the Middle Old Red Sandstone of Scotland (Middle Devonian in age). A recent revision of *Meemannia*, with the aid of high-resolution computed tomography, has shown additional characters that support its inclusion as the most basal actinopterygian from the Early Devonian of China (Lu et al. 2016), and that it is closing the gap between the earliest known sarcopterygians and actinopterygians. These findings support a Silurian radiation of both the sarcopterygians and actinopterygians, suggesting a northern hemisphere radiation center for both clades; however, it must be acknowledged that there has been far greater work on northern hemisphere actinopterygians compared with the southern hemisphere. The Holostei and the Teleostei diverged from each other possibly in the early Carboniferous or Devonian based on molecular estimates (Friedman 2015).

The actinopterygians have undergone several radiations that can be constrained into three main events: a Devonian–Triassic basal actinopterygian radiation; a Triassic – Jurassic radiation, and a teleost radiation, which occurred from the Jurassic to the present (Benton 2015). The diversification of the actinopterygians post the end-Devonian mass extinction event was possibly seeded by a few or possibly even by one lineage of actinopterygians and is typical of a post extinction recovery followed by adaptive radiation (Henderson et al. 2023 and references therein) with actinopterygians filling vacant niches left by extinct taxa, primarily sarcopterygians and placoderms which suffered a significant decline in diversity for the former and extinction for the latter.

The end Permian mass extinction is recognized as the world's most severe extinction event with 70% of terrestrial species and between 80 % and 96 % on marine species effected (Sahney and Benton 2008). Marine organisms that existed for most of the Paleozoic, especially invertebrates with a calcium carbonate skeleton were more effected including tabulate and rugose corals, graptolites, blastoid echinoderms, trilobites and eurypterids. Marine vertebrates were less affected with only the acanthodians (stem chondrichthyans) becoming extinct (Sahney and Benton 2008; and references therein). This extinction event led to the Mesozoic marine revolution and radiation of the chondrichthyans and actinopterygians, the latter which are divided into the basal actinopterygians and a more crownward group, the neopterygians (Long 2011; Smithwick and Stubbs 2018 and references therein). The non-teleost lineages represent <2% of extant fish species (Friedman 2015). The neopterygians radiation was characterized by changes in jaw morphology and movement that allowed for inertial suction feeding (Lauder 1982) and has been associated with the success of the clade. The basal groups consist of the Polypteriformes (bichirs and reedfishes) and Chondrostei (sturgeons and paddlefishes). Neopterygians are mostly made up of extant members and include the Lepisosteiformes (gars), Amiiformes (bowfins) and the Teleostei (including the vast majority of extant fishes) (Long 2011). The early Jurassic saw the first radiation of the teleosts following the Late Triassic mass extinction event. The teleosts developed a second innovation in relation to feeding, a flexible, kinetic musculoskeletal system associated with the skull and axial skeleton (specifically dorsal and ventral body muscles) that allowed for protrusion feeding (Holtzman et al. 2008). The innovation allows for a significant improvement in prey capture, through increasing the speed of the attack and increasing the hydrodynamic forces on prey (Wainwright, et al. 2015).

The Polypteriformes were originally thought to have diverged from the rest of the actinopterygians during the Early-Middle Devonian (Benton 2015) because of their unique mix of primitive and advanced traits. Polypteriformes are first evident in the fossil record from the ‘mid’ Cretaceous, implying a very long ghost lineage (Giles et al. 2017). Scanilepiformes became widely distributed as a result of radiations during the Triassic across continental or marginal marine deposits in Europe and North America. They show many primitive features of extant polypterids and have been resolved phylogenetically as stem polypterids, primarily due to increased morphological knowledge from high-resolution micro-computed tomography of the skull anatomy of *Fukangichthys* (Giles et al. 2017). This suggest that the Polypteriformes more likely diverged a lot later than previously thought. The fossil record of Polypteriformes indicates that the group were never species rich with the majority of fossils known from Cretaceous deposits of Africa and comprise at least nine genera (Gayet et al. 2002). Cavin (2008) indicates that there was a potential Cretaceous radiation of the Polypteriformes however this is based on fragmentary remains (Cavin 2008). Despite surviving the K-T mass extinction the modern a Polypteriformes are greatly reduced to only two genera (Nelson 2006). The modern distribution of the Polypteriformes is restricted to continental Africa (Gayet et al. 2002; Nelson 2006). There is currently no record of the Polypteriformes from Mesozoic deposits of Australia (Berrell et al. 2020) and it be highly unlikely that there would be since they evolved after Gondwana began to separate and are exclusively freshwater (Nelson 2006).

The crown group Chondrostei have a fossil record that commenced in the Early Jurassic (~200 million years ago) (Bemis et al. 1997). Stem Chondrostei are difficult to recognise due to all basal actinopterygian share similar morphological traits that were previously used to seperate the Chondrostei from other actinopterygians (Argyriou et al. 2018). Bayesian analysis of mitochondrial genome suggest a divergence from the actinopterygians in the Devonian (Thorne et al. 1998) although current fossil evidence is ambiguous. The total age for the group, as suggested by morphological and/or molecular phylogenetics, predates the first appearance in the fossil record, which is a common occurrence amongst basal actinopterygians (Friedman 2015). Recent studies by Argyriou et al. (2018) removed Saurichthys and *Belichthys* from the ingroup. Cavin, (2008) considered the group had an initial radiation in Asia during the Early Cretaceous with a Late Cretaceous or early Tertiary dispersal to North America.

Extant species of Chondrostei comprise paddlefishes and sturgeons. Sturgeons are anadromous and freshwater, while paddlefishes are almost exclusively freshwater (Nelson 2006). They are restricted to Europe, Asia, and North America (Nelson 2006). The paddlefishes and the sturgeons have followed a similar evolutionary progression as the dipnoans, becoming less diverse through geological time with the Sturgeons having 25 extant species and the paddlefishes having only two extant species (Peng et al. 2009).

The record of the Chondrostei in the Mesozoic outcrops of Australia presents a poor record. The Australian records of '*Coccolepis'* are now known tentatively as *Condorlepis* from the Late Jurassic and Early Cretaceous of the Talbragar and Koonwarra fish beds (López-Arbarello et al. 2013), there is also a potential Acipenseriformes, *Psilichthys selwyni* (Hilton & Forey 2009; Berrell et al. 2020) from the Cretaceous deposits of Victoria, although this assignation appears incorrect on the current known radiation and dispersal events of the group (Cavin 2008).

Neopterygians

The Holostei are a diverse and ancient clade, of which the crown group contains the extant, Ginglymodi and Halecomorphi, or the gars and bowfins (López-Arbarello and Sferco 2018). Together with the Teleostei, they form the actinopterygian crown group Neopterygii (López-Arbarello and Sferco 2018). The Holostei are considered the sister group to the Teleostei and have their roots in the Palaeozoic, but underwent major diversification during the Mesozoic

(López-Arbarello and Sferco 2018). Their modern-day range and species numbers are greatly reduced, with the Halecomorphi only having two extant valid species of *Amia* that are restricted to the freshwater rivers and lakes of North America (Wright et al. 2022). The only surviving genus of the Ginglymodi is the Gars (family Lepisosteidae) which are also restricted to waters of North and central America (Nelson 2006), but which were once more widely distributed in Africa and Eurasia.

The record of Halecomorphi is reasonably supported by fossils from the Mesozoic of Australia. The earliest representative of the Halecomorphi from Australia is *Promecosomina formosa* from the Middle Triassic of the Sydney Basin (Berrell and Trinajstic, In Press, Chapter 3). There is currently an undescribed species of Holostei from the Late Jurassic of the Talbragar fish beds (Bean 2021). A possible species of Ionoscopiformes, *Canaryichthys rozefelds,* is also known from the Early Cretaceous of the Toolebuc Formation of Queensland (Bartholomai 2015). *Calamopleurus* has also been recognised based on isolated jaw elements from the Late Cretaceous freshwater deposits of the Griman Creek Formation, New South Wales, Australia (Berrell et al. 2023 and Chapter 4). There are currently no records of the Ginglymodi in the Mesozoic of Australia (Berrell et al. 2020).

Teleostei

The Teleostei are a monophyletic group divided into four subgroups, all of which contain extant members (Arratia 2001; Patterson and Rosen 1977). The teleosts are united by a single unique character: the presence of an elongate posteroventral process on the quadrate (Arratia 2001). The timing for the origins of the Teleostei depends on how the group is defined (Arratia 2001); however, it is generally accepted that the teleost lineage originated at least by the Late Triassic with the Pholidophoriformes found from limestone deposits in Italy (Arratia

2017) and diversified during the Jurassic (Benton 2015). From 450 extant teleost families (Nelson 2006), only 15 families can be recognized in the Cretaceous (Arratia 1997) indicating that the K-T mass extinction event had a profound effect on teleost families. This event is now widely accepted that an asteroid was the cause for the extinction of non-avian dinosaurs, marine reptiles, ammonites and some fish groups including the ichthyodectiforms and pachycormiforms (Chiarenza et al. 2020; Long et al. 2018). The extinction appears to have selectively targeted fish with large body size and limited jaw-closing apparatus (Friedman 2009). While this event had lasting impact on some teleost groups, it ultimately led to the diversification of the Acanthomorpha (spiny-finned teleosts) and the Ostariophysi during the Paleogene (Long et al. 2018, and references therein).

The taxa described across the Mesozoic localities (Talbragar and Koonwarra) account for ~ 1/3rd of fish taxa described for the Australian Mesozoic (Berrell et al. 2020, Chapter 1, Table 1). Both these localities typically contain a small (<10 cm-sized), primitive, freshwater fish assemblage that includes stem group teleosts and holosteans (Bean 2017). Another large component of the Australian Mesozoic fish fauna is the large macro fossils consisting of taxa from the families Ichthyodectiformes, Aspidorhynchidae, pachycormiform pachyrhizodontids several probable elopomorphs, and a possible ionoscopiformes, from the Early Cretaceous formations of the Great Artesian Basin, specifically the Eromanga Basin (Bartholomai 1969; 2004; 2008; 2010; 2012; 2013; 2015). Very little is known about the evolution and diversification of the Acanthomorpha and Ostariophysi fishes during the Mesozoic of Australia. Because of the lack of knowledge of these groups in the Mesozoic of Australia were omitted from Berrell et al. 2020 and Chapter 1.

Aims and objectives.

The objective of this thesis is to determine if the Australian Mesozoic fish fauna was depauperate. The modern Australian freshwater fish fauna is described as depauperate with ~200 species, the majority of which originated from marine ancestors (Merrick 1996), since there were radiations of teleost in the Mesozoic are there links between Mesozoic and Cenozoic events that led to this depauperate nature of the modern Australian fauna. Whilst the currently described fauna (both modern and Mesozoic) is highly endemic, the Mesozoic actinopterygian fauna is not well understood. This will be achieved in this thesis through the following aims:

> Aim 1: Establish if the lack of documented actinopterygian diversity in the Mesozoic of Australia is a result of a depauperate fauna or the understudied nature of the Australian Mesozoic fauna.
>
> Aim 2: Describe new actinopterygian taxa from the Eromanga and Perth basins and assess their significance.
>
> Aim 3: Apply modern phylogenetic methods to investigate the relationships of a halecomorph and a teleost, to test whether their historical taxonomic placements were accurate.

Chapter overview and thesis structure:

The thesis is organized in chapters that reflect geological time.

Gondwanan actinopterygians are poorly known (López-Arbarello 2004; Merrick 2006) and no prior review had been undertaken on Mesozoic actinopterygians. As my aim is to better understand the origination and diversification patterns of Mesozoic actinopterygians, I produced a review in Chapter 1, which included analysis of some microfossils. This review consolidates knowledge on the topic “Mesozoic fishes of Australia” and compiles current understanding of taxonomy, distribution, palaeobiogeography and palaeoenvironmental significance. It concludes that the Mesozoic actinopterygian fauna is not depauperate but a result of incomplete sampling and the lack of study of microfossils.

In Chapter 2, I chose the Early Triassic Kockatea Shale (Perth Basin) of Western Australia to investigate aim 2.

Investigate sites in Western Australia, New South Wales and Queensland for the presence of fauna that has not been described before.

This locality from the Early Triassic is located inland on the East Gondwana interior rift-sag system but is still considered marine. No actinopterygian fossils had previously been described from Western Australia in this time-period and this was a good locality to test if Permian taxa endemic to Gondwana had persisted through the Permo-Triassic extinction or if a diversification event occurred after the extinction event. We describe two new fish taxa which increases the diversity. However, the preservation does not allow to assign them to Permian species and morphologically they appear to be more likely Triassic species. It does show, however, that increased exploration and description of fragmentary material can improve our understanding of faunal composition.

In Chapter 3, I examine a large collection (including mass mortally beds) of well-preserved and complete actinopterygians from the Middle Triassic of the Sydney Basin. These fishes are referred to the genus *Promecosomina*. These larger individuals than the smaller, originally described *Promecosomina formosa* (Woodward 1908) were originally placed in the European Permian genus *Acentrophorus,* with multiple authors rejecting a later revision by Wade 1935, who included these fish within the Parasemionotiformes.

Since these descriptions are pre-phylogenetic, a unique opportunity to test Wade's (1935) original hypothesis. There are more than 20 individual fish-bearing localities across the Sydney Basin, with at least several of these containing *Promecosomina.* The type locality at St Peters is within the Ashfield Shale and is considered shallow marine to Brackish (Herbert 1997). The Somersby locality is approx. 70 km to the north of St Peters, is preserved within the Hawkesbury Sandstone and is considered to represent a freshwater (lacustrine) environment (Herbert 1997). These assemblages represented an opportunity to redescribe and analyse these fishes in a modern phylogenetic context.

Chapter 4 investigates isolated toothed elements from the freshwater deposits of the Late Cretaceous Griman Creek Formation, New South Wales, Australia. The Griman Creek Formation was deposited in the freshwater streams and rivers on the edge of the Eromanga Sea, so it provides a good opportunity to observed what is "typically" freshwater taxa and those that are 'typically' marine and their overlap. I describe the first halecomorph from the Cretaceous of Australia. Halecomorpha are often resolved as the sister group to teleosts. I assigned these toothed elements to the genus *Calamopleurus*, a euryhaline fish common to the Early–'mid' Cretaceous seas and rivers of South America and Africa.

In Chapter 5, I chose the Early Cretaceous Toolebuc Formation, Queensland, Australia, which was deposited in part of the Eromanga Sea. This is a significant site for understanding the biogeography of Australian taxa as it records an of extensive marine transgression and regression event and could provide information on the contributions of the Tethys Ocean to Australian endemic fauna. My co-author and I chose to redescribe *Dugaldia* because it was attributed to the Neoteleostei, as a basal teleost. We reassign

Dugaldia to the Ichthyodectiformes and resolve the position of two freshwater Ichthyodectiformes. I show that the Australian ichthyodectiform fauna was more speciose than originally thought. Establishing taxa within in the correct taxonomic framework is important as some modern taxa can be found both in marine and freshwater habitats and this can be true for some Mesozoic forms e.g., (*Cladocyclus gardineri*).

Material and Methods

To avoid replication in this thesis, details of the geological settings studied are presented as part of the published papers that comprise subsequent chapters. A summary of the stratigraphic relationship among sites is detailed in Chapter 1. Methodology for each publication is clearly presented in each chapter. Items not represented in each published paper are discussed below.

Taxonomy follows that set out in The Code from the International Commission on Zoological Nomenclature. If exact taxonomic identification to species rank was impossible, the specimens were referred to open nomenclature at the family or genus level (Mathews 1973). Descriptive terminology for chondrichthyan fossils was undertaken using the terminology of Cappetta (2012). Halecomorph fishes were described based on terminology in Grande and Bemis (1998). Teleost fishes were described based on terminology in Arratia (1997).

Comparative and studied material were photographed with a digital camera; a 20-megapixel Olympus OMD using a macro lens. Fossils were photographed with the inclusion of a millimetre scale. Fossils were measured using digital callipers with a 1mm accuracy. Angles were measured using an angle/linear ruler.

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Chapter 1. A Review of Australia's Mesozoic Fishes

The study presented in Chapter 1 was accepted in the peer-reviewed journal '*Alcheringa'* on the 3rd of March 2020.

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1.1 ABSTRACT

The Australian Mesozoic fish fauna is considered to be depauperate in comparison with fish faunas in the Northern Hemisphere. However, due to its geographical location as a potential radiation centre in the Southern Hemisphere, Australia's Mesozoic fish fauna is important for understanding fish radiations. During the Mesozoic, most of the modern fish groups originated, but the first records of a modern fish fauna (freshwater and marine) in Australia does not occur until the lower Paleogene. Here, we review all known fossil fish-bearing localities from the Mesozoic of Australia, to improve the understanding of the record. The apparent low Australian Mesozoic fish diversity is likely due to its understudied status of the constituent fossils rather than to a depauperate record. In addition, we review recent work with the aim of placing the Australian Mesozoic fish fauna in a global context. We review the taxonomy of Australian fossil fishes and conclude that the assignments of many actinopterygians need major revision within a modern phylogenetic context. The vast majority of chondrichthyans are yet to be formally described, to the contrary all of the known lungfish specimens have been described. This study considers the microscopic and fragmented remains of Mesozoic fish already found in Australia, allowing a more complete view of the diversity of the fishes that once inhabited this continent.

1.2 INTRODUCTION

Mesozoic fish faunas from Gondwanan terrains are poorly known and considered depauperate when compared to faunas from the northern hemisphere (López-Arbarello 2004, Merrick 2006). However, well-understood and documented faunas from Australia are known from marine and freshwater environments. The known Australian Mesozoic faunas consist mostly of teleosts, other basal actinopterygians and chondrichthyans with several lungfish species, some of them, such as

Ptychoceratodus philippsi, having a global distribution (Kemp 1996). However, recent taxonomic studies suggest that the assignation of many Australian Mesozoic fishes to genera firstly reported for northern hemisphere terrains is erroneous (e.g., *Leptolepis*). More recent studies, as Sferco *et al*. (2015), indicate, that at the species level, the Australian bony fish fauna is endemic to Australia and that at the genus and family level, their range appears to be limited to Gondwana (Arratia *et al.* 2004, López-Arbarello 2004, Bean 2005, 2006, Sferco *et al*. 2015). The same cannot be said for the chondrichthyans; as an example, the lamniform shark *Cardabiodon ricki* has an incomplete but global distribution in the Cenomanian stage of the Cretaceous, being found in Australia, North America, and Europe (Newbrey et al. 2015).

A detailed knowledge of Australian Mesozoic fish faunas is important to gain an understanding of fish evolution and the biogeography of both modern and ancient groups. The Mesozoic represents a time of major continental reconfiguration due to tectonic processes, which had a profound impact on the origin, diversification, and distribution of these living organisms (Briggs 2003), leading to marked endemism of Australia's modern fish fauna (Unmack 2001). According to López-Arbarello (2004), the few studies that have been conducted on Australian Mesozoic fishes indicates a major shift in the diversity of fishes between the Triassic and the Cretaceous, delimited by a loss of diversity during the Cretaceous. This loss of diversity is probably a result of the break-up of Gondwana that resulted in loss of connectivity between freshwater species coupled with climatic changes (López-Arbarello 2004). However, it may instead reflect the lack of study, different taphonomic effects and depositional environment of Mesozoic fishes within Australia. In contrast, the dipnoans are characterised by low taxonomic diversity, globally throughout the

Triassic–Cretaceous aged deposits. Further studies on the Australian fish fauna are required to determine if there is a general trend in decreasing diversity from the Cretaceous to present time or if instead clades respond differently and there is a collection bias.

To address the above issue, and uncertainties associated with taxonomy, recent work has been undertaken (Bartholomai 2010, 2013, 2015, Berrell *et al.* 2013, Kear 2007, Kemp 1997a and b, Kemp 1998, Newbrey *et al*. 2015, Siverson 1996, 1997, 1999 & 2011, Siversson *et al*. 2015, Siversson *et al*. 2018) to better characterise the Australian Mesozoic fish faunas. These studies have largely concentrated on macrofaunas with the exception of the chondrichthyan faunas from the Southern Carnarvon Basin of Western Australia (Siverson 1996, 2011, Siversson *et al*. 2018). As a result, much of the Australian Mesozoic micro-remains (teeth and scales of actinopterygians and chondrichthyans) remain undescribed. Extensive sampling and description of microvertebrates from Devonian strata increased the taxonomic diversity, stratigraphic range, and species distribution for this time period (Turner 1993, Trinajstic & George 2009, Burrow *et al*. 2010, Roelofs *et al*. 2015) and there is the potential for similar results from the under-sampled Mesozoic strata of Australia. In the Cretaceous section, we present previously undescribed teleost microfossils recovered from the Toolebuc Formation along with descriptions of new specimens of the chondrichthyan *Echinorhinus australis.* The microvertebrate fossils for most of the Mesozoic of Australia are currently undescribed and their taxonomy is uncertain. This indicates a great need for further description and inclusion into phylogenetic analyses where possible distribution and biogeographic studies to reach an integrated understanding of these fish faunas within a global and regional context. Herein, we review all the Australian Mesozoic sites yielding fossil fishes (Figure 1.1) and discuss uncertainties surrounding the previous taxonomic assignment of chondrichthyans, actinopterygians and sarcopterygians.

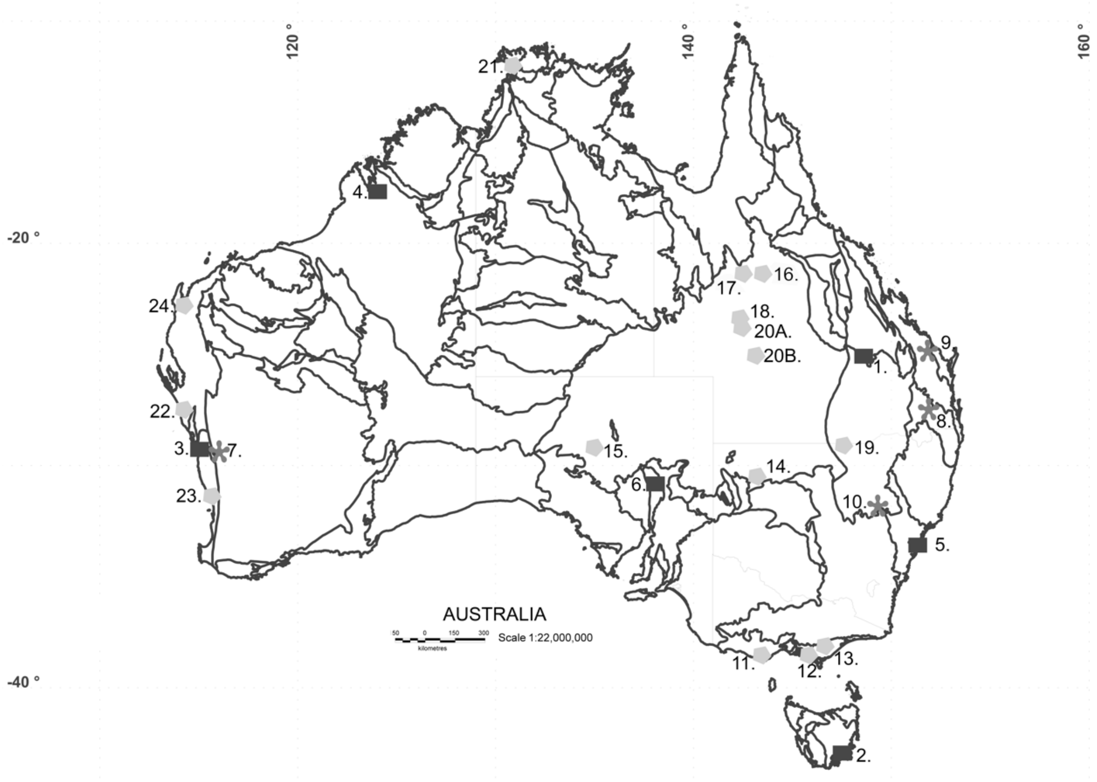

Figure 1.1. Map of Australia, showing sites that have produced Mesozoic fishes in time sequence order (oldest–youngest). Squares represent Triassic localities; stars Jurassic localities and pentagons represent Cretaceous localities.

1. Arcadia Formation, Queensland (Triassic, Griesbachian). 2. Knocklofty Formation, Tasmania (Triassic, upper Induan – lower Olenekian). 3. Kockatea Shale, Perth Basin (Triassic, Olenekian). 4. Blina Shale, Western Australia (Triassic, Olenekian). 5. Narrabeen, Hawkesbury Sandstone and Wianamatta Shale, Sydney Basin, New South Wales (Lower Triassic, Olenekian-lower Anisian). 6. Leigh Creek, South Australia (Triassic, Carnian – Norian). 7. Colalura Sandstone, Perth Basin (Jurassic, Bajocian). 8. Walloon Coal Measures, Queensland (Jurassic, upper Bajocian - lower Callovian). 9. Mulgildie Coal Measure, Mulgildie Basin (Jurassic, upper Bajocian - lower

Callovian). 10. Purlawaugh Formation, Surat Basin (Jurassic, Kimmeridgian). 11. Eumeralla Formation, Otway Basin (Cretaceous, upper Aptian – lower Albian). 12. Wonthaggi Formation, Gippsland Basin (Cretaceous, lower-middle Aptian). 13. Korumburra Group, Gippsland Basin (Cretaceous, upper Aptian – lower Albian). 14. Wallumbilla Formation, Eromanga Basin (Cretaceous, Aptian). 15. Bulldog Shale, Eromanga Basin (Cretaceous, Aptian-lower Albian). 16. Allaru Formation, Eromanga Basin (Cretaceous, upper Albian). 17. Toolebuc Formation, Eromanga Basin (Cretaceous, upper Albian). 18. Mackunda Formation, Eromanga Basin (Cretaceous Albian – lower Cenomanian). 19. Griman Creek Formation, Surat Basin (Cretaceous, middle Albian). 20a. Winton Formation at Isisford, Eronmanga Basin (Cretaceous upper Albian). 20b. Winton Formation at Winton, Eronmanga Basin (Cretaceous – Turonian). 21. Moonkinu Formation, Money Shoal Basin (Cretaceous, Cenomanian – Turonian). 22. Alinga Formation & Beedagong Claystone, Carnarvon Basin (Cretaceous, Cenomanian). 23. Molecap Greensand and Gingin Chalk, Perth Basin (Cretaceous, Cenomanian – Coniacian). 24. Gearle Siltstone, Haycock Marl, Toolonga Calcilutite & Miria Marl, Giralia Anticline, Southern Carnarvon Basin (Cretaceous, upper Maastrichtian).

1.3 MATERIAL AND METHODS

Institutional abbreviations: AM, Australian Museum, Sydney, New South Wales, Australia; KKF, Kronosaurus Korner, Richmond, Queensland, Australia; NHM, Natural History Museum, London, United Kingdom; LRF, Lightning Ridge Opal and Fossil Centre, Lightning Ridge, New South Wales, Australia; MV, Museum Victoria, Melbourne, Victoria, Australia; QM and GSQ (formally held by the Geological Survey Queensland), Queensland Museum, Brisbane, Queensland Australia; SAM, South Australian Museum, Adelaide, South Australia, Australia; TMAG, Tasmanian Museum and Art Gallery, Hobart Tasmania, Australia. UWA, University of Western Australia, Perth, Western Australia. WAM, Western Australian Museum, Perth, Western Australia, Australia.

Methods: Limestone samples (~ 1Kg) from the Toolebuc Formation were collected from a quarry approximately 12 km northwest of Richmond along the Richmond – Woolgar Road (20°38’45. 3” S 143°05’58. 0E), in north-west Queensland (Figure 1.1., Locality 18). The limestone was disaggregated in ~10% acetic acid (Toombs & Rixon 1959). Sediment was washed and sieved using a 1mm mesh size. Heavy and light fractions of the limestone residue were separated using heavy liquid separation with polytungstate (Jeppsson & Anehus 1999). The heavy fraction was picked using a stereo dissecting microscope. Samples were imaged on a Leica M165C Stereo microscope with a DFC7000T colour camera as a 3D montage using the LAS software 4.9.0. Shark teeth were described using the terminology of Cappetta (2012). Angles were measured using an angle/linear ruler between the root and the tooth junction and the apex of the cusp on the lingual side of the tooth. The fossil specimens referred to in the microvertebrate section below are deposited in Kronosaurus Korner (KKF), Richmond, Queensland, Australia.

1.4 AUSTRALIAN FOSSIL FISH LOCALITIES

Triassic

The Triassic fishes are the best-known and most diverse of the Mesozoic fishes described from Australia. Currently, Triassic taxa are known to occur in six formations: The Knocklofty Formation, Tasmania Basin, Tasmania; the Arcadia

Formation, Bowen Basin, Queensland; the Kockatea Shale, Perth Basin, Western Australia and Blina Shale, Canning Basin, Western Australia; the Narrabeen and Hawkesbury Sandstones and Wianamatta Shale, New South Wales and the Leigh Creek Coal Measures, Telford Basin, South Australia (Figure 1.2.). These deposits range from the earliest Induan (Griesbachian) to Carnian-Norian, with over 20 discrete fish-bearing localities known within these strata (e.g., the Sydney Basin faunas). The upper Middle (Ladinian) and the upper Upper (Rhaetian) Triassic are not represented in Australia. Spore-pollen data confirms that the Knocklofty, Arcadia, and Kockatea formations as well, as the Blina shale, are all Early Triassic in age, potentially coeval providing a palaeobiological "snapshot" of the Neotethys and South-western Panthalassa fauna during the Early Triassic.

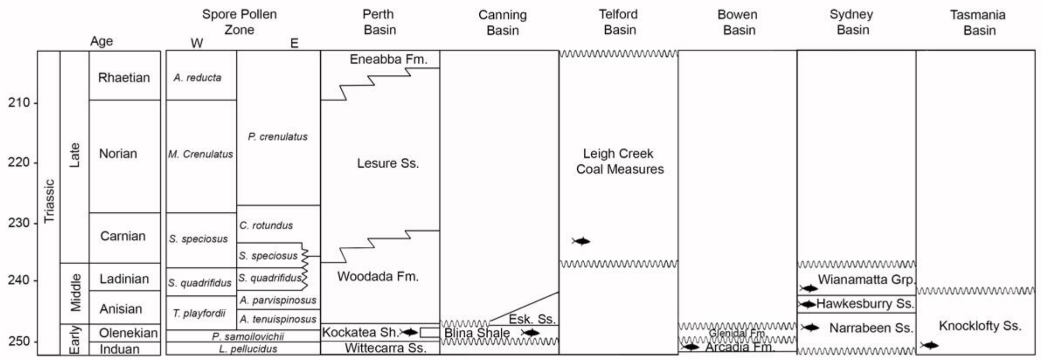

Figure 1.2. Stratigraphy of Triassic fish sites across Australia. Abbreviations: Esk. Erskine; Sh. Shale; Ss. Sandstone; Mbr. Member; Grp. Group; Fm. Formation. The black fish symbol represents the approximate stratigraphic position of fish sites and does not differentiate between actinopterygians, chondrichthyans or piscine sarcopterygians.

1. Arcadia Formation, Bowen Basin, Queensland

The Arcadia Formation crops out in southeastern Queensland (Figure 1.1., locality 1). The majority of the fossils recovered from this formation are from The Crater

(Queensland Museum Locality 78) and Duckworth Creek (QML215) localities (Northwood 2005). The formation has been dated earliest Triassic, Griesbachian, lower Induan corresponding to the vertebrate *Lystrosaurus* Zone of South Africa (Thulborn 1983), corresponding to the Australian pollen zone *Lunatisporites pellucidus* zone (= APT1 zone Price 1997) (Figure 1.2.). The depositional environment is interpreted as a braided watercourse with seasonal flooding indicated by the deposition of red, quartz-dominated sandstone (Jensen 1975). Although skeletal fish remains are rare from this formation, fossil coprolites show that fishes were a common element within this ecosystem (Northwood 1999, Warren 2006). Isolated and partial aggregates of scales show that basal actinopterygians representing at least six actinopterygian taxa, including perleidids and acrolepids, were present in the Arcadia Formation (Northwood 1999). Northwood (1999) highlighted the importance of scale descriptions for fossil taxa since often only scales are preserved. Description of the diversity of scales types present of an individual has been successfully undertaken for the Devonian (Trinajstic 1999, Basden *et al.* 2006, Choo 2009). A partial *Saurichthys* skull has also been described (Turner 1982) along with the lungfish (*Aphelodus anapes* (Figure1.3.A), *Ptychoceratodus phillipsi* and *Namatozodia pitikanta*). The first two are represented by tooth plates (Figure 1.3.A) and partial skulls (Kemp 1993, 1996), and *N. pitikanta* by a small juvenile skull only.

2. Knocklofty Formation, Tasmania Basin, Tasmania

Six localities of the Knocklofty Formation are exposed near Hobart, Tasmania, Australia (Figure 1.1., locality 2) and are dated as Lower Triassic (upper Induan – lower Olenekian) determined by spores (*Densoisporites playfordi* and *Lundbladispora brevecula*) (Figure 1.2.), macroflora (*Cylostrobus sydeneyensis*), temnospondyls (cf. *Blinasaurus henwoodi*) and archosauromorphs (Banks 1987). The temnospondyls are correlated with the vertebrate fauna biozones in the Beaufort Series of South Africa, based on the co-occurrence of temnospondyls (cf. *Blinasaurus henwoodi*) and archosauromorphs (Banks and Naqvi 1967, Cosgriff 1974, Camp and Banks 1978). The depositional environment has been interpreted to be fresh water based on the presence of clay-pebble conglomerate and sandstones considered to be a channel fill deposit (Dziewa 1980). The fossils (Table 1.1) occur as isolated bones, tooth plates and/or partial and complete body fossils (Figure 1.3.B), and possible chondrichthyan fin spines from the Old Beach Site, Hobart (Bender 2008).

3. Kockatea Shale, Perth Basin, Western Australia

The Kockatea Shale crops out in the northern part of the Perth Basin (Figure 1.1., locality 3). Prior to the discovery of a quarry site near Geraldton (Haig *et al.* 2015), fossils from this formation were limited to a petroleum drill core (B.M.R. 10, Cosgriff 1965, Metcalfe *et al.* 2008). This formation is dated as early Olenekian based on spore-pollen zones *Densoisporites playfordii* and *Kraeuselisporites saeptatus*, and the conodont *Neospathodus wageni* corresponds to the *Protohaploxypinus samoilovichii* and *Krauselisporites saeptatus* Zones (Metcalfe *et al.* 2008, Haig *et al.* 2015). Previously the Kockatea Shale was assigned to be broadly of Scythian age due to its microflora and the occurrence of the ammonites *Ophiceras* cf. *subkyoticum* and *Subinyoites kashmiricus* (Cosgriff 1965). Dating based on conodont elements and spore-pollen has refined the date of the Kockatea Shale as Olenekian in age (Haig *et al.* 2015) (Figure 1.2.). The formation is exposed as a variably weathered <40m-exposed thin shale interbedded with thin ripple laminated strata and dominantly capped by sandstone. The depositional environment is interpreted as a coastal marine to estuarial (Haig *et al.* 2015). The formation has previously been noted to contain disarticulated fish remains (Dickens & McTavish 1963, Metcalfe *et al.* 2008) including dentigerous elements, thick rhombic scales with peg and socket articulations indicative of basal actinopterygians (Figure 1.3.D) and broad oval scales representing coelacanthid sarcopterygians (Haig *et al.* 2015) (Figure 1.3.C).

4. Blina Shale, Canning Basin, Western Australia

The Blina Shale contains horizons that are bone bed accumulations in the Erskine Ranges, West Kimberly District ~480 kilometres southeast of Derby, Western Australia (Figure 1.1., locality 4) (Cosgriff 1965). McKenzie (1961) mapped multiple localities within the area, which have been broadly assigned to an Early Triassic age based on the presence of the temnospondyls *Deltasaurus kimberleyensis* that is correlated with *Deltasaurus pustulatus* from the Kockatea Shale (Cosgriff 1965). However, as noted above, the Kockatea Shale has recently been refined as Olenekian in age (Haig *et al*. 2015; see above). This indicates that based on the common vertebrate fauna the Blina Shale should also now be considered Olenekian in age. Sandstone with crossbedding and conglomerate, siltstones, and shales with glauconite provide evidence of a fluviatile – marine transgression – regression sequence that is supported by faunal evidence (Cosgriff 1965, Gorter 1978). The vertebrate fauna is dominated by temnospondyls (Rhytidosteidae, mastodonsaurids and some brachyopids (Warren 2006)) in addition to fragmented remains of actinopterygian fishes and isolated dipnoan tooth plates (Figure 1.3.E) (Long 1991; Kemp 1991), (Table 1). The composition of the fauna from Blina Shale has suggested that it is more closely related to the Lower Triassic deposits of Madagascar than to deposits from eastern Australia (Warren 2006).

5. Narrabeen Sandstone, Hawkesbury Sandstone, and Wianamatta Shale, Sydney Basin, New South Wales

The Narrabeen Sandstone, Hawkesbury Sandstone, and Wianamatta shale crop out over a vast area of about 52, 000 km^2 within the Sydney Basin (Figure 1.1., locality 5) (Mayne *et al.* 1974)). Within the shales and sandstone over 20 individual fish and vertebrate fossil localities are known, mostly because of commercial quarrying of shale and sandstones (Willis 1996). The Sydney Basin is part of the larger Sydney-Gunnedah-Bowen Basin in which the Triassic fossils are dated as Olenekian-lower Anisian based on the presence of fossil plants of the *Dicrodium zuberi* oppel zone (Retallack 1997) and palynomorphs of *Aratrisporites tenuispinosus* (Helby *et al.* 1987) (Figure 1.2.). Based on the presence of temnospondyl amphibians, insects and fish along with shales and sandstones, the formations have been interpreted to represent a fluvial-estuarine environment (Long 1991 & Willis 1996). Vertebrate fossils include labyrinthodont amphibians, stem neopterygians representing Perleidiformes, and basal actinopterygians including Redfieldiiformes (Figure 1.3.G) and *Cleithrolepis*. Dipnoans are preserved as whole fish but unfortunately without tooth plates or any other diagnostic characters (*Gosfordia truncata* & *Ariguna formosa* (Figure 1.3F)) (Ritchie 1981, Wade 1935). The Ashfield Shale has a partially preserved specimen of *Archaeoceratodus avus* (Kemp 1997a). Xenocanth sharks (Table 1.1.) in addition to several undescribed taxa are preserved as incomplete body fossils and isolated teeth (Turner 2011).

6. Leigh Creek Coal Measures, Telford Basin, South Australia

The Leigh Creek Coal Measures of South Australia are located in an active coal-mining district in the mid-north of the state (Figure 1.1, locality 6) (Pledge & Baulch 2013). The formation is dated as upper Triassic (Carnian – Norian) based on the correlation of *Samaropollenites speciosus* and *Craterisporites rotundus* spore-pollen zones (Barone-Nugent *et al.* 2003, among others) (Figure 1.2.). Despite mining activity turning over vast quantities of rock, vertebrate fossils are rare (Pledge & Baulch 2013). Wade described the first fish fossil in 1953, but it was not until 1993 and 2000 that two additional partial fish fossils were discovered from the same area (Pledge & Baulch 2013). Unfortunately, due to their poor preservation, SAM F15094 (Figure1.3.H) and SAM P34796 can only be considered indeterminate Actinopterygii remains; however, the better-preserved SAM P40103 has been tentatively identified as representative of the family Brookvaliidae (Pledge & Baulch 2013), which is a common faunal element in the Sydney Basin. However, this taxonomic determination would extend the taxon from Early to Late Triassic.

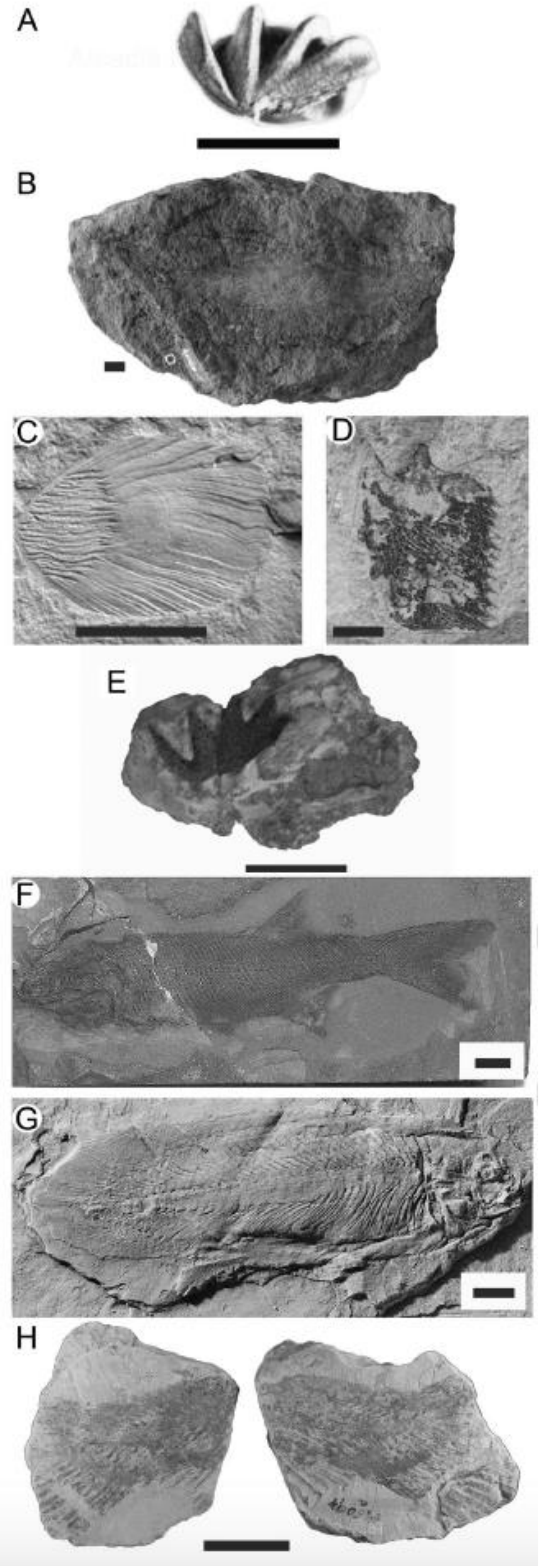
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Figure 1.3. Triassic fishes of the Neotethys and South-western Panthalassa areas during the Triassic. **A**. Lower toothplate of *Ptychoceratodus philippsi* (QM F11206) from the Lower Triassic Arcadia Formation, Queensland, Australia. Scale bar = 1 cm. **B**. *Acrolepis hamiltoni* (TMAG Z 1377) from the Lower Triassic Knocklofty Formation of Tasmania. Scale bar = 1 cm. **C**. Coelacanth scale from the Lower Triassic Kockatea Shale, Western Australia. Scale bar = 5mm. **D**. Palaeonscoid scale from the Lower Triassic Kockatea Shale, Western Australia. Scale bar = 1mm. Specimens from the Kockatea Shale UWA163873 and UWA163874. **E**. *Ptychoceratodus philippsi* (AM F64151) from the Lower Triassic Blina Shale, Western Australia. Scale bar = 1 cm. **F**. *Brookvalia gracilis* (AM F19764) from the Lower Triassic Sydney Basin, New South Wales. Scale bar is 1 cm. **G**. *Ariguna formosa* (NHM P16828) from the Lower - Middle Triassic Sydney Basin, New South Wales. Scale bar is 2 cm. **H**. *Leighiscus hillsi* (SAM F15094 a, b) from the Leigh Creek Coal Measures, South Australia. Scale bar = 5 cm.

Jurassic

Only four Jurassic localities are currently recognised as yielding fishes in Australia. These are the middle Jurassic Colalura Sandstone, Western Australia, the middle Jurassic Walloon Coal Measure at Balgowan Colliery, the middle Jurassic Hutton Sandstone, Monto, and the upper Jurassic Purlawaugh Formation at Gulgong (Figure 1.1. and Figure 1.4.). These localities range in age from Bajocian, being the oldest, to Kimmeridgian, being the youngest. No localities yielding fishes of Early Jurassic Age are known. The Colalura Sandstone is interpreted as nearshore marine, with the other localities interpreted as continental freshwater assemblages. The Jurassic faunas of these sites are not as diverse as those known from the Triassic; however, this may be a result of a lack of sampling or preservation bias, rather than representative of a true loss of diversity.

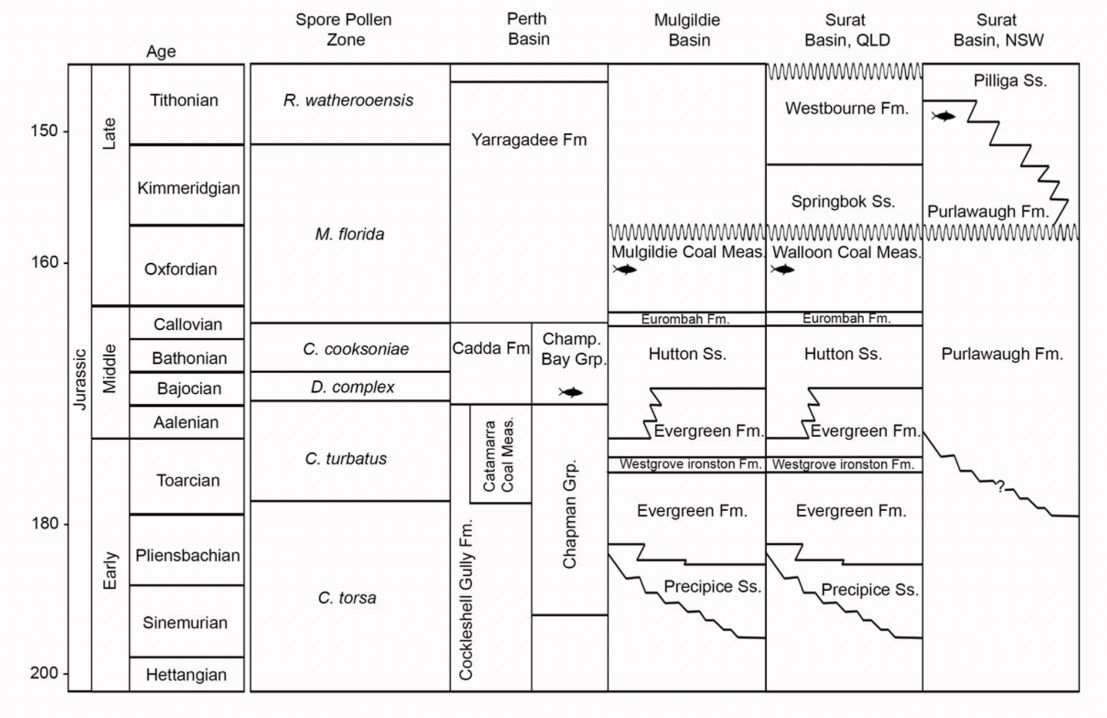

Figure 1.4. Stratigraphy of Jurassic aged fish sites across Australia. Abbreviations: Champ. Champion; Sh. Shale; Ss. Sandstone; Mbr. Member; Grp. Group; Fm. Formation. The black fish symbol represents the approximate stratigraphic position of fish sites and does not differentiate between actinopterygians, chondrichthyans or piscine sarcopterygians.

7. Colalura Sandstone, Perth Basin, Western Australia

The Colalura Sandstone occurs in outcrop in a railway cutting ~ 20 kilometres east of Geraldton, near the town of Bringo, Western Australia (Figure 1.1., locality 7) (Long & Molnar 1998). The formation is dated Middle Jurassic (Bajocian) as it conformably underlies the Newmarracarra Limestone (Long & Molnar 1998). The Newmarracarra Limestone has been dated as middle Bajocian based on ammonites and their correlation to ammonite zones from Europe (Playford *et al*. 1975), hence implying a

Middle Jurassic age for the Colalura Sandstone (Figure 1.4). The formation is a thin, shallow marine transgressive lag deposit (see Playford *et al.* 1975). It yields a mixture of terrestrial and shallow marine biota, including fossilized wood, marine bivalves, rare remains of pliosaurs, a theropod tibia (Long & Molnar 1998) and an isolated sauropod caudal vertebra (Kear & Hamilton-Bruce 2011). The only fishes known from this locality are isolated teeth belonging to an undescribed hybodont shark, (Long pers. comm. 2015).

8. Walloon Coal Measures, Surat Basin, Queensland

The Balgowan Colliery is located near Oakey in the Darling Downs region of southeastern Queensland (Figure 1.1., locality 8). The earlier Middle Jurassic (upper Bajocian - lower Callovian) age for the Walloon Coal Measures corresponding to the range of *Aequitriradites norrisii* - *Murospora florida* in the local palynology zonation (Gould 1968, Cranfield *et al.* 1976), has been revised recently as Oxfordian age (162.55 +/- 0.05 Ma and 158.86 +/- 0.04 Ma) using U-PB dating of volcanic tuffs (Wainman *et al.* 2015) (Figure 1.4). The depositional environment of this stratum is considered to be a major channel, flood basin and mire environments interpreted from interbedded coal, mudstone and siltstone (McLoughlin & Drinnan 1995). Six carbonized, partial fish specimens, showing rhombic scales with one specimen exhibiting a dorsal fin (Figure 1.5.A), represent the Walloon Coal Measures fauna. These specimens are of poor quality because of their partial preservation and carbonaceous nature, and this means that higher taxonomic assignment is not possible (Turner & Rozefelds 1987). Turner & Rozefelds (1987) have placed these specimens as neopterygian although they may also belong to a stem teleostean fish like *Hulettia* from the western USA based on scale shape and orientation.

9. Mulgildie Coal Measure, Mulgildie Basin, Queensland

The Milgildie Coal Measures occur near the town of Monto in Queensland (Figure 1.1., locality 9). This formation is thought to be the equivalent of the Walloon Coal Measures in the Surat Basin (Wainman *et al.* 2015). Therefore, the dating of this formation is based on the correlation with palynological zones J4-J5 of Evans (1966) or the *Dictyotosporites complex*, *Contingnisporites cooksoniae* and lower *Murospora florida* spore-pollen zonation scheme of Helby *et al.* 1987 (Figure 1.4.). The presence of the plant *Osmundocaulis gibbiana* also supports a Middle Jurassic age (Gould 1974, Thies & Turner 2002). It is expected that with similar palynology, the Mulgildie Coal Measures would have a similar detrital zircon age as the Walloon Coal Measures in the Surat Basin. Recovered plant fragments pertaining to *Osmundocaulis gibbiana* along with shale, mudstone, sandstone, and coal beds confirm that this formation was deposited in a freshwater environment (Thies & Turner 2002). Only a single, partially preserved fish has been recovered from these strata and is assigned to the 'semionotiforms' (currently named ginglymodians) based on the presence of rhombic scales (Thies & Turner 2002) (Figure 1.5.B).

10. Purlawaugh Formation, Surat Basin, New South Wales

The Talbragar Fish Bed belongs to the Purlawaugh Formation and represents Australia's best-preserved Jurassic continental assemblage. This fish site is located near Gulgong in central New South Wales (Figure 1.1., locality 10). The formation is dated 151.55 ± 4.27 Ma, corresponding to the Upper Jurassic (Kimmeridgian) based on zircons from a nearby tuff (Veevers 2000; Bean 2006). The finely laminated sediments with fossil plants and insects indicate a freshwater, shallow lacustrine depositional environment. The presence of stoneflies has indicated that it was an oligotrophic lake (Beattie & Avery 2012, Bean 2006). Preservation of the lake system is interpreted as a mass kill assemblage potentially from volcanic activity (Bean 2006). It has produced Australia’s earliest teleost, *Cavenderichthys talbragarensis* (Figure 1.5.C) (Woodward 1895, Long 1995, Arratia 1997, Bean 2006), a single basal actinopterygians genus and five holostean genera (Bean 1997, Turner *et al.* 2009). A partial body fossil of a possible hybodontid shark has recently been described by Turner & Avery (2017). However, taxonomic conclusions are uncertain as the specimen is only partially preserved, showing only the posterior region of the head (Turner & Avery, 2017). A large predatory fish with thick rhomboid scales is also known but its preservation is too fragmentary for taxonomic assignment other than that it is likely to be a halecomorph (Bean & Long 2016). The Talbragar Fish Bed represents Australia’s best-preserved Jurassic continental assemblage. The absence of lungfish and tetrapods in the Purlawaugh Formation is unusual given the environmental deposition and global distribution of these vertebrates in the Jurassic.

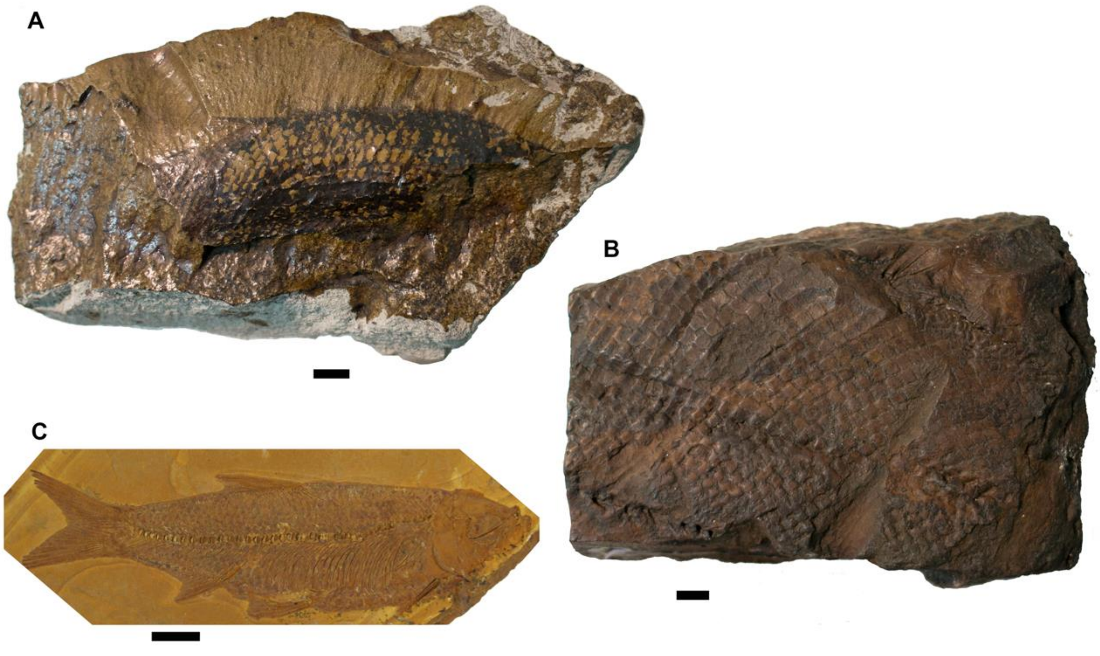

Figure 1.5. Continental (freshwater) Jurassic fishes of Australia. **A**. neopterygian indet. from the Walloon Coal Measures, Queensland (GSQ F12975). Scale = 1 cm. **B**. A potential semionotiform from the Mulgildie Coal Measures Monto, Queensland (QM F25080). Scale = 1 cm. **C**. *Cavenderichthys talbragarensis* (AM F119231) from the Upper Jurassic Talbragar Fish Beds. Scale bar = 1cm.

Cretaceous

Cretaceous fossil fish localities in Australia are much more diverse in depositional setting than Jurassic localities and, as a result, many more species are known from these formations. Currently, nineteen formations are known to produce fossil fishes with multiple localities within each formation. The eastern half of the continent only produces localities of Aptian to lower Turonian age. The western half of the continent produces localities from Aptian to Maastrichtian in age. Currently, no fish fossils of the earliest Cretaceous age (Berriasian – Barremian) are known (Figure 1.6.).

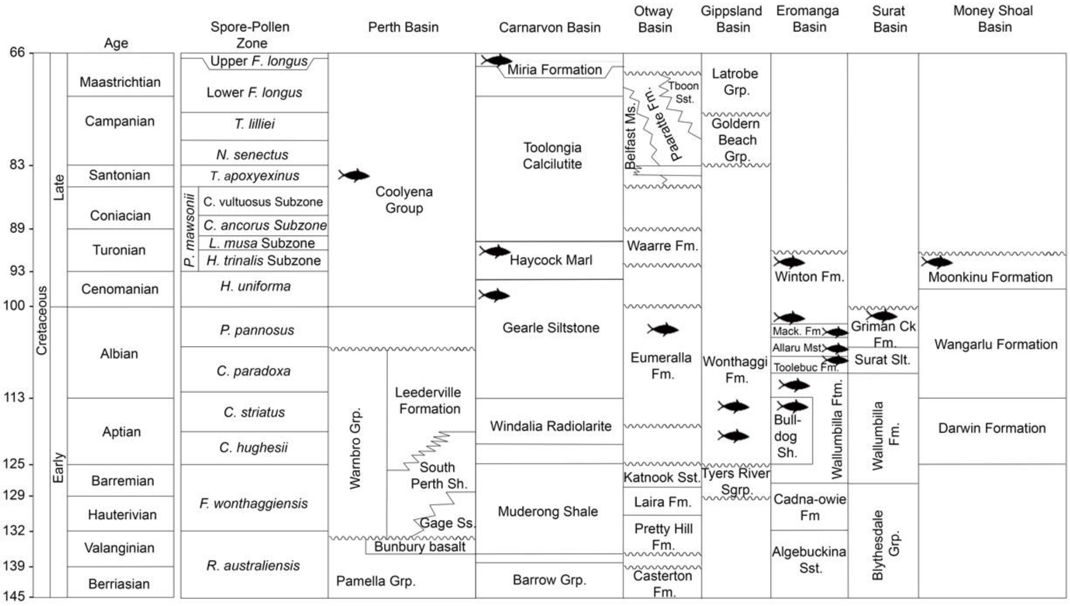

Figure 1.6. Cretaceous stratigraphy showing the relationship of fish sites across Australia. Abbreviations: Sh. Shale; Ss. Sandstone; Sst. Siltstone; Mbr. Member; Grp.

Group; Fm. Formation. The black fish symbol represents the approximate stratigraphic position of fish sites and does not differentiate between actinopterygians, chondrichthyans or piscine sarcopterygians.

11. Eumeralla Formation, Otway Basin, Victoria

The Eumeralla Formation is located on Victoria's south coast, to the west of Melbourne, and is exposed between the areas of Lorne and Knowledge Creek (Figure 1.1., locality 11). Multiple individual localities are known to produce vertebrates (Rich & Vickers-Rich 2000). These localities have been dated as upper Aptian – lower Albian corresponding to the *Crybelosporites striatus* and *Pilosisporites notensis* palyno-stratigraphic zones (Morgan *et al.* 1995). The sediments represent sandstones, shales, conglomerates, and minor coal seams deposited in a fluvial-lacustrine setting (Felton 1992). Dinosaur Cove and the surrounding Lower Cretaceous strata along the Otway Ranges are well known for producing small bipedal ornithopod dinosaurs (Agnolin *et al.* 2010) and to a lesser extent early mammals (Rich & Vickers-Rich 2004). The only fossil fishes described from the Otway Ranges are the toothplates of lungfish (Kemp 1997a & b) and a single basal actinopterygians (Hill 1900) (Table 1.1.). However, due to poor preservation little of the morphology of these taxa can be determined. Hilton and Forey (2009) have suggested that *P. selwyni* may be allied to Acipenseriformes based on its heavy dorsal caudal fulcra, rhombic caudal scales, and the absence of vertebral centra and body scales (Hilton & Forey, 2009). Further remains of teleosts from the Eumeralla Formation at Dinosaur Cove consist of partial to nearly complete body fossils e.g., MV P186235 (Figure 1.7.A). A summary of vertebrate fossils from this formation has recently been provided by Poropat *et al*. (2018).

12. Wonthaggi Formation, Gippsland Basin, Victoria

The Strzelecki Group comprises fluvial sediments deposited in the Gippsland Basin during the early stages of rifting between Australia and Antarctica (Tosolini *et al.* 1999) and contains outcrops of the Wonthaggi Formation and the Korumburra Group (below), occurring over a broad area from San Remo in the west to Inverloch in the east (Figure 1.1., locality 12). Upwards of 10 individual localities of the Wonthaggi Formation exist along Victoria's south-eastern coast, with the most notable (heavily excavated) being Inverloch. This formation is considered lithologically equivalent to the Eumeralla Formation, being dated as lower-middle Aptian corresponding to the upper part of the Lower *Pilosisporites notensis* to *Phimopollenites pannosus* zones (Dettmann & Douglas 1988, Morgan *et al.* 1995) (Figure 1.6.). The Wonthaggi fish material consists of isolated lungfish tooth plates assigned to *Archaeoceratodus avus* (Kemp 1997a) (Figure 1.7.B) and isolated bones and partial skeletons of undescribed actinopterygians. A summary of vertebrate fossils from this formation has recently been provided by Poropat *et al*. (2018).

13. Korumburra Group, Gippsland Basin, Victoria

The Koonwarra Fish Bed near Koonwarra, Victoria (Figure 1.1., locality 13), was originally discovered in 1962 during road works (Waldman 1971). Koonwarra has been dated based on fusion track ages of volcanic apatite from strata above and below the fish bed, which give ages of 115 +/- 6 MY and 118 +/- 5MY respectively (Lindsay, 1982) (Figure 1.6.). The individual preservation of vertebrate fossils in addition to the presence of fossils of insects and a diverse plant biota indicate a palaeoenvironment representative of a long-standing lake. The fossil fish bed is thought to represent a varved lake deposit with freeze-thaw cycles that killed off the fauna (Waldman 1971); however, Jell *et al.* (1986) have commented that this ice-covered lake scenario is unlikely as terrestrial/flying insects are preserved within the finest sediment possibly representing when the lake was thought to be covered in ice. A diverse fauna of actinopterygians (Figure 1.7.C) and a single lungfish are represented in this deposit (Waldman 1971) (Table 1.1). This fauna is comparable to that of the Talbragar Fish Beds based on the similar freshwater actinopterygian diversity (Waldman 1971, Long 1991) representative of a primitive Gondwana mid to late Mesozoic Lake (Long 1991) where body fossils of terrestrial vertebrates are absent. The fish are preserved as either complete body fossils or isolated scales in fine-grained laminated siltstone and claystone. A summary of vertebrate fossils from this formation has recently been provided by Poropat *et al*. (2018).

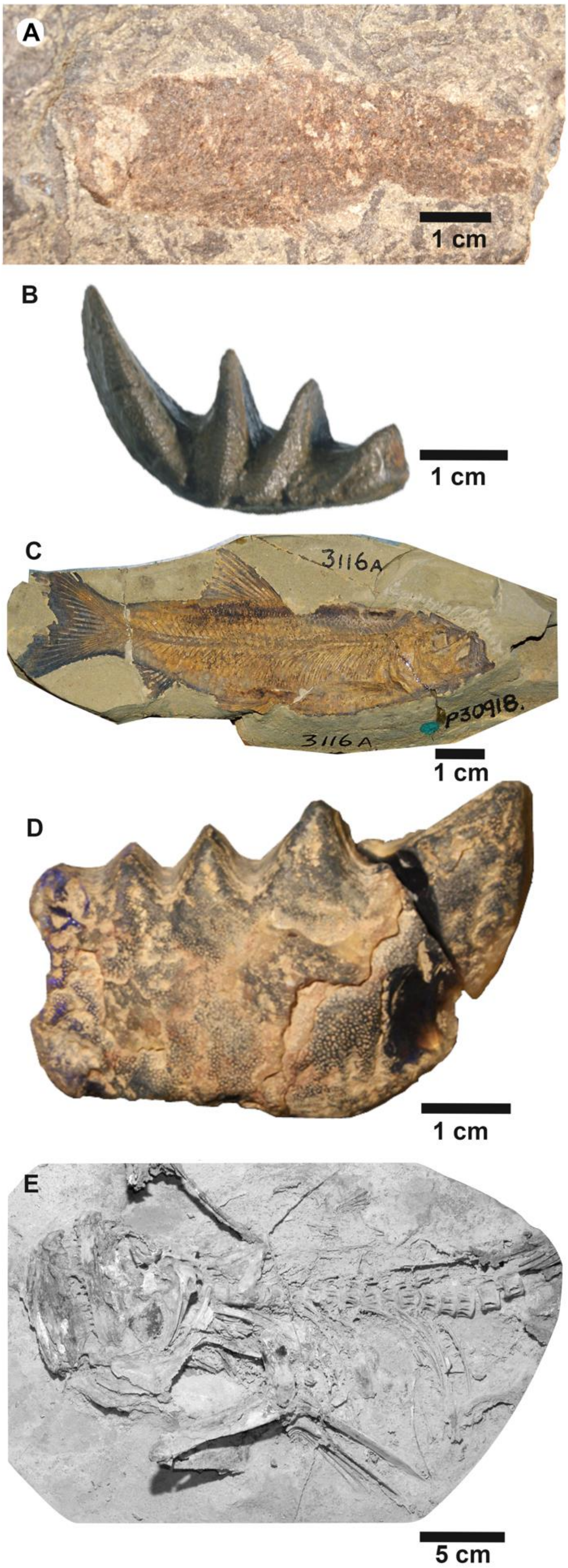

Figure 1.7. Fluvial – lacustrine Lower–Upper Cretaceous fishes from eastern Australia (western Gondwana). **A**. An undescribed teleost (MV P186235) from

Dinosaur Cove, Eumeralla Formation, Victoria, Australia. Scale bar = 1cm. **B**. Lower toothplate of *Archaeoceratodus avus* (MV P186138) from the Lower Cretaceous Strzelecki Group, San Remo, Victoria, Australia. This specimen shows some dental caries on the mediolingual face (Kemp and Berrell 2013). Scale bar = 1cm. **C**. *Waldmanichthys Koonwarri* (MV P30918) from the Koonwarra Fish Beds, Victoria, Australia. Scale bar = 1cm. **D**. A large lungfish toothplate *Ceratodus diutinus* (LRF 0726) from the Griman Creek Formation of Lightning Ridge New South Wales. Australia. Scale bar = 1cm. **E**. *Cladocyclus geddesi* (QM F44329) from the Upper Cretaceous Winton Formation, Isisford, Queensland, Australia. Scale bar = 5cm.

14. Wallumbilla Formation, Eromanga Basin, New South Wales

The Wallumbilla Formation occurs in northwestern New South Wales at White Cliffs and isolated outcrops within the Surat Basin (Figure 1.1, locality 14) (Haig & Barnbaum 1978). Active opal mining in this formation continues to yield fossils. The formation is dated as Aptian from ammonites corresponding to the *Maccoyella barklyi* zone discovered from the type section in Queensland (Haig & Barnbaum 1978) (Figure 1.6). Sediments from this formation were deposited in the early phases of the marine inundation of the Eromanga Basin (Haig & Barnbaum 1978). Currently, the only fish specimen described from this geological unit is an isolated vertebra, tentatively assigned to *Cladocyclus* sp. (AM F.9223). The specimen awaits formal description.

15. Bulldog Shale, Eromanga Basin, South Australia

The Bulldog shale crops out at Andamooka, Coober Pedy and surrounds (Figure 1.1., locality 15), and is dated at Aptian-lower Albian due to the occurrence of microplankton corresponding to the *Odontochitina operculata*, *Diconodinium davidii* and *Muderongia tetracantha* zone, and spore-pollen spanning the *Cyclosporites hughesii* and *Crybelosporites striatus* zones (Helby *et al.* 1987) (Figure 1.6.). The environment is a shallow marine with cool-cold conditions interpreted from dropstones and fossil wood (Kear 2006a, Dettmann *et al.* 1992). The fossil strata of the South Australian opal fields preserve a diverse Lower Cretaceous fauna of marine reptiles, chimaerids, and osteichthyans with rare sharks and dinosaurs (Kear 2006a). Fossils are found mostly as a by-product of opal mining, which results in the fossils being broken or partially disarticulated. Actinopterygian remains consist of isolated vertebrae, e.g., SAM P39684, and as fossilized gut contents of marine reptiles (Kear *et al.* 2006). Fossil tooth plates of the chimaerid *Edaphodon eyrensis* are known from similar non-opal bearing deposits near Lake Eyre (Kear & Hamilton-Bruce 2011) (Figure 1.8.A). Most of these fossils are currently not identified to a lower taxonomic level than Teleostei because of their isolated nature.

16. Toolebuc Formation, Eromanga Basin, Queensland

The Toolebuc Formation occurs in a similar arc to the Allaru Formation (below) cropping out in central-northern Queensland (Figure 1.1., locality 17). It is a thin <40m thick unit of organic-rich calcareous and carbonaceous mudstones, generally buff or cream in colour (Henderson 2004, Kellner *et al.* 2010). The formation has been dated as lower upper Albian based on the ammonites *Goodhallietes goodhalli*, *Labeceras* and *Myloceras* and their correlation to biostratigraphic occurrences in South Africa (Henderson & Kennedy 2002). The depositional environment has been interpreted to represent a restricted, shallow, stratified, partially dysaerobic marine environment, evident by dark organic-rich layers (Morgan 1980, McMinn & Burger

1986, Kellner *et al.* 2010). Bone beds generally consist of an agglomeration of elongated round bones such as vertebrae, conical teleost teeth, shark teeth, fin rays and ribs (microfossils) as well as occurrences of complete body fossils. The actinopterygians fish fauna, where complete or near complete body fossils are preserved, is dominated by medium to large-sized (ca. 50cm – 1m) predatory fishes which include the ichthyodectiform *Cooyoo australis* (Figure 1.8.B) and *Pachyrhizodus marathonensis* (Figure 1.8.C), *Pachyrhizodus grawi* (Bartholomai 1969, 2010b, Lees & Bartholomai 1987). Lees (1990) described and named *Dugaldia emmilta*, a fish known by a single specimen comprising the head and the anterior part of the trunk. Lees referred this species to the neoteleosteans, order and family unknown. A recent review of this specimen, together with other, more recently found specimens housed in the Kronosaurus Korner in Richmond, Queensland, suggests that *Dugaldia* is an ichthyodectiform (Cavin and Berrell 2019). Smaller teleosts likely to disarticulate on decomposition have been identified from microfossils and include an aulopiform fish (Berrell *et al.* 2016). Studies on chondrichthyan diversity are ongoing and include at least 8 taxa (Table 1.1).

The record of the anacoracid genus '*Microcorax*' (= *Nanocorax* Cappetta, 2012 as *Microcorax* Cappetta & Case, 1975 is a junior homonym) (Kemp, N 1991, pl. 4, fig. x) is based on a pathological, non-anacoracid lamniform tooth of uncertain affinity. The record of saw sharks (Kemp, N 1991, pl. 3, figs f-g) rests on misidentified jaw sections of bony fishes (MS, personal observation). Additional elasmobranch species await formal description. This undescribed material includes new species and genera (Figure 1.12.D-G). Compared with more open marine deposits of Albian age in Western Australia (Alinga Formation and part of the Gearle Siltstone), the chondrichthyan diversity in the Toolebuc Formation is low, largely because of the poor representation of strictly benthic taxa. Kemp N. & Ward (1997) indicated the presence of benthic orectolobiform taxa in the Toolebuc Formation although none have yet been encountered in samples from roadside quarries in the Richmond area. Two poorly preserved dipnoan tooth plates (*Metaceratodus wollastoni*) have also been found in the Toolebuc Formation (Kemp, 1997b).

17. Allaru Formation, Eromanga Basin, Queensland

The Allaru Formation occurs in north-central Queensland in a broad arc between Hughenden in the east to Boulia in the west (Figure 1.1., locality 18) (Cook *et al.* 2013). The Allaru Mudstone is presumed to be of early late Albian age based on the ammonites *Goodhallietes goodhalli*, *Labeceras* and *Myloceras* and their correlation to biostratigraphic occurrences in South Africa (Henderson & Kennedy 2002). The dominance of *Endoceratium ludbrookiae* dinocysts and *Phimopollenites pannosus* sporomorphs allows this formation to be assigned to the *Endoceratium ludbrookiae* dinocyst and *Phimopollenites pannosus* sporomorph Zone (Helby *et al.* 1987) (Figure 1.6.). The Allaru Mudstone is conformable with the Toolebuc Formation also representing part of the shallow marine transgression of the Eromanga Sea (Cook *et al.* 2013). The fossil fishes are preserved in nodules. The Toolebuc and Allaru Formations contain bony fishes identified as the same genera, however, different species may be present and additional taxonomic study is required to determine this. Kemp, N. (1991) reported '*Lamna*' *arcuat* [sic.] and a lamniform vertebral centrum from the Allaru Mudstone (in addition to several teeth that are possibly derived from this unit). '*Lamna*' *arcuat* most likely refers to '*Lamna*' *arcuata* Woodward 1894, which is a junior synonym of *Archaeolamna kopingensis* (Davis 1890). The tooth is clearly of lamniform type, but its generic identity is uncertain. Given the abundance of cardabiodontid teeth in the underlying Toolebuc Formation, it is possible that the Allaru specimen belongs to this family. *Archaeolamna* does not seem to be present in the Toolebuc Formation but is common in the Mackunda Formation.

18. Mackunda Formation, Eromanga Basin, Queensland

The Mackunda Formation conformably overlies the Allaru Mudstone and is the transitional formation from marine conditions to the terrestrial Winton Formation, which conformably overlies the Mackunda (Figure 1.1., locality 19) (Cook *et al.* 2013). Similar to that of the Winton Formation, this unit has poor outcrop due to extensive weathering and covering by recent black soil plains. The Mackunda Formation is interpreted to correspond to APK6 and APK7 spore-pollen zones of upper Albian – lower Cenomanian age (Cook *et al.* 2013) based on its stratigraphic position above the Allaru Formation (APK6). However, the Mackunda Formation has recently been estimated to be 102.5 – 104 Ma (upper Albian) based on the detrital zircon age of the Winton Formation (Tucker *et al.* 2013) and the interpretation that the basal parts of the Winton Formation were syndepositional with the Mackunda Formation (Syme *et al.* 2016). Therefore, this formation should be considered to be of upper Albian age (Figure 1.6.).

Kemp, N. (1991, pl. 3, fig. w) recorded an indeterminate lamniform tooth from the Mackunda Formation in addition to teeth that may originate from this deposit. Undescribed material (collected by David Ward and Noel Kemp) comprises poorly to relatively well-preserved teeth of about a dozen species (MS, pers. observation). In contrast to the Toolebuc Formation, teeth of strictly benthic elasmobranchs are abundant in this assemblage. Several of the species represent new taxa. Indeterminate actinopterygian remains have also been reported by Cook *et al.* (2013). The only other vertebrate known from this formation is the ornithischian dinosaur, *Muttaburrasaurus langdoni* (Cook *et al.* 2013). A single toothplate referred to the dipnoan *Metaceratodus wollastoni* occurs in the Mackunda Formation (Kemp 1997b).

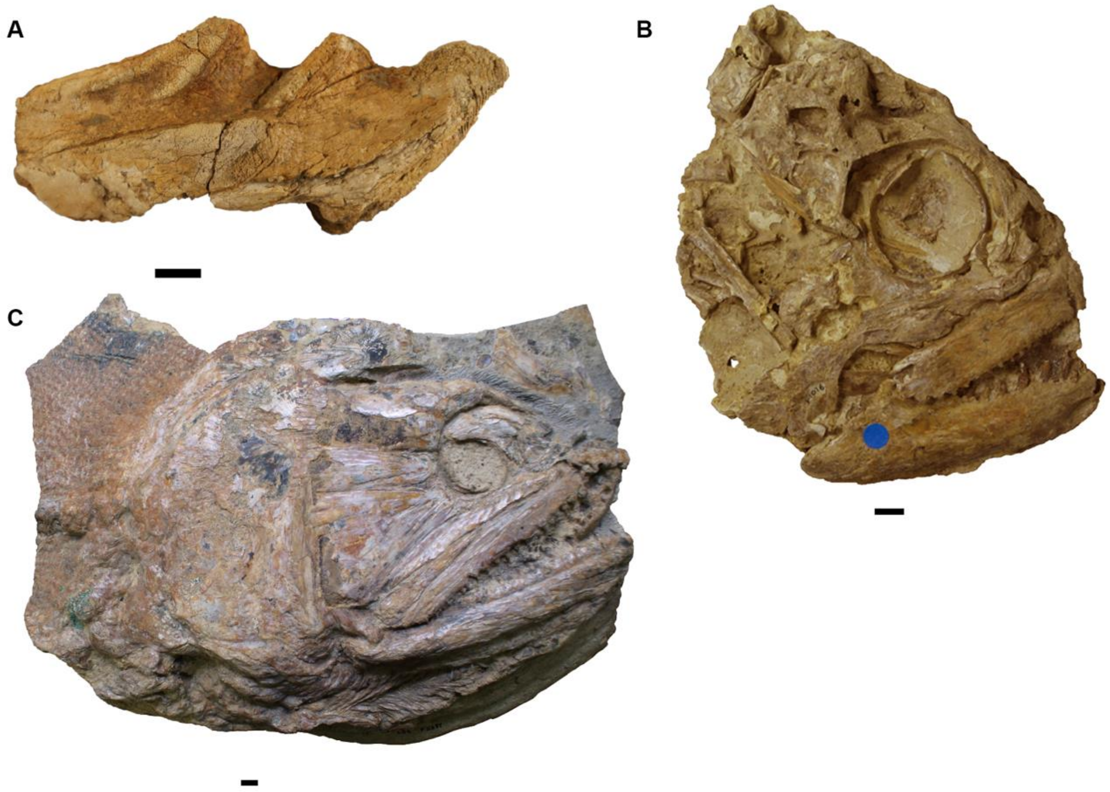

Figure 1.8. Marine Lower–Upper Cretaceous fishes from eastern Australia (eastern Gondwana). **A**. *Edaphodon eyrensis* (SAM P24770) from the Lower Cretaceous, Bulldog Shale, Lake Phibbs, South Australia. **B**. *Cooyoo australis* (QM F12711) from the Lower Cretaceous, Allaru mudstone, Mountain Creek near Hughenden Queensland. **C**. *Pachyhrizodus marathonensis* (QM F5687) from the Lower Cretaceous, Toolebuc Formation, Bore Park Station near Richmond Queensland.

19. Griman Creek Formation, Surat Basin, New South Wales

The Griman Creek Formation is located in central-northern New South Wales and is centered on the opal-mining town of Lightning Ridge (Figure 1.1., locality 19). The fossil-bearing strata (Finch Claystone) are dated as middle Albian based on correlation to the *Coptospora paradoxa* spore-pollen zone (Burger 1980) (Figure 1.6.). More recently the stratigraphic unit above the Finch Claystone, the Wallangulla Sandstone has been dated based on detrital zircons with a maximum depositional age of 100.2–96.6 Ma (Bell et al. 2019). The formation is interpreted as being deposited in a freshwater–estuarine environment based on the faunal assemblage comprising viviparid gastropods, and freshwater bivalves (hydrillids?). In addition to the fish fauna (Table 1.1.) other vertebrate remains include turtles (Testudinata) (Smith 2010, Smith & Kear 2013), crocodylians (Molnar & Willis 2001), pliosaurs and elasmosaurs (Kear 2006b), pterosaurs and dinosaurs (Bell *et al.* 2015, Smith 1999, Molnar & Galton 1986), mammals (Archer *et al.* 1985, Flannery *et al.* 1995). The recovery of mainly isolated teeth from chondrichthyans and sarcopterygians indicates a high degree of taphonomic sorting (Kear & Hamilton-Bruce, 2011; Smith 1999).

20. Winton Formation, Eromanga Basin, Queensland

The Winton Formation occupies large geographic areas of central-western Queensland, and parts of northeastern South Australia (Gray *et al.* 2002) (Figure 1.1., locality 20). Outcrops are often poorly exposed, being covered by 'black soil' (recent soil accumulation, predominantly of smectitic clays) and other regolith products such as gibber stone plains. Analysis of detrital zircons, from multiple localities, indicates a maximum depositional age of 100.5– 102.2 Ma for the localities at Isisford and 92.5 (± 1.2) and 93.3 (± 1.2) Ma for localities around Winton (Bladensburg, Lark Quarry, etc.) (Tucker *et al.* 2013) (Figure 1.6.). The basal part of the Winton Formation at

Isisford is considered syndepositional with the Toolebuc / Allaru / Mackunda formations which lie farther to the north (Figure 1.1.) (Syme *et al.* 2016).

The basal parts of the Winton Formation represent a delta system prograding out into the Eromanga Sea with the Isisford localities deposited in a more landward estuarine position. This is supported by the faunal assemblage and strontium isotope data (Syme *et al.* 2016), whereas the Toolebuc / Allaru / Mackunda Formations are more seaward, and deposited under restricted marine conditions. The upper (younger) horizons of the Winton Formation represent fluvial conditions of braided river systems. The age differences and differences in depositional environments may account for the faunal differences between sites (Table 1.1.). Two large teleostean fishes are known from this deposit (Faggottor et al 2007 and Berrell et al. 2014) with the dipnoans only known from the upper (Cenomanian–Turonian) Upper cretaceous portions of the Winton Formation (Kemp 1991, 1997b; Dettmann *et al.* 1992) (Table 1.1.).

21. Moonkinu Formation, Money Shoal Basin, Northern Territory

The Moonkinu Formation, Bathurst Island (Figure 1.1., locality 21) (Campbell 2003) is dated as Cenomanian -Turonian based on standard ammonite zonations (Wright 1963) and correlated with foraminifera *Rotalipora reicheli*, *R. cushmani* and *Whiteinella archaeocretacea* (Campbell 2003a) and palynomorph content that includes *Classopollis* sp. nov., *Asteropollis asteroids, Camarozonosporites* sp. nov., *Gleicheniidites* cf. *G. trijugatus* and *Liliacidites* sp. (Hughes 1978) (Figure 1.6). Sparse chondrichthyan remains (seven isolated selachian scales) have been recovered from an inner neritic environment (shallow marine) (Campbell 2003b) (Table 1.1.).

22. Windalia Sandstone Member of the Muderong Shale, Alinga Formation, 'upper' Gearle Siltstone, Haycock Marl and Toolonga Calcilutite, lower Murchison River area, Southern Carnarvon Basin, Western Australia

The Windalia Sandstone Member of the Muderong Shale, which is up to 15 metres thick, crops out along the southern edge of the Pillawarra Plateau in the lower Murchison River area north of Kalbarri, Western Australia (Mory *et al*. 2005) (Figure 1.1. locality 22). The uppermost 1-2 metres yield abundant fossil wood with *Teredo*-like borings, ammonite fragments, isolated bones and partial skeletons of ichthyosaurs and plesiosaurs and extremely rare and heavily abraded teeth of indeterminable elasmobranchs (e.g., WAM 92.10.2). The ammonites indicate an Aptian age for the fossil-bearing, uppermost part of the unit (see McLoughlin *et al*. 1995). The Windalia Sandstone Member is overlain by the upper Aptian – lower Albian Windalia Radiolarite, which in turn is succeeded by the lower to middle Albian Alinga Formation (Mory *et al.* 2005). The age of the latter is based on unpublished calcareous nannofossil data (samples collected and examined by David Watkins). Preliminary bulk sampling in the Alinga Formation has shown that selachian teeth and dermal denticles are relatively rare but exceptionally well preserved at certain levels. This material is yet to be formally described but indicates well-oxygenated bottom waters (a diverse assemblage of orectolobiform species) and relatively cool water temperatures (faunas strongly dominated by a squaloid of *Protosqualus* type). The Alinga Formation is overlain unconformably by the Santonian (or possibly upper Coniacian)-lower Campanian Toolonga Calcilutite at most localities in the area. However, a lens of 'upper' Gearle Siltstone and Haycock Marl (the latter referred to as the Beedagong Claystone by Siverson 1996), at least two kilometres long and up to 2.5 m thick and sandwiched between the Alinga Formation and the Toolonga Calcilutite, is present between the Thirindine Point and Stonewall localities (Siversson *et al*. 2018). Siverson (1996) recorded 15 nominal species of lamniform sharks from the Alinga Formation – Haycock Marl interval in the Thirindine Point area, but most of these records are based on surface collected material, lacking precise stratigraphic data. (See Table 1.1. for up-to-date taxonomic assignments).

Extensive bulk sampling of the 'upper' Gearle Siltstone has produced thousands of elasmobranch teeth but research on these important faunas has been held back by the lack of stratigraphic control, both in terms of high-resolution biostratigraphy and coherence of excavated sections (Siversson *et al*. 2018). It is only relatively recently that sections largely unaffected by slumping were cleared; permitting identification of four discrete units in the 'upper' Gearle Siltstone, sampling for calcareous nanofossil analysis and a characterisation of the Alinga Formation-'upper' Gearle Siltstone contact (Siversson *et al*. 2018).

In a review of anacoracid sharks from the 'upper' Gearle Siltstone and the Haycock Marl, Siversson *et al*. (2018) identified multiple taxa, including three new species (Table 1.1.).

23. Molecap Greensand and Gingin Chalk, Perth Basin, Western Australia

Molecap Greensand covers a large area with scattered outcrops throughout the Perth Basin, Western Australia (Figure 1.1., locality 23) (Kear *et al*. 2010). The formation is dated on the basis of correlation to spore/pollen/dinocyst zonations and is considered

Cenomanian – Coniacian (McWhae *et al.* 1985, Shafik, 1990 & Mory *et al.* 2005) (Figure 1.6.).

The mixed assemblage of sharks, and teleosts, within glauconitic sand indicates a shallow marine environment (Kear *et al*. 2010). Teeth from elasmobranchs are rare and poorly preserved relative to age-equivalent units in the Southern Carnarvon Basin. McNamara *et al*. (1993) illustrated 10 species of elasmobranchs from the Molecap Greensand and Gingin Chalk but several of the illustrated specimens are not of Australian origin (see Siverson 1997, p. 454). Isolated indeterminate teleost vertebrae are also known.

24. Gearle Siltstone, Haycock Marl, Toolonga Calcilutite & Miria Marl, Giralia Anticline, Southern Carnarvon Basin, Western Australia

Siverson (1997) described a number of elasmobranchs from the mid-Albian part of the Gearle Siltstone (Figure 1.1., locality 24; Table 1.1.).

The middle Cenomanian part of the Gearle Siltstone has yielded a diverse chondrichthyan fauna but only a handful of species have been illustrated (Siverson 1999; Siversson et al. 2015; Figure 1.12. A, H-J, Table 1.1.). Chondrichthyan teeth are also abundant in the upper lower Turonian part of the Haycock Marl in the Giralia Anticline but are yet to be described. Shark teeth are present in the upper Maastrichtian Miria Marl but are poorly preserved and indeterminable at the species level (see Siverson 1997, p. 453 regarding the ‘record’ of *Cretoxyrhina mantelli*).

1.5 MICROVERTEBRATE MATERIAL FROM THE TOOLEBUC FORMATION

With the purpose of updating the list of the fish fauna of Australia, the central theme of this work, we show in this section the taxonomic designation of some fragmented and isolated remains of fish collected from a single site within the Toolebuc Formation.

Systematic Palaeontology

Class CHONDRICHTHYES Huxley, 1880

Order ECHINORHINIFORMES De Buen, 1926

Family ECHINORHINIDAE Gill, 1862

Genus *Echinorhinus* de Blainville 1816

Type species. Squalus brucus Bonnaterre, 1788,

Echinorhinus australis (Chapman, 1909) (Figure 1.9)

1991 *Pseudocorax australis* (Chapman) [*partim*]; Kemp, p. 507, pl. 4, figs n-w. Tooth in fig.m is *Squalicorax* sp.

2012 *Echinorhinus australis* (Chapman); Adnet et al., fig. 3a, c, d.

Material. 5 isolated teeth (KKF1070-KKF1074). (Figure 1.9).

Description. Teeth are labio-lingually compressed and wider than high. The triangular crown is posteriorly angled from the root. There are no accessory cusplets. The thin root is broadly rectangular in shape.

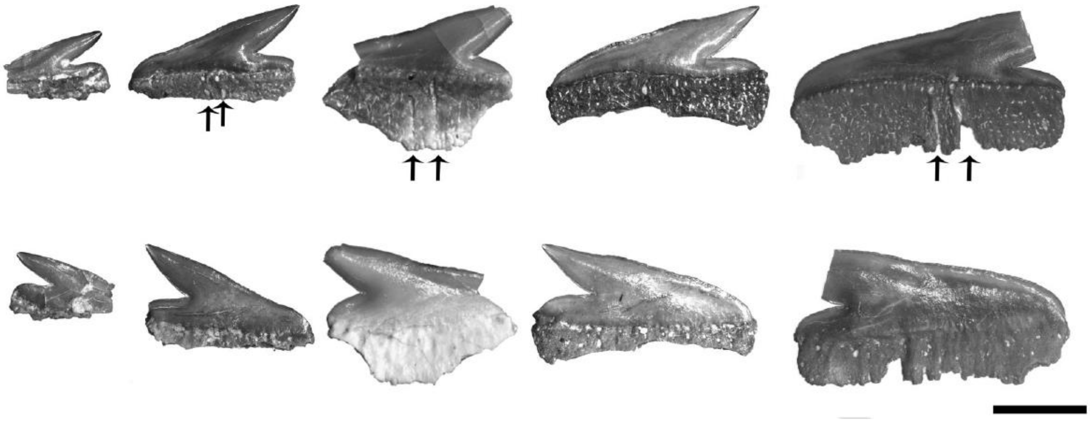

Figure 1.9. Isolated teeth of the bramble shark *Echinorhinus australis* (KK F1070 – KK F1074, in number sequence left to right) from the Lower Cretaceous, Toolebuc Formation, Richmond north-west Queensland, Australia. Scale bar is 1 mm. Arrows indicate root canals.

Two dorsoventrally directed nutritive grooves are present centrally on the basal face of the root in large teeth (black arrows Figure 1.9.). Smaller teeth have these nutritive grooves although not as developed as in the larger teeth, and most notable as two opposed circular holes. The teeth have a keel where the enameloid meets the root. A shallow furrow that deepens centrally is also present where the enameloid meets the root at the base of the tooth on the lingual side.

Remarks.

Species of *Echinorhinus* can be differentiated by the presence or absence of additional tooth cusps, the projection of the main cusp (vertically inclined like a typical shark tooth or directed posteriorly as noted in all Mesozoic and Paleogene specimens (Bogan *et al*. 2017)). The small sample size coupled with their incomplete preservation means that heterodonty cannot be discussed.

Modern bramble shark teeth can be differentiated from Mesozoic bramble sharks because Mesozoic teeth are simpler, lacking basal cusplets (Cappetta 1987). Extant *Echinorhinus* are characterised by distinct dermal scales with a thorn-like ornament and lack of fin spines (Cappetta 1987). To date, no scales or denticles have been recovered, possibly because of the small sample size. Dermal thorns of Cenomanian/Turonian *Echinorhinus* have been collected in the Southern Carnarvon Basin, but these are greatly outnumbered by oral teeth (MS, personal observation). A description of the enameloid microstructure of this species is presented in Adnet *et al*. (2012), where they compared the microstructure of a modern species (*E. brucus*) with *E. australis*. These authors conclude that there are few diagnostic features in the microstructure between species. Therefore, it was not investigated here.

OSTEICHTHYES
ACTINOPTERYGII
TELEOSTEI Müller, 1845
CROSSOGNATHIFORMES Taverne, 1989
PACHYRHIZODONTIDAE Cope, 1872
Pachyrhizodus Dixon, 1850
Pachyrhizodus sp. (Figure 1.10)

Remarks: Pachyrhizodus, originally described from jaw fragments, is defined as having compressed jawbones forming elongate rods with a single row of robust teeth supported by swollen tooth bases (Woodward 1902, Shimada 2015).

Type species: *Pachyrhizodus basalis* Dixon, 1850, English Chalk, Burham Kent.

Material: An isolated maxilla (KKF1075), and isolated dentary (KKF1076)

Description: Maxilla: The maxilla is only partially preserved with the posterior section missing (Figure 1.10. A & B). The maxilla is ovoid in lateral view and relatively shallow compared to the holotype *Pachyrhizodus grawi* (Bartholomi 2012). The maxilla is slightly curved anteriorly creating a concave internal scallop on the lingual side of the element (Figure 1.10. A). On the external (labial) surface of the bone are two small grooves, elongated and opposite to each other, (Figure 1.10. B arrows).

Teeth are formed as a single row, attached to the maxilla with swollen bases. The teeth are broad at the base, conical in shape and lack cutting edges. Only one tooth is preserved attached to the maxilla with an additional~ 17 tooth sockets with partial teeth. KKF1075 has been assigned to *P. grawi* as the maxilla is elongate and shallow, and the curvature is less sigmoidal in lateral view than compared with *P. marathonensis* Bartholomai 2012.

Dentary: The dentary is generally rectangular in shape where preserved in its entirety (Figure 1.10. C & D). The exterior of the bone preserves a deep groove that runs the whole length of the preserved portion of the dentary for the mandibular sensory canal. This groove separates the dorsal part containing the teeth and lamina of bone lateral to the row of teeth and the ventral lamina orientated medially. The teeth, strongly fixed to the bone, are more reminiscent of a pachyrhizodontid rather than, for instance, an ichthyodectiform. The internal surface of the bone preserves swollen tooth bases with scalloped depressions between teeth (Figure 1.10. D).

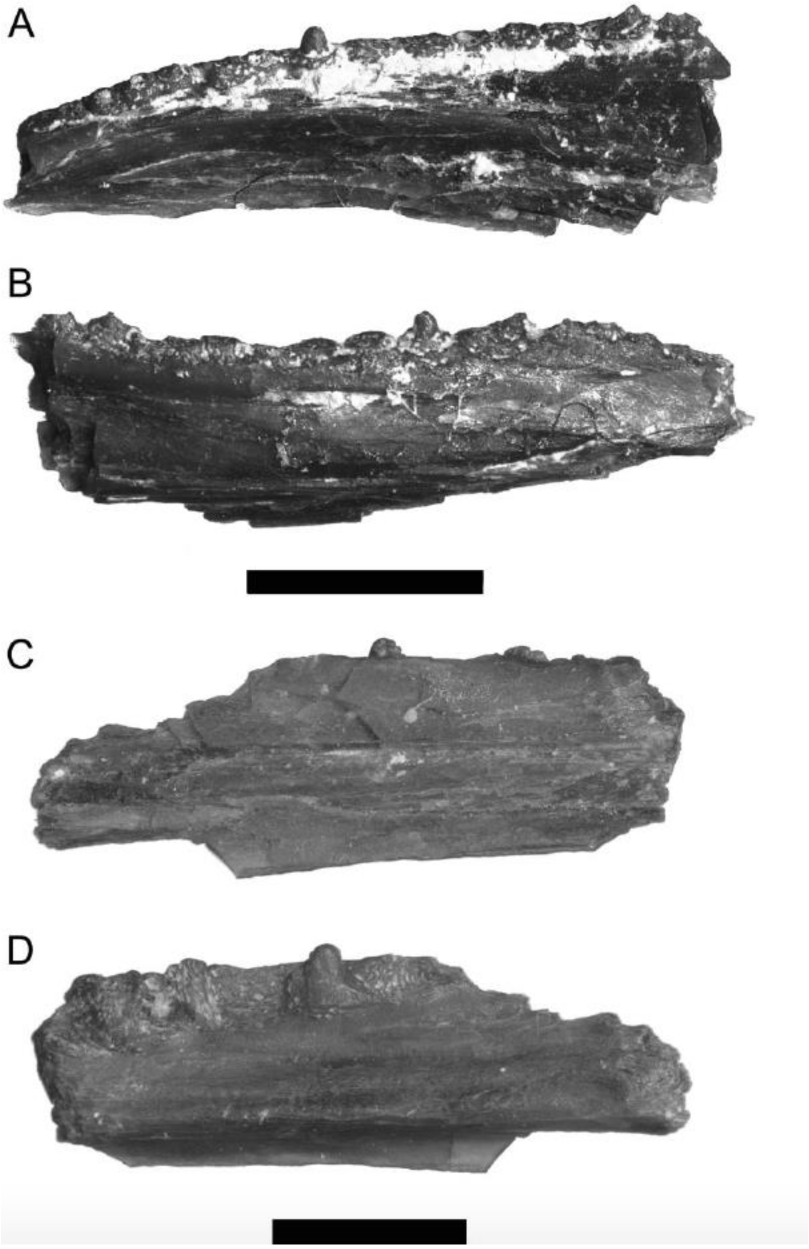

Figure 1.10. Isolated *Pachyrhizodus* jaw elements from the Lower Cretaceous Toolebuc Formation of Queensland. **A** & **B**. Internal and external views of the maxilla (KKF1075). **C** & **D**. Internal and external views of dentary (KKF1076). Scale bar is 1 mm.

Remarks: The genus *Pachyrhizodus* has been found in Cretaceous marine sediments worldwide (including multiple sites in the USA (Shimada 2015), Canada (Bamforth & Tokaryk 2016), Mexico (Giersch et al. 2010), Italy (Taverne 1987), France (Wenz

& Fricot 1985), England (Woodward 1902), Sweden (Bazzi et al. 2016), Australia (Bartholomai 2012) and New Zealand (Wiffen 1983)). Due to the generic nature of the dentary presented here and its partial preservation, it cannot be assigned further than *Pachyrhizodus* sp.

AULOPIFORMES Rosen, 1973
ICHTHYOTRINGOIDEI Goody 1969
ICHTHYOTHRINGIDAE Jordan 1901
Apateodus Woodward 1901
Apateodus sp. (Figure 1.11)

Remarks: Teeth of *Apateodus* are diagnostic in possessing anterior and posterior cutting edges and the lack of a post-apical barb (Kriwet 2003).

Type species: Apateodus glyphodus Woodward, 1901, English Chalk.

Material: one dentary tooth (KKF1077) and one ectopterygoid tooth (KKF1078). (Figure 1.11).

*Description***:** Dentary teeth: Tooth shape varies from straight to gently sigmoidal having a more slender appearance and curves slightly at the tooth apex (Figure 1.11.A & B). Vertical striations are present on the base of all teeth extending upwards to 1/3 the length of the tooth. Well-preserved teeth are oval in section that flares to become bell-shaped at the anterior and posterior cutting edges. Teeth do not appear to have a post-apical barb. Based on the diverse range in tooth size we suggest that this taxon possessed dentary fangs.

Ectopterygoid teeth: Only represented by a single tooth (Figure 1.11. C & D).
An isolated ectopterygoid tooth (KKF1078) is also present among the teeth. This tooth is laterally compressed and broadly an equilateral triangle with cutting edges on the anterior and posterior sides of the tooth.

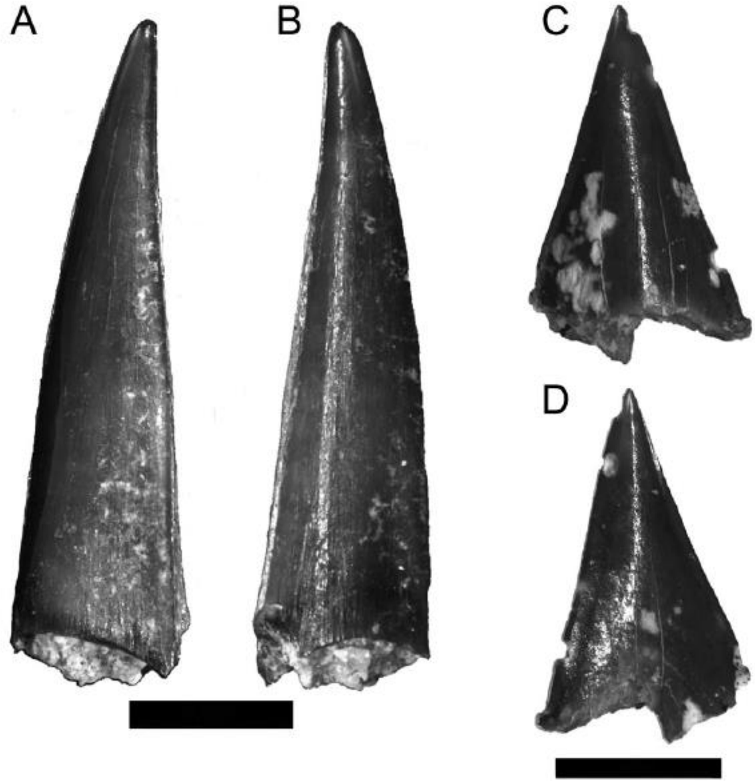

Figure 1.11. Isolated teleost teeth assigned to *Apateodus* sp. from the Lower Cretaceous Toolebuc Formation of Queensland. **A**. (KKF1077) labial view, and **B** (KKF1077). Lingual view of same tooth. **C** and **D** ectopterygoid tooth (KKF1078). Scale bar is 1 mm.

Remarks: The only parts of the fish that are preserved consist of isolated teeth that have a rounded lateral face and an anterior and posterior cutting edge. Teeth of different size and shape in the assemblage are thought to either represent teeth from different dentary positions or from different sized individuals rather than different species. The anterior and posterior cutting edges are diagnostic of Aulopiformes and the lack of a post-apical barb that is present in basal forms of the group and in *Cimolichthys* (Kriwet 2003) exclude the teeth from this group. *Apateodus* and some Enchodontidae lack this post-apical barb. However, Enchodontidae are only known from the Late Cretaceous whereas *Apateodus* is known from the Early Cretaceous as well. Based on the geological time ranges of these fishes, the absence of a post-apical barb and the anterior and posterior cutting edge, the teeth are assigned to *Apateodus* sp.

1.6 FAUNAL COMPOSITION OF THE AUSTRALIAN MESOZOIC

Historically, Australian fossil genera were placed within known European genera with early workers assuming commonality between northern and southern hemisphere faunas (Woodward 1895, Waldman 1971). Taxonomic assignment of new discoveries from Antarctica (Arratia *et al.* 2003) South America and Australia (Sferco *et al.* 2015) indicate that much of the Australian Mesozoic fauna required redescription in addition to taxonomic revision. The challenge of this work is that the vast majority of the Australian material is fragmentary, lacking the necessary morphological data to resolve their taxonomic affinity.

Within the current known taxa, the most problematic group (probably because it is the most diverse group) is the Actinopterygii. The chondrichthyans are better resolved, but since a large amount of the microvertebrates remain undescribed, the number of species is under-reported (Siverson 1997). The taxonomy of lungfish is based mainly, but not entirely, on tooth plate characteristics and that of coelacanths on scale morphology and isolated bones because of a lack of body fossils (Kemp 1991, Dziewa 1980, among others) suggesting that these taxa are under-reported in the Australian record due to preservation of isolated skull elements and scales for the coelacanths (Dziewa 1980 & Haig et al. 2015).

Triassic Fauna

Chondrichthyans

Triassic chondrichthyans present in Australia consist of the xenacanthiforms, a successful freshwater and marginal marine clade common in worldwide faunas in the mid-late Palaeozoic and early Mesozoic (Turner & Burrow 2011). To date, their occurrence in Australian Mesozoic rocks is restricted to the Sydney Basin (Woodward 1908). This record includes a near complete specimen from the brick pits at St Peters, Sydney identified as “*Pleuracanthus*" *parvidens* by Woodward (1908). More recently Ginter *et al.* (2010) reassigned “*Pleuracanthus*" *parvidens to Mooreodontus* because of the morphological similarity of the Australian teeth to *Mooreodontus* already known from the Triassic localities of Brazil, Europe, and the United States of America (Turner 2011). Further work on these specimens indicates that there are multiple species present in Australia, which have morphological differences in the pelvic claspers that could be diagnostic (Schultze and Soler-Gijon 2004, Turner 2011).

Actinopterygians

The Triassic record of *Pholidophorus gregarius* (Woodward 1890) from the Sydney Basin was previously considered to represent the earliest record of the

Pholidophoridae in the world (Arratia 2013). The Australian specimen was assigned to *Pholidophorus* based on the presence of thick rhombic scales and its fusiform shape (Woodward 1890), characters thought to define the marine Upper Jurassic Northern Hemisphere genus *Pholidophorus*. However, further discoveries showed these characters were not unique to *Pholidophorus* (Arratia 2013), with the Pholidophoridae defined as a monophyletic family based on the skull bones fused into a single plate and the anterior of the extrascapular is characterised by a flange of bone that curves from the external face and onto the visceral face (Arratia 2013). This work supports Wade (1940), who assigned this Australian specimen to a new genus and species, *Chrotichthys gregarius*, within the family Perleididae using the combination of a fusiform body shape, thick rhombic scales and the position of the dorsal fin to support this proposition.

Piscine Sarcopterygians

Globally, Mesozoic lungfish became exclusively freshwater by Early Triassic times. Triassic lungfish are recovered from all earliest Triassic freshwater locations and appear to be abundant but not diverse. The lungfish fauna during the Early Triassic was dominated by *Ptychoceratodus*, which has been recovered from freshwater localities globally. A possible gnathorhizid occurs in the Arcadia Formation (Kemp 1993) in Queensland and suggests that the Gnathorhizidae may have been restricted in Australia to the southwest Panthalassic. The same applies to the possible sagenodontid lungfish, also from the Arcadia Formation (Kemp 1993).

Coelacanths are a rare component in the Mesozoic faunas of Australia (Table 1.1.) and no complete specimens are known. The majority of remains are isolated scales from the Kockatea Shale (Haig *et al.* 2015) and an isolated skull element from the Knocklofty Formation (Dziewa 1980). This confirms their presence in the Tethys and southwest Panthalassic Seas.

Jurassic Fauna

Chondrichthyans

A single specimen of a Jurassic chondrichthyan is the only shark described from the Jurassic of Australia (Turner & Avery 2017), although other specimens are known (see Table 1.1.) but are yet to be described.

Actinopterygians

Recent systematic revisions of the former *Lepidotes-Semionotus* complex and phylogenetic analyses have provided a new scheme for ginglymodians interrelationships (López-Arbarello 2012). In most studies, a Semionotiformes clade is distinguished from a Lepisosteiformes clade (for instance López-Arbarello 2012). Both clades contain representatives from both marine and fresh waters, and in the present state, the Queensland material cannot be referred to one or the other groups, or to a peculiar genus among ginglymodians as the material is too fragmentary. Often because Semionotiformes have thick rhombic scales, the group becomes a “bucket taxon” for fragmentary remains of fishes with thick rhombic scales. Based on the widespread occurrence of thick rhombic scales in Mesozoic fishes (Arratia 2013) the Queensland material may, in fact, have no phylogenetic relationship to the Semionotiformes (currently named ginglymodians) and further skeletal material is required to determine this.

Piscine Sarcopterygians

A single isolated fin from the Jurassic Talbragar Fish Bed is described as belonging to the Coelacanthidae (Woodward 1895). Examination of the figure shows a bone of the pectoral girdle, probably a scapulocoracoid, against which articulate four hour-glass shaped radials. About 40 rays, segmented from their base and with one dichotomy at least, are present. This pectoral fin belongs to an actinopterygian because of the arrangement of the radials, and more specifically, it probably belongs to a chondrostean as indicated by the numerous segmented rays. The misidentification of Woodward is explained by the poor knowledge of the paired fins of coelacanths at his time and by the comparison he made of this fossil with *Polypterus*, which was included in the “crossopterygians” at that time. Forey (1998: 365) already referred this fin to an actinopterygian and noticed its resemblance to a polypterid fin. No Jurassic lungfish have been identified in Australia.

Cretaceous Fauna

Chondrichthyans

Australian Mesozoic chondrichthyans are known primarily from Cretaceous rocks with most specimens preserved as isolated teeth/tooth-plates and fin spines. The most productive units that have been sampled include the lower upper Albian Toolebuc Formation in Queensland, the middle Albian to middle Cenomanian part of the Gearle Siltstone in Western Australia and the uppermost Cenomanian to lower Turonian part of the Haycock Marl in Western Australia. Although the quality of the material is commonly exceptional in all three units, most taxa have not yet been described. Cretaceous elasmobranchs have been reported from other units in Australia (see e.g., Kemp N. & Turner 2002) but some of these assemblages have not been studied and others are lacking in both quality and quantity (Molecap Greensand, Gingin Chalk, Toolonga Calcilutite and Miria Marl), preventing a meaningful discussion of the faunas.

Strictly benthic elasmobranchs are either rare (Kemp N. & Ward 1997) or absent (Richmond area, MS, pers. observ.) in the Toolebuc Formation. The benthopelagic/pelagic assemblage is numerically dominated by *Echinorhinus australis* and, to a lesser degree, Cardabiodontidae sp. (of all ontogenetic stages; Figure 1.12K-N depicts a lower jaw tooth from a large individual) and *Squalicorax* (sensu lato) sp. (undescribed; see Figure 1.12.B-C). Collecting in the Richmond area has thus far yielded four additional species, all belonging to the Lamniformes (one of these is illustrated in Figure 1.12.D-G). This newly collected material is yet to be formally described but includes, e.g., an undescribed species of *Johnlongia* Siverson, 1996 (Shimada *et al*. 2015), which constitutes the oldest known occurrence of this genus.

The vast majority of chondrichthyan material collected from the Gearle Siltstone in the Giralia Anticline of Western Australia is undescribed. However, Popov & Machalski (2014) listed several taxa of chimaeroids, including *Elasmodectes* cf. *kiprijanoffi* (Figure 1.12A). Because this unit is not readily processed by wet sieving most of the species are represented by surface-collected teeth. Siverson (1997) described a mid-Albian assemblage comprising hexanchids, paraorthacodontids, orectolobids and several lamniforms. Lamniforms likewise dominate surface collected material from the middle Cenomanian part of the Gearle Siltstone (see Siverson 1999; Siversson *et al*. 2015; Newbrey *et al*. 2015; Figure 1.12H-J). Unpublished results from limited bulk sampling indicate that *Protosqualus* Cappetta, 1977 was the most common elasmobranch taxon in the middle Cenomanian of the area. In the lower

Murchison River area, north of Kalbarri, the Gearle Siltstone is more readily wet-sieved and has produced rich microvertebrate faunas. Most of this material remains to be described but is numerically dominated by squaloids of *Protosqualus* type and small orectolobiforms (see Siversson *et al*. 2018). Like in the Gearle Siltstone of the Giralia Anticline, teeth of hexanchids are relatively common. *Paraorthacodus* Glikman, 1957, recently linked to the Synechodontiformes Duffin & Ward, 1993 as well as to the Hexanchiformes Buen, 1926 (see Cappetta 2012), occurs throughout the 'upper' Gearle Siltstone in the area but is less common than in the Molecap Greensand (Supplementary Fig. S1).

The Haycock Marl in the Southern Carnarvon Basin contains the highest concentration of Cretaceous elasmobranch teeth in Australia. An isolated phosphatic lens in the lowermost lower Turonian part of the Haycock Marl in the lower Murchison River area (Siversson et al. 2018, fig. 4c) has thus far produced 30 species of chondrichthyans (MS, unpublished data), the second highest number recorded for a narrow stratigraphic interval of Mesozoic age in Australia (Bed 1 of the 'upper' Gearle Siltstone, of uppermost Albian age, has thus far yielded 33 species; MS unpublished data, see also Siversson et al. 2018, fig. 2). By comparison, and at the other end of the diversity spectrum, the lower upper Albian Toolebuc Formation has yielded about a dozen species. The Haycock Marl assemblages are indicative of fully marine, outer shelf conditions. Unlike the Alinga Formation, the Gearle Siltstone and the Mackunda Formation, teeth of *Protosqualus* type are rare whereas teeth of scyliorhinids are abundant above the basal, laminated part of the Haycock Marl. Teeth of benthic orectolobiforms are extremely rare in lower Haycock Marl in the lower Murchison River area (uppermost upper Cenomanian – lowermost lower Turonian) but are common in a highly condensed interval of the Haycock Marl of upper lower Turonian age, exposed in the Giralia Anticline. Teeth of lamniform sharks are common throughout the Haycock Marl, but Carcharhiniformes are the numerically dominant elasmobranch group, largely because of a single, extremely abundant and most likely pelagic species (*Diprosopovenator hilperti*).

The fossil record of Holocephalans in Australia is sparse, comprising isolated tooth plates and rare dorsal-fin spines. The tooth plates are assigned to *Ptyktoptychion* containing two species (*P. tayyo* and *P. wadeae)* and *Edaphodon eyrensis*. Popov (2011) has reported the presence of *Callorhinchus, Ischyodus, Elasmodectes* (Figure 1.12. A), *Harriotta* and *Belgorodon* from the Cretaceous of Australia, but these identifications do not represent formal taxonomic description and are yet to be published. Tooth plates and fin spines are found in isolation, and this means that associating fin spines to tooth plates of individual genera has not been possible (Bartholomai 2015).

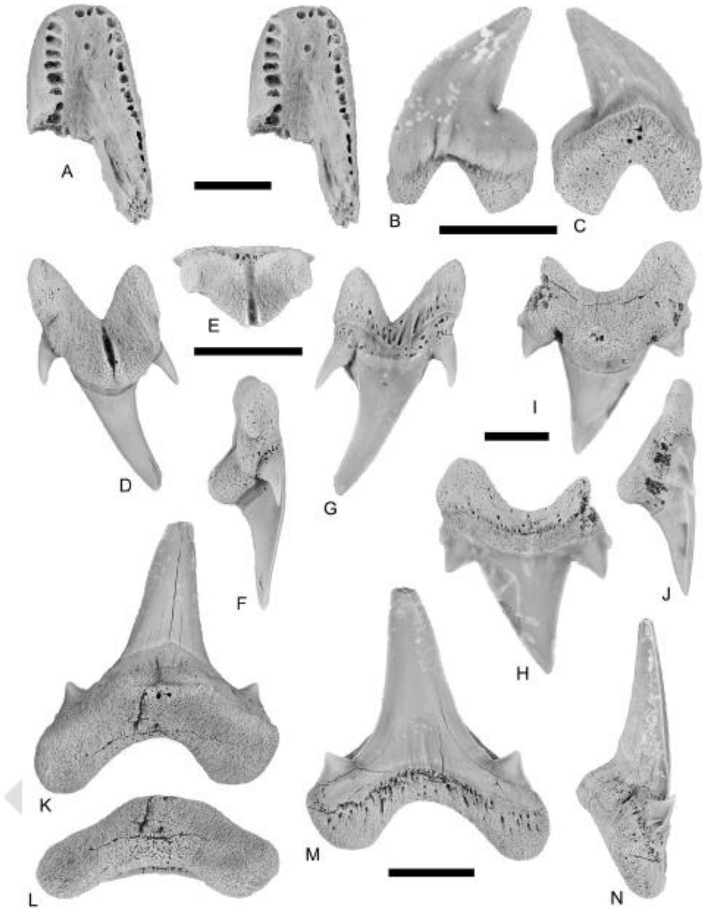

Figure 1.12. **A**, *Elasmodectes* sp.; **B-C**, *Squalicorax* sp. (undescribed); **D-G**, Lamniformes sp. (undescribed); **H-J**, *Dwardius* aff. *D. woodwardi* (Herman, 1977); **K-N**, Cardabiodontidae sp. (undescribed). **A**, Left palatine tooth plate, WAM 18.8.3, Occlusal view (stereo); **B-C**, Anterolateral tooth, WAM 18.8.5; **B**, Labial; **C**, Lingual views; **D-G**, Upper? lateroposterior tooth (tooth terminology *sensu* Siverson 1999), KKF1079; **D**, Lingual; **E**, Basal; **F**, Profile; **G**, Labial views; **H-J**, Upper lateroposterior tooth, WAM 18.8.4; **H**, Labial; **I**, Lingual; **J**, Profile views; **K-N**, Anteriorly situated lower lateroposterior tooth, WAM 18.8.7; **K**, Lingual; **L**, Basal; **M**, Labial; **N**, Profile views; lower upper Albian, Toolebuc Formation (‘fish-mash layer’), Council Quarry, Richmond, Queensland (**B-G**, **K-N**); middle Cenomanian (most likely lower part), ‘upper’ Gearle Siltstone, C-Y Creek, Giralia Anticline, Western Australia (**A**, **H-J**). Scale bars 3 mm (**A**), 5 mm (**B-J**) and 10 mm (**K-N**).

Actinopterygians

The diagnosis of a new species, *Pachyrhizodus grawi*, Bartholomai 2012, based on several skulls recovered from the Toolebuc and Allaru Formations, is problematic as only general teleostean features, such as size, angled gape (a feature common in ichthyodectiform fishes), expanded preopercular and the size and shape of the operculum and size and overall skull shape have been used (Bartholomai 2012). Although, the most informative diagnostic characters are most common in the postcranial anatomy, particularly within the caudal fin to date most taxonomy has been restricted to the head due to the unavailability of postcranial material of *Pachyrhizodus* from Australia. Similar palaeoenvironments such as the Niobrara Chalk in the USA yield multiple species of *Pachyrhizodus,* which suggests that the Eromanga Sea would also yield multiple species. Further, more complete specimens of *P. grawi* and *P. marathonensis* are required to determine if the current specimens from the Allaru and Toolebuc Formations represent a single species with ontogenetic variation, or if multiple species are present.

The series of elopomorph teleosteans described by Bartholomai (2013) includes four genera, *Flindersichthys*, *Euroka*, *Marathonichthys* and *Stewartichthys*, obviously belong to basal teleosts, but because most of them are known by very incomplete specimens, mostly isolated heads or isolated braincases, a new assessment of their phylogenetic positions among basal teleosts that can bring interesting biogeographical signals, is pending.

Piscine Sarcopterygians

All the post-Triassic lungfish known from Australia occur as isolated tooth plates. Within lungfish taxa, the toothplates are diagnostic to species level making identification, even in the absence of a body fossil, robust (Kemp 1991, 1997a, b). Tooth plates of the lungfish *Ceratodus tiguidiensis* were described by Tabaste (1963) from the Cretaceous of Niger, and these were later placed in the genus *Arganodus* by Martin (1982a, 1982b). Kemp (1994, 1998) has proposed that the tooth plates of *Asiatoceratodus* from the Early Triassic are synonymous with *Arganodus*, and since *Asiatoceratodus* was described first, it takes precedence. Hence, all toothplates referred to as *Arganodus* should be referred to as *Asiatoceratodus* until more complete material can prove otherwise. This expands the geographic occurrence of *Asiatoceratodus* throughout Pangea including Australia.

Toothplates identified as indistinguishable from *Neoceratodus forsteri*, the extant Australian lungfish have been recorded from strata dated as Early Cretaceous suggesting this species could have remained evolutionarily static for ~110 million years (Kemp & Molnar 1981). To date, no Cretaceous coelacanths are known from Australia.

1.7 DISTRIBUTION AND COMPARISON OF THE AUSTRALIAN MESOZOIC FAUNA.

Chondrichthyans

The vast majority of the collected chondrichthyan material remains undescribed or is only briefly mentioned in abstracts. The best-known faunas, both in terms of material collected and taxa described is the elasmobranch material from the Toolebuc and Mackunda Formations in the Eromanga Basin, Queensland and the Gearle Siltstone and Haycock Marl in the Southern Carnarvon Basin (lower Murchison River area and Giralia Anticline), Western Australia (Kemp 1991; Siverson 1996, 1997, 1999; Siversson et al. 2015, 2018). A direct comparison of coeval faunas between the restricted Eromanga Basin and the more open marine Southern Carnarvon Basin is currently only possible for the upper Albian interval, during deposition of the Mackunda Formation and Beds 1 and 2 of the ‘upper’ Gearle Siltstone in the lower Murchison River area (see Siversson et al. 2018 for calcareous nannofossil age data for the latter unit) and shows few common species e.g., *A haigi* (Bed 1) and a large orectolobiform illustrated in Siverson 1997, fig. 3d-g (Table 1.1.). The chondrichthyan diversity is more than twice as high in the Gearle Siltstone than in the Mackunda Formation. The different faunal composition is most likely a function of the more offshore palaeoenvironment of the Gearle Siltstone.

Adult Cardabiodontidae sp. (undescribed species and genus, seemingly closely related to *Cardabiodon* Siverson, 1999; Figure 1.12. K-N) from the Toolebuc Formation were probably the largest lamniform sharks in the Cretaceous having a vertebral diameter of up to ~140mm. Assuming a similar ‘maximum vertebral diameter/total body length’ ratio as in *Cardabiodon ricki* (5.4 m TL in the holotype, independently estimated from extrapolated jaw circumference; Newbrey *et al*. 2015) this species may have had a maximum TL exceeding 8 metres. Comparable (i.e., similar tooth positions) teeth of this species range from very small to large in the Toolebuc Formation but most teeth are from juvenile individuals, suggesting that the Eromanga Basin was a centre for reproduction in this taxon. The absence of this species in the Albian of Western Australia might, in part, be a result of the lack of exposed strata of lower upper Albian age in the Southern Carnarvon Basin. Teeth (Williston 1900, pl. 30, fig. 6) and vertebrae (Fredrickson 2015) from the upper Albian of Texas, USA, very similar to those of Cardabiodontidae sp., indicate a wide but possibly patchy distribution. Remains of *Cardabiodon* are relatively rare in the Southern Carnarvon

Basin (*Cardabiodon ricki* in the Cenomanian and *C. venator* in the Turonian [see Siverson 1996, pl. 4, figs 8-10]) and, with one exception (Newbrey *et al*. 2015, fig. 3a), comprise teeth and vertebrae from large individuals. Teeth of small, juvenile individuals of *Cardabiodon* are locally common in the Cenomanian-Turonian of the Western Interior Seaway of North America (see Siverson & Lindgren 2005), indicating that the seaway was an important area for reproduction. The spatial distribution of teeth from small, juvenile cardabiodontids of *Cardabiodon*-type thus indicates dependence on restricted seaways and partially enclosed intercontinental seas for reproduction and/or nursery sites.

A surface collected and partly undescribed, middle Cenomanian elasmobranch fauna from the uppermost Gearle Siltstone in the Giralia Anticline area comprise a mixture of cosmopolitan (e.g., *Cardabiodon ricki*, *Cretoxyrhina denticulata* [Glikman, 1957], *Ptychodus decurrens* Agassiz, 1838) and more endemic species (e.g., *Cretalamna catoxodon* Siversson *et al*., 2015, *Kenolamna gunsoni* [Siverson, 1996]) (Table 1.1.). Global sea level rose towards the end of the Cenomanian stage and deeper water anoxia (the OAE2 event) developed in many parts of the oceans and epicontinental seas. In the onshore Southern Carnarvon Basin, laminated black sediments in the basal Haycock Marl attest to strongly dysaerobic to anaerobic bottom waters (Dixon *et al*. 2003). Sampling of this interval revealed a highly anomalous chondrichthyan fauna with >80 % of the teeth originating from a most likely pelagic, carcharhiniform (*Diprosopovenator hilperti*) and juvenile bramble sharks and only ~0.1 % of the teeth coming from strictly benthic species.

Holocephalans

The Gondwana record of holocephalans is not restricted to only Australia (Bartholomai 2015) with occurrences in Antarctica (Stahl & Chatterjee 1999), Africa (Ward et al. 2014) and South America (Otero et al. 2013). Holocehalans appear more widespread throughout Laurasia (Popov & Machalski 2014) and are dominated by the genera *Edaphodon* and *Ischyodus* (Popov & Machalski 2014). The Australian fauna contains the endemic *Ptyctoptychion* plus the cosmopolitan genera *Ischyodus*, *Callorhinchus*, and *Elasmodectes* (Figure 1.12. A).

Actinopterygians

The Triassic actinopterygians consist of basal actinopterygian fishes found globally in freshwater sediments with endemic speciation found at the genus level. Cavin (2017) pointed out that the phylogeny of Redfieldiiformes provided by Schaeffer (1984) indicates that most of the basal genera occurred in the Southern Hemisphere (South Africa and Australia), while the more derived genera are from the Northern Hemisphere (North America and North Africa). Although, as suggested by Lombardo (2013), the phylogeny of this clade is still uncertain, it may indicate the occurrence of a radiation of Redfieldiiformes in the Austral region. Similarly, the Australian Cleithrolepidae from Australia shows strong affinities with the South African ones (López-Arbarello and Zavattieri 2008, Sun et al., 2012). During the Jurassic, the palaeoniscoid grade assemblages were slowly replaced by teleosts. These teleosts are thought to be related to Luisiellidae from South America (Patagonia) (Sferco *et al.* 2015). It is possible that they evolved from a common ancestral marine species which then migrated and diversified in the freshwater ecosystems of the Southern Hemisphere. The invasion into freshwater could have resulted in species isolations and account for a large number of endemic species found in Patagonia and Australia.

The predominantly marine Cretaceous sediments from the large epi-continental Eromanga Sea have yielded a largely cosmopolitan fauna comparable to Gondwana faunas at the family and genus level. For example, aspidorhynchids (e.g., *Richmondichthys;* Bartholomai 2004) and Ichthyodectiforms (e.g., *Cooyoo* Lees & Bartholomai 1987) are also found in the Araripe Basin of northeastern Brazil, in South America. In their phylogeny of Ichthyodectiformes, Cavin et al. (2013) found the Australian *Cooyoo* as the sister of *Unamichthys espinosai*, a species from the middle or late Albian Tlayúa Formation, Mexico (Alvarado-Ortega, 2004), but later, Cavin & Berrell (2019) found *Cooyoo* as the sister of *Ichthyodectes ctenodon*, a Late Cretaceous species from North America. These contrasting results show that the phylogeny of the ichthyodectiforms, and consequently their paleobiogeographical signal is still unclear. The opening of the South-Atlantic and Proto-Indian Oceans during the Early Cretaceous would have provided new niches for shallow-water marine fishes to diversify and result in related but endemic faunas in the southern hemisphere. Generalist cosmopolitan taxa speciate into a relatively empty niche as they become available.

Piscine Sarcopterygians

The majority of sarcopterygians from the Australian Mesozoic are dipnoans. Triassic lungfish fauna is considered diverse, with representatives from many northern hemisphere groups, characterised by well-preserved tooth plates, but with other body parts inadequately conserved. They are mostly confined to eastern regions of continental Australia, with a single record of the ubiquitous genus *Ptychoceratodus* from Tasmania and Western Australia, and a single record of *Asiatoceratodus* from Western Australia (Table 1.1.). It is considered that all lungfish taxa of the Mesozoic were freshwater, and that fossil remains found in estuarine–marine conditions were transported seaward post-mortem. Schultze (2004) suggested that the increase in fluvial sediments during the Triassic could explain the relatively diverse dipnoan fauna. The Australian record supports that there were many fluvial deposits as well as a high number of specimens of lungfish recovered but does not explain their absence in the Jurassic record where many specimens were recovered from fluvial sediments in the northern hemisphere. Schultze (2004) suggests that the increase in marine conditions during the Jurassic led to a reduction in the freshwater habitats and migratory pathways available to lungfish resulting in their ultimate decline in abundance. In Australia, dipnoans are abundant in freshwater deposits. Phylogenetic hypotheses using fossil taxa suggest that modern lungfish lineages evolved during the Early Cretaceous (Kemp et al. 2017). The presence of *Metaceratodus* in the Early–Late Cretaceous of Australia (Kemp 1997b) and the Late Cretaceous of South America (Cione & Gouiric-Cavalli 2012) suggests that *Metaceratodus* was present in both Australia and South America prior to the two continents separating. It also may suggest that Antarctica acted as a land bridge from Australia to South America.

1.8 BIOGEOGRAPHY

The Mesozoic is characterised by a series of significant changes (continental fragmentation, rising sea levels, faunal exchange, etc.) (Dunhill *et al.* 2016; Holtz *et al.* 2004.

During the Triassic, Pangaea persisted, spanning both hemispheres (Seton *et al.* 2012). By the Jurassic, Pangaea began to fragment into two supercontinents, a northern landmass known as Laurasia, containing modern-day Asia, Europe, and North America, and the southern landmass, Gondwana, containing the modern landmasses of Africa, Antarctica, Australia, India, Madagascar and South America. Continental fragmentation and reconfiguration continued throughout the Cretaceous (Upchurch 2008). The persistence of Pangaea into the Triassic could be an explanation as to why some Palaeozoic taxa, particularly freshwater forms (xenacanth sharks) persisted throughout the Triassic, and the latest Triassic, marine regression – transgression (Hallam & Wignall 1999) would have impacted their habitats, with some taxa becoming extinct by Early Jurassic times.

The associated opening up of the seaways and sea-level rise triggered a number of speciation events and colonisation of new waterways throughout the Mesozoic (Cavin 2008; Cavin & Forey 2007). However, placing the Australian fish fauna, particularly the actinopterygians within this global biogeographic context is difficult due to the lack of taxonomic robustness and description of a large part of the fauna.

1.9 DISCUSSION

The disparate nature of the preservation among various fossil-bearing formations in Australia increases the difficulty in determining the actual faunal diversity and abundance of fishes during the Mesozoic. The fauna from the Triassic strata in the Sydney Basin is overwhelmingly represented by articulated whole-body fossils with little deformation from a freshwater low-energy lacustrine–estuarial environment (Willis 1996). Triassic marine deposition for this period comprises mostly disarticulated elements of actinopterygians, and coelacanths devoid of diagnostic features and, therefore, the taxonomic assignment cannot be resolved. Thus, taphonomic bias may be responsible for freshwater deposits appearing to have a higher diversity and abundance than corresponding marine deposits. Compounding this problem is that material such as coprolites, which contain examples of vertebrate taxa previously not recorded in the region are understudied (Niedźwiedzki *et al.* 2016, Northwood 2005). Continuing work in marine localities in understudied areas of Western Australia has the potential to yield more complete material than sites currently known in eastern Australia and will hopefully address this issue.

The majority of Jurassic localities in Australia are represented by freshwater deposits (excluding the nearshore marine locality of Colalura Sandstone) with the majority of taxa known from a single site, the Talbragar Fish Bed. This may not be a true representation of the Jurassic fauna. For example, lungfishes are common in both the Triassic and Cretaceous of Australia but are absent at Talbragar as are other faunal elements such as labyrinthodonts, pterosaurs, dinosaurs, turtles and crocodiles known from other Jurassic strata globally (Solnhofen and Tiaojishan Formation as examples) (Zhou & Wang 2017).

The most common vertebrate marine fossils from the Eromanga Basin are isolated teeth and dermal denticles of chondrichthyans, with actinopterygians being represented by large predatory fishes, over one metre long, often preserved only as the head and anterior part of the trunk region suggesting detachment of the caudal fin during decay. In addition, microvertebrate remains of small actinopterygians from the Toolebuc Formation are also very common and represent fishes that have undergone various taphonomic processes and are disarticulated as a result. The microvertebrates are known but understudied and further work will increase our understanding of this faunal assemblage. Cretaceous freshwater sediments preserving fish fossils of fluvial nature are restricted to the eastern half of the continent. The fossils are undescribed but are preserved as partial body fossils; the head is often separated from the body prior to fossilisation making identification difficult. Lacustrine deposits where a whole fish assemblage is preserved are only found at Koonwarra, which has the best preservation of basal teleosts where complete body fossils in mass kill assemblages are preserved. These fossils have already provided interesting biogeographical information with respect to the South American freshwater fauna.

1.10 CONCLUSION

There are many Mesozoic localities yielding fossil fishes in Australia and a large number of fossils have been found. However, most of the actinopterygians are still undescribed, improperly assigned, due to their description prior to cladistics or based on fragmentary material that limits the taxonomic resolution. Both the chondrichthyans and dipnoans are still undergoing research, but their taxonomy is relatively well understood. The Mesozoic fish fauna of Australia is not depauperate but requires further descriptive, taxonomic and phylogenetic work to be placed properly in the global context.

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SUPPLEMENTARY INFORMATION 1.1

Supplementary Fig. S1.1. Paraorthacodus sp., juvenile antero-lateral tooth measuring 4.8 mm in maximum root width, WAM 18.8.1; Bed 1, ‘upper’ Gearle Siltstone (uppermost upper Albian), Thirindine Point east, Murchison House Station, Western Australia.

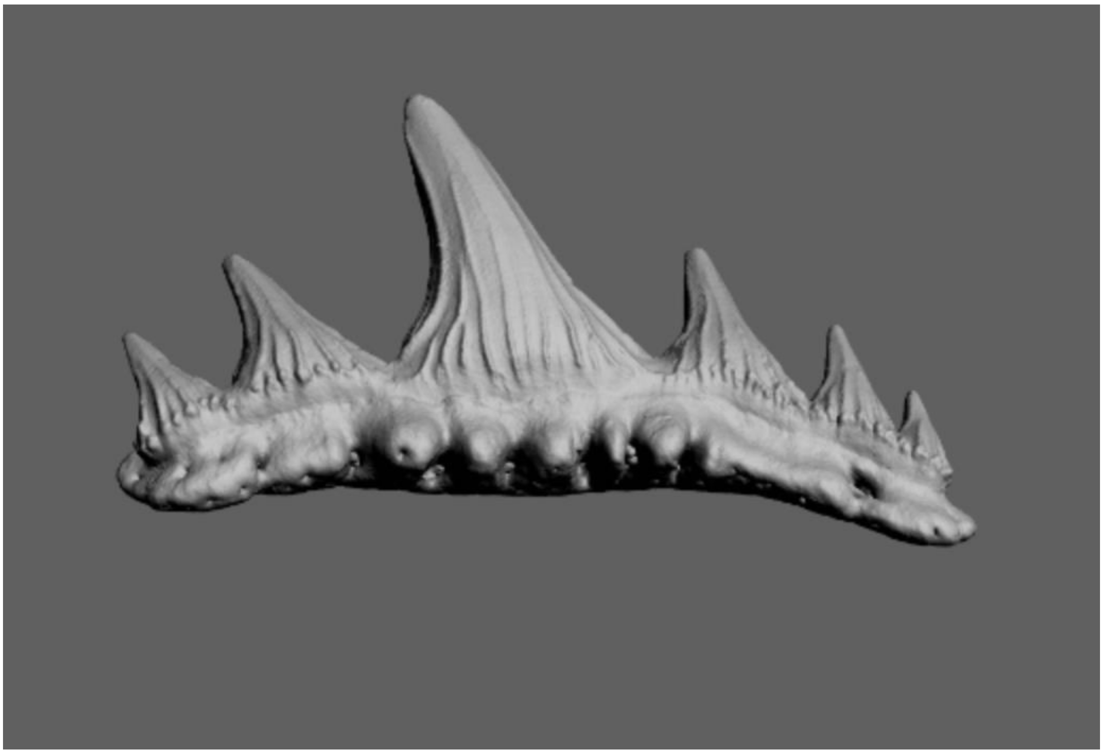

Table 1.1. Taxa of Mesozoic fish based on age and locality. Locality numbers 1-21 are localities 1-21 in the main text. The Western Australian localities (22-31) expanded to represent different Formations presented within the text.

		Formation	Triassic						Jurassic				Cretaceous																					Reference
			Arcadia Formation	Knocklofty Formation	Kockatea Shale	Blina Shale	Narrabeen Sandstone	Leigh Creek Coal Measures	Colalura Sandstone	Walloon Coal Measures	Mulgildie Coal Measures	Purlawaugh Formation	Eumeralla Formation	Wonthaggi Formation	Korumburra Group	Wallumbilla Formation	Bulldog Shale	Toolebuc Formation & Normanton Formation	Allaru Formation	Mackunda Formation	Griman Creek Formation	Winton Formation	Moonkinu Formation	Windalia Sandstone	Molecap Greensand	Alinga Formation	Gearle Siltstone mid-Albian	Gearle Siltstone 'Vraconnian'	Gearle Siltstone early middle Cenomanian	Gearle Siltstone late middle-late Cenomanian	Haycock Marl	Gingin Chalk	Toolonga Calcilutite	
		Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
	Chimaerida	*Edaphodon eyrensis*															X																	Long 1985
		Ptyktoptychion tayyo																X																Lees 1986
		Ptyktoptychion wadeae																X																Bartholomai 2008
		Ptyktoptychion cf. *tayyo*																									X							Popov 2011
		Ptyktoptychion cf. *wadeae*																							X									Popov & Machalski 2014
		Elasmodectes cf. *kiprijanoffi*																											X					Popov & Machalski 2014; this study
		Callorhinchus cf. *borealis*																									X		X					Popov 2011; Popov & Machalski 2014
		Ischyodus cf. *thurmanni*																											?					Popov 2011
		Ischyodus sp.																			X								X					Popov 2011, Popov pers comm.
		Harriotta sp.																									X	X						Popov 2011; Popov & Machalski 2014
		Belgorodon sp.																							X									Popov & Machalski 2014
Elasmobranchii	Xenocanthiformes	*Pleuracanthus parvidens*					x																											Woodward 1908
	Ptychodontiformes	*Ptychodus decurrens*																											X					Siverson 1999
		Echinorhinus sp.																													X			this study

	Echinorhiniformes		*Echinorhinus australis*																X																Chapman 1909; also see Siverson 1996
			Anomotodon sp.																							X	?		?		?	?			Kemp N. 1991 (as *Scapanorynchus* sp. [partim]); Siverson 1996
			Archaeolamna haigi																								?		X		?	?			Siverson 1996, stratigraphic provenance uncertain; this study
			Archaeolamna spp.																		X							X							Siverson 1997; this study
			Carcharias' sp. A																													X			Siverson 1996 (text-fig. 5g-j)
			Carcharias' sp. B																							X	?		?		?	?			Kemp N. 1991 (as *Scapanorynchus* sp. [partim]); Siverson 1996 (text-fig. 6a-d), stratigraphic provenance uncertain
			Carcharias' sp. C																								?		?		?	?			Siverson 1996 (text-fig. 6e-h), stratigraphic provenance uncertain
			Carcharias' sp. D																														X		Kemp N. 1991 (as *Hispidaspis* sp. and *Hispidaspis* [?])
			Carcharias' striatula																									X							Siverson 1997
			Cardabiodon ricki																											X		X			Siverson 1999; Newbrey et al. 2015
			Paraisurus aff. P. compressus																									X							Siverson 1997
			Cardabiodon venator																													X			Siverson 1996 (as *Pseudoisurus*? sp. [*partim*], pl. 4, figs 8-10)
			Cardabiodontidae sp.																X																Kemp N. 1991 (as *Cretolamna appendiculata*); this study
			Cretalamna catoxodon																								?		?	X	?	?			Siverson 1996 (as *Cretolamna appendiculata* [partim], pl. 3, figs 5-6); Siversson et al. 2015

			Cretoxyrhina denticulata																											X					Siversson et al. 2018
			Cretoxyrhina agassizensis																												X	X			Siverson 1996 (as *C. mantelli*; Newbrey et al. 2015; Siversson et al. 2018 (as *Cretoxyrhina* aff. *C. agassizensis*)
			Cretalamna? sp.																									X							Siverson 1997 (as *Cretolamna* sp.)
			Cretalamna spp.																								?		?		?	?	X		Kemp N. 1991 (as *Cretoxyrhina* cf. *mantelli*); Siverson 1996 (as *Cretolamna appendiculata* [*partim*], pl. 3, figs 1-4, 7-8), stratigraphic provenance uncertain
			Cardabiodontidae sp.																																Siverson 1997 (as Cretoxyrhinidae gen. et sp. incertae sedis)
			Diprosopovenator hilperti																													X			this study
			Dwardius aff. *D. woodwardi*																								?		?		?	?			Siverson 1996 (as *Archaeolamna* aff. *kopingensis* [*partim*], pl. 2, figs 1-4 and *Pseudoisurus tomosus*), stratigraphic provenance uncertain
			Dwardius sp.																								?		?		?	?			Siverson 1996 (as *Archaeolamna* aff. *kopingensis* [*partim*] pl. 2, figs 5-6), stratigraphic provenance uncertain
			Kenolamna gunsoni																										?	X					Siverson 1996 (as *Cretolamna gunsoni*); Siversson et al. 2015
			Johnlongia allocotodon																													X			Siverson 1996
			Johnlongia sp.															X																	this study
			Lamna' daviesii															X																	Etheridge 1888 (most likely Cardabiodontidae sp.)

			Paraisurus sp.																X																Kemp N. 1991
			Paranomotodon sp.																								?		?		?	?			Siverson 1996, stratigraphic provenance uncertain
			Protolamna spp.																							X	?	X	?		?	?			Kemp N. 1991; Siverson 1996 (as *Leptostyrax* sp.), 1997 (as *Leptostyrax* sp.)
			Squalicorax acutus																												X				Siversson et al. 2018
			Squalicorax bazzii																												X				Siversson et al. 2018
			Squalicorax aff. *S. bernardezi*																													X			Siversson et al. 2018
			Squalicorax mutabilis																													X			Siverson 1996 (as *S. volgensis*); Siversson & Cook in Siversson et al. 2018
			Squalicorax sp. A																										X						Siversson et al. 2018
			Squalicorax sp. B																										X						Siversson et al. 2018
			Squalicorax primaevus																									X							Siverson 1997
			Squalicorax sp. (unnamed)																X																this study, originally described as Pseudocorax sp. by Kemp N. 1991
			Anacoracidae sp.																X																Rozefelds 2003
			Squalicorax spp.																								?		?		?	?			Siverson 1996 (as *Squalicorax* ex gr. *curvatus*)
			Lamniformes sp.																X																Fig. 12D-G
	Orectolobiformes		Orectolobiformes sp.																									X							Siverson 1997
	Squaliformes		*Protosqualus* sp.																							X				X					Kemp N. 1991 (one of the teeth described as *Centrophoroides* sp.); this study
	Squatiniformes		*Squatina* sp.																							X									Kemp N. 1991
	Hexanc hiforme		*Gladioserratus aptiensis*																									X							Siverson 1997 (as *Notorynchus aptiensis*)

			Hexanchidae sp.																							X									Kemp N. 1991 (as *Notorynchus* sp.)
			Paraorthacodus spp.																							X		X	X						Kemp N. 1991 (as *Synechodus* sp. and 'batoid dermal denticles'); Siverson 1997; this study
Actinopterygii			*incertae sedis*						X																										Pledge & Baulch 2013
			Leighiscus hillsi						X																										Wade 1953
		Coccolepididae	*Coccolepis australis*										X																						Wooward 1895
			Coccolepis sp.?													X																			Waldman 1971
			Coccolepis woodwardi													X																			Waldman 1971
			Chondrostei incertae sedis					X																											Wade 1935
			Belichthys longicaudatus					X																											Wade 1935
			Belichthys magnidorsalis					X																											Wade 1935
			Belichthys minimus					X																											Wade 1935
	Saurichthyiformes		*Saurichthys* cf. *S. gigas*	X																															Woodward 1890 and Turner 1982
			Saurichthys gigas					X																											Woodward 1890
			Saurichthys gracilis					X																											Woodward 1890
			Saurichthys parvidens					X																											Wade 1935
			Saurichthys sp.		X		X																												Turner 1982
		Palaeonisicidae	*Acrolepis hamiltoni*		X																														Johnston & Morton 1890
			Acrolepis tasmanicus		X																														Johnston & Morton 1891
			Agecephalichthys granulatus					X																											Wade 1935
			Apateolepis australis					X																											Woodward 1890
			Elonichthys armatus					X																											Woodward 1908
			Elonichthys semilineatus					X																											Woodward 1908
			Elpisopholis dunstani					X																											Woodward 1908
			Leptogenichthys longus					X																											Wade 1935
			Megapteriscus longicaudatus					X																											Wade 1935
			Mesembroniscus longisquamosus					X																											Wade 1935
			Myriolepis clarkei					X																											Egerton 1864
			Myriolepis latus					X																											Egerton 1864
			Myriolepis pectinata					X																											Wade 1931
			Palaeoniscus antipodeus																																Egerton 1864
			Palaeoniscus crassus					X																											Woodward 1908

		Platysomidae	*Platysomus* sp.					X																											Woodward 1908
		Redfieldiformes	*Beaconia spinosa*					X																											Wade 1935
			Brookvalia gracilis					X																											Wade 1933
			Brookvalia parvisquamata					X																											Wade 1933
			Brookvalia propennis					X																											Wade 1933
			Brookvalia sp.						X																										Pledge & Baulch 2013
			Clethrolepis alta					X																											López-Arbarello & Zavattieri 2008
			Clethrolepis granulatus					X																											López-Arbarello & Zavattieri 2008
			Clethrolepis sp.		X																														López-Arbarello & Zavattieri 2008
			Dictyopleurichthys latipennis					X																											Wade 1935
			Dictyopyge illustrans					X																											Woodward 1890
			Dictyopyge robusta					X																											Woodward 1890
			Dictyopyge symmetrica					X																											Woodward 1890
			Geitonichthys ornatus					X																											Wade 1935
			Molybdichthys junior					X																											Wade 1935
			Phlyctaenichthys pectinatus					X																											Wade 1935
			Schizurichthys pulcher					X																											Wade 1935
		Perleidiformes	*Manlietta crassa*					X																											Wade 1935
			Procheirichthys ferox					X																											Wade 1935
			Tripelta dubia					X																											Woodward 1890
			Chrotichthys gregarius					X																											Woodward 1890
			Pristisomus gracilis					X																											Woodward 1890
		Pholidopleuridae	*Macroaethes altus*					X																											Wade 1935
			Macroaethes brookvalei					X																											Wade 1932
	Acipenseriformes		*Psilichthys selwyni*											X																					Hilton & Forey 2009
	Paraseminotiformes		*Promecosomina beaconensis*					X																											Wade 1935
			Zeuchthiscus australias					X																											Wade 1940
			Promecosomina formosus					X																											Wade 1935

	Macrosemiiformes		*Uarbryichthys latus*										X																						Wade 1935
Holostei			*Pristisomus latus*					X																											Woodward 1890
			Aphenlepis australis										X																						Woodward 1895
			Aetheolepis mirabilis										X																						Woodward 1895
	Ionoscopiformes		*Canaryichthys rozefelds*																X																Bartholomai 2015
		Family Non. Det.	*Enigmatichthys attenuatus*					X																											Wade 1935
Teleosteomorpha	Pachycormiformes		*Australopachycormus hurleyi*																X																Kear 2007
Teleostei	Aspidorhynchiformes		*Richmondichthys sweeti*																X	X															Bartholomai 2004
	'Pholidophoriformes'	Pholidophoridae	*Pholidophorus australis*					X																											Woodward 1908
		Archae	*Archaeomaene tenuis*										X																						Bean 2017

			Wadeichthys oxyops													X																		Waldman 1971
		Luisiellidae	*Cavenderichthys talbragarensis*										X																					Sferco et al. 2015
			Leptolepis' crassicauda											X																				Hall 1900
			Waldmanichthys koonwarri													X																		Sferco et al. 2015
	Ichthyodectiformes		*Cooyoo australis*																X	X														Less and Bartholomai 1987
			Cladocyclus geddesi																				X											Berrell et al. 2014
			Dugaldia emmilta																X															Cavin and Berrell 2019
			Koonwarria manifrons													X																		Waldman 1971 & Cavin pers. comm.
	Elopiformes		*Flindersichthys deameni*																X	X														Bartholomai 2010a
			Marathonichthys coyleorum																	X														Bartholomai 2013
			Stewartichthys leichhardti																	X														Bartholomai 2013
			Euroka dunravenensis																	X														Bartholomai 2010
	Crossognathiformes		*Pachyrhizodus marathonensis*																X	X														Bartholomai 2012
			Pachyrhizodus grawi																X	X														Bartholomai 2012
			Pachyrhizodus sp.																											X				Siversson pers. comm.
	Aulopiformes		*Apateodus* sp.																X															Berrell et al. 2016 and this study
	Clupeiformes		Undescribed specimen																	X														Smith pers. Comm.
Sa rc	C oe		Knocklofty FTM specimen		X																													Dziewa 1980

			Kockatea Shale specimen			X																												Haig et al. 2019
	Dipnoi	Sagenodontidae	*Apheiodus anapes*	X																														Kemp A. 1993a
		Gnathorhizidae	*Namatozodia pitikanta*	X																														Kemp A. 1993a
		Ceratodontidae	*Ariguna formosa*					X																										Wade 1935
			Ceratodus diutinus																x			x												Kemp A. 1993b
			Ceratodus sp.													X																		Waldman 1971
			Gosfordia truncata					X																										Woodward 1890
			Metaceratodus ellioti																				X											Kemp A. 1997b
			Asiatoceratodus tiguidensis				X																											Kemp A. pers comm.
			Metaceratodus wollastoni											X			X		X			X	X											Kemp A. 1997b
		Ptychoceratodontidae	*Ptychoceratodus philippsi*	X	X		X																											Kemp A. 1996, Bender 2008
		Neoceratodontidae	*Archaeoceratodus avus*					X							X																			Kemp A. 1997
			Neoceratodus sp.																			X												Kemp pers comm.
			Neoceratodus nargun											X	X																			Kemp A. 1997

Note added after publication: *Neoceratodus* sp. from the Cretaceous Griman Creek Formation, is now described as *Neoceratodus potkooroki*. Kemp, A., & Berrell, R. 2020. A New Species of Fossil Lungfish (Osteichthyes: Dipnoi) from the Cretaceous of Australia, Journal of Vertebrate Paleontology, 40:3, DOI: 10.1080/02724634.2020.1822369. *Coccolepis woodwardi* and *Coccolepis australis* have been excluded from the Coccolepidid by López-Arbarello and Ebert 2021. López-Arbarello, A., and Ebert. M. 2021. Diversity of the *Coccolepis* AGASSIZ, 1843 (Coccolepididae, Chondrostei) from the Upper Jurassic Solnhofen-

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? in text represent uncertain taxonmny.

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Chapter 2. Early Triassic (early Olenekian) marine fishes of East Gondwana (Kockatea Shale) Western Australia, Australia.

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and

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2.1 ABSTRACT

A new terrestrial–marine assemblage from the lower beds of a thin outcrop section of the Kockatea Shale in the northern Perth Basin, Western Australia, contains a range of fossil groups, most of which are rare or poorly known from the Lower Triassic of the region. To date, the collection includes spinose acritarchs, organic-cemented agglutinated foraminifera, lingulids, minute bivalves and gastropods, ammonoids, spinicaudatans, insects, austriocaridid crustaceans, actinopterygians, a temnospondyl-like mandible, plant remains, and spores and pollen. Of these groups, the insects, crustaceans and macroplant remains are recorded for the first time from this unit.

Palynomorphs permit correlation to nearby sections where conodonts indicate an early Olenekian (Smithian) age. The locality likely represents the margin of an Early Triassic shallow interior sea with variable estuarine like water conditions, at the southwestern end of an elongate embayment within the East Gondwana interior rift–sag system preserved along the Western Australian margin. Monospecific spinose acritarch assemblages intertwined with amorphous organic matter may represent phytoplankton blooms that accumulated as mats and suggest potentially eutrophic surface waters. The assemblage represents a mixture of marine and terrestrial taxa, suggesting variations in water conditions or that fresh/brackish-water and terrestrial organisms were transported from adjacent biotopes. Some of the lower dark shaly beds are dominated by spinicaudatans, likely indicating periods when the depositional water body was ephemeral, isolated, or subjected to other difficult environmental conditions.

The biota of the Kockatea Shale is insufficiently known to estimate biotic diversity and relationships of individual taxa to their Permian progenitors and Triassic successors but provides a glimpse into a coastal-zone from the interior of eastern Gondwana. Specialist collecting is needed to clarify the taxonomy of many groups, and comparisons to other Lower Triassic sites are required to provide insights into the pattern of biotic decline and recovery at the end-Permian crisis.

2.2 INTRODUCTION

During the end-Permian mass extinction, particular marine environments have been considered refuges, encouraging the distribution and multiplication of environmentally opportunistic organisms (e.g., the bivalve *Claraia* or brachiopod '*Lingula*'; Benton and Twitchett, 2003; Rodland and Bottjer, 2001), and harbouring rare organisms that were later re-established as Lazarus taxa (Flessa and Jablonski, 1983; Wignall and Benton, 1999). Based on studies of post-extinction ichnofaunas, Beatty et al. (2008) and Zonneveld et al. (2010) suggested that broad shallow-marine shelf environments above storm-wave base, and with a well-oxygenated seafloor, acted as refuges for some burrowing animals, although Hofmann et al. (2011) questioned this geographic restriction. Other postulated refuges have included marginal normal-marine environments with mixed siliciclastic–carbonate facies showing evidence of periodic salinity and temperature fluctuations (e.g., Mata and Woods, 2008), and brackish-water deltaic settings (e.g., Gall and Grauvogel-Stamm, 2005). Estuarine-like environments subjected to great diurnal, seasonal, and longer-period variability in water quality, and inhabited by a highly adaptable biota, may have allowed some species to survive the extinction event (e.g., the conservative organic cemented agglutinated foraminifera that were prolific in shallow, restricted, intracratonic seas from the Carboniferous to the Cretaceous, as outlined by Haig and McCartain, 2010). Estuarine environments can be localized within the tidal ranges of rivers; e.g. see Ostrognay and Haig (2012) for a discussion of the high seasonal variability in modern microtidal rivers of southwestern Australia. Alternately, estuarine-like conditions may exist in large interior seas with periodic freshwater influx (e.g., the present-day Baltic Sea, and the large Permian and Cretaceous interior seas of Australia; Kunzendorf and Larsen, 2002; Haig, 2004). Therefore, the identification of estuarine-like Early Triassic environments, particularly in large interior seas, may lead to a greater understanding of why some groups survived the end-Permian extinction event. Although no single location is likely to preserve stratigraphically continuous estuarine-like facies, documentation of various facies at multiple localities and from different ages will allow reconstruction of the evolutionary history of a region’s biota. Additionally, marginal marine deposits of interior seas or estuaries may contain evidence of the terrestrial fauna and flora from the adjacent coastal plain, thereby providing a glimpse into biotas not otherwise preserved.

During the Early Triassic, an interior rift–sag system of basins—the East Gondwana rift of Harrowfield et al. (2005)—extended southwest, far into the interior of the supercontinent (Fig. 2.1A). Lower Triassic epicontinental marine deposits are known from a series of rift and sag basins along the western margin of Australia, extending from the Timor orogen in the north to the Perth Basin 2500 km to the south (Fig. 2.1B). Further southwest within this system, sedimentation along the Antarctic–

Indian margin was primarily non-marine (Turner, 1991, 1993; Veevers and Tewari, 1995; McLoughlin and Drinnan, 1997). Marine mudstone is a major component of the Lower Triassic succession in most of the Western Australian basins, and regularly includes estuarine-like facies. Except in Timor-Leste, where stratigraphic sections were disrupted by late Neogene orogenesis, these rift–sag basins are relatively undeformed and become thinner towards basin margins. Consequently, outcrop along basin margins reveals incomplete stratigraphic successions; the most complete sections are from boreholes in central parts of these basins, but few of these are even partially cored.

The basin most distal from the continent–ocean boundary to come under marine influence during the Early Triassic was the Perth Basin (Fig. 2.1A, locality A), in which the Lower Triassic succession consists of the shallow-marine Kockatea Shale in the present-day north and the coeval fluviatile Sabina Sandstone in the present-day south. Fossils have long been known from the Kockatea Shale, but most groups are sparse in both outcrop and subsurface sections. Exceptions are the abundant palynomorphs (especially acritarchs) found at all levels, and beds low in the formation in which the bivalve Claraia is concentrated (Thomas et al., 2004). The shelly fauna (excluding Claraia) is dominated by pelagic and nektonic groups, rather than by benthic forms. Although many groups have been identified in previous studies, relatively few have been thoroughly described. Noted fossils include stromatolites and other microbialites (McLoughlin and McNamara, 2001; Lipps and Culver, 2002; Thomas et al., 2004; Mory et al., 2005; Metcalfe et al., 2008; Chen et al., 2012, 2014; Luo and Chen, 2014),marine phytoplankton (Balme, 1963, 1967; Medd, 1966; Dolby and Balme, 1976; Sappal, 1978; Thomas et al., 2004), organic-cemented agglutinated foraminifera (Jones, 1970; Metcalfe et al., 2008), inarticulate brachiopods (Dickins and McTavish, 1963), bivalves (Dickins and McTavish, 1963; Skwarko and Kummel, 1972; McTavish and Dickins, 1974; Thomas et al., 2004; Metcalfe et al., 2008), gastropods (Metcalfe et al., 2008), nautiloids (Skwarko and Kummel, 1972), ammonoids (Edgell, 1964; Skwarko and Kummel, 1972; McTavish and Dickins, 1974; Bolton et al., 2010; Chen et al., 2012), echinoid spines (tentatively identified; Metcalfe et al., 2008), spinicaudatans (previously referred to as ‘conchostracans’; Fig. 2.1.

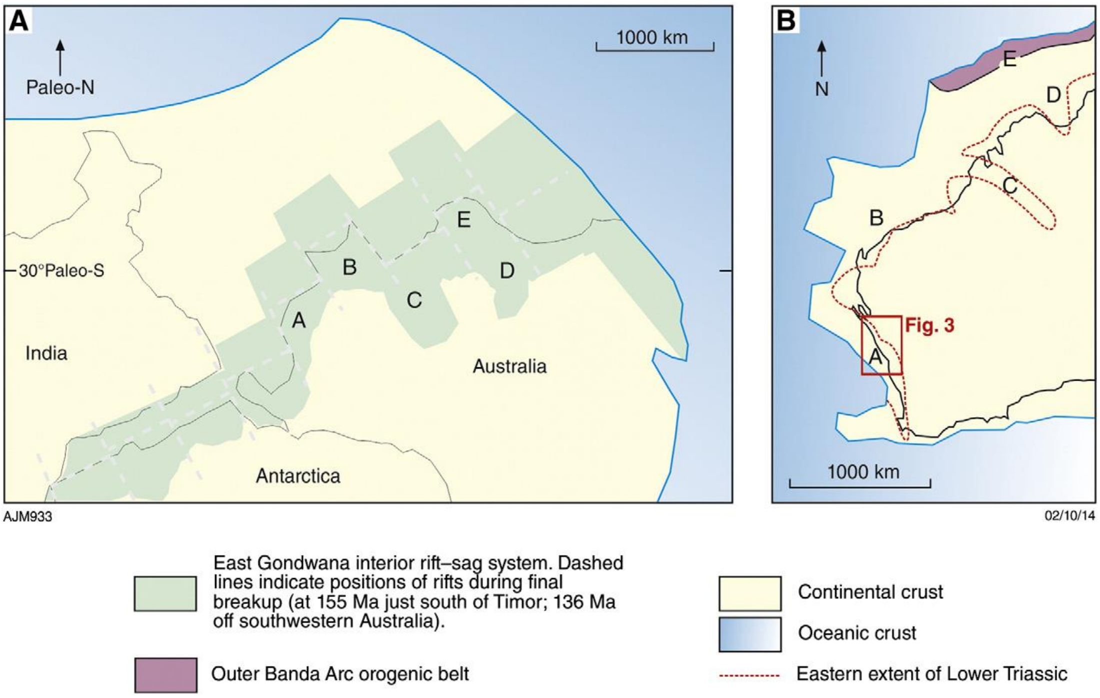


Figure 2.1. Geological setting: A. Early Triassic palaeogeographic reconstruction, showing the basins within the East Gondwanan interior rift–sag system (modified from Harrowfield et al., 2005); B. Distribution of basins containing Lower Triassic strata in Western Australia. A= Perth Basin (Playford et al., 1976a; Mory and Iasky, 1996; Metcalfe et al., 2013), B= Northern Carnarvon Basin (Gorter, 1994), C =

Canning Basin (Mory, 2010); D= Bonaparte Basin (Mory, 1988; Nicoll and Foster, 1998; Gorter et al., 2010); E = Timor-Leste (Charlton et al., 2009).

Dickins and McTavish, 1963; Cockbain, 1974; Tasch and Jones, 1979b), ostracods (Jones, 1970; Metcalfe et al., 2008), microconchids (previously considered spirorbid annelids; Dickins and McTavish, 1963; Thomas et al., 2004), conodonts (McTavish, 1973; Nicoll and Foster, 1998; Metcalfe et al., 2008, 2013), fish debris (Dickins and McTavish, 1963; Thomas et al., 2004; Metcalfe et al., 2008), amphibians (Dickins and McTavish, 1963; Cosgriff, 1965), land-plant spores and pollen (Balme, 1963, 1967; Dolby and Balme, 1976; Thomas et al., 2004; Metcalfe et al., 2008), and trace fossils (Dickins and McTavish, 1963; Bolton et al., 2010; Chen et al., 2012; Luo and Chen, 2014).

Fossil preservation in outcrop of the Kockatea Shale, from which most of the rarer macrofossils have been collected, is typically poor owing to heavy oxidization caused by intense weathering during the Cenozoic, with contacts between permeable quartz-sandstone beds and impermeable shale usually highly ferruginized (e.g., see figures of Luo and Chen, 2014). Here, we identify an outcrop section containing shale that, in the lowermost beds, is both far less weathered than normal and lacks the typical iron-oxide overprint. Furthermore, the site has yielded a large fossil assemblage (diverse only at the highest taxonomic levels, and low in specimen numbers) comprising both marine and terrestrial components, including groups not previously recorded from the formation. This paper provides a preliminary inventory of the groups from the site, comparing this material both with prior records from the formation and with fossils from coeval beds (Fig. 2.2) elsewhere in the East

Gondwana interior rift–sag system. The information presented here provides substantial insights into the biota of Early Triassic shallow-marine estuarine-like environments at the margins of an interior sea within eastern Gondwana.

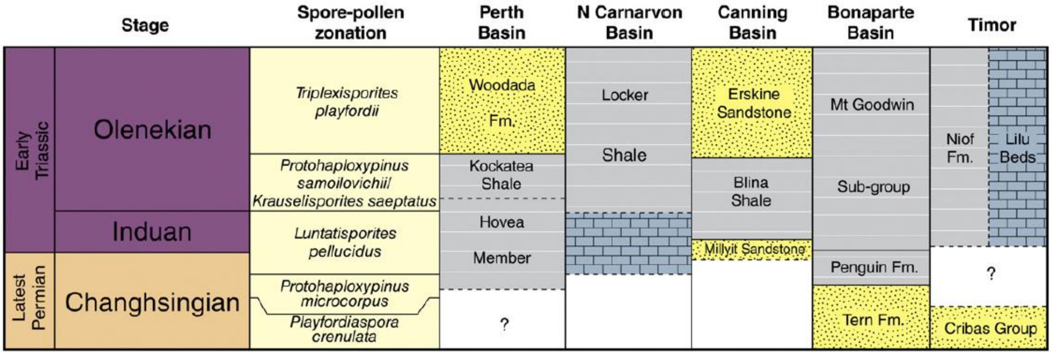


Figure 2.2. Correlation of the uppermost Permian – Lower Triassic succession in basins shown on Fig. 2.1. The Hovea Member is the lowest part of the Kockatea Shale (Thomas et al., 2004).

2.3 GEOLOGICAL SETTING

The Kockatea Shale is exposed as several isolated, thin (b40 m; Playford et al., 1976a,b) sections along the northern margin of the Perth Basin, up to 120 km north northwest and 75kmeast of the coastal city of Geraldton (Fig. 2.3). The exposures lie unconformably on Precambrian crystalline basement or lower Palaeozoic sandstone, and are overlain disconformably by Jurassic strata (Playford et al., 1976a,b). In the subsurface, the Kockatea Shale extends at least 200 km to the south and southeast of Geraldton, where it thickens to at least 1060 m (Mory and Iasky, 1996), and lies between Permian and Middle Triassic strata (Figs. 2.3, 2.4).

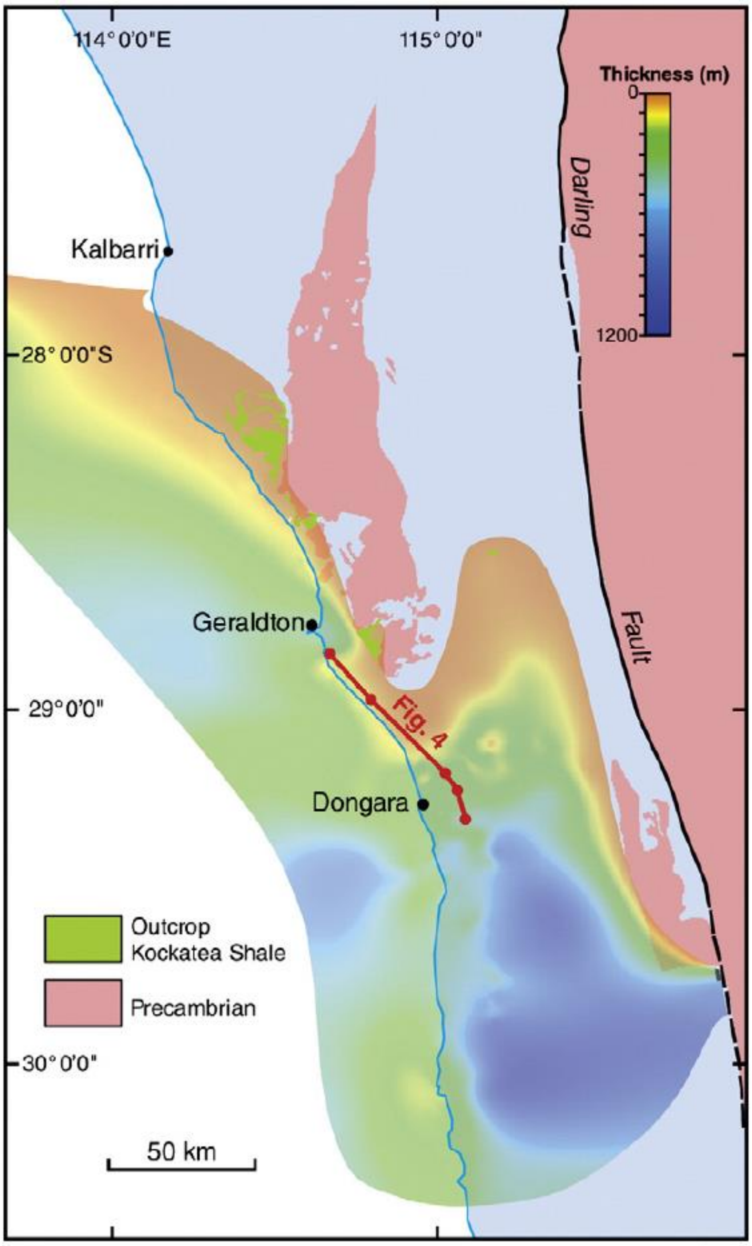


Figure 2.3. Isopach map of the Kockatea Shale, northern Perth Basin.

In the subsurface, the unit encompasses uppermost Permian to more widespread Induan intervals, in places preserving the Permian–Triassic boundary (Thomas et al., 2004; Metcalfe et al., 2008, 2013). Strata exposed at the basin margins appear to represent the upper part of the formation, based on Olenekian ammonoids from some localities (Edgell, 1964; Skwarko and Kummel, 1972). Although penecontemporaneous fault movement is required to explain at least some of the southward thickening in the subsurface, onlap onto the Precambrian basement, or Palaeozoic strata at the margin of the basin, best explains why only the uppermost part of the formation is preserved in outcrop (Fig. 2.4). In the subsurface, the unit is within the oil window and forms an important source rock and seal unit for ten small gas fields with minor oil shows (Owad-Jones and Ellis, 2000), some of which are now depleted. By comparison, the pale colours of palynomorphs from outcrop indicate only shallow burial, thereby suggesting that the overall northward thinning of the Mesozoic succession, and breaks within it, are due to non-deposition rather than erosion.

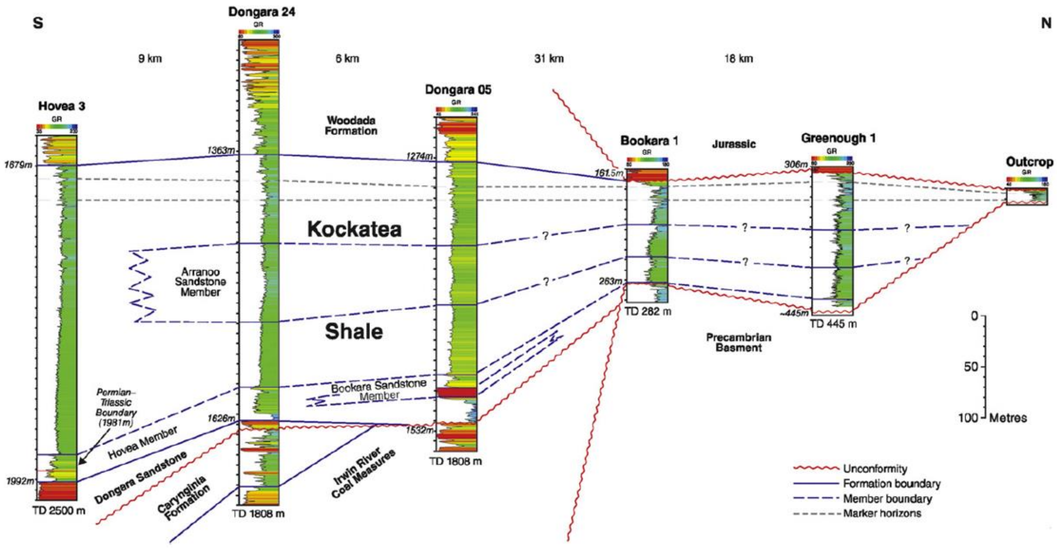


Figure 2.4. North–south correlation of the Kockatea Shale from Hovea 3 to outcrop near Geraldton showing progressive onlap to the north. The three members of the Kockatea Shale are labelled next to their respective type sections. Line of section shown on Fig. 2.3; detailed outcrop gamma-ray measurements shown on Fig. 2.5. For descriptions of units older than the Kockatea Shale,
see Mory and Iasky (1996).

The present study is based on the lower 1m of an 11-m-thick exposure of the Kockatea Shale (Fig. 2.5), which consists of fresh, grey, laminated, pyritic mudstone at its base, succeeded by mainly shale for the bottom 1 m of the section. Thin beds of fine-grained quartz sandstone, alternating with shale layers, are more common above 1 m, with sandstone beds becoming thicker, coarser grained, and more closely spaced up-section. The sandstone generally displays ripple laminations, and the progradational nature of the succession suggests a shoaling-upward trend. The whole section is increasingly oxidized up-section. The fossil assemblage was collected from the same stratigraphic level at two localities about 60m apart; above this level, the rocks are extremely weathered, and fossils are rare and very poorly preserved.

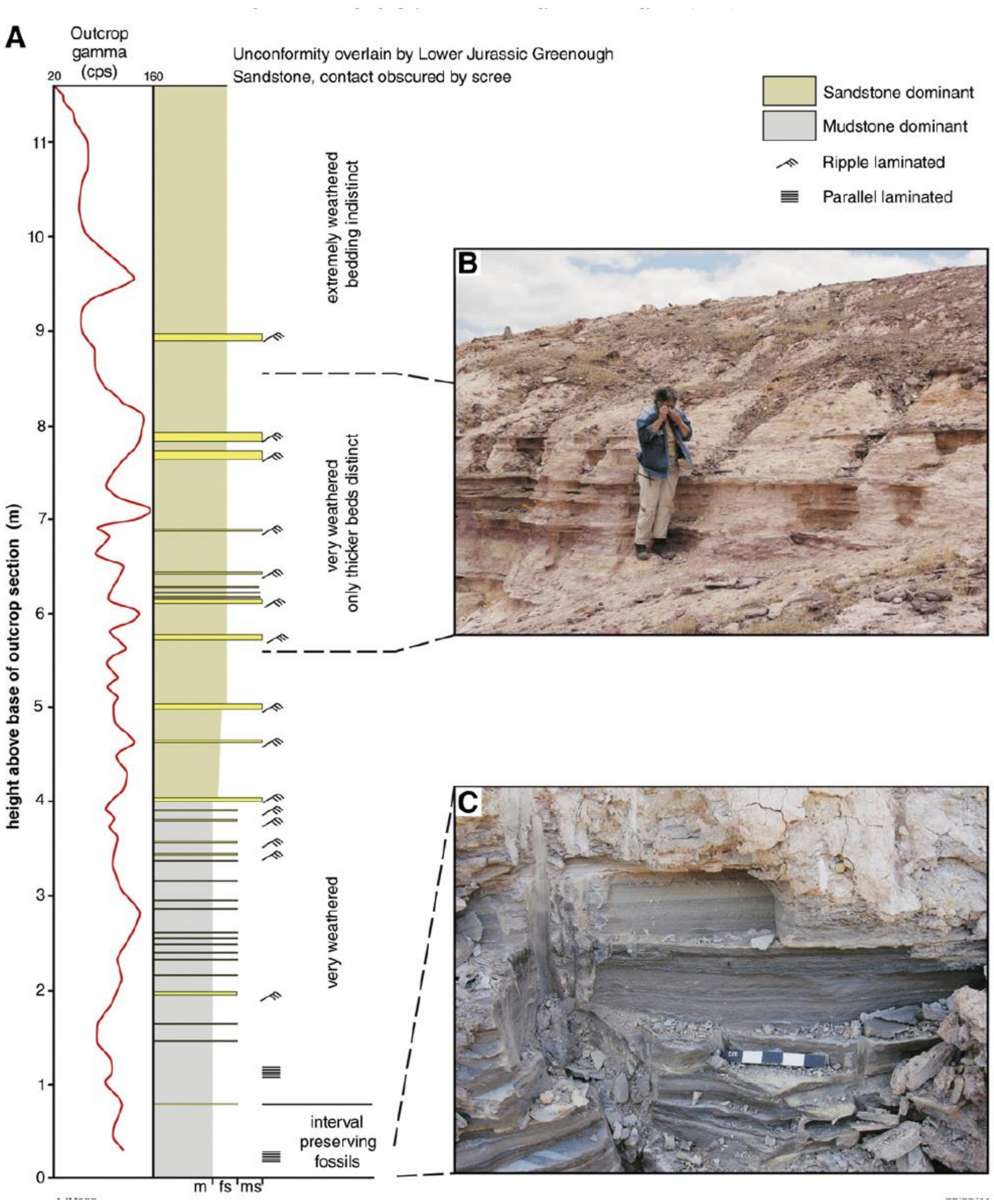


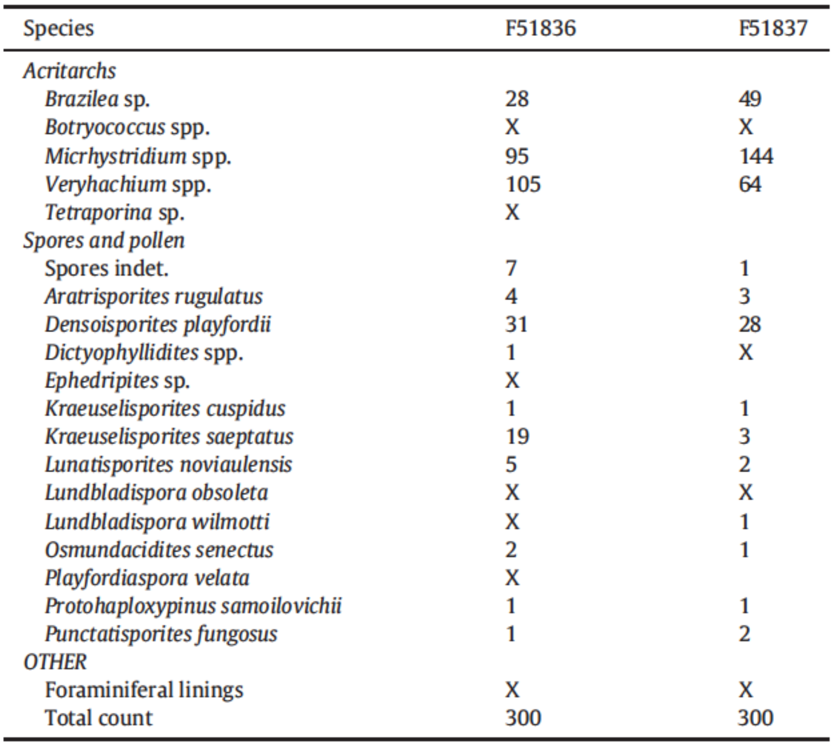
Figure 2.5. Studied outcrop section (A) of the Kockatea Shale correlated to uncalibrated outcrop gamma-ray measurements (in counts per second); images B and C show nature of outcrop at particular heights within the section.

The fossils are preserved on bedding surfaces in compact but very friable laminated shale. On exposure to air, fine gypsum rosettes form on the surfaces of the samples as they dry out, thereby obscuring some specimens. Most of the fossils are impressions; calcium carbonate in particular has been completely removed during diagenesis. Low in the section, plant remains retaining relict carbonized matter, spinicaudatans retaining their chitinous carapaces, well-preserved palynomorphs and small pyritized gastropods and bivalves are present, suggesting variable taphonomic and diagenetic influences throughout the section. Locality details for this new site have been lodged with the Geological Survey of Western Australia (GSWA), Western Australian Museum (WAM), and the Earth Science Museum at The University of Western Australia (UWA). All specimens are housed in the Earth Science Museum under acquisition numbers UWA163873 and UWA163874. Palynomorph slides F51836 and F51837 are housed in the Paleontological collection of the Geological Survey of Western Australia. England finder coordinates for the illustrated acritarchs and pollen are stored with the slides.

2.4 METHODS

Large slabs of shale were collected in the field and then carefully split in the laboratory where the surfaces were examined under low magnification in reflected light. Recognizable fossils, most of which are small, were numbered and photographed. Two samples of grey laminated shale excavated from the lowest part of the outcrop were processed for palynomorphs by digestion in hydrofluoric acid (HF)— higher beds were considered too oxidized to sample. The sample points were collected close together, with F51837 (Table 2.1) about 0.5mhigher in the section than F51836. Both samples were highly productive and counts of 300 palynomorphs were made on each assemblage as a quantitative evaluation. An additional sample of the grey shale was disaggregated in boiling water with detergent, and wet-sieved through 63 μm and 150 μm meshes. The washed residues were examined under a stereomicroscope in reflected light.

Table 2.1. Counts of acritarch, microspore and pollen species. X = species present but not included in specimen count.



Species	F51836	F51837
Acritarchs		
Brazilea sp.	28	49
Botryococcus spp.	X	X
Micrhystridium spp.	95	144
Veryhachium spp.	105	64
Tetraporina sp.	X	
Spores and pollen		
Spores indet.	7	1
Aratrisporites rugulatus	4	3
Densoisporites playfordii	31	28
Dictyophyllidites spp.	1	X
Ephedripites sp.	X	
Kraeuselisporites cuspidus	1	1
Kraeuselisporites saeptatus	19	3
Lunatisporites noviaulensis	5	2
Lundbladispora obsoleta	X	X
Lundbladispora wilmotti	X	1
Osmundacidites senectus	2	1
Playfordiaspora velata	X	
Protohaploxypinus samoilovichii	1	1
Punctatisporites fungosus	1	2
OTHER		
Foraminiferal linings	X	X
Total count	300	300

Because several megaspores were recovered from the washed residues, which also contained foraminifera and pyritized micro-bivalves and micro-gastropods, a small amount of the basal grey shale was processed specifically to find more megaspores.

About 45 g of sample was broken into 5–10 mm pieces and soaked in distilled water for seven days, breaking the sample down into a clay–silt slurry. Siliceous grains were removed by treatment with ~30% HF solution for an additional seven days; after neutralizing the solution, the residue was wet-sieved through 150 µm mesh.

Centrifuging was not used in the processing. No whole megaspores were found using this process, although wall fragments up to 250 µm in length were present in the preparations, as were large mat-like fragments, 1–5 mm long and containing abundant acritarchs.

The section was measured using a Jacobs’s staff and Abney level, with gamma readings taken every 10 cm as an aid for correlation across minor faults in the section and to the subsurface. A detailed log of the section (Fig. 2.5.) is provided to support the correlation to petroleum exploration wells to the south (Fig. 2.4.).

2.4 FOSSIL ASEMBLAGE

Microplankton

Acritarchs dominate the palynomorph assemblages, contributing 76% and 86% of the content in slides F51836 and F51837, respectively (Table 2.1.). Acanthomorph and polygonomorph (spinose) acritarchs are dominant, although sphaeromorph acritarchs in the form of *Brazilea* sp. are also common. All acanthomorph forms are assigned to *Micrhystridium* spp., although the most common form (Fig. 2.6.A) has similarities to *Filisphaeridium* spp. They range from spherical forms with over 50 slender processes, to forms with a spherical to subspherical test and fewer than 30 processes (Fig. 2.6.B–D). Polygonomorph forms are all assigned to *Veryhachium* spp.; unsculptured forms (Fig. 2.6.G, H) are the most abundant, although forms with finely sculptured tests (Fig. 2.6.F) are also present in significant numbers.

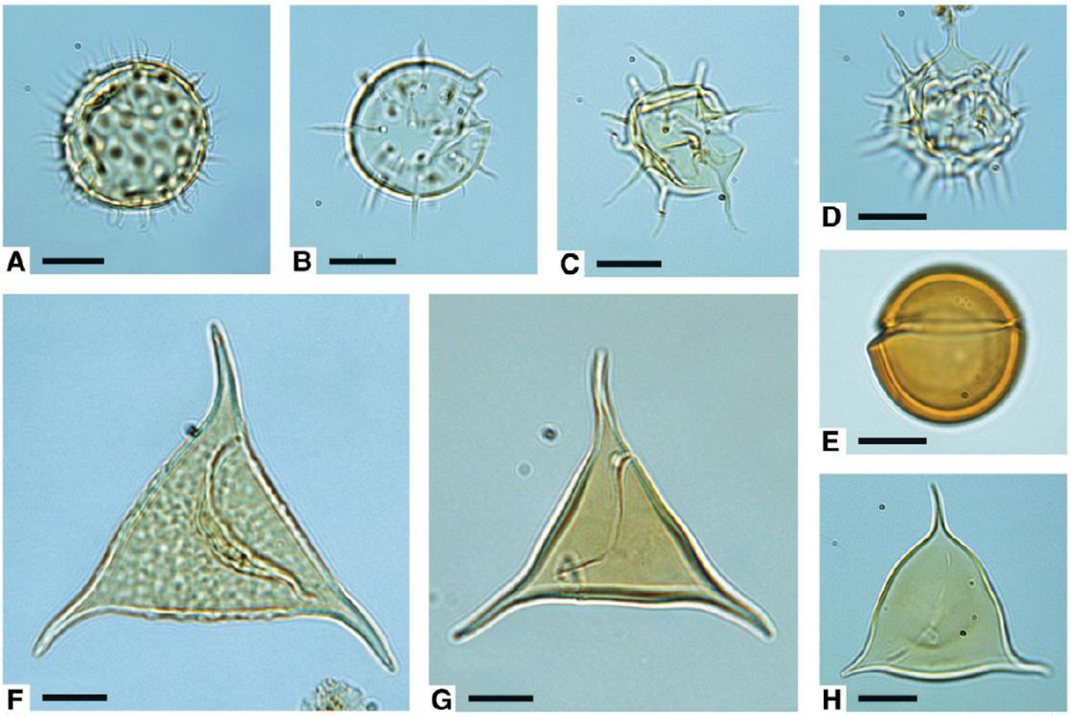


Figure 2.6. Acritarchs: A–D. *Micrhystridium* spp.; E. *Brazilea* sp.; F–H. *Veryhachium* spp. All specimens from basal grey shale. Scale bars= 10 µm.

Gentle processing of the shale for megaspores (see Section 3) revealed clusters of acritarchs, usually monospecific mats of *Micrhystridium* spp. but less commonly of *Veryhachium*, embedded within amorphous organic matter (Fig. 2.7.).

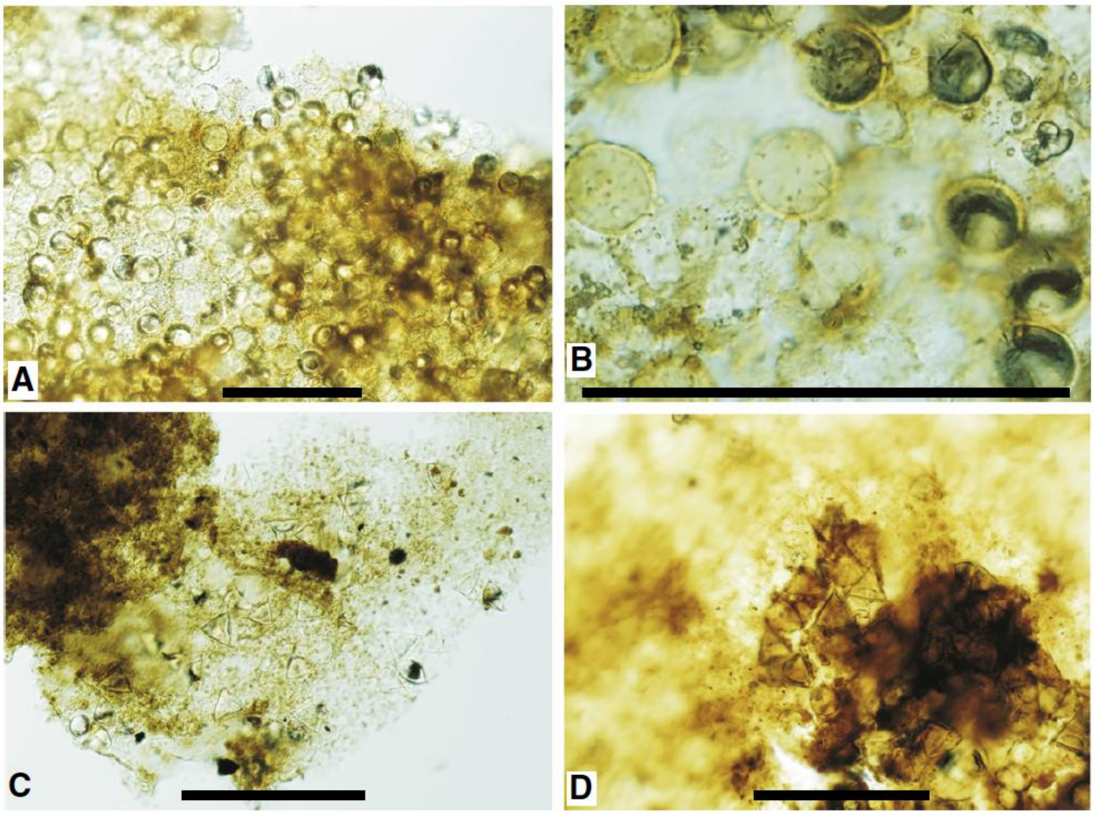


Figure 2.7. Mats from basal grey shale composed of monospecific clusters of acritarchs (resting cysts) and amorphous organic matter: A, B. Clusters of *Micrhystridium* sp.; C, D. Clusters of *Veryhachium* sp. Scale bars= 100 µm.

Individual specimens are 18–20 µm in diameter and uncompressed, as shown by single air bubbles within individual cysts. Thomas et al. (2004) reported similar clusters of acritarchs in the subsurface sections of the Kockatea Shale, within the sapropelic interval of the Induan Hovea Member in Hovea 3. Furthermore, both Balme (1963) and Sappal (1978) demonstrated the great numerical dominance of acritarchs in samples from several boreholes to the east and south of Geraldton. The preservation of the mats and great abundance of the acritarchs may indicate both the presence of phytoplankton blooms in surface waters of the interior sea, and that resting cysts formed intertwined organic mats with amorphous organic matter or its precursor on the seafloor. Grice et al. (2005) found the biomarker C33nalkylcyclohexane, which is related to the association of abundant acritarchs and amorphous organic matter, in the Kockatea Shale. Acritarchs of the types found in our samples are well known from units of similar age in other basins of the East Gondwana interior rift– sag system—i.e. the Locker Shale of the Northern Carnarvon Basin (Dolby and Balme, 1976), Blina Shale of the Canning Basin (Gorter, 1978a), and upper Hyland Bay Formation and Mount Goodwin Subgroup of the Southern Bonaparte Basin (Foster et al., 1997; Gorter et al., 1998; Fig. 2.1.A, localities B–D, respectively). Medd (1966) and Sappal (1978) provided the only descriptions of material specifically from the Kockatea Shale. Examples of the brackish−freshwater, planktonic green alga *Botryococcus* sp. (Fig. 2.8.) are present but rare in the palynological preparations. These would have been transported to the depositional site by rivers flowing into the interior sea.

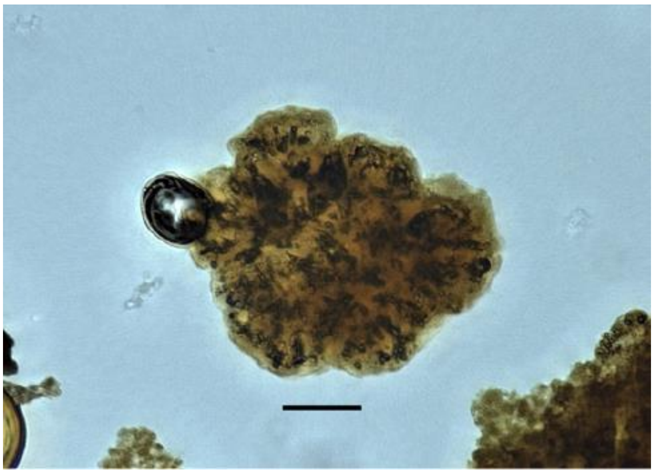


Figure 2.8. *Botryococcus* sp. from basal grey shale. Scale bar = 10 µm.

4.2. Foraminifera

Very rare, small, organic-cemented siliceous agglutinated foraminifers referable to *Ammodiscus* (Fig. 2.9. C, D) have been recovered from washed residues of the grey shale at the base of the section. These resemble *Ammodiscus parapriscus* Ho, which was recorded by Haig and McCartain (2010, p. 373, figs. 3.31–3.33) from the Anisian to Rhaetian of Timor-Leste (Fig. 2.1., locality E), but there is presently insufficient material from the Kockatea Shale to confirm this identification or to determine intraspecific variability. The recovery of rare organic linings of foraminiferal tests in the palynology preparations indicate that there is a more diverse suite of foraminifera at this site than recovered from washed residues. Organic linings include a trochospiral test, perhaps of the organic-cemented agglutinated *Trochammina* (Fig. 2.9.A), and an apparently biserial form, possibly belonging to the organic-cemented agglutinated *Palustrella* (see Haig and McCartain, 2010; Fig. 9B). This sparse foraminiferal assemblage may be widespread in the Kockatea Shale because Jones (1970) also reported poorly preserved foraminifera, mainly *Ammodiscus* spp., from subsurface samples. Other records of foraminifera from the Kockatea Shale include unnamed small forms noted by Metcalfe et al. (2008) from acid-insoluble residues of shale and thin limestone beds, collected from core of the sapropelic interval within the Induan part of the Hovea Member. Elsewhere in the East Gondwana interior rift–sag system, a more diverse Lower Triassic foraminiferal assemblage of lagenids and involutinids (attributed to *Lingulina* and *Trocholina*) were described by Heath and Apthorpe (1986) from the Locker Shale in the Northern Carnarvon Basin; McTavish (1973) also mentioned unnamed agglutinated foraminifera from this formation. Gorter (1978b) reported abundant foraminifera from subsurface sections of the Blina Shale in the Canning Basin, although only specimens of *Ammodiscus* spp. were identified, and similar foraminifera were reported by Gorter et al. (2010) from the Mount Goodwin Subgroup in the Southern Bonaparte Basin. From Timor-Leste, Haig and McCartain (2010) recorded species of

Ammobaculites and *Tolypammina* from acid-insoluble residues of limestone from the Olenekian part of the Lilu Beds. Lower Triassic foraminifera are not known elsewhere in the Australian region. *Ammodiscus* is a major component of the Ammobaculites Association, which was characteristic of very shallow marine shale facies of late Paleozoic and Mesozoic epeiric seas in the Australian region (Haig, 2004; Haig and McCartain, 2010). The association is indicative of estuarine like conditions that were seasonally variable in terms of salinity, dissolved-oxygen, turbidity, and temperature. Conversely, the lagenid–involutinid fauna present in the Northern Carnarvon Basin suggests more open-marine conditions within that part of the rift–sag system.

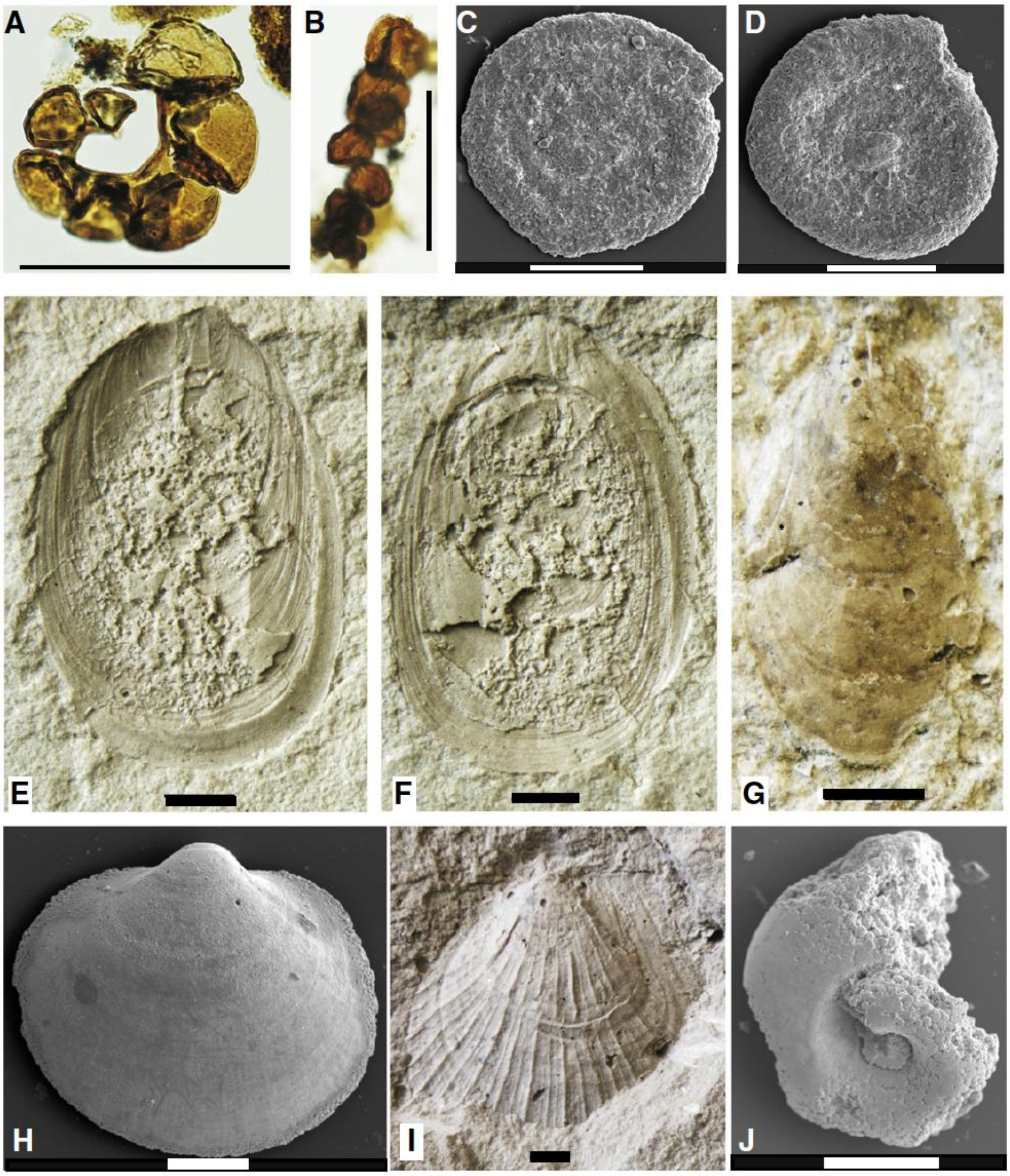
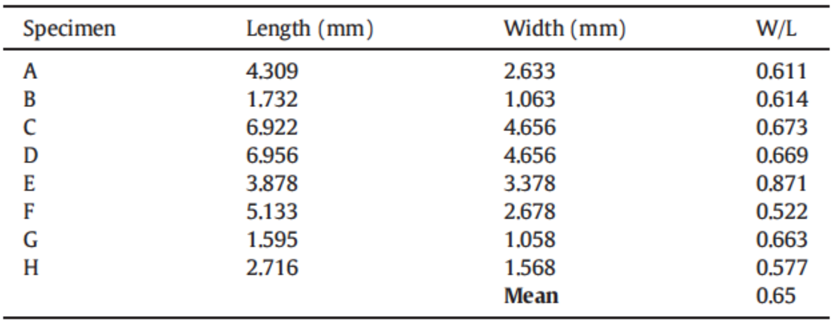


Figure 2.9. Representatives of the shelly fauna. A–D. Foraminifera: A. Organic lining observed in palynomorph preparation, ?*Trochammina* sp.; B. Organic lining observed in palynomorph preparation, ?*Palustrella* sp.; C, D. *Ammodiscus* sp., scanning electron micrographs; scale bars =100 µm. E–G. Lingulid brachiopod moulds: E, F. Counterpart specimens; scale bars = 1 mm. H. Pyritic internal mould of micro-bivalve, scanning electron micrograph, scale bar = 100 µm. I. *Leptochondria* sp., internal mould, bar scale= 1 mm. J. Pyritic internal mould of microgastropod, scanning electron micrograph, scale bar= 100 µm.

4.3. Brachiopods

Lingulid brachiopods are rare at the studied site and are preserved as incomplete internal and external moulds of disassociated valves (Fig. 2.9. E–G). Due to a lack of muscle-scar traces and other internal features within the valves, which are critical for generic identification, it is impossible to ascribe these lingulids to any particular genus. However, based entirely on shell size and shape (Table 2.2.), especially the width to length ratio, they likely belong to either Lingularia or Sinolingularia. Early Triassic lingulids have been reported from East Greenland, Spitzbergen (Norway), Italy, Hungary, Iran, western Pakistan, South China, Siberia, southeastern and northeastern Japan, Western Australia, western Canada and northwestern USA. Although Lingula s.s. is now largely restricted to Cenozoic and extant forms, the most recent taxonomic revision of this genus (Peng, 2007; Peng and Shi, 2008) showed that there were at least five lingulid genera globally in the Early Triassic: Lingularia Biernat and Emig, Sinolingularia Peng and Shi, Sinoglottidia Peng and Shi, Semilingula Popov, and an as yet unnamed genus.

Table 2.2. Dimensions of lingulid brachiopods.



Specimen	Length (mm)	Width (mm)	W/L
A	4.309	2.633	0.611
B	1.732	1.063	0.614
C	6.922	4.656	0.673
D	6.956	4.656	0.669
E	3.878	3.378	0.871
F	5.133	2.678	0.522
G	1.595	1.058	0.663
H	2.716	1.568	0.577
		Mean	0.65

Some of the specimens of ‘*Lingula*’ sp. described by Dickins and McTavish (1963, p. 128, pl. 1, Fig. 1) from core of the Kockatea Shale resemble those figured here

(Fig. 2.9.E–G). Elsewhere in Western Australia, Early Triassic lingulids have been recorded from the Locker Shale in the Northern Carnarvon Basin (McTavish, 1973), the Blina Shale in the Canning Basin (Teichert, 1950; Brunnschweiler, 1957; McKenzie, 1961; Gorter, 1978a,b), and the Mount Goodwin Subgroup in the Southern Bonaparte Basin (Tasch and Jones, 1979b). Due to their preferred infaunal lifestyle in muddy substrates, lingulids are adapted to variable salinity, dissolved-oxygen, and pH conditions (Posenato et al., 2014). The lingulids found in the present study are all within the range of the small-sized Triassic lingulids documented by Posenato et al. (2014, Fig. 5), which may indicate locally stressful marine environmental conditions during deposition of the Kockatea Shale.

4.4. Bivalves

The bivalve assemblage recovered includes both heteroconchs and pteriomorphs. Apparently monospecific clusters of abundant, millimetre-sized pyritic internal moulds of heteroconch bivalves (Fig. 2.9. H) are preserved on bedding surfaces in the basal grey shale, where they are associated with pyritic internal moulds of similar sized gastropods. Larger, very rare, aviculopectinoids have also been found in more weathered shale layers, as both internal and external moulds. These include specimens that may be attributable to Leptochondria (Fig. 2.9. I). Claraia has been reported in large numbers from borehole sections of the lower Kockatea Shale (Dickins and McTavish, 1963; McTavish and Dickins, 1974; Thomas et al., 2004; Metcalfe et al., 2008). Other records of bivalves from the formation include Trigonucula sp., Bakevellia sp., and ‘Anodontophora’ cf. griesbachi Bittner described by Dickins and McTavish (1963); a ‘Pteriacea indet.’ illustrated by Skwarko and Kummel (1972); and a similar association of pyritized micro-bivalves and micro-gastropods illustrated from the sapropelic unit in the Hovea Member by Metcalfe et al. (2008). Elsewhere in the East Gondwana rift–sag system, Gorter (1978a) noted forms previously reported as Anomia sp. and cf. Pseudomonotis sp. from the Blina Shale of the Canning Basin; and Claraia sp. has been found in variegated shale attributed to the Ni of Formation in Timor-Leste (E. McCartain and D.W. Haig, unpublished observations). The monospecific assemblage of small heteroconchs may have been part of a shallow infauna living in organic-rich mud, or else may represent mass mortality of very thin shelled planktonic D-larval stages of a species that inhabited more favourable conditions elsewhere. The aviculopectinoids were probably byssate-attached bivalves, either resting on the seafloor or attached to floating algae or other degradable objects (e.g., Kauffman, 1969).

4.5. Gastropods

The pyritic internal moulds of millimetre-sized, relatively low aspect, trochospiral gastropods (Fig. 2.9. J) are associated with the pyritic moulds of heteroconch micro-bivalves mentioned in 4.4. Like the bivalves, these gastropods appear monospecific and similarly may be part of a shallow infauna, or else represent the larval stages of a gastropod species whose mature individuals lived elsewhere. Elsewhere in the Kockatea Shale, Metcalfe et al. (2008) reported similarly pyritized micro-gastropods in the subsurface sapropelic interval from the upper part of the Hovea Member. In their compilation of Lower Triassic micro-gastropod records, Fraiser et al. (2005) listed their presence within core of Kockatea Shale from an unnamed well. McTavish (1973) also reported ‘microscopic’ gastropods from the Locker Shale in the Northern Carnarvon Basin.

4.6. Ammonoids

Several distinct ammonoid genera are preserved as laterally flattened impressions (Fig. 2.10), with some being smooth, some having fine, dense, sinuous growth lines, and all showing varying degrees of shell involution. Because of the style of preservation, no details of the venter (whether tabulate, rounded, or sharp) or the umbilical wall (whether sloping, vertical, or undercut) can be determined; these being the key features for the taxonomy of Early Triassic ammonoids. Even the nature of the shell coiling (degree of involution/evolution) is difficult to discern in most specimens due to crushing.

Numerous smooth forms with varying degrees of involution have recently been illustrated from the Lower Triassic of Spiti (northern India; Brühwiler et al., 2010b), South Primorye (far eastern Russia; Shigeta et al., 2009), South China (Brühwiler et al., 2008), and southern Tibet (Brühwiler et al., 2010a). Similar forms from the studied Kockatea site (e.g., Fig. 2.10. F, G, I) resemble genera from the Griesbachian, Dienerian, and Smithian of South Primorye, such as *Clypeoceras*, *Arctoceras*, *Paranorites*, *Proptychites*, *Pseudoproptychites*, and *Ambitoides*; *Tulongites* from the Smithian of south Tibet; and *Shangganites* and *Proptychites* from the Griesbachian–Dienerian of South China. As noted above, more precise generic assignments are not possible without additional information on the nature of the venter, umbilical wall, and shell involution.

Forms with stronger shell ornamentation are similar to the inner whorls of *Xenodiscoides* and *Flemingites* species from beds near the Dienerian–Smithian boundary in Spiti (our Fig. 2.10J) and to *Radioprionites* from the Smithian of South

Primorye (our Fig. 2.10H). The larger, involute forms with fine and densely spaced growth lines (our Fig. 2.10K, L) resemble some Induan species of *Clypeoceras*, *Paranorites*, and *Pseudoproptychites*.

Lying near the aperture of the body chamber of one of the smooth, involute ammonoid shells are an upper and lower jaw (Fig. 2.10F). In addition, approximately 19 isolated upper (e.g., Fig. 2.10A, B, D) and lower (e.g., Fig. 2.10C, E) jaw elements have been found on other bedding planes.

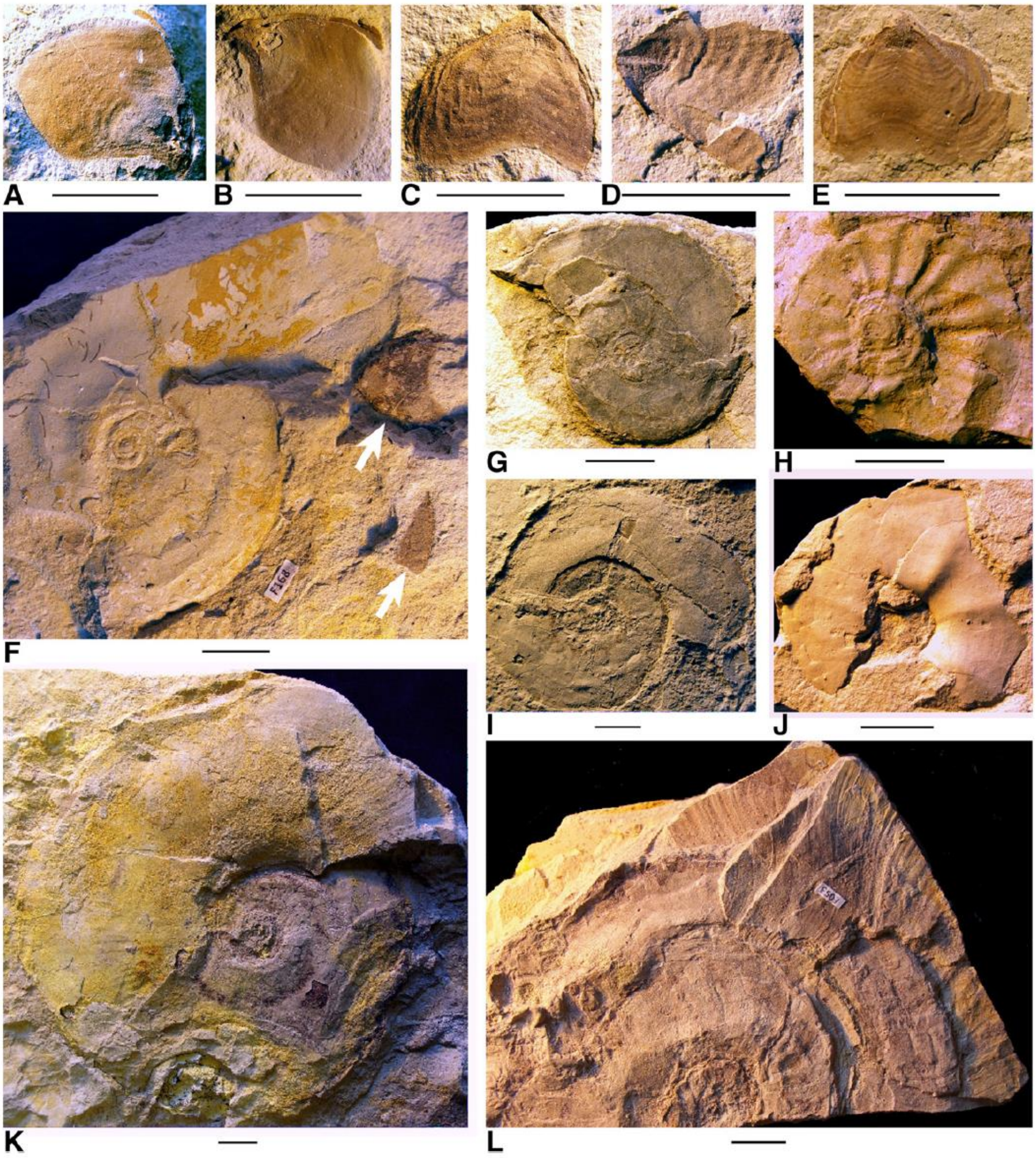


Figure 2.10. Ammonoids. A–F, ammonoid jaw elements: A, B. Upper jaw showing rostrum, faint growth lines, and small part of right wing separated by thin sediment layer in B; C–E. Lower jaws showing rostrum, coarse growth lines, and broad embayment on posterior margin; F. Lateral impression of smooth, involute ammonoid with jaw elements (arrowed) preserved adjacent to aperture of last whorl. G–L. Lateral impressions of ammonoids: G. Moderately involute, smooth shell with possible tabulate venter; H. Involute form with strong, slightly sinuous, simple ribs; I. Evolute form with very faint, sinuous growth striations; J. Smooth form with widely spaced folds on lower flanks; K, L. Larger involute forms with faint, dense, sinuous growth striations. Scale bars= 1 cm.

The wings of the upper jaws are 12–15 mm long in the anterior–posterior direction and 9–16 mm high, and are preserved as light pink-brown surfaces with faint, arcuate growth lines. The anterior ends of the jaws have a sharp, downward curved rostrum preserved as a darker coloured substance, suggesting a different composition (perhaps calcitic) to the remainder of the jaw structure. The lower jaws are broadly bilobed, with only a wide, rounded indentation separating the posterior margins of the two wings, which also bear faint growth lines; a pointed rostrum forms at the anterior end of the lower jaws. These structures closely resemble reconstructed jaw apparatuses from Lower Jurassic ammonites illustrated by Lehmann (1976, figs. 76, 78).

Several published studies have dealt with ammonoids from surface and subsurface sources in the Kockatea Shale; however, the ages assigned to these assemblages used now superseded stage and substage names. Edgell (1964) illustrated ammonoids from outcrop of the ‘Minchin Siltstone’ in the Northampton area, tentatively assigning specimens to aff. *Owenites* sp., aff. *Proptychoides* sp., and aff. *Kashmirites* sp.. Based on these identifications, he assigned an Early Triassic age to this unit and proposed its transfer to the Kockatea Shale (a designation that is now widely accepted). Dickins and McTavish (1963) identified *Ophiceras* (Discophiceras) cf. *subkyokticum* (Spath), *Subinyoites kashmiricus* (Diener) and ?*Glyptophiceras* sp. indet. in core from BMR 10 (Beagle Ridge) 61 km south of Dongara, and thereby assigned a Scythian (Otoceraten) age to this section. Skwarko and Kummel (1972) described ammonoids from two sections through the Kockatea Shale: from Dongara 4 (8 km northeast of Dongara) they identified *Proptychites* sp. indet., ?*Koninckites* sp. indet., and ?*Paranorites* sp. indet., to which they assigned an age equivalent to the Ceratite Marls of West Pakistan; and from outcrop at Mount Minchin (58 km north of Geraldton) they recognized *Arctoceras* sp. indet., *Prionites* sp. indet., *Hemiprionites* sp. indet., and *Anasibirites kingianus* (Waagen), giving a middle Scythian age.

Ammonoids of similar ages have been recognized in the Locker Shale of the Northern Carnarvon Basin (McTavish, 1973), the Blina Shale of the Canning Basin (Gorter, 1978a), and both the Niof Formation (Bird and Cook, 1991; unpublished observations of E. McCartain and D.W. Haig) and Lilu Beds (Haniel, 1915; Welter, 1922; Nakazawa and Bando, 1968; Berry et al., 1984; Charlton et al., 2009) in Timor-Leste.

4.7. Spinicaudatans

Spinicaudatans (formerly known as ‘Conchostraca’, a taxon now considered paraphyletic; Fryer, 1987; Olesen, 1998) are common at this locality, and are abundant on some bedding surfaces. Fossils are predominantly preserved in strictly lateral view, making it difficult to determine whether the carapace valves are still articulated (Fig. 2.11A), although one specimen is preserved slightly obliquely showing the valves attached at the hinge (Fig. 2.11B). There is no indication of soft tissue elements in any examples recovered to date. Most specimens are preserved as detailed impressions (commonly with both part and counterpart); however, many examples from the lower shaly layers show colour and texture variations that suggest the preservation of altered chitinous material (Fig. 2.11A). As features of the microscopic carapace ornament are important to spinicaudatan taxonomy (Tasch, 1969), finding compression material will greatly aid future attempts to formally identify these branchiopods. All of the spinicaudatans found so far possess growth lines and lack radial carinae, seemingly excluding them from the leaioids.

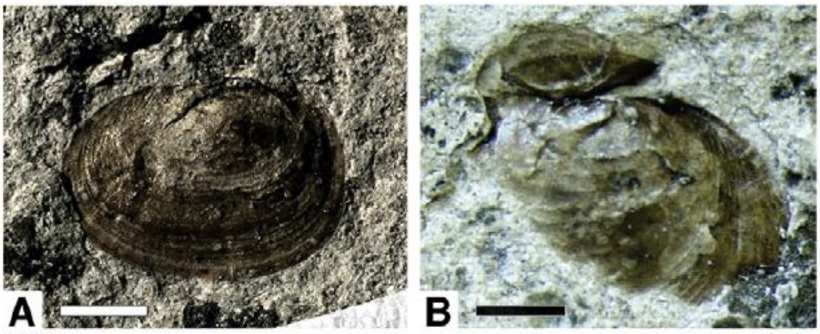


Figure 2.11. Spinicaudatans: A. disarticulated carapace valve showing preservation including altered chitin; B. carapace showing two articulated valves. Scale bars = 1 mm.

Spinicaudatans from the Kockatea Shale were first mentioned, but not formally described or figured, by Dickins and McTavish (1963) from cores 25 and 26 of BMR 10 (Beagle Ridge). Cockbain (1974) described specimens from outcrop of the Kockatea Shale near Kalbarri as Cyzicus (Euestheria) minuta (von Zeiten), but this identification was queried by Tasch and Jones (1979b), who highlighted the use of measurements of the carapace height over length, and the angle between the posterior and anterior margins, to clarify taxonomy. Elsewhere in the East Gondwana interior rift–sag system, Early Triassic spinicaudatans have been recorded from the Blina Shale of the Canning Basin (Chapman and Parr, 1937; Teichert, 1950; Brunnschweiler, 1954, 1957; McKenzie, 1961; Veevers and Wells, 1961; Gorter, 1978a; Tasch and Jones, 1979a; Tasch, 1987) and the Mount Goodwin Subgroup of the Bonaparte Basin (Etheridge, 1907; Dickins et al., 1972; Tasch and Jones, 1979b; Tasch, 1987; Gorter et al., 2010). Further southwest along this rift system, Ravich et al. (1977) reported poorly preserved spinicaudatans from strata now attributed to the Lower Triassic Ritchie Member of the Flagstone Bench Formation in the Prince Charles Mountains, Antarctica. In eastern Australia, coeval spinicaudatans are known from the Ross Sandstone and Knocklofty Formation in Tasmania (Tasch, 1975, 1987) and from the Rewan Group (including Arcadia Formation) in the Bowen Basin, southeastern Queensland (Jensen, 1975; Tasch, 1979, 1987). Tasch (1979) noted similarities between the spinicaudatan faunas of the Canning, Bonaparte, and Bowen basins, with two shared species between the Bowen and Canning basins and several genera common to all three. The genus described from the Kockatea Shale was one of those shared genera, but at the subgenus level, Cyzicus (Euestheria) was only seen in the Perth and Bonaparte basins.

4.8. Insects

Assorted insect fossils, mostly disarticulated and fragmentary wings, have been collected for the first time from the Kockatea Shale. Most of this material is preserved as impressions, and this, plus their generally incomplete nature, hinders identification. The best-preserved wing is a large, complete tegmen (forewing), clearly attributable to the auchenorrhynchan hemipterans (true bugs; Fig. 2.12A).

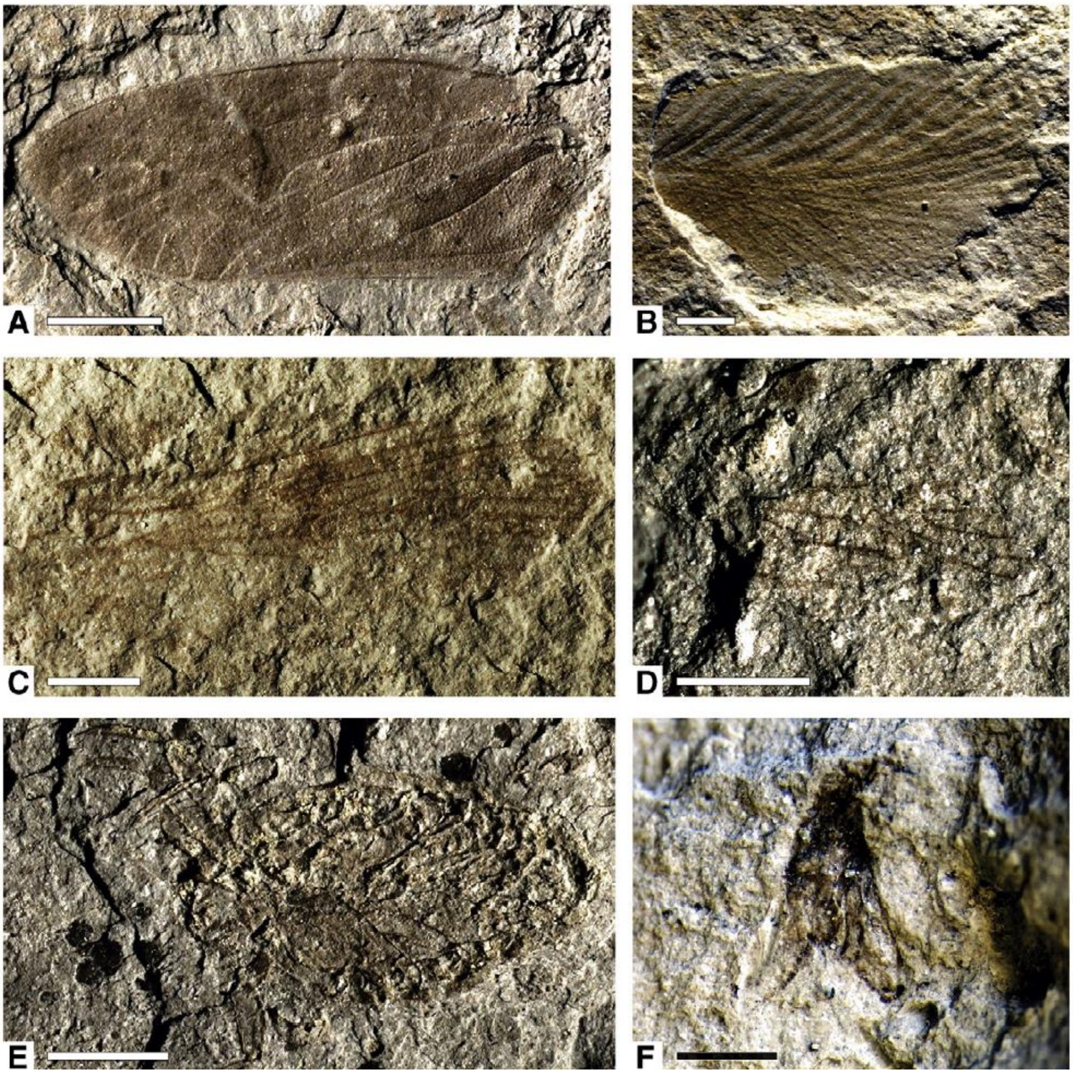


Figure 2.12. Insects: A. Complete hemipteran tegmen, likely belonging to Fulgoromorpha; B. Partial blattodean tegmen; C. Over lapping membranous forewings; note the darkened patch at the centre of the wings, which may be a macula or wing colouration; D. Fragmentary forewing showing dense venation network; E. Complete insect body, possibly of an aquatic heteropteran (Hemiptera); F. Small indeterminate ?insect; Scale bars: A, E = 2 mm; B, C, D, F = 1 mm.

Although further work is required to clarify its identity, the shape of the anal loop and presence of a distinct ‘basal cell’ suggests a link to the Fulgoromorpha. The wing is also distinctively textured, allowing a tiny fragment on a different block to be tentatively compared to this beautifully preserved fossil. Also recovered was a partial tegmen (Fig. 2.12B) attributable to the ‘Blattodea’ (stem-group cockroaches, or ‘roachoids’ as defined by Grimaldi and Engel, 2005). Although the absence of part of the base, the apex, clavus, and distal cubital field makes the wing unidentifiable, the apparently short subcostal field, narrow radial region with branched radial veins, and independent stems of medial and cubital veins are more characteristic of Mesozoic roachoid families, particularly the Caloblattinidae (Vršanský, 2000; Vršanský et al., 2002; Vršanský and Ansorge, 2007).

Another specimen consists of two nearly complete, but overlapping wings, possibly representing a forewing–hindwing pair (Fig. 2.12C). The wings are clearly membranous, but the darker sections seen at wing centre imply original patterning or colouration. The anal veins, although present, are faint, suggesting weaker sclerotization in that region of the wing. The costal section of the ?forewing appears extensively cross veined and has a rounded margin. Together, these features suggest a polyneopteran identity, albeit tentatively. The last wing is a more difficult to identify fragment showing a relatively dense, forking set of veins linked by numerous cross-veins (archaedictyon; Fig. 2.12D). This pattern is seen predominantly in hemimetabolous groups, such as the Odonata (dragonflies and damselflies), Ephemeroptera (mayflies), and Plecoptera (stoneflies), although densely veined holometabolous groups, such as the Neuroptera (lace wings) cannot be entirely discounted.

The most intriguing fossils of this set are three complete or nearly complete bodies preserved as impressions in dorso-ventral aspect, and with both part and counterpart available (Fig. 2.12E). The overall shape is highly suggestive of the nepomorphan Hemiptera, all of which are aquatic or riparian predators (Schuh and Slater, 1995; Andersen and Weir, 2004). The body is rounded, and the head appears short, with large eyes placed laterally. The lateral margins of the abdomen appear strongly sculptured, and have rounded features that could be abdominal spiracles. The legs are the clearest preserved features; the fore femora appear broad and possibly raptorial, and all three pairs of legs bear long hairs, presumably for swimming. Other characteristic features, such as wings and rostrum, are unclear on this material. As the best preserved of these specimens is now partly covered by ‘spots’ of gypsum, the taxonomic identity of this species will likely remain uncertain until more examples can be recovered or the material better prepared. If correct, the identity of this fossil will be of great interest, as the previous oldest nepomorphan is Anisian in age, from the Grés à Voltzia locality in France (Shcherbakov, 2010). The last fossil worthy of mention has the outward appearance of a small (~2mmlong) insect body with its wing folded back over its abdomen, an interpretation supported by a hint of venation on one of the ‘wings’ (Fig. 2.12F). Unfortunately, its small size and generally poor preservation means there are no obvious features that allow it to be confirmed as an insect—additional material is required to clarify its identity.

In Western Australia, the first record of Triassic fossil insects was by Wade (1936, Table 1), listed as from a locality ‘1. miles north of White Rocks – Noonkanbah’. Whereas Wade considered the material to be Pleistocene to Miocene, the locality lies within an area since mapped as the Lower Triassic Blina Shale (Guppy et al., 1958;

Gorter, 1978a). However, no additional specimens have been found from the formation and Wade's material should be reassessed if it can be found. Although Riek (1968) reported insects of 'probable Triassic age' from the Hill River area of the Perth Basin, Western Australia, his samples were later shown to come from the Lower Jurassic Cattamarra Coal Measures (Martin, 2008). Early Triassic insects are otherwise unknown from the Western Australia – Timor-Leste portion of Gondwana.

Elsewhere in Australia, an assemblage of Early Triassic insects was recorded from the Arcadia Formation of Queensland (Northwood, 2005), which is considered Induan or Olenekian in age (Foster, 1982; Balme and Foster, 1996; Brakel et al., 2009) and is, therefore, roughly contemporaneous with the assemblage described here. However, the Arcadia material is preserved within vertebrate coprolites, in which the insects have been disarticulated and fractured, so much so that the remains are difficult to identify. At present, the small and highly fragmentary Arcadia arthropod assemblage is unstudied, but is similar to the Kockatea material in that it is dominated by spinicaudatans as well as containing a roachoid wing and a range of other non-insect an sclerites (S.K. Martin, unpublished observation). Of interest is the shared record of roachoid material, the earliest finds of this order in Australia (Jell, 2004). However, blattodeans are very common and diverse in both the Middle and Late Triassic insect assemblages of eastern Australia (Tillyard, 1916, 1919, 1936, 1937; Dodds, 1949; Riek, 1955, 1962, 1967), a dominance that continues into the later Mesozoic Australia-wide (Riek, 1968; Jell and Duncan, 1986; Vršanský, 2004; Martin, 2010; McLoughlin et al., in press).

4.9. Other arthropods

At least four large bivalved carapaces (~35 mm long including posteroventral spine) have been recovered, all of which appear to preserve at least some carbonized chitinous material (Fig. 2.13A). Their large size, dorsal hinge line on the carapace, distinctive anterior horn, mesolateral ridge, and excavate posterior margin favour assignment to Austriocarididae or a similar family (G.D.F.Wilson,written comm., 2014). Although initially considered part of the Phyllocarida: Archaeostraca (Rolfe, 1969), this family has more recently been reassigned to the enigmatic ?crustacean class Thylacocephala within the Order Concavicarina (Briggs and Rolfe, 1983; Rode and Lieberman, 2002). Triassic austriocaridids are presently known from the Middle Triassic of China and Upper Triassic of Austria, and as the family extends back to the Devonian, its presence here in the Lower Triassic is not surprising (Rolfe, 1969). Another large arthropod fossil recovered from the Kockatea locality is a poorly preserved, shallow impression, severely limiting the prospect of identifying it (Fig. 2.13B). The body seems rounded without an obvious telson or tail, with other features including ?ten long, segmented legs, and a strongly textured ?carapace. No antennae, head, mouthparts or body subdivisions can be seen, and more material is required to reveal the true affinities of this specimen; however, the number of legs clearly rules out an association with the Hexapoda and probably the Arachnida. Other small fragments, preserved as carbonized cuticle, may also represent arthropod sclerites, although their incomplete nature means that their taxonomic affinities will likely remain unknown. Other than spinicaudatans, marine ostracods are the only arthropod body fossils recorded from subsurface samples of the Kockatea Shale (Jones, 1970; Metcalfe et al., 2008); although none have been found at the current locality, this may change with additional sampling. A rather different record of crustaceans from outcrop of the Kockatea Shale in the Northampton area was presented by Luo and Chen (2014), who interpreted abundant scratching traces on bedding surfaces as feeding behaviour by decapods or other arthropods. The number of traces they recorded indicates that grazing crustaceans were a common part of the Early Triassic marine ecosystem within the Perth Basin.

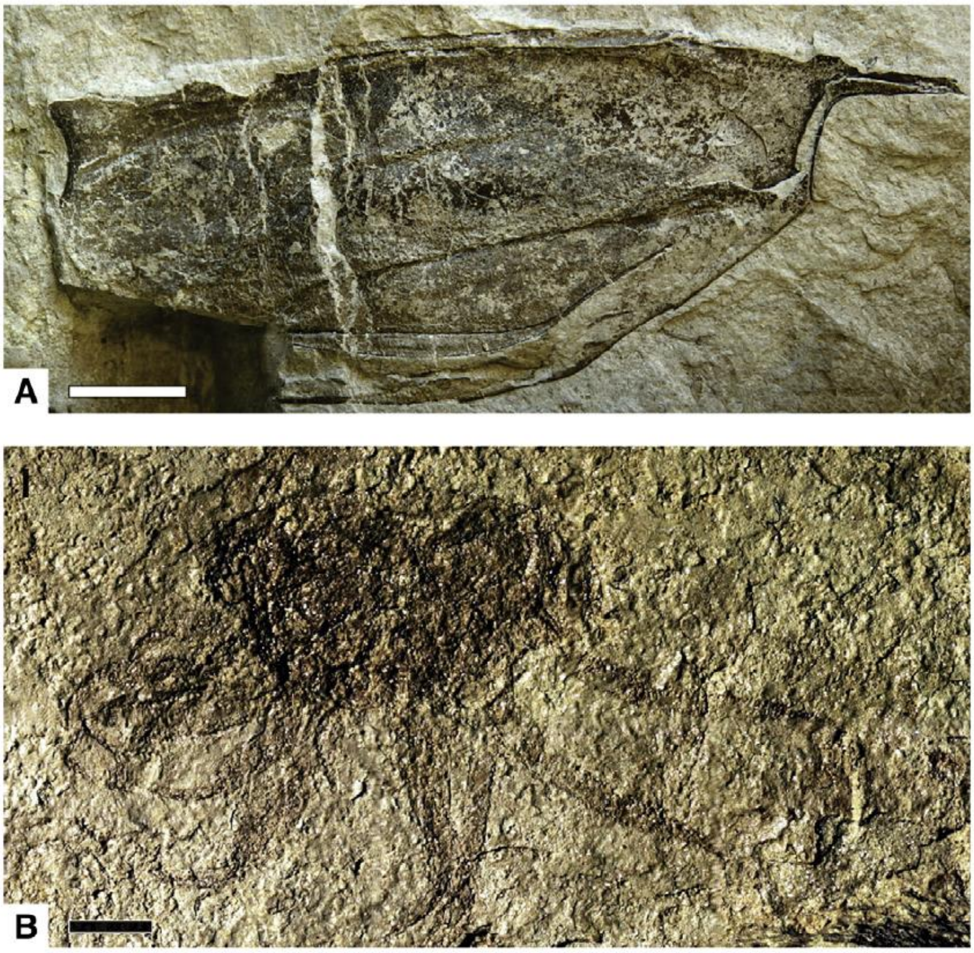


Figure 2.13. Other arthropods: A. Austriocaridid carapace; B. Large, unidentified arthropod. Scale bars: A = 4mm; B = 2mm.

Elsewhere in the East Gondwana interior rift–sag system, insects and spinicaudatans are the only arthropods known from contemporaneous formations apart from abundant hirsute ‘scales’ attributed to an unknown arthropod recovered from the non-marine McKelvey Member of the Flagstone Bench Formation, Price Charles Mountains, East Antarctica (McLoughlin et al., 1997). In eastern Australia, unidentifiable arthropod sclerites were found within the coprolites of the Lower Triassic Arcadia Formation (Northwood, 2005), and Tasch (1975) described a malacostracan carapace valve from the Lower Triassic Knocklofty Formation of Tasmania. Probable insect tracks from 25–50 cm above the base of the Coal Cliff Sandstone in the Sydney Basin, and interpreted by Retallack (1996) to be earliest Triassic in age, are now dated as latest Permian based on assignment of the host strata to the *Protohaploxypinus microcorpus* Zone (Helby et al., 1987; Shi et al., 2010), and recent radiometric dating (Metcalfe et al., in press).

4.10. Vertebrates

Vertebrate material from this site includes jaw fragments (e.g. Fig. 2.14A) and isolated fish scales (Fig. 2.14B, C) that are compatible with actinopterygians, and in particular, palaeonisciforms. This group can be recognized by a thick, rhombic scale structure with ‘peg and socket’ articulations. In addition, sarcopterygian scales consistent with coelacanthids—the first evidence of this clade from the Triassic of Australia—are indicated by a broadly oval morphotype incorporating an exposed field of about one-third the maximum length and ornamented with elongate ridges (Fig. 2.14D, E). At least one specimen (Fig. 2.14F) shows overlapping fields consisting of superimposed fibrous layers that were separated and juxtaposed into their present positions, possibly during post-mortem decay (see Yabumoto and Neuman, 2004).

A very small tetrapod mandible (maximum length 13.5 mm) is preserved as part (Fig. 2.14G) and counterpart impressions (Fig. 2.14H) that reveal limited bone surface detail. Despite this, a reticulate external sculpturing pattern of shallow pits and ridges resembles the ‘temnospondyl-like’ mandibular ornamentation defined by Ruta and Bolt (2008). Sutures between individual bones are indistinct, yet, based on topology, at least the dentary, angular, and surangular are present. The ventral edge of the angular displays a marked curvature, forming a narrow distal dentary ramus; such dorsoventral constriction might have been accentuated by disarticulation of the splenial and post splenial, although the uninterrupted surface sculpture along the exposed ventral margin implies that the mandible is intact. It is unclear how much of the seemingly short glenoid extremity (sensu Jupp and Warren, 1986) is preserved; however, a well developed dentary sulcus is clearly visible beneath the tooth row. The dentition is unusual, comprising a single row of 27 marginal teeth that become long and filamentous towards the midline of the jaw (up to 0.8 mm high). This feature renders affinities ambiguous, a problem potentially compounded by osteological immaturity. Nevertheless, the small size of the specimen is compatible with some diminutive rhytidosteans (Yates, 2000) and lapillopsids (Warren and Hutchinson, 1990), the latter also displaying reduced numbers of teeth (Yates, 1999).

Vertebrate fossils reported from other localities in the Kockatea Shale consist mainly of unidentified scales together with isolated and partially articulated osteichthyan skeletal elements (e.g., Dickins and McTavish, 1963; Metcalfe et al., 2008). Cosgriff (1965) also described an incomplete temnospondyl amphibian skull from core 28 of BMR 10 (Beagle Ridge), which he attributed to the rhytidostean *Deltasaurus pustulatus*.

Compositionally, the Kockatea Shale vertebrate assemblage is consistent with the coeval, but much more intensively sampled, Blina Shale in the Canning Basin, which records a deltaic – marginal-marine fauna of palaeoniscoids, represented by scales and vertebrae reminiscent of the Australian endemic genera *Myriolepis*, *Apateolepis*, and *Brookvalia* (Brunnschweiler, 1957; McKenzie, 1961), lungfish tooth plates referred to *Asiatoceratodus* (Kemp, 1996), and dentigerous elements of the ubiquitous Triassic actinopterygian *Saurichthys* (Long, 1991, p. 374, fig. 26). These elements have been encountered in Triassic localities in eastern Australia that also contain actinopterygians, dipnoans, and rare sharks (Woodward, 1890; Wade, 1935; Dziewa, 1980; Long, 1991; Turner, 2011). Cosgriff (1965, 1969), Cosgriff and Garbutt (1972), and Warren (1980) reported examples of various temnospondyls from the Kockatea and Blina shales, including species of the rhytidostean *Deltasaurus*, brachiopid *Blinasaurus*, widespread Early Triassic mastodonsaurid *Watsonisuchus*, and the endemic trematosaurid *Erythobatrachus* (see Kear and Hamilton-Bruce, 2011, for a recent summary). The presence of trematosaurids, together with anecdotally identified ichthyopterygian bone fragments (see Cosgriff and Garbutt, 1972; Kear, 2004) is significant because it suggests a euryhaline setting for both units (e.g., Steyer, 2002). Gorter (1978a) likewise inferred mixed marine and freshwater influences based on the association of vertebrate assemblages with conodonts and spinicaudatans.

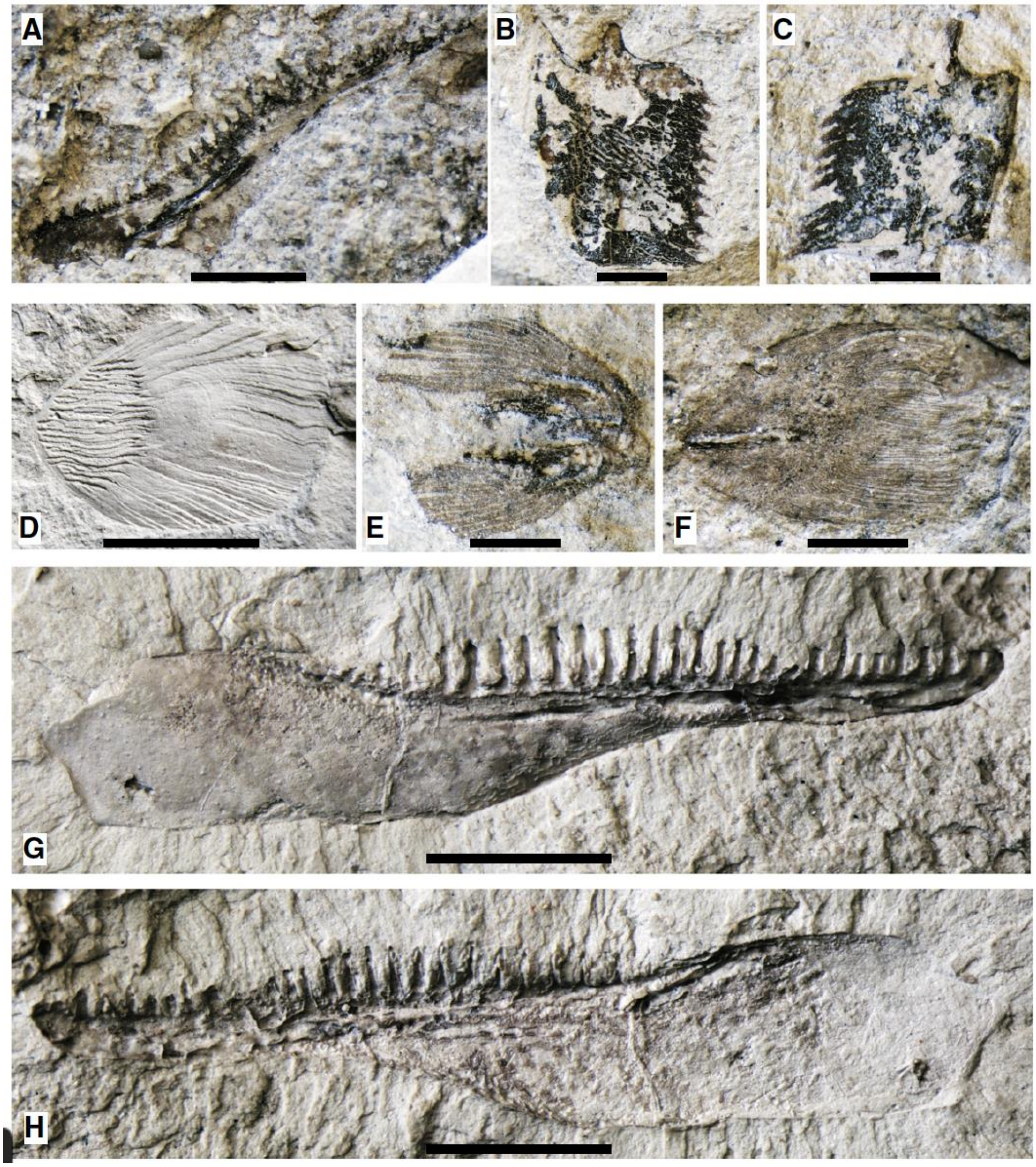


Figure 2.14. Vertebrate remains: A–F. Fish remains; A. Jaw fragment; B, C. Palaeonisciform fish scales; D–F. Sarcopterygian scales. G, H. Counterpart moulds of tetrapod mandible. Scale bars: A–C, E, F = 1 mm; D, G = 5 mm.

4.11. Plant macrofossils

Plant macrofossils are represented by a sparse suite of fragmentary foliar, axial, and thalloid remains. Most plant fossils cannot be identified to species level due to their fragmentary state, and lack of cuticular or reproductive structures. Nevertheless, around eight distinct plant organs can be differentiated within the assemblage. None of the small fragments shows evidence of arthropod herbivory. Several specimens in the collection represent unequally dichotomous thalloid liverworts (Fig. 2.15.A–C). Most of these show some degree of medial thickening indicating a line of abaxial rhizoids, but all are fragmentary, suggesting a modest degree of transport. Several specimens bear surficial darkened spots or dashes that probably represent thickenings in the thallus associated with air pores (see Schönherr and Ziegler, 1975 for examples in modern liverworts). These liverworts have shorter segments between dichotomies than Middle Triassic examples described from eastern Australia (Webb and Holmes, 1982; Holmes, 2000).

A single 0.5mmdiameter axis, bearing spirally arranged, slightly imbricate, 2 mm long, b1 mm wide, broad-based, awl-shaped leaflets (Fig. 2.15.D), probably represents a moss or herbaceous clubmoss fragment as the leaves and parent axis are notably smaller than similar scale-leafed Mesozoic conifers, such as *Pagiophyllum* (e.g., Harris, 1979) or *Rissikia* (e.g., Holmes and Ash, 1979; Anderson and Anderson, 1989). Moreover, the absence of a discernible central vein in the leaves favours an affiliation with the mosses.

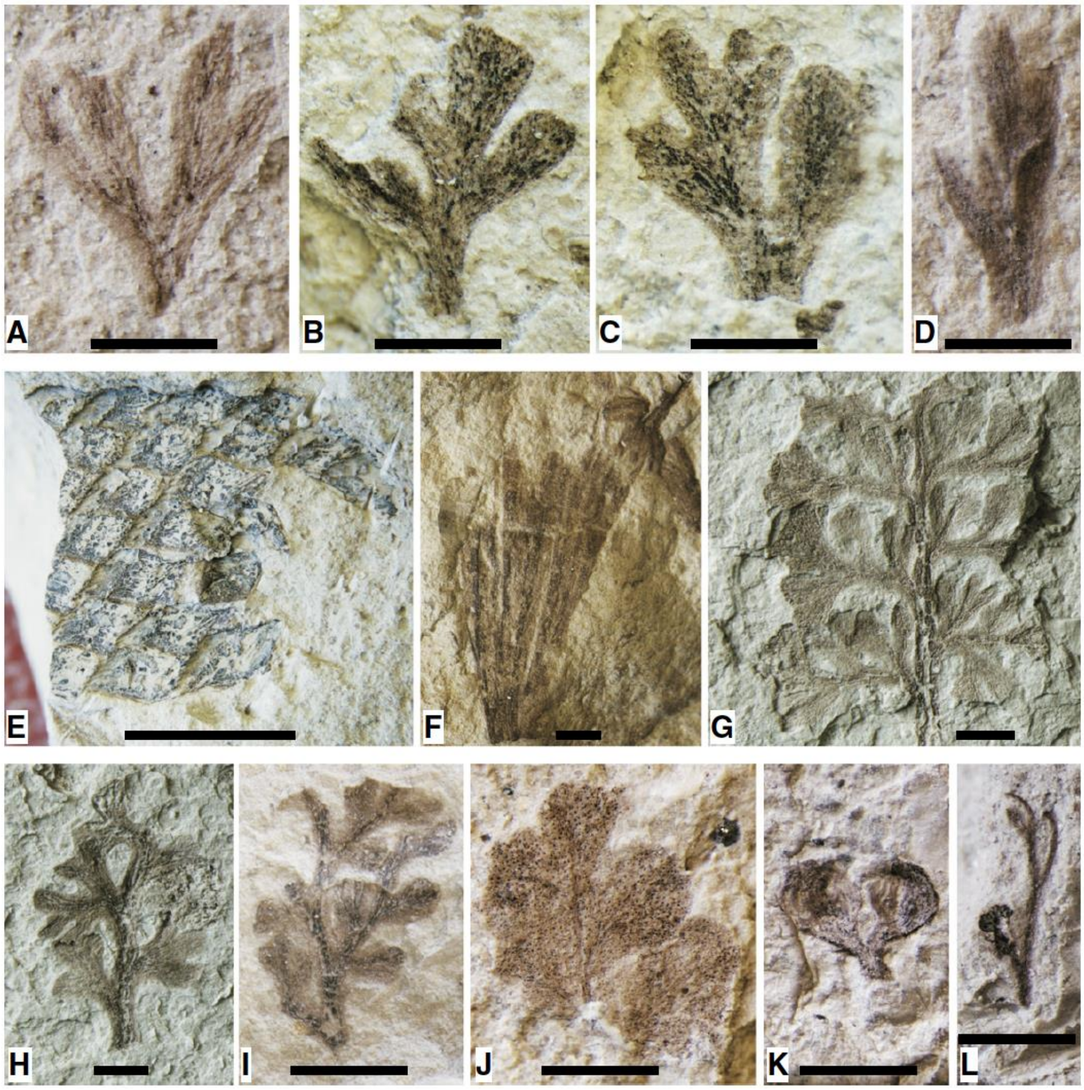


Figure 2.15. Plant remains: A–C. Thalloid liverworts; D. Moss or herbaceous clubmoss; E. Isoetalean corm fragment; F. Equisetalean leaf sheath; G–I. cf. *Nymboidiantum multilobatum* Holmes; J. cf. *Ptilonymba* or *Nymbopteron* sp.; K. Possible sporangiate fern pinnules; L. Branched filamentous axes with sporangia. Scale bars = 1 mm, except E = 5 mm.

Two specimens with diagonal rows of tightly spaced rhombic structures (Fig. 2.15.E) are similar in size, shape, and arrangement to ‘Lycopod stem b’ of Holmes and Ash (1979, fig. 3.3) from the Early Triassic of the Lorne Basin, New South Wales. These specimens probably represent the distal portions of isoetalean corms with tightly spacedmicrophyll scars, and are generally smaller with more compact leaf scars than the axes of related pleuromeian lycophytes. Preservation is inadequate to detect clear vascular traces on the rhomboid features, but their form and arrangement suggests that they are leaf scars on a globose corm and not superficially similar fish scales. Isoetalean corms are common constituents of Early Triassic floras globally (Pigg, 1992; Skog and Hill, 1992; Retallack, 1997; Cantrill andWebb, 1998), and similar small forms typically assigned to Isoetites or Nathorstianella persisted in Australia throughout the Mesozoic (Karrfalt, 1986; McLoughlin, 1996; McLoughlin et al., 2014).

A single specimen represented by a sheath of 10 mm long, laterally fused, univeined leaves, attached to a 0.7 mm diameter finely striate axis (Fig. 2.15.F), is referred to Equisetales. Similar diminutive equisetalean axes and leaf whorls have been described from the Early and Middle Triassic of eastern Australia (Holmes and Ash, 1979; Holmes, 2000, 2001). Several fragments of bi- to tri-pinnately divided fern fronds, reaching maximum dimensions of only 5 Å~ 6 mm (Fig. 2.15.G–I), strongly resemble the unevenly divided pinnae with obovate pinnules of Nymboidiantum multilobatum Holmes described from the Middle Triassic Basin Creek Formation of New South Wales (Holmes, 2003), although the Kockatea Shale specimens are markedly smaller (~25%).

All known fragments are infertile and their familial affinities are unresolved. A single fragmentary pinna in the assemblage has obovate to rhombic, apically rounded pinnules, with weak primary veins giving off acutely orientated secondary veins (Fig. 2.15.J). This fragment is broadly similar to species of the ferns *Ptilonymba* and

Nymbopteron, which Holmes (2003) reported from the Middle Triassic of New South Wales. Several specimens consist of 0.2 mm diameter short axes dichotomously divided into a pair of terminal club-like appendages b1 mm long and ~0.8 mm wide (Fig. 2.15.K). These structures are superficially similar to a range of dichotomously divided cupulate ovuliferous organs of Ginkgoales (Hamshawvia, Avatia), Corystospermales (Umkomasia), and Matatiellales (Matatiella) (Holmes and Ash, 1979; Anderson and Anderson, 2003), although the Kockatea Shale specimens are markedly smaller (10–20%) than these gymnospermous reproductive structures. They may represent the diminutive detached fertile pinnules of a fern, since a darkened or creased periphery on most specimens is reminiscent of sporangial positions on the margins of wedge-shaped pinnules of a range of delicate extant ferns, such as Lindsaea and Adiantum. Two examples of branched filaments are preserved in which circular or irregular structures b0.2 mm in diameter are inserted terminally on some ultimate branchlets (Fig. 2.15.L). Their branched nature and terminal sporangia-like bodies are superficially similar to various pteridospermous or ginkgoalean microsporangiate organs but the Kockatea Shale fossils are much smaller and an algal affinity cannot be excluded.

4.12. Megaspores

Although megaspores are extremely rare, the specimens recovered have coarse granular, low conate, or weakly verrucate ornament (Fig. 2.16.) and are, therefore, dissimilar to forms from Lower Triassic formations in eastern Australia. Metcalfe et al. (2008) figured four species from the ‘inertinitic interval’ at the base of the Kockatea Shale in Corybas 1 (drilled 16 km northeast of Dongara), which was dated as late Wuchiapingian–Changhsingian. Amongst these, specimens of ?*Singhisporites* spp. appear most similar to our material. Elsewhere in the Eastern Gondwana interior rift–sag system, Gorter (1978a) noted megaspores from the Blina Shale in the Canning Basin. Further along the Eastern Gondwana interior rift-sag system, megaspores with broadly similar granular to verrucate ornamentation are recorded from the Lower Triassic of India (Maitur Formation: *Biharisporites* sp. of Maheshwari and Banerji, 1975; Nidhpuri beds: *Duosporites indicus* Bhomik and Das, 2011) and the Prince Charles Mountains, East Antarctica (*Verrutriletes* sp. A of McLoughlin et al., 1997).

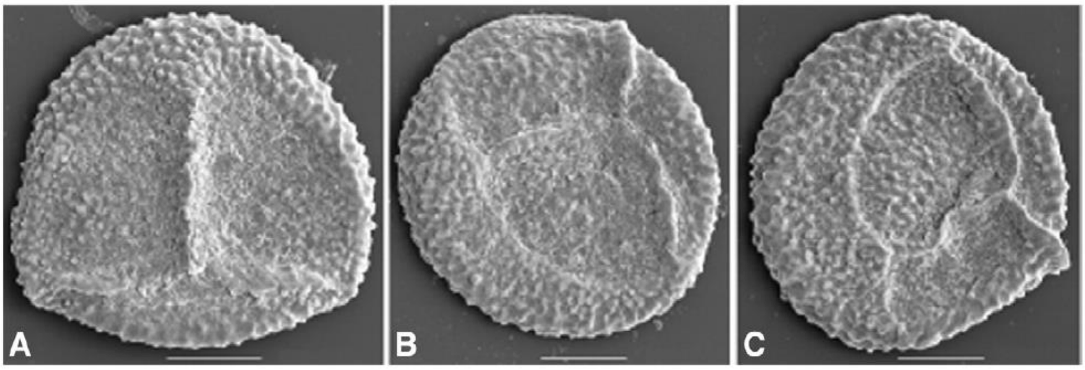


Figure 2.16. Megaspores from washed residue of basal grey shale; scanning electron micrographs, scale bars = 100 μm.

4.13. Microspores and pollen

The two samples analysed contain broadly similar assemblages of spores and pollen (Fig. 2.17.; Table 2.1.). Both are dominated by *Densoisporites playfordii* (Balme) Dettmann (Fig. 2.17.C), with *Kraeuselisporites saeptatus* Balme (Fig. 2.17.D) also common in the lower sample—these key species are derived from lycopod plants (Balme, 1995). Several other species of spores are moderately common, but this is not reflected in the counts due to the overwhelming abundance of acritarchs. *Aratrisporites* is represented by *A. rugulatus* de Jersey (Fig. 2.17.B), a species originally described from the Scythian of the Arcadia Formation (upper Rewan Group) of Queensland. The current samples clearly belong to the *Kraeuselisporites saeptatus* Assemblage Zone as originally erected by Dolby and Balme (1976), with most species described by Balme (1963). These assemblages are also consistent with the *Protohaploxypinus samoilovichii* Oppel Zone of Helby (1974), redescribed by Helby et al. (1987). The boundary with the immediately younger *Triplexisporites playfordii* Oppel Zone is somewhat transitional, but the absence of *Falcisporites* australis (de Jersey) Stevens, spinose forms of *Aratrisporites*, and the prevalence of lycopsid spores suggest that this sample is still some distance below the top of the zone.

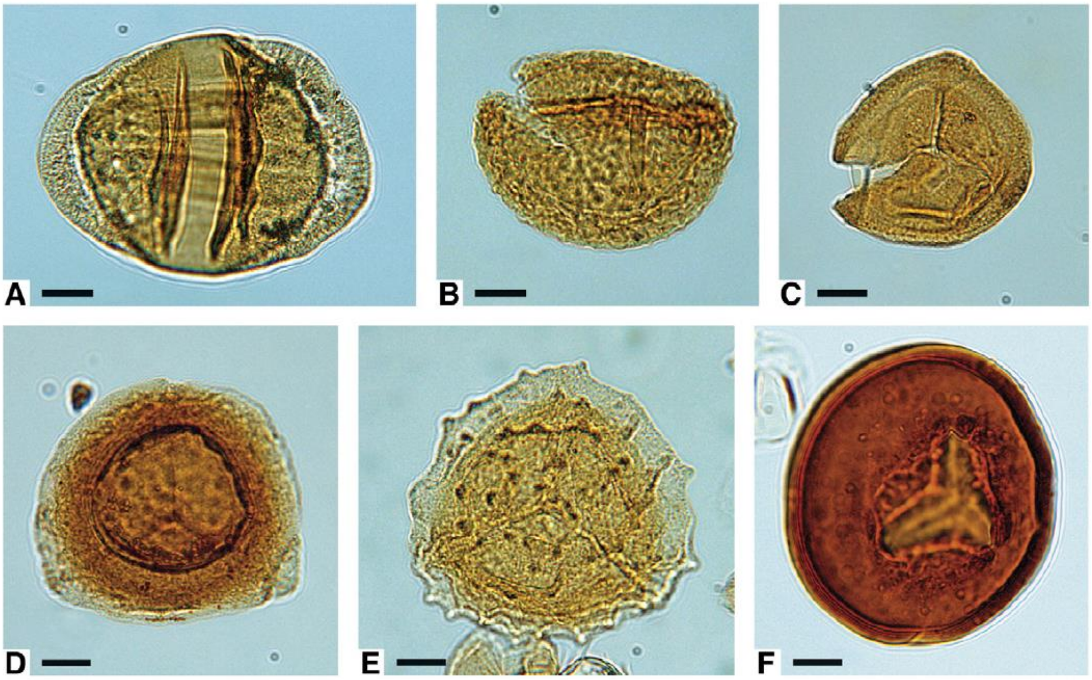


Figure 2.17. Microspore and pollen: A. *Lunatisporites noviaulensis* (Leschik) Foster; B. *Aratrisporites rugulatus* de Jersey; C. *Densoisporites playfordii* (Balme) Dettmann; D. *Kraeuselisporites saeptatus* Balme; E. *Kraeuselisporites cuspidus* Balme; F. *Punctatisporites fungosus* Balme. Scale bars= 10 µm.

The only extensive descriptions of spores and pollen from the Kockatea Shale were by Balme (1963, 1967). Dolby and Balme (1976) selected an interval of 359 m in the Kockatea Shale in BMR 10 (Beagle Ridge) borehole as the reference stratotype for the *K*. saeptatus Assemblage Zone, but did not describe material from this locality. The *K*. saeptatus Zone is also recorded in the Locker Shale (Carnarvon Basin) and the Blina Shale (Canning Basin), all with similar environments and all within the East Gondwana interior rift–sag system. Equivalent palynofloras, with entirely non-marine signatures are present further southwest along the rift–sag systemin the middle Ritchie Member, Flagstone Bench Formation (Lambert Graben, Antarctica: McLoughlin et al., 1997; Lindström and McLoughlin, 2007) and the Panchet Formation (Godavari Basin, India: Jha and Aggarwal, 2012). A comparison of the spore–pollen assemblages can be made with recent work on the Salt and Surghar ranges of Pakistan (Hermann et al., 2011, 2012). The best correlation with material from the Kockatea Shale is with the PTr 2 palynozone recorded in the Ceratite Marls and the Ceratite Sandstone, which is dated as early Smithian to early middle Smithian (i.e., earliest Olenekian) based on ammonites (Hermann et al., 2012).

2.5. DISCUSSION

2.5.1. Age implications

The *K. saeptatus* Zone, to which our section belongs, extends throughout much of the Kockatea Shale (Nicoll and Foster, 1998) in the northern Perth Basin, and the Locker Shale in the Northern Carnarvon Basin. According to Nicoll and Foster (1998), this palynozone is associated with the upper Induan *Neospathodus dieneri* and overlying Smithian *N. waageni* conodont zones (Metcalfe et al., 2013). In addition, R. Nicoll (pers. comm., 2014) recovered the Smithian conodont *Neospathodus bicuspidatus* (Müller) from the Kockatea Shale section in Greenough

Shallow No. 13 water bore (7.5 km northeast of Bookara 1; Fig. 4) at a level that also yielded palynomorphs of the *P. samoilovichii* Zone (Backhouse, 1994). This and the correlations discussed in Section 4.13 indicate that the studied section is no younger than Smithian (early Olenekian). Due to its position in onlapping strata at the edge of the basin (Section 2; Fig. 4), the studied deposit is probably high in the *K. saeptatus*.

2.5.2. Taphonomy

Although the mixed marine–terrestrial nature of this assemblage has likely increased the range of organisms preserved at this site, it has also had a strong taphonomic influence on fossil preservation. There is a clear bias towards aquatic organisms, whether fresh-water or otherwise, in the assemblage, with purely terrestrial groups—plant remains, amphibians, and some insects—generally the rarest and least diverse parts of the assemblage. These groups also tend towards preservation as disarticulated or incomplete elements, indicating the longer pathways to burial and more numerous taphonomic barriers faced by terrestrial organisms. Whether transport into the preserving environment had an effect on other aspects of preservation for these terrestrial organisms, such as size sorting, or biases towards robust taxa or body elements, has yet to be tested, but seems likely. For aquatic organisms, the levels of disarticulation and fragmentation appear far lower than for the terrestrial groups.

This is exemplified by the insects, where the aquatic insects (?nepomorphans) are numerous and preserved as complete bodies, whereas other groups (hemipterans, blattodeans) are generally represented as single, incomplete specimens, particularly wings. The close association of ammonoid mouthparts and shells, likely indicating burial close to their life habitat, is another example of the more complete preservation of aquatic taxa in comparison to terrestrial groups.

In terms of diagenesis and alteration, both calcite and aragonite have been preferentially leached from the studied beds, including the lowest grey shale containing pyrite and well-preserved palynomorphs. Carbonate dissolution probably took place in organic-rich seafloor sediment shortly after deposition. Thin-shelled hyaline foraminifera, ostracods, and even bivalves and gastropods may have left no record of their presence in this environment. The preservation of chitin also appears affected by diagenesis, with remnants seen prominently in the lower darker shales; arthropods recovered from higher levels are mostly preserved as impressions.

In a wide-ranging review of fossil preservation in the Lower Triassic, Fraiser and Bottjer (2005, p. 308) concluded that preservation bias did not affect what they called the ‘fossilization low’ in this interval. This may be so, but at the present fossil site the diagenetic influence on the recovered fossil assemblage, caused by the dissolution of carbonate skeletons, appears significant. Only some of the thicker-shelled forms are preserved as moulds, but these crumble rapidly when the friable mudstone is exposed to air. In the unweathered shale, pyritized internal cavities indicate the presence of small, closed shells that likely have been completely removed in the weathered zone.

Ferruginization of the sandstone sections above the fossiliferous shales took place at the permeability interface between sandstone and mudstone beds, and is probably the result of iron-oxide cement precipitation from relatively recent iron-rich groundwater flowing through the sandstone layers. Similarly, the growth of gypsum on freshly exposed fossils appears to be due to the effect of recent groundwater chemistry: the gypsum does not indicate the environmental conditions at the time of deposition.

5.3. Palaeoenvironment and palaeogeography

Continental reconstructions based largely on palaeomagnetic evidence have placed the northern Perth Basin variably at ~45°S (Blakey, 2005), 50°S (Scotese, 2001), 55–60°S (Torsvik et al., 2012), and up to 70°S (Veevers, 2000) in the Early Triassic. In general, these studies imply a middle- to high-latitude setting for the northern Perth Basin, although globally elevated temperatures during the Early Triassic super greenhouse phase (Retallack et al., 2011; Retallack, 2013) suggest conditions substantially warmer than at equivalent modern latitudes.

The acritarchs, foraminifera, lingulid brachiopods, aviculopectinoid bivalves, and ammonoids all indicate shallow-marine depositional conditions for the mixed assemblage layers in the centre of the studied section (see Section 4). Although the organic-cemented agglutinated foraminifera, lingulids, and spinicaudatans may have tolerated brackish water (see Sections 4.2, 4.3, and 4.7), the ammonoids were clearly inhabitants of normal-marine salinity. The presence of jaw structures together with ammonoid shells indicates that these individuals did not posthumously drift from more open, normal-marine environments and so were presumably living in, or close to, the depositional environment. Therefore, the mixed fossil assemblage and the predominance of mud with interlaminations of silt and fine-grained sand may be due to seasonal variations in the amount of freshwater and nutrient influx into a very shallow water environment near the margins of the interior sea, with coarser sediment, terrestrial organic detritus, and fresher, more oxygenated, water periodically flooding into the quiet-water mud-bottomed environment. Consequently, this Early Triassic sea is likely to have been estuarine in character, similar to the Permian and Early Cretaceous interior seas in Australia (Haig, 2004), and possibly was analogous to modern microtidal estuaries of southwestern Australia (Ostrognay and Haig, 2012) in experiencing great seasonal variability in water quality.

Throughout the fossiliferous interval, laminations, the absence of bioturbation, and the presence of framboidal sedimentary pyrite in the unweathered shale suggest low levels of dissolved oxygen in the bottom waters. Benthic faunal components are rare, consisting of a sparse assemblage of organic-cemented siliceous agglutinated foraminifera, few lingulid brachiopods, and extremely rare aviculopectinids. More common in the grey shale at the base of the outcrop section are clusters of pyritized micro-bivalves and micro-gastropods. These may have been benthic, but alternatively may have been planktonic larval stages or epiplanktonic on floating algal masses. Also seen in the basal darker shale layers are beds where accumulations of spinicaudatans are the dominant fossils. These crustaceans are considered highly adapted to changes in water depth and salinity, with extant species primarily inhabiting small, ephemeral, inland ponds (Tasch, 1969, 1987), and suggest that the early depositional phase of this section of the Kockatea Shale included periods when the water body was ephemeral, isolated, subjected to extreme environmental conditions, or some combination of the three. Higher in the section, spinicaudatan and micromolluscan layers give way to mixed assemblages, interpreted as the more normal estuarine-like conditions. Spinicaudatans have been recovered from Mesozoic facies representing freshwater lacustrine through to open-marine conditions, and there has been debate as to whether the group lived in fully marine environments or whether their remains were transported there from their preferred marginal marine habitats (Kobayashi, 1954; Tasch, 1969, 1987). Considering that the spinicaudatans in our Kockatea Shale assemblage are often preserved in mixed assemblage layers, the latter interpretation is supported for this locality.

In the very weathered stratigraphic section above the studied fossil site, rare ripple-laminated sandstone beds interbedded in the shale (Fig. 5) have ferruginized mud cemented to their lower and upper surfaces. These thin layers of red cemented mudstone contain a poorly preserved trace-fossil assemblage similar to that recorded by Chen et al. (2012) and Luo and Chen (2014) from outcrop of the Kockatea Shale north of Geraldton. Although the sections probably represent the same stratigraphic level, correlating these outcrops is somewhat perilous without more solid means for correlation. The trace-fossil assemblages are representative of bioturbation within the mud, not of traces on the sand surface, and imply that although bottom waters during deposition of the fossiliferous shale were likely dysaerobic or, at times, anaerobic, there was adequate dissolved oxygen available in the bottom water to sustain a mud infauna as progradation led to shallower water depths. The cross-laminated sandstone beds are devoid of burrows and indicate that current movements across the substrate periodically re-oxygenated the water. As described by Chen et al. (2012), the trace-fossil assemblages are relatively diverse and are, therefore, similar in general diversity to Early Triassic ichnofaunas recorded from shallow-marine facies in northern Pangea (e.g., Pruss et al., 2005; Zonneveld et al., 2010; Hofmann et al., 2011).

The great abundance of acritarchs in the Kockatea Shale, as in other coeval units of the East Gondwana rift–sag system (Balme, 1963, 1967; Medd, 1966; Dolby and Balme, 1976; Sappal, 1978; Thomas et al., 2004) and in some (Nautiyal and Sahni, 1976; Eshet and Cousminer, 1986) but not all (Tewari et al., in press) marine deposits of the Gondwanan Tethyan margin, are preserved within intertwined, essentially monospecific, mats that are associated with amorphous organic matter (Section 4.1; Fig. 7). These may represent phytoplankton blooms in the eutrophic surface-waters of the shallow sea, preserved as resting cysts incorporated into organic mats that covered the seafloor. Although we have not observed microbialites in the studied section, such facies are present in borehole sections low in the Kockatea Shale (Thomas et al., 2004; Metcalfe et al., 2008) and at the base of some outcrop sections north of Geraldton (Mory et al., 2005; Chen et al., 2012; Luo and Chen, 2014). Phytoplankton blooms may have caused periodic de-oxygenation of the water and the mortality of ammonoids and small fish.

Although uncommon in comparison to the marine and marginal marine taxa in the assemblage, the macroplant and insect fossils recorded for the first time from the Kockatea Shale (Sections 4.8 and 4.11) provide a small but intriguing window into the Early Triassic austral terrestrial biota that emerged in the wake of the end-Permian mass extinction event. The Early Triassic is characterized by a global coal gap, indicating an absence of peat-forming plant communities (Retallack et al., 1996). Widespread aridity or strongly fluctuating water tables in the Early Triassic, and the lack of suitable habitats for peat accumulation, have contributed to a scant plant-fossil record and a poor understanding of vegetation recovery in Gondwana following the end-Permian biotic crisis (Hill et al., 1999; Retallack, 1999; Vajda and McLoughlin, 2007). Records of Early Triassic insects or of insect damage on plants are similarly scant worldwide, so little is known about the mechanics and timing of diversification of this ecologically important group following the end- Permian mass extinction event (Zherikhin, 2002a; Grimaldi and Engel, 2005; Shcherbakov, 2008; Labandeira and Currano, 2013).

The recovered macroflora contains few species and is notably lacking in gymnosperms. Apart from a single equivocal microsporangiate organ, all of the plant fossils appear to represent remains of diminutive free sporing groups, which are typically confined to moist habitats due to their dependence on water for gamete transfer. All plant groups represented in the assemblage are typical components of pioneer communities that colonize bare, moist substrates. The presence of isoetalean lycophyte macrofossils is consistent with that group's dominance of the terrestrial palynomorph assemblages. Modern isoetaleans also grow in shallow submerged freshwater settings, and related pleuromeians may have occupied saltmarsh or mangrove-like niches in the Triassic (Retallack, 1977, 1997). A moist, coastal setting dominated by herbaceous vegetation is favoured as the source of the plant fossils. The delicate nature of the pteridophytic remains and lack of rooting structures indicate that the plant suite was transported only modest distances before preservation in a relatively quiet-water setting. Rare examples of the green alga *Botryococcus* sp. and fragments of woody tissue within the palynological preparations also demonstrate input from freshwater environments.

Overall, the composition of the floras is broadly consistent with the few Early Triassic plant assemblages reported fromeastern Australia, particularly the Lorne (Holmes and Ash, 1979), Sydney (Retallack, 1975, 1977, 1980), and Bowen (Cantrill and Webb, 1998) basins, and the small assemblages reported from the Canning Basin in Western Australia (White, 1961; White and Yeates, 1976; Tasch and Jones, 1979b; Retallack, 1995). Small Early Triassic floras reported from Peninsular India (Saksena, 1974; Srivastava, 1988) and East Antarctica (McLoughlin and Drinnan, 1997; McLoughlin et al., 1997), which at the time were located further southwest along the East Gondwana interior rift-sag system, have a similar low-diversity representation of lycophytes and ferns, but differ by their inclusion of key gymnosperms, such as *Lepidopteris* (Peltaspermales) and *Dicroidium* (Corystospermales).

Interestingly, even the small number of insect fossils recovered so far indicates that they inhabited diverse Early Triassic non-marine ecosystems in this part of Gondwana. Assuming the tentative taxonomic identifications presented in this paper are accurate (if not precise), the assemblage includes aquatic predators (?nepomorphan), strongly phytophilous herbivores (fulgoromorph), and ground-dwelling scavengers/ detritivores (blattodean). Although the fulgoromorph implies a vegetated area adjacent to the depositional water body, more work is needed before any real palaeoenvironmental or palaeoecological interpretation can be undertaken.

Despite the variable preservation of the material discussed here, the number and obvious diversity of the insects already recovered from this locality after only a short period of investigation is highly encouraging; insect fossils tend to be uncommon within shallow-marine facies compared to lacustrine, lagoonal, or swamp deposits, with recovery rates as Low as a few specimens per ton of rock (Zherikhin, 2002b; Grimaldi and Engel, 2005). Therefore, intensive investigation of this site in the future should yield a much larger insect fauna. Outside Australia, records of Early Triassic insects are becoming increasingly common, although almost all Induan records found so far are from Russia and Mongolia (Zherikhin, 2002a; Grimaldi and Engel, 2005; Shcherbakov, 2008). A study of these generally low-diversity assemblages has revealed that faunas of this time strongly resemble those of the latest Permian, with few endemic Triassic families (Shcherbakov, 2008); whether this trend also holds for Gondwanan assemblages will be of interest to continuing studies of Triassic post-extinction biotic recovery.

Associations of organic-cemented agglutinated foraminifera (mainly Ammodiscus), lingulids, spinicaudatans, ammonoids, and abundant acritarchs are widespread in the northern Perth Basin, both in probable Smithian outcrops of the Kockatea Shale at the northern margin of the basin, and in coeval borehole sections of the formation. This suggests that shallow-water conditions were extensive across the interior sea. A similar association is present in the Blina Shale of the Canning Basin, and some elements of the association are also evident in the Locker Shale in the Northern Carnarvon Basin (see Section 4), indicating highly uniform environmental conditions along the interior sea that spanned much of the 3000 km length of the East Gondwana interior rift–sag system during at least part of the Early Triassic.

5.4. Evolution and Early Triassic biotic recovery

Because of the scarcity of most groups (apart from the palynomorphs), the full diversity of the Early Triassic biota cannot be determined from the Smithian assemblage we have studied, and cannot be used quantitatively in comparisons with other earliest Mesozoic assemblages. However, similar assemblages characterized by low fossil numbers, usually in the presence of abundant acritarchs, have been recorded from marginal-marine facies of late Early Triassic or early Middle Triassic age in Europe (e.g., Wills, 1910; Rose and Kent, 1955; Pollard, 1981; Gall and

Grauvogel-Stamm, 2005; Źyła et al., 2013). Furthermore, some of the terrestrial (plants) and marine (brachiopods, bivalves, gastropods) taxa in the Kockatea Shale are diminutive compared to equivalent groups of the Late Permian or Late Triassic. Although taphonomic sorting may have played some role in the accumulation of small remains, the diminutive size of individual architectural components, such as fern pinnae, is consistent with the ‘Lilliput effect’ recognized in Early Triassic fossil assemblages globally, which is commonly attributed to harsh environmental conditions and simplified food chains in the wake of the end-Permian crisis (Twitchett, 2007). Although it is presently difficult to assess the influence of winnowing or size biasing on these diminutive groups, together these features suggest that the studied assemblage is typical of a widespread biofacies in the Early Triassic. It is hoped that with additional collecting the taxonomy of these fossils can be clarified, thereby allowing more comprehensive comparisons with equivalent biofacies elsewhere and a better assessment of the biogeographic range of the biota.

The sedimentology and low fossil numbers of the Kockatea Shale are also not unusual when compared to mud-dominated successions in some Permian and Cretaceous shallow-marine interior basins of Australia (Haig, 2004), which have been interpreted as large estuarine systems analogous to the modern Baltic Sea (Ketchum, 1983; Kunzendorf and Larsen, 2002). These Permian and Cretaceous successions include great thicknesses of mudstone and fine-grained sandstone that are apparently devoid of macrofossils, although the mudstone contains variable assemblages commonly dominated by organic-cemented agglutinated foraminifera.

The presence of microbialites and acritarch mats seems unique to the Kockatea Shale, but this may be due to warmer sea conditions in the Early Triassic (see Section 5.3) compared to the Permian and Cretaceous interior seas.

Therefore, the biota of the Kockatea Shale is currently insufficiently known to allow the estimation of the biotic diversity, or to determine relationships of individual taxa to their Permian progenitors or later Triassic successors. However, given the short period of investigation at the site, and the wide range of fossils already found, more intensive collecting by specialists will undoubtedly lead to a far richer inventory of species and a better appreciation of their role in the Early Triassic biotic recovery. As Pruss et al. (2005) concluded, an examination of many facies in a variety of palaeoenvironments is required. The challenge for basins of the East Gondwana rift–sag system is to find outcrop that is relatively unaffected by the severe Western Australian weathering, as well as obtaining additional cored borehole sections.

2.6 Conclusion

This preliminary survey of a new fossil biota from the Kockatea Shale of the northern Perth Basin, Australia, reveals:

(1) The site is no younger than Smithian (early Olenekian), and is probably Olenikian rather than Induan, based on spores and pollen of the *K. saeptatus* Zone, which elsewhere are associated with conodonts from the upper Induan *N. dieneri* and overlying Smithian *N. waageni* zones (Metcalfe et al., 2013), and on correlations to the subsurface indicating significant onlap of the Kockatea Shale onto granitic basement.

(2) Many groups are present in the fossil assemblage, but for most an estimation of diversity cannot be made due to poor preservation and the small numbers of representatives so far recovered. To date, the assemblage consists of acritarchs, Botryococcus, organic cemented siliceous agglutinated foraminifera, lingulid brachiopods, heteroconch and pteriomorph bivalves, micro-gastropods, ammonoids, spinicaudatans, insects, a possible austriocaridid, palaeonisciform and sarcopterygian scales and jaws, a temnospondyl-like mandible, plant leaves, thalli, and corms, megaspores, microspores, and pollen. Of these groups, the plants, insects, and non-branchiopod crustaceans are first records from this unit.

(3) The assemblage includes normal-marine, brackish-water, freshwater, and terrestrial organisms. The depositional environment is interpreted as being very shallow marine with variable water quality, perhaps changing on a daily, seasonal, or longer cycle. It may have had an estuarine character similar to the Permian and Early Cretaceous interior seas of Australia and to the modern Baltic Sea. Similar fossil associations are present in the Lower Triassic of other East Gondwana interior rift-sag system basins, indicating uniform conditions extended through much of the interior seaway.

(4) An unusual feature of the fossil assemblage is the extraordinary abundance of acritarch cysts, preserved in monospecific assemblages intertwined with amorphous organic matter. They may represent phytoplankton blooms in the nutrient-rich surface waters of the shallow sea, and were preserved as resting cysts incorporated in mats that covered the seafloor.

(5) At present, the Kockatea Shale assemblage is insufficiently known to allow the estimation of biotic diversity and analysis of connections between these taxa, their Permian progenitors, and later Triassic successors, especially in relationship to proposals of biotic decimation and recovery following the end-Permian crisis. More detailed specialist collecting from the site, and an examination of other facies in a variety of palaeoenvironments from many more localities, is required to properly evaluate such claims for the East Gondwana interior rift-sag system.

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Chapter 3. New morphological information and a redescription of the basal halecomorph fish, Promecosomina formosa Woodward 1908 from the Middle Triassic of the Sydney Basin, New South Wales, Australia.

Chapter 3 has been type set to be submitted to the peer-reviewed journal ‘*Gondwana Research’*.

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3.0 ABSTRACT

New fossil specimens, comprising complete fish previously identified as belonging to the genus *Promecosomina,* are here referred to *Promecosomina formosa*. The new material collected from Glendale Quarry, located near Somersby within the Sydney Basin of New South Wales, Australia, demonstrates a greater size range than previously realised for the taxa and shows additional morphological data indicating the need for redescription of not only *Promecosomina formosa* but also specimens attributed to *Promecosomina beaconensis*. We show here that specimens previously attributed to *Promecosomina beaconensis* instead represent part of an ontogenetic series of the single species *Promecosomina formosa*. A cladistic analysis of the basal halecomorphs resolved a monophyletic Parasemionotidae, which includes *Promecosomina formosa, Parasemionotus labordei* and *Stensionotus dongchangensis,* but excludes other taxa previously referred to the Parasemionotidae. We show that the Parasemionotidae clade comprises predominantly Gondwanan taxa.

Keywords: Basal halecomorph, Parasemionotidae, *Promecosomina*, ontogenetic series, Middle Triassic, Sydney Basin, Australia

3.1 INTRODUCTION

In the early 1900s, many fossils were discovered as a result of increased quarrying activity in and around the burgeoning Sydney centre, New South Wales, Australia. The most commonly found vertebrate fossils were of early actinopterygians. One of these fishes, *Promecosomina formosa,* has had a convoluted history of classification having been previously assigned to various orders including the Semionotidae Woodward, 1908, a Late Triassic – Early Jurassic order that pertains to the ginglymodians and currently resolved as monogeneric containing only the genus *Semionotus* (López-Arbarello, 2012); the

Pholidophoridae, a group of stem teleosts from the Late Triassic of Europe (Arratia, 2013); and the Platysomidae, an extinct group of typically deep-bodied fishes of uncertain phylogenetic relationships (Gardiner, 1960; Mickle, 2015; Wade, 1931; Woodward, 1908).

However, the attribution of *Promecosomina* to the genus *Semionotus* was disputed (Wade, 1941), as work on the Australian fossil fish faunas through the 1920s and 1930s changed the previously held view that all Australian taxa could be placed within the known European clades (Wade, 1941). Wade (1935) erected a new family Promecosominidae and genus *Promecosomina* to which he assigned *P. beaconensis* (Wade, 1935) and later described *P. formosa* (Woodward, 1908 revised Wade, 1941). Subsequently Wade (1941) recognised *P. formosa* as a subadult and both species of *Promecosomina* were synonymised (Wade, 1941), but incomplete and poorly preserved specimens resulted in not all juvenile characters being recognised and described. Additional specimens of *Promecosomina* were collected through the 1980s but identified only to the genus level *Promecosomina*, based on the earlier work of Wade (1941) with no further morphological study undertaken. Here we redescribe all specimens previously referred to the genus *Promecosomina* and present new morphological and ontogenetic features, not noted in the original (Woodward, 1908) or revised (Wade, 1941) descriptions.

The Parasemionotiformes comprise multiple taxa known from well-preserved materials that range in age from late Permian to Triassic, have a global distribution and are predominantly marine (See Romano et al., 2016, for a recent commentary on the Parasemionotidae, which excluded the Australian taxa). However, despite the large amount of morphological information known from the Parasemionotiformes, most have never been included in a phylogenetic analysis (Arratia, 2000) raising questions as to the robustness of previous phylogenetic analyses (Grande and Bemis, 1998; Ebert, 2018), which resolve the Parasemionotiformes as a monophyletic clade, which included the family Promecosominidae.

However, the erection of the Promecosominidae by Wade (1941) was disputed by Lehman (1952) based on a different interpretation of the preopercle. Wade (1941) determined the presence of a divided preopercle; however, as both sections contained the preopercle canal Lehman (1952) determined that the upper portion was not the suborbital but the upper extension of the preopercle. Based on this reinterpretation Lehman suggested *P. formosa* was a true Parasemionotid and that the Promecosominidae should be abandoned (Lehman, 1952). Although Wade (1953) agreed with Lehman (1952), Gardner (1960) considered the Promecosominidae as valid. Here we present a phylogenetic analysis, using multiple taxa assigned to the Parasemionotiformes, for the first time.

3.2 GEOLOGICAL SETTING

The Sydney Basin, New South Wales, Australia is a sedimentary basin comprising Permo-Triassic clastic sediments (Conolly and Ferm, 1971) (Fig. 3.1A, B). It is divided into four main groups: the late Permian-Middle Triassic (Anisian) Narrabeen Sandstone, the Middle Triassic (Anisian) Hawkesbury Sandstone; the Middle Triassic Mittagong Formation and the Middle Triassic (Ladinian) Wianamatta Group (Bryan, 1966; Damiani, 1999; Farman & Bell, 2020) (Fig.3.1C).

The deposition of the Narrabeen Sandstone is considered to have occurred under marine conditions (Naing, 1991) whereas the Hawkesbury Sandstone and Wianamatta Group are interpreted as a transgressive system with associated floodplain deposits represented by the Mittagong Formation (Dehghani, 1994). The Hawkesbury Sandstone represents an extensive north-eastern flowing braided river system connected to the sea towards the northeast of the modern-day Australian coastline (Herbert, 1997). The Wianamatta Group represents a subsequent marine transgressive event (Herbert, 1997).

Specimens of *Promecosomina* occur within the fossil bearing shale and sandstone horizons of the Hawkesbury Sandstone from the Gosford and Somersby areas north of Sydney (Fig. 3.1A, B) (Ritchie, 1981) and Wianamatta Group including the Ashfield Shale from around the inner Sydney metropolitan area (Fig. 3.1C) (Wilson & Edgecombe, 2003).

Fig 3.1.

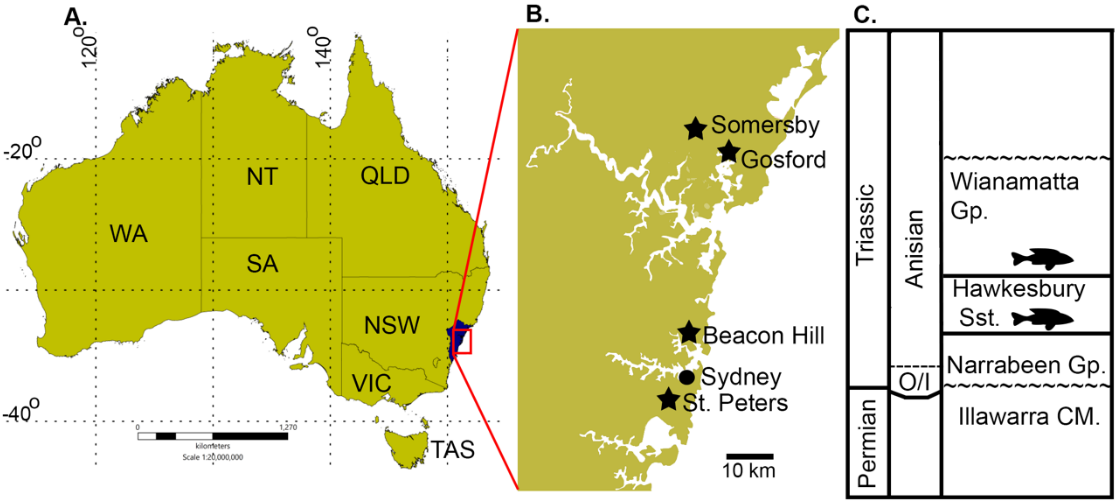

Fig. 3.1. Fossil localities where specimens of *Promecosomina formosa* were collected. **A,** Map of Australia indicating the position of the Sydney Basin (in purple), in New South Wales (NSW). Grid in latitude and longitude. Red rectangle denotes map area in B. **B,** Fossil bearing sites within the Sydney Basin (indicated by stars). **C,** Stratigraphic chart of the Sydney Basin indicating *Promecosomina*-bearing strata as fish silhouettes. Abbreviations for map: States of Australia: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria; WA, Western Australia. Abbreviations for stratigraphic chart: CM, Coal Measure; Gp, Group; O/I, Olenekian / Induan; Sst, Sandstone; ~, unconformity. Fig. 3.1C redrawn from Herbert (1979).

3.3 TAPHONOMY

Fossils of *P. formosa* are found as isolated specimens in many of the fish-bearing localities across the Sydney Basin (See Berrell et al., 2020; and McLean, 2024 for a summary); however, in several locations (including Somersby) they are recovered from mass mortality beds, where several hundred individuals are preserved across multiple bedding planes. Lithological descriptions, architectural elements and interpreted depositional settings for the fossil-bearing localities, as discussed below, are supported by sequence stratigraphic analysis conducted by Herbert (1997) and summarised in Table 3.1.

3.4 LOCALITY INFORMATION

St Peters Brick Pit, fauna previously described by (Woodward, 1908)

At St Peters (Ashfield Shale), fishes are preserved, articulated and complete; however, some individuals have sustained damage due to collecting methods. The fossils are generally preserved as carbonaceous films on the shale surfaces, although several fossils are preserved within siderite concretions. The presence of freshwater bivalves (unionids) was considered indicative of a freshwater lacustrine environment (Herbert, 1976); however, this interpretation has been revised and the bivalves are now considered to represent a lag deposit on the transgressive surface between the low stand and transgressive system (Herbert, 1997). This interpretation is further supported by Helby (1973), who regarded acritarchs from the Ashfield Shale as indicative of a shallow marine to brackish environment. The inclusion of some fossils within siderite nodules indicated intermittent periods when the environment was anoxic.

Somersby (Glendale Quarry locality)

All the fossil fish from the Glendale Quarry locality (Hawkesbury Sandstone), Somersby, are articulated and complete, showing little evidence of scavenging or disarticulation. The fishes' completeness, in particular intact fins and lepidotrichia, in addition to complete scale cover, indicate minimal post-mortem transport of the carcasses. The lack of bloating and floating can be attributed to low water temperatures <16º C (Elder & Smith, 1988), which is within the accepted temperature range estimates from climate modelling for the Early–Middle Triassic (Miller & Baranyi, 2019). Furthermore, locations with a high diversity of taxa and a variety of body shapes, including deep-bodied fishes (in this case *Cleithrolepis* and to a lesser extent *Promecosomina*) are indications of a low-gradient water body (Miller & Baranyi, 2019). There is an absence of scavenging, which suggests dysoxic or anoxic bottom conditions. This combination of evidence supports the Somersby location (Hawkesbury Sandstone) as representing a palaeoenvironment comprising a stratified water column with little or no water flow, i.e., a stratified lake or cut-off loops in a large meandering river system (Ritchie, 1981; Willis, 1996). The faunal overlap (Table 3.1) from the Gosford Railway Ballast Quarry (discussed below) and Somersby could indicate that the strata Glendale Quarry is a more deeply weathered section of the Gosford Formation (McDonnell, 1973).

Gosford, Railway Ballast Quarry, fauna described by (Woodward, 1890)

The fossils at Gosford are found as complete individuals within a shale lens of the Gosford Formation, (Edgeworth David in Woodward, 1890). A description of the stratigraphy is presented by Edgeworth David in Woodward, (1890) with the depositional setting probably represented as a similar scenario to Somersby, above.

Beacon Hill, Brookvale, fauna described by (Wade, 1935)

The shales at Beacon Hill Quarry, Brookvale, preserve a very diverse flora and fauna including Equisetalean plants (Holmes, 2001), unionid bivalves (David, 1950), insects

(Tillyard, 1925; McKeown, 1937), two species of conchostracans, a xiphosauran (Riek, 1968), at least 20 genera of fish (Wade, 1935) (Table 3.1) and a labyrinthodont amphibian (Watson, 1958). This fauna supports the interpretation of a freshwater braided-plain channel depositional environment (Herbert, 1997).

Table 3.1. Summary of facies identified from the study areas, with environmental architectural elements and dominant lithology. The vertebrate fauna column shows faunal overlap between the formations. *P. formosa* in bold to highlight commonality. Abbreviations: eq. Equivalent.

Formation / Locality	**Lithology / facies description**	**Depositional setting**	**Architectural element**	**Dominant Grain Size**	**Pooled Architectural Elements**	**Vertebrate Fauna**
Wianamatta Group/St. Peters Brick Pit	Dark indurated shale/grey mudstone (Woodward, 1908)	Shallow marine (Herbert, 1980)	Prograding shoreface/coastal plain sedimentation (Herbert, 1997)	Mud/clay	Estuarine/coastal plain	*Pleuracanthus parvidens* *Sagenodus laticeps* *Palaeoniscus crassus* *Elonichthys armatus* *Myriolepis pectinate* *Elpisopholis* ***P. formosa***
Gosford Formation, distal eq. Hawkesbury Sandstone (McDonnell, 1973)/Gosford Railway Ballast Quarry	Sandy Shale & purplish-grey laminated mudstone (Woodward, 1890)	Freshwater (McDonnell, 1973)	Flood Plain and associated channel environments (McDonnell, 1973)	Mud/clay	Flood plain	Indet. Chondrichthyes *Gosfordia* *Myriolepis* *Apateolepis* *Dictyopyge* *Pristisomus* *P. formosa* *Cleithrolepis* *Belonorhynchus*
Hawkesbury Sandstone/Glendale Quarry, Somersby	Buff micaceous sandstone	Freshwater – fluvial to lacustrine (Watson 1991)	Stratified lake, part of an N-E meandering river (Watson 1991)	Very Fine Sand	Flood plain	*Gosfordia* ***P. formosa*** *Saurichthys* *Cleithrolepis* Undescribed Chondrichthyes
Hawkesbury Sandstone/Beacon Hill, Brookvale	Micaceous shale	Freshwater (Riek, 1967)	Low-laying coastal plain (Herbert, 1997)	Mud/clay/Silt	Flood plain	*Ariguna fomosa* *Megapteriscus* *Belichthys* *Leptogenichthys* *Mesembroniscus* *Myriolepis* *Brookvalia* *Beaconia* *Dictyopleurichthys* *Geitonichthys* *Molybdichthys* *Phylctaenichthys* *Schizurichthys* *Cleithrolepis* *Manlietta* *Procherichthys* *Macroaethes* *Saurichthys* *Enigmatichthys* ***P. formosa***

3.5 MATERIALS AND METHODS

3.6 INSTITUTIONAL ABBREVIATIONS

AM F., Australian Museum, William Street, Sydney, New South Wales (NSW), Australia; **NHMUK**, The Natural History Museum, London, United Kingdom; **U. S. G. D** The University of Sydney Geology Department, with specimens from this collection now housed at the Australian Museum, Sydney.

3.7 ANATOMICAL ABBREVIATIONS

Anatomical abbreviations follow those used by Wade (1935), Olsen (1984) with modification from Ebert (2018). **af**, anal fin; **ang**, angular; **bop**, branchiopercle; **br**, branchiostegal ray; **cf**, caudal fin; **co**, coracoid; **cl**, cleithrum; **clav**, clavicle; **d**, dentary; **df**, dorsal fin; **dpt**, dermopterotic; **dsp**, dermosphenotic; dspo, exposed portion of the sphenotic **fr**, frontal; **ff**, fringing fulcra; **g**, gular plate; **io**, infraorbitals; **mx**, maxilla; **n**, nasal; **op**, opercle; **or**, orbit; **pa**, parietal; **pcf**, pectoral fin; **pcl**, postcleithrum; **pmx**, premaxilla; **pop**, preopercle; **psp**, parasphenoid; **ptt**, posttemporal; **pvf**, pelvic fin; **rar**, retroarticular**;** **sc**, scale cover; **sca**, scapular; **scl**, supracleithrum; **smx**, supramaxilla; **so**, supraorbital; **sop**, suboperculum; **suo**, suborbital; **t**, teeth; tab, tabular (=supratemporal). Sensory canal abbreviations: **ioc**, Infraorbital canal; **lc**, lateral line canal; **md**, mandibular canal; **prc**, preopercle canal; **soc**, supraorbital canal. (l) or (r) suffix indicate left or right bone.

3.8 DESCRIPTIVE TERMINOLOGY

Bone identification and terminology follows that of Wade (1935), Olsen (1984) with modification from Ebert (2018).

Scale descriptions follow the terminology of Esin (1990).

Environmental architectural elements follow that of Pickering et al., (1986).

3.9 PREPARATION

The majority of fish described by Woodward (1908) including the holotype were recovered by quarrymen splitting blocks of shale with a hammer and chisel. The holotype was stabilised by setting it in a concrete supported by a wooden frame, followed by the application of an unknown lacquer.

Fossils found in the 1980s from the Somersby locality were recovered either by the method described above; or by collecting exposed material lying at the bottom of the quarry. Fossils were removed from large blocks using a brick saw and later trimmed to size. Due to their friable nature, fossils were stabilised by soaking them in a solution of paraloid.

3.10 MEASUREMENTS

Standard fish measurements (Mous et al., 1995) were used in measuring specimens of *Promecosomina.* Measurements were taken with either a digital calipers or tape measure with 1mm increments and are presented in Appendix I.

The elongation ratio was calculated as a ratio of length to depth by taking the standard length (Mous et al., 1995) and then dividing this by the maximum body depth (Katz and Hale, 2016; and references therein).

Predorsal length was calculated by measuring the distance from the premaxilla to the start of the dorsal fin divided by the standard length and then calculated as a percentage (Grande, 2010).

Skull length was measured from the anterior tip of the premaxilla to the posterior junction of the opercle and subopercle as per Neuman (1986). Head depth was measured from the intersection of the dentary and angular in a vertical line to the top of the frontals. In juveniles where the angular is unable to be established, the termination of the dentary is approximated and measured from the approximate posterior position of the dentary to the top of the frontals. Where the skull roof was crushed flat, we have measured to the junction of the two frontals to represent one whole side of the fish; however, where fish are dorso-laterally crushed this exaggerates the head length to head depth ratio.

The head depth to head length ratio was calculated by dividing the head depth by head length.

Scale row count methodology followed Masuda et al., (1984). Horizontal scale rows were counted along the lateral line, referred to as longitudinal row (LR). Vertical scale row (also called transverse row (TR)) were counted at the widest part of the fish, in this case from the start of the dorsal fin to the start of the anal fin as per Masuda et al., (1984). Vertical scale rows were counted as per Ebert (2018), from the postcleithra to the hinge line along the lateral line (Ebert, 2018; character 41).

3.11 COMPARATIVE MATERIAL

To obtain and/or check previously coded characters for the phylogenetic analysis, representatives of the Parasemionotiformes were studied using photographs and line drawings presented in: Romano et al., (2019) for *Candelarialepis argentus*; Liu et al., (2002) for *Jurongia fusiformes*, *Qingshania cerida*, *Stensionotus dongchangensis* and *Suius brevis*; Li (2009) for *Peia jurongensis*; and Priem (1924) for *Parasemionotus labordei.* Character states for all other taxa were the codes of Ebert (2018) and were accepted.

3.12 RESULTS

Systematic palaeontology

Subclass ACTINOPTERYGII Cope, 1887 sensu Rosen et al., 1981

Series NEOPTERYGII Regan, 1923

Unranked HALECOSTOMI Regan, 1923 sensu Sallan, 2014

Division HALECOMORPHI Cope, 1872

Order PARASEMIONOTIFORMES Lehman, 1966

Family PARASEMIONOTIDAE Stensiö, 1932

Promecosominidae

3.13 Emended Diagnosis

The Parasemionotidae are diagnosed by the following combination of characters: head length is 35% or less of standard length; abbreviated heterocercal tail, nearly vertical, or slightly forked caudal fin with long medial fin rays; scales of reduced lepisosteid type; small posterior myodome and post-temporal fossa; vomers present and attached weakly to parasphenoid; short parasphenoid; ventral limb of preopercle placed vertically beneath dorsal limb; relatively long maxilla that extends below the orbit; a single antorbital; large nasals; the upper postinfraorbital is approximately the same length as the lower postinfraorbital; hyomandibular facet almost horizontal; presence of an interopercle; maxilla free from preopercle and infraorbitals; dentary with high coronoid process; presence of a clavicle; 4-6 epaxial caudal basal fulcra and number of lepidotrichia equal in number to their endoskeletal supports and lepidotrichia few in number and undivided for a rather long proximal portion of their length;

3.14 Remarks

In his diagnosis of the Parasemionotidae Lehman (1966) included general Halecomorphi characters. Here the presence of a supramaxilla, interopercle and vertical or subvertical suspensorium are excluded as diagnostic characters of the Parasemionotidae because all these characters are shared amongst the Halecomorphi clade. An additional character: large nasals meeting in the midline which was previously considered diagnostic for the Parasemionotidae (Neuman 1986) has been modified to exclude the nasals meeting midline because not all taxa (*Promecosomina formosa*) within this group possess this character.

Genus *PROMECOSOMINA* Wade, 1935

PROMECOSOMINA FORMOSA (Woodward, 1908)

Fig 3.2 – 3.8.

Semionotus formosus Woodward, 1908

Pholidophorus (*Semionotus*) *australis* Woodward, 1908

Acentrophorus sp. Woodward, 1908

Promecosomina beaconensis Wade, 1935

Promecosomina formosa Wade, 1941

Fig. 3.2.

Fig. 3.2. *Promecosomina formosa* (AM F.135068) preserved in lateral view from Glendale Quarry, near the town of Somersby, New South Wales, Australia. Scale bar: 1 cm.

3.15 Emended Diagnosis

A Parasemionotidae with the following combination of characters: nasals are large; a single antorbital; presence of an interopercle; maxilla free from preopercle and infraorbitals; dentary with high coronoid process. Wade (1941) used the characters of a blunt snout; eyes central and placed above oral margin; tail forked; cranial roof dermal bones with poorly defined ornamentation, forwardly inclined suspensorium to diagnose *P. formosa* and these characters are supported here. *P. formosa* contains the following apomorphies: Possessing a long and narrow preopercle that is crescent shaped; a predorsal length of 41.8 % (calculated from AM

F.101712); vertical scale rows contain 50 scale rows; principal caudal fin rays of 21 rays and a maximum standard length of 28.5 cm (AM F.101749).

5.1.3 Remarks

The retention of a large single median gular; a single supramaxilla; a long, and a narrow crescent-shaped preopercular (Neuman, 1986; Ebert, 2018) support the placement of *Promecosomina* within the Halecomorph.

The retention of a comparatively short parasphenoid; hyomandibular facet almost horizontal; preopercular in combination with the suborbital create a broad kidney shaped outline; ventral limb of preopercle placed vertically beneath dorsal limb; maxilla remains relatively long; clavicle and abbreviated heterocercal tail and scales of reduced lepisosteid type place *Promecosomina as a* parasemionotid.

The character of a fusiform body (Wade, 1941) has here been determined to be present only in juveniles and so is removed as a diagnostic character.

5.1.4 Stratigraphic and Geographic Range

All localities are located within the Middle Triassic (Anisian), Hawkesbury Sandstone and Wianamatta Group, Sydney Basin, New South Wales, Australia (Fig. 3.1):

St. Peters – see below under type locality.

Manly Brick and Tile Coy, Beacon Hill (commonly referred to as Beacon Hill Quarry), near the town of Brookvale, New South Wales, Australia. Beacon Hill Quarry, now Beacon Hill Reserve, is located at 33°45'13.6"S 151°15'47.7"E. The horizon is a shale lens, located within the Hawkesbury Sandstone (Wade, 1935).

Glendale Quarry, located near the town of Somersby, New South Wales, Australia. Glendale Quarry – Somersby is located at S33°22'52.9"S 151°15'53.6"E. Hawkesbury Sandstone, ~ 25m above the contact with the Narrabeen Group (Watson, 1991).

Gosford, (Rail ballast quarry) located near the town of Gosford, New South Wales, Australia. This rail ballast quarry is located approximately in vicinity to President Hill, Gosford, near 33°25’34.7” S 151°20’18.0”E. Gosford Formation interpreted to be a distal equivalent of the Hawkesbury Sandstone (McDonnell, 1973).

5.1.6 Holotype

AM F.38905 (part) and NHMUK PV P 18091 (counterpart). The holotype was separated with the part remaining at the Australian Museum and the counterpart curated to the collections of the Natural History Museum, London, United Kingdom.

5.1.7 Type Locality

St. Peters Brick Pit, S 33° 54.800 E 151° 11.000 (now Sydney Park) New South Wales, Australia. St. Peters Brick Pit operated from the 1880’s—1970.

5.1.8 Type Horizon

Ashfield Shale, Wianamatta Group, Sydney Basin, New South Wales, Australia (Fig. 3.1). Ladinian, Middle Triassic.

5.1.9 Material

Promecosomina formosa NHMUK PV P18072 (Gardiner 1960); AM F.148, AM F.17954, AM F. F.14263, AM F. 17953, AM F.29729, AM F.29731, AM F.142857 (original number F3196C), AM F. 3196, AM F.142858 and AM F.142859 (originally F. 3196 E and D) (Wade, 1941) AM F.39545.

Promecosomina beaconensis NHMUK PV P16823-4, part and counterpart (figured by Wade, 1935); AM F.66968 (Originally numbered U.S.G.D 192).

Promecosomina AM F.101321, AM F.101368, AM F.101439 — AM F.101447, AM F.101449 — AM F.101450, AM F.101645 — AM F.101653, AM F.101657 — AM F.659161, AM F.101666 — AM F.101669, AM F.101671, AM F.101673, AM F.101679, AM F.101712, AM F.101749, AM F.101799, AM F.100918, AM F.100930, AM F.134935, AM F.135068.

5.1 Description of adult specimens

5.21 Remarks

The ventral and dorsal morphology of the species has not previously been described; however, the lateral morphology with the exception of the axial skeleton morphology and dermal ornamentation, has previously been described but only for small and mid sized individuals (Woodward, 1908; Wade, 1935; Wade, 1941). In light of larger adult specimens being recovered the whole fish is re-described.

5.3.1 Skull

In lateral view, the skull is slightly longer than deep (~1.3 times (Appendix I)) showing a triangular outline in lateral view (Fig. 3.3A-D). The anterior margin of the skull is rounded and the mouth is terminal (Figs. 3.4, 3.5). In dorsal and ventral views, the skull has a semi-circular outline.

Fig. 3.3.

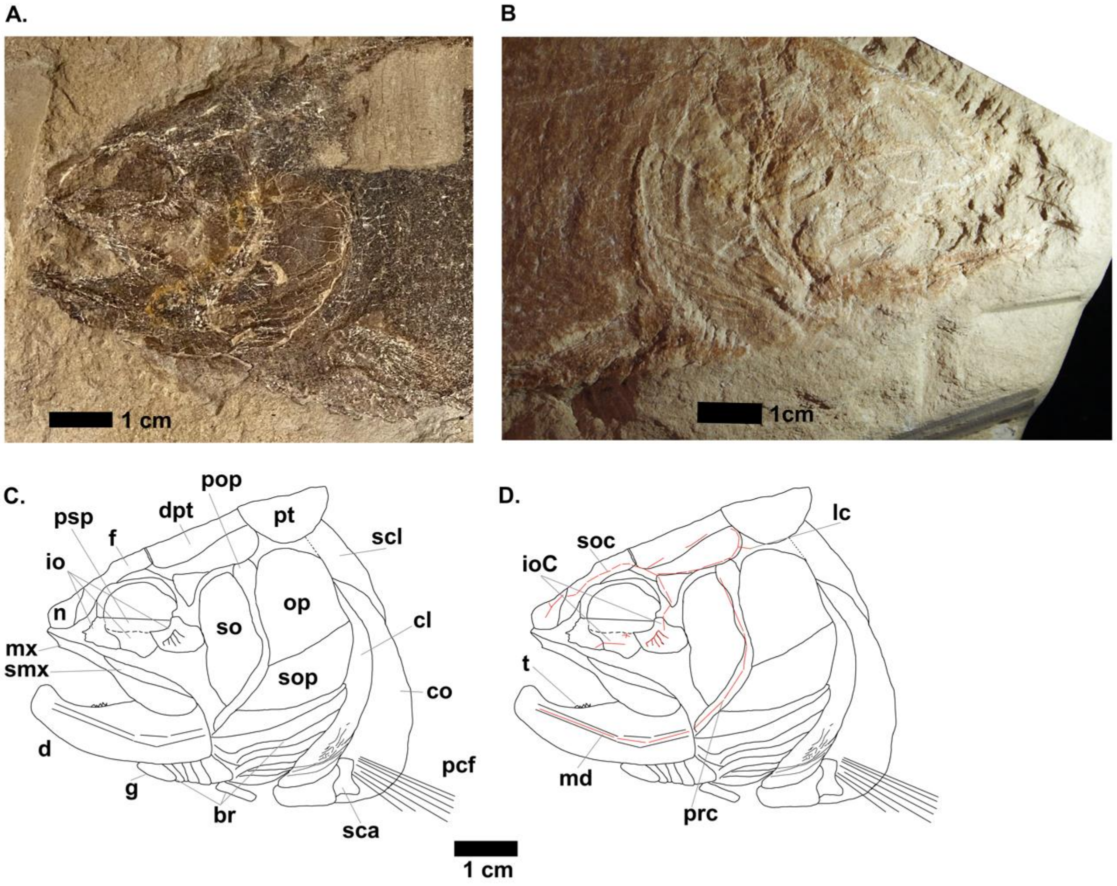

Fig. 3. 3. **A**, Skull of *Promecosomina formosa* AM F.101368 preserved in left lateral view. **B,** Skull of *Promecosomina formosa* AM F.101671 preserved in right lateral view. **C,** line drawing of A, indicating the bones of the skull. **D,** line drawing of A, indicating the path of the sensory line canals as they are preserved. Scale bar = 1 cm.

The dermal bones of the head comprise paired nasals, frontals, parietals dermopterotics, supratemporals and posttemporal bones. The dermal ornament on the frontals comprises a series of indistinct irregular circular bumps. Sutures between the dermal bones of the skull are not prominent, although this may be an artefact of preservation. The presence of sensory line canals on the skull bones and along the bone boundaries, further obstructs the sutures (Fig. 3.3D).

Nasals are rectangular in shape and do not meet along the midline (AM F. 100918). Anteriorly the nasals connect to the premaxilla and posteriorly to the frontals (Fig. 3.4).

Fig. 3.4.

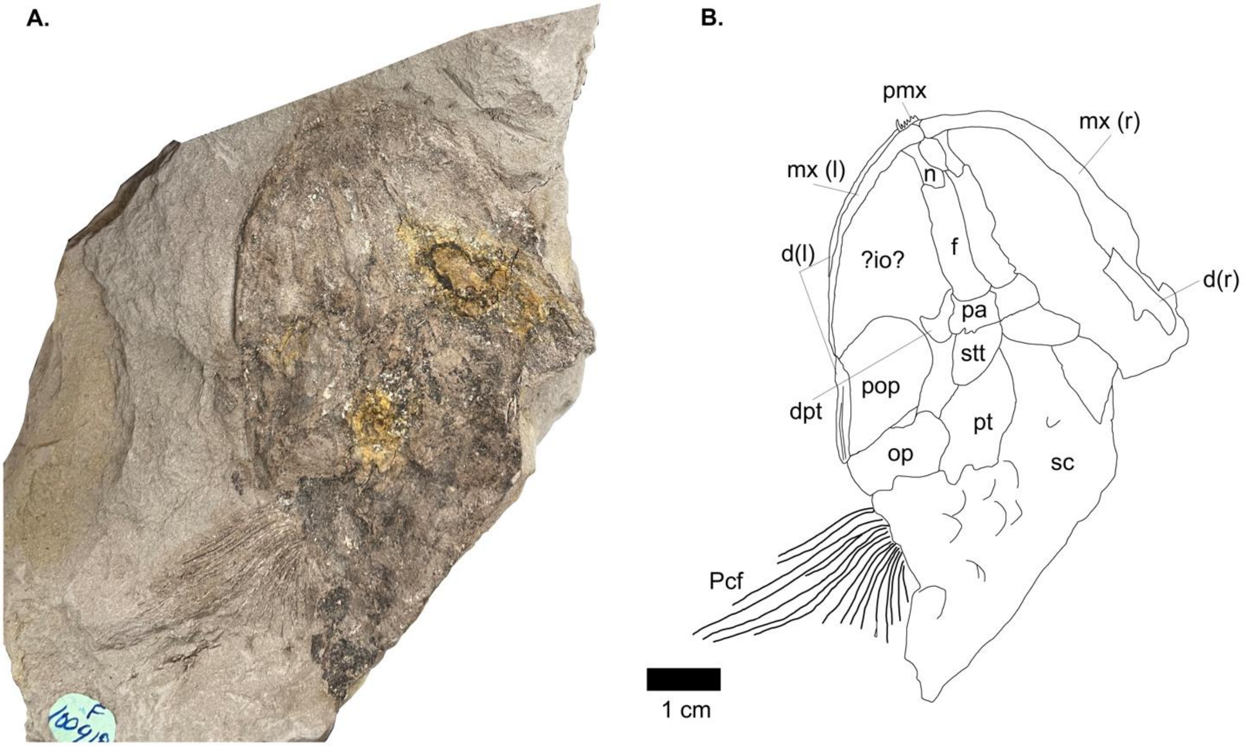

Fig. 3.4. **A**, Skull of *Promecosomina formosa* AM F.100918 preserved in dorsal view. **B**, line drawing of the dorsal skull roof bones. Scale bar = 1 cm.

The frontals (=parietal of Mickle, 2015) are elongated and positioned above the orbit. They are thin and long, being the largest bones of the skull roof, extending from the nasal and lacrimal bones anteriorly, to above the halfway point of the dermopterotic. The frontals meet medially, and the margin is straight. The frontals are six-times as long as wide (width-to-length ratio = 0.16) (Appendix I). The dermopterotic bone forms part of the skull roof, posterior to the orbit and anterior to the opercular bones (Fig. 3.4). Posteriorly, the frontals connect with the two rectangular, non-fused parietals (=post parietals of Mickle, 2015). The parietals are relatively short, being wider than long.

There is a single, broadly triangular tabular (=supratemporal of Olsen, 1984) on each side of the skull, posteriorly to the dermopterotic. It is assumed that these two bones meet anteriorly at the midline of the skull. There is a single, triangular posttemporal on either side of the skull that is larger than the tabular (Fig. 3.4). It extends and overhangs the back of the skull, extending beyond the limit of the supracleithrum.

An exposed portion of the sphenotic (AM F. 101671) extends into the orbit and appears knob-shaped, and lacks dermal ornament.

5.3.2 Infraorbital series

The infraorbital series is not well preserved in most specimens, making the margins of the bones hard to differentiate. There are at least six bones that make up this series, (including the lacrimal and dermosphenotic). These bones connect between the dermosphenotic, located posterodorsally to the orbit, and the lacrimal anteroventral, located anteroventrally. The first infraorbital (= lacrimal of Grande and Bemis, 1998; Fig. 3.3) is a large, sub-rectangular, slightly concave bone, longer than deep, and occupying the anteroventral corner of the orbit, where it meets the maxilla. Because of poor preservation, and due to its size, it cannot be determined if the first infraorbital comprises one or two bones. It is thought unlikely to consist of two bones as the lacrimal is typically large in early neopterygians (Grande and Bemis, 1998 and figures therein).

The second infraorbital is an elongate, rectangular bone that connects with the first and third infraorbitals. The third infraorbital is posteroventrally enlarged, being almost "D" shaped and the largest bone in the infraorbital series, reaching the anterior margin of the preopercle. The fourth infraorbital appears to come in contact with or near contact with the dermosphenotic. The infraorbital sensory canal can be seen to run through all elements of the infraorbital series, appearing as a simple pipe in the first and second infraorbitals, becoming branched in io3 (Fig. 3.3D), with at least 5 branches diverging ventrally (AM F.101799). There does not appear to be ornament or pitting on any of the infraorbitals (Fig. 3.3).

The suborbital is a large, ovoid bone that fills the space between the preopercle posteriorly and the infraorbitals anteriorly. Due to its preservation, it is not certain if the suborbital is one bone or multiple bones making up a suborbital series.

5.3.3 Jaws

The premaxilla is transversely elongate and rod-shaped, bearing at least eight conical teeth in a single row along the margin (Fig. 3.4). In most specimens, few teeth are visible, tooth sockets are also obstructed by matrix, so a total tooth count is not possible. Where visible, the teeth reduce in size posteriorly (Fig. 3.5).

The dentary is strongly ossified, bears an ornament of fine striations, is anteriorly narrow and widens in the posterior region behind the orbit (Fig. 3.3). A large groove, for the mandibular sensory canal, is centrally located along the length of the dentary (Fig. 3). Posteriorly the dentary connects with the angular and retro-articular (Fig. 3.6).

The teeth form a single row along the margin of the dentary and decrease in size in an anterior to posterior direction (Fig. 3.5). The teeth are elongate, conical in shape with a pointed apex, and recurve posteriorly.

Fig. 3.5

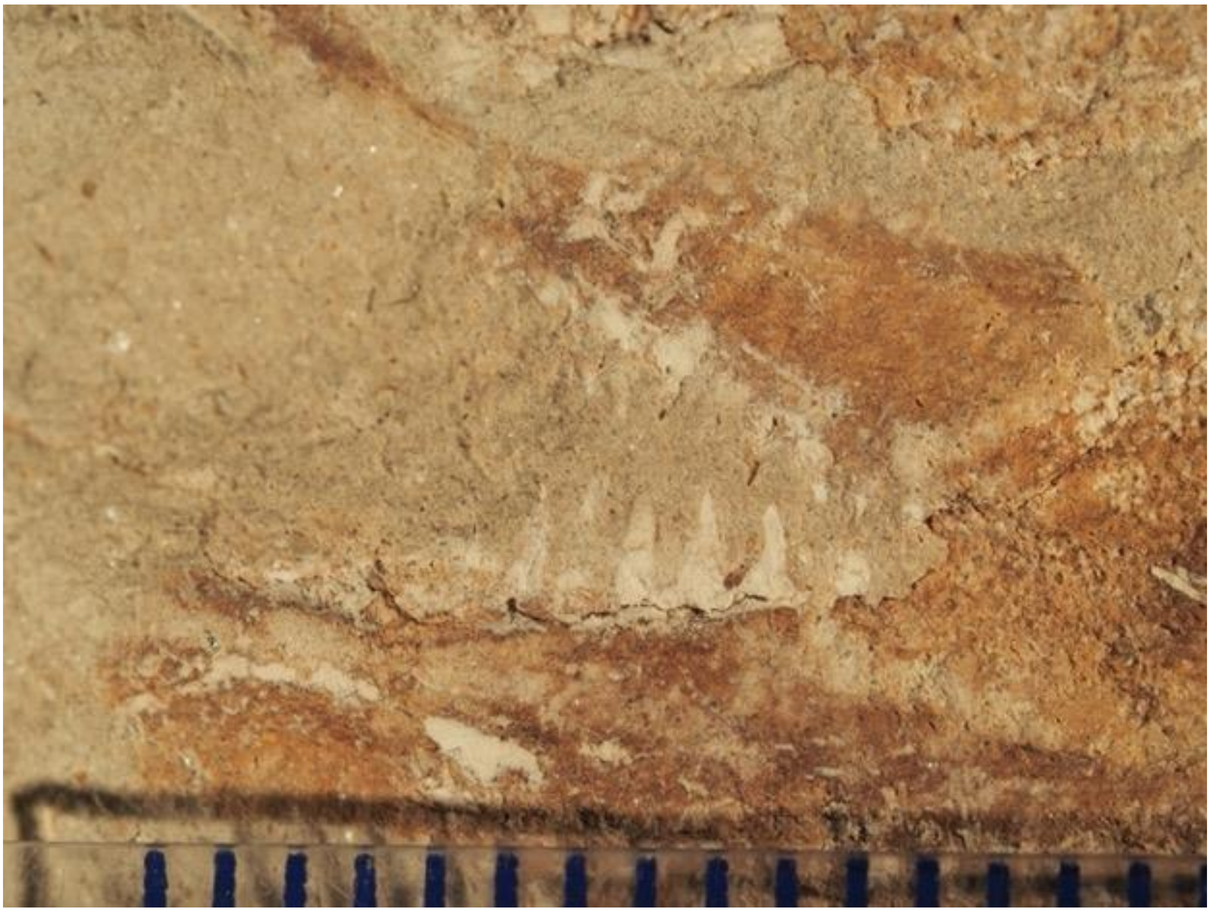

Fig. 3.5. AM F.134935, showing dentary and maxillary teeth. Scale is in millimetres.

The maxilla approximates the length of the dentary and extends posteriorly behind the orbit by at least 2/3rds of the total length of the maxilla. There is a single supramaxilla, which is elongated and tapers towards each end located towards the anterior portion of the maxilla. There is a single row of equal-sized, conical, recurved teeth along its margin; the teeth are smaller in height than those on the dentary teeth (Fig. 3.5).

5.3.4 Opercular series and branchiostegals

The preopercle is long and narrow, becoming slightly curved in shape towards the dentary. The anterior preopercle sensory canal comprises a dorsal and ventral portion that together form a gentle crescent “(” shaped canal that runs the posterior length of the preopercle (Fig. 3.3D).

The opercle has rounded corners with an overall square shape and represents one of the larger bones of the opercular series.

The subopercle is slightly smaller than the opercle and rectangular in shape. The interopercle is a small, triangular bone that is located near the ventral end of the preopercle and anterior to the subopercle.

There are at least two branchiopercles (slightly larger than the other branchiostegal rays) that are generally rectangular in shape that sit below the subopercle and form part of the branchiostegal array.

There are at least 8 branchiostegal rays on each side of the gular plate (Fig. 3.6). The branchiostegal rays are generally elongated in shape with rounded ends (Fig. 3.6).

There is a single flat gular plate that is oval, with its longest axis aligned antero-posteriorly. The gular does not occupy the entire void between the left and right lower jaw bones and the gular overlaps the proximal parts of the branchiostegal rays (AM F.101321, Fig. 3.6).

Fig. 3.6.

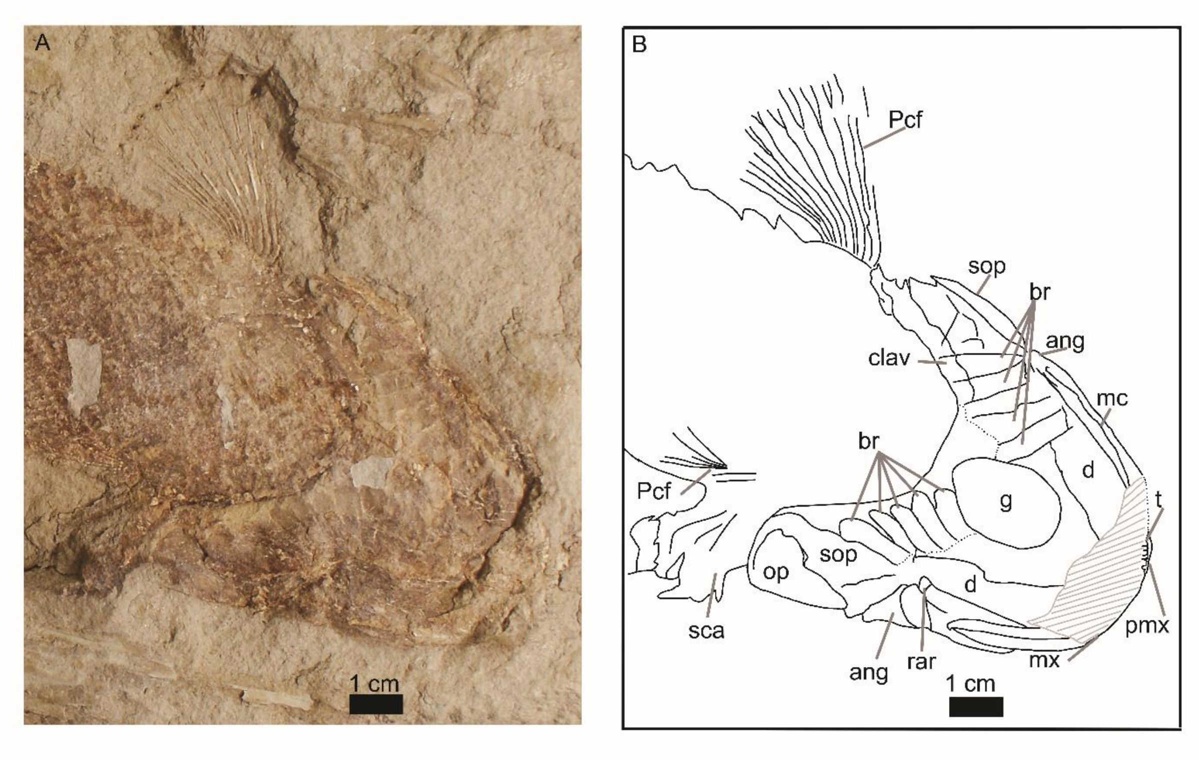

Fig. 3.6. Ventral view of the head and pre-pelvic region of *Promecosomina formosa* AM F.101321. **B**, line drawing indicating the skull and anterior part of the body in ventral view. Shaded part in the anterior region represents sediment covering the bones. Scale bar = 1 cm.

5.3.6 Axial skeleton

Due to the thick covering of scales, an exact vertebral count is not possible. The two parallel lines along the ventral flank of the fish suggest that the vertebrae were not ossified. The “double” line identified along the scales (Fig. 3.2) indicates the presence of paired neural spines, and ribs.

5.3.7 Paired fins

Specimens from the Glendale Quarry preserve paddle-shaped pectoral fins which comprise a primary ray, covered in fringing fulcra scales and at least an additional 13 fin rays that bifurcate distally, into two fin rays branches (AM F.10132, Fig. 6).

The triangular pelvic fins are located in the mid ventral area of the body, with the first fin ray originating more anteriorly than the first ray of the dorsal fin. The first ray of the pelvic fin is covered by fringing fulcra scales followed by at least an additional 6 rays that bifurcate distally (Fig. 3.7).

Fig. 3.7.

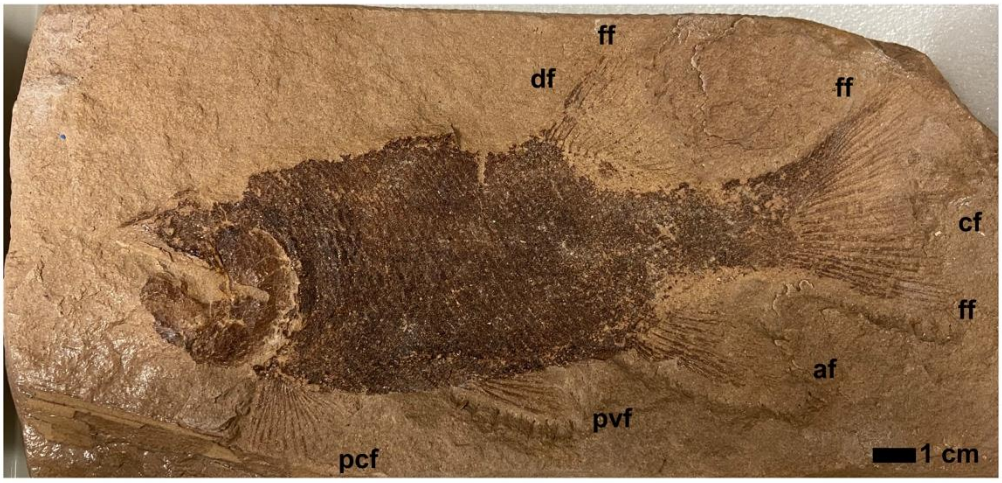

Fig. 3.7. *Promecosomina formosa* AM F. 101338, in left lateral view with all fins preserved. Scale in centimetres.

5.3.8 Unpaired fins

The single dorsal fin approximates an equilateral triangle in shape (in lateral view), commences at the 21st scale row, anteriorly to the anal fin and spans eight scale rows (Fig. 3.7). The fin possesses at least 12 segmented fin rays that bifurcate distally. The first fin ray is the longest and is not segmented or bifurcated, but is covered in fringing fulcra scales. Each successive fin ray is decreased in height in an anterior to posterior direction.

The anal fin starts at about the 29th scale row and, like the dorsal fin, has a long fin base that spans ~8 scale rows. It comprises at least 11 primary fin rays that bifurcate, the first fin ray being covered in fringing fulcra scales.

5.3.9 Caudal fin

The caudal fin is heterocercal. The forked caudal fin comprises 21 fin rays, each of which bifurcates and then bifurcates again, resulting in four total branches (Fig. 8). There appear to be 4 -5 unsegmented procurrent rays dorsally (Fig. 8). The dorsal lobe of the caudal region has a sigmoidal outline, with the fin rays of the ventral lobe commencing anterior to the start of the dorsal lobe fin rays. The dorsal lobe includes the 1st – 7th principal caudal rays. The first ray is covered in fringing fulcra, with at least an additional 6 fin rays. Which bifurcate twice posteriorly (four branches in total for each). The median rays (principal caudal rays 8 – 14) are slightly shorter than the fin rays that make up the dorsal and ventral lobes, making the caudal fin forked. These fin rays bifurcate posteriorly at least once (two branches in total). The ventral lobe contains principal caudal rays 15 – 21 that are tightly packed together in this specimen. In these rays the lepidotrichia are taller than wide. These ventral rays bifurcate twice posteriorly (four branches in total). There is also a ventral ray covered in fringing fulcra. Lepidotrichia segments meet other lepidotrichia by flat connections, unlike those of more advanced neopterygians where there are z-like junctions between segments (Fig. 3.8). There are approximately 6 epaxial caudal basal fulcra.

Fig. 3.8.

Fig. 3.8. Caudal and anal fin of *Promecosomina formosa* AM F. 100930. Scale is in centimetres.

Scales

There are 50 scale columns, horizontally, from post cleithra to caudal fin (counted along the lateral line).

Scales located between post cleithra, and the dorsal fin are elongated dorso-ventrally, being rectangular in shape. Scales posteriorly of the dorsal fin are square in shape.

6 3.9

7 Juvenile specimens

6.12 Remarks

Only those characters unique to juveniles are described below.

Material

The holotype of *Promecosomina formosa* (AM F.38905 (part) and NHMUK PV P 18091 (counterpart) is here recognised as a juvenile following the collection of larger adult specimens in the 1980s.

AM F.66968, NHMUK PV P 12466, NHMUK PV P 12472, NHMUK PV P 18097, AM F. 142858, AM F. 142859.

6.1.1 Preservation

All specimens are preserved in either right or left lateral view.

6.1.2 Ontogenetic Changes

The body shape changes through ontogeny (Fig. 3.9, 3.10) with juveniles having an elongate or torpedo body shape (Fig. 3.9A), whilst adults are deeper bodied (Fig. 3.9D and Fig. 3.10). Fishes with a standard length between 14 cm and 15 cm show an expansion of the body along the dorsal margin extending from the posterior margin of the head to the anterior margin of the dorsal fin, resulting in the fish exhibiting a hunchback appearance (Fig. 3.9C). This represents a transitional stage between the adult and juvenile shapes (Fig. 3.9C) and indicates that the anterior region of the body deepens prior to the posterior region. There is a strong correlation between length and depth throughout growth (Fig. 3.10).

Fig. 3.9.

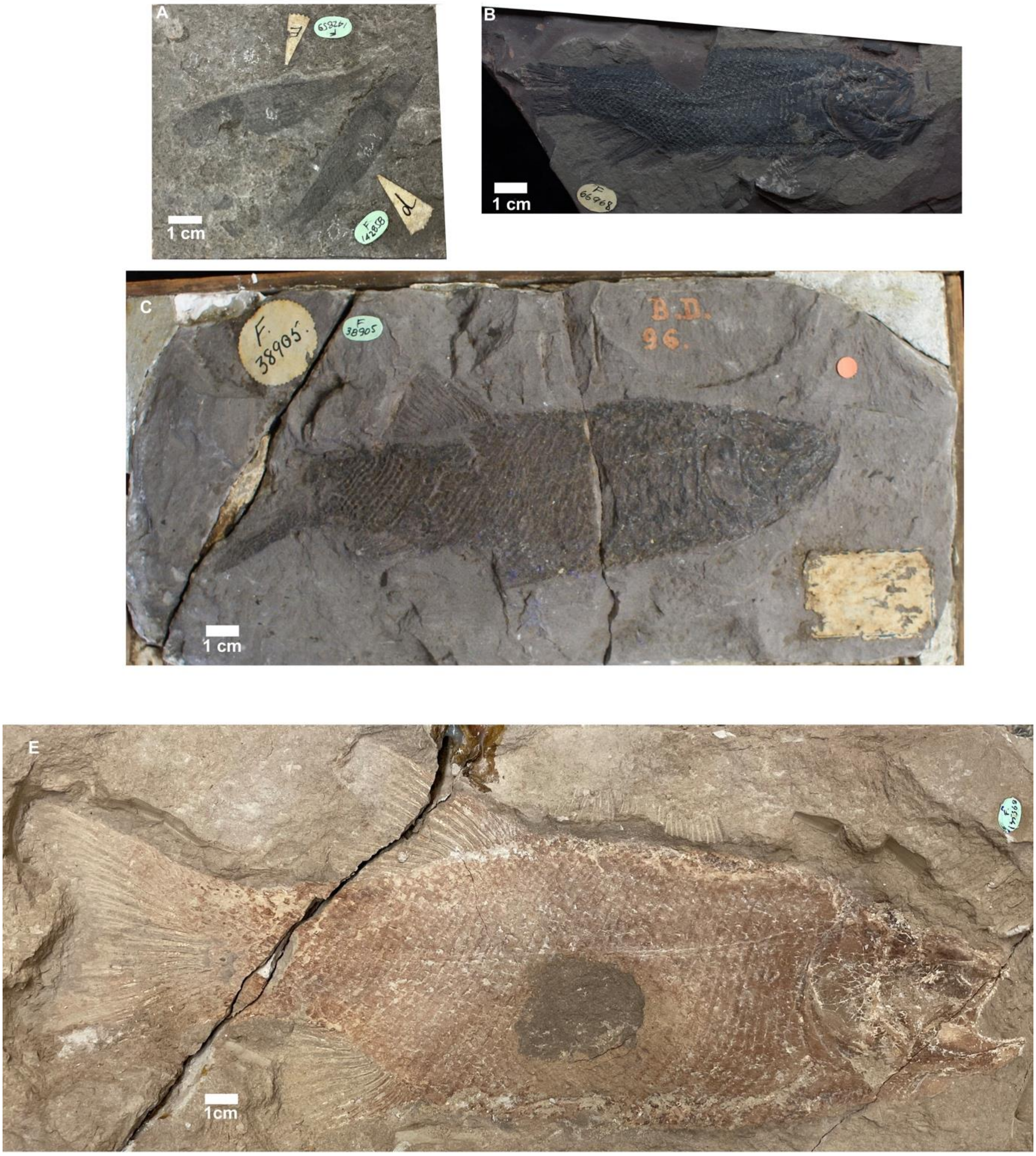

Fig. 3.9. Ontogenetic series of *Promecosomina formosa*. **A**, AM F. 142858 and AM F. 142859, juvenile fishes from St Peters Brick Pit locality. **B**, AM F. 66968 from Beacon Hill, Brookvale. **C**, AM F. 38905 (holotype) from St Peters Brick Pit locality, subadult fish. **D**, Adult fish, AM F.135068 from Glendale Quarry, Somersby. Scale = 1 cm. Note the changes

of proportions in body shape and fin shape, along with differences in preservation from juvenile to adult.

Fig. 3.10.

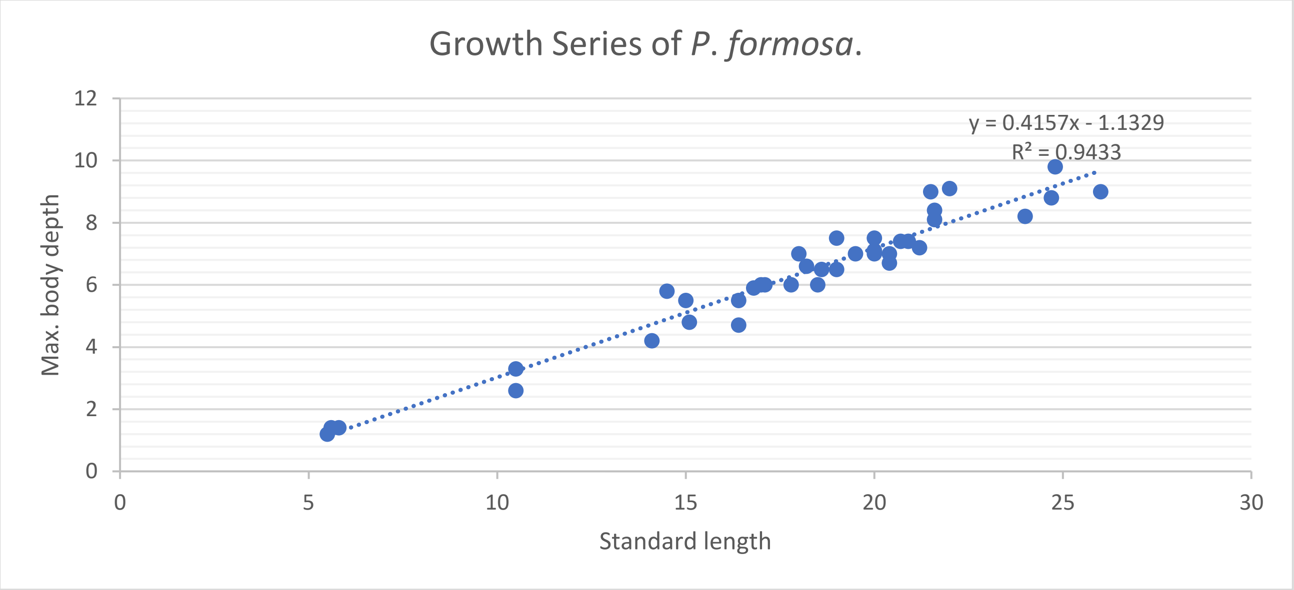

Fig. 3.10. Regression analyses of a growth series of *Promecosomina formosa*. Blue dots represent measurements of individuals with the R2 line a regression line of best fit.

6.1.3 Skull

The smallest fish, based on standard length (Appendix I) tend to have skulls that are ~20% of standard length. Overall the skulls have a triangular shape (Fig. 3.9). Skulls enlarge by up to 10 % through ontogeny to adult size.

Specimens (AM F.38905 (part) (Fig. 3.9C) and NHMUK PV P 18091 (counterpart) along with AM F.66968) (Fig. 3.9B) show a narrow gap between the edge of the opercle and cranial roof bones, exposing part of the hyomandibular head, whilst AM F.101799 shows the opercle and suborbital almost touching the cranial roof bones, with the hyomandibular being completely covered. This indicates that bones are not fully grown in smaller individuals and this gap between the skull bones allows for continuous growth during the life of the fish.

A feature common to many vertebrate juveniles is large eyes relative to the body size; this is also seen in *P. formosa*. The ratio of eye size compared to body size decreases through ontogeny with eye size remaining constant, whereas the body size increases greatly.

Juveniles have little or no preservation of sensory line canals which suggests that these too were not ossified until a later ontogenetic stage.

6.1.4 Jaws

The premaxilla is poorly preserved, and no detail can be determined. No teeth are visible in any of the specimens determined to be juvenile (Fig. 3.8A). The surface of the maxilla is ornamented with elongate ganoid ridges. This suggest that this feature develops early in ontogeny. No teeth can be seen on the maxilla.

The dentary teeth are elongate and conical in cross-section with flared bases; in life, there were likely more teeth, which are not preserved.

The position of the mouth in juveniles is superior (Fig. 3.9, B and C).

6.1.5 Opercular series and branchiostegals

The preopercle is long and narrow, rounded, expanded at the dorsal end, and tapers ventrally, having a slightly concave margin where it meets the maxilla. The opercle together with the subopercle makes up the posterior 1/3rd of the skull, in combination forming a kidney-shaped series. The subopercle is almost 2/3rds the size of the opercle, whereas in adults they are approximately equal in size. The shape and exact number of branchiostegal rays cannot be determined as no juvenile specimens are preserved in ventral view.

6.1.6 Pectoral girdle

There is no reticulate rugae ornament on the cleithrum. The lack of fine dermal ornament on the external, lateral face of the cleithrum is also considered a juvenile characteristic and the appearance of ornament on only some of the larger specimens indicates that it is a feature that developed late in ontogeny (e.g., AM F.101712).

6.1.7 Axial skeleton

Juvenile fishes, in general, lack a fully ossified skeleton (Johanson & Trinajstic, 2014) and the presence of a single line along the flank of the fish corresponding to the vertebral column, observed along the scale surface in juveniles, is indicative of only the neural spines being fully ossified and the parapophyses yet to fully ossify. In adults "two lines" are visible along the scales covering the vertebral column indicating that both the neural spine and the parapophysis are fully ossified. The vertebrae in both adults and juveniles are not mineralised which is a common feature of other basal halecormorphs.

6.1.8 Fins

The dorsal and pelvic fins do not change shape between adults and juvenile stages and the dorsal and pelvic fins have a long fin base.

The pectoral fin shape changes from triangular in juveniles to paddle shaped in adults and the position changes from ventral to lateral as the fish reached adulthood. The lateral position of the pectoral fins may be a consequence of an increased girth of the fish as it grows. In general, the internal skeleton of the paired fins appears less mineralised in juveniles whereas it is rigid in adults. This is evident in AM F.66968 (interpreted to be a juvenile) where the pectoral and pelvic fins appear bent posteriorly.

6.1.9 Caudal fin

The caudal fin is less broad than that of adults.

6.2 Scales

Scales in adults and juveniles have the same vertical scale row counts, however, scales in the adults are taller than wide and it is proposed that the flank scales between the skull and dorsal fin continue to grow dorsally and ventrally (AM F.38905) until adulthood (AM F.101749) which helps account for the change in body shape from torpedo to oblate in shape (becoming deeper bodied in adults). In both sub-adult specimens, the widest part of the body is just posterior of the head. The lateral line appears to have an ossified rod on the scale surface that may indicate modified lateral line scales.

DISCUSSION OF ONTOGENY IN P. FORMOSA

Wade (1935) suggested that *Promecosomina beaconensis* and *P. formosa* were the same taxon and represented different ontogenetic stages, but lacked the larger adult specimens described here and was therefore unable to confirm this. In juveniles of *P. formosa* the dermal bones of the skull roof are thinner than in adults also a common feature amongst extinct and extant juvenile vertebrates (Christopher Bennett, 1996; Hone et al., 2016; Kyomen et al., 2023). Poorly ossified skull roof bones were reported in juveniles of the Cretaceous pycnodontiform, *Flagellipinna rhomboides* (Cawley & Kriwit, 2019) the extant Japanese Catfish *Silurus* (*S. asotus*, *S. biwaensis* and *S. lithophilus*) (Kobayakawa, 1992), the extant Barred Surfperch *Amphistichus argenteus* (Morris, 1975) and within extinct placoderms (Johanson & Trinajstic, 2014). The sensory lines of the head are not visible in juveniles of *P. formosa* and are thus interpreted to be poorly ossified. In adult specimens, the sensory line canals are represented by white lines over the skull (described by Wade 1941 as being calcified). This is a common trait in bony fishes, with sensory line canals becoming ossified for support and protection late in ontogeny (Jollie, 1984a,b; Grande & Bemis, 1998).

The axial skeleton in juveniles of *P*. *formosa* is not fully ossified and this also is common to both extinct and extant fishes (Johanson & Trinajstic, 2014). The presence of a single line along the path of the vertebral column in juveniles of *P*. *formosa* is indicative of only the neural spines being fully ossified. In adults two lines are visible along the scales covering the vertebral column indicating that both the neural spine and the parapophysis are fully ossified. The vertebrae in both adults and juveniles are not mineralised which is a common feature of other basal halecormorphs (i.e., *Cerinichthys*) (Ebert, 2018) and is considered a primitive gnathostomata character that is persistent in primitive actinopterygians and sarcopterygians (Arratia et al., 2001).

All specimens in this study possessed a full scale cover, which suggests that earlier ontogenetic stages of this fish were not present. A common feature of early ontogeny in placoderms (Cloutier et al., 2009), acanthodians (Zidek, 1985), sharks (Johanson et al., 2008), and actinopterygians (Wade, 1935; Schultze & Bardack, 1987; Cloutier, 2010) is that a full complement of scales appears later in ontogeny. However, the presence of transitional scales on the flank (Fig. 3.8) supports the interpretation that these fishes represent a subadult stage.

Changes in body shape and proportions are common throughout ontogeny and are often associated with changes in ecology (Klingenberg, 1998; Katz & Hale, 2016). The shift from an elongate body in juveniles to a deeper bodied adult has been noted amongst many early actinopterygian taxa including *Elonichthy hypsilepis* (Schultze & Bardack, 1987) from the Francis Creek Shale, U.S.A., and multiple instances of ontogenetic series in taxa: *Notagogus ferreri, Rublesichthys gregalis* and *Vidalamia catalunica* from the Late Cretaceous, Las Hoyas, Spain (Wenz & Poyato-Ariza, 1994; Wenz, 1995). Within

Promecosomina formosa, the body initially deepens dorso-ventrally behind the head (Fig. 8B, C) and then progressively deepens in a caudal direction resulting in the deepest portion of the body being immediately anterior to the dorsal fin (Fig. 3.8D, Fig. 3.9). Changes in body shape within multiple actinopterygian lineages indicate that this morphological shape transformation is a widespread occurrence within extant and extinct actinopterygian fishes (Searle et al., 2021 and references therein).

Changes in body shape are related to changes in locomotion. An elongated body shape is typically associated with locomotion by undulating the body and caudal fin, whereas deeper-bodied taxa are typically associated with locomotion that utilises the median and paired fins (Friedman et al., 2021). Fishes with an elongate body are typically considered rapid accelerators, beneficial for both prey capture and escape from predation in juveniles (Cade et al., 2020). A deeper body is more stable in the water column as the body shape reduces drag and roll (Weihs, 2002) and fishes with deep bodies are often generalists in terms of locomotion (Fletcher et al., 2014). The ontogenetic shift in body shape and hence locomotion indicates that juveniles and adults of *P. formosa* obtain prey differently and suggest that they inhabit different parts of the water column or even feed at different localities. Studies have shown that, in modern fishes, water velocity is a strong predictor of intraspecific variation (Langerhans, 2008), and therefore that body shape is a predictor of the environment inhabited by the fish.

The shapes of the cleithrum and pectoral fins across teleosts show little morphological variation (Tanaka et al., 2022), although in more basal actinopterygians the number of radial bones in the pectoral fins can be used to distinguish between species (Tanaka et al., 2022 and references therein). The shape of the cleithrum through ontogeny in *P. formosa* does not change greatly, although it does become more robust and develops a fine reticulate rugae on the lateral surface of the cleithrum in those individuals considered to be adults. In extant fishes, the cleithrum is associated with both locomotion and feeding (Gudo & Homberger, 2002). The lack of change in *P. formosa* suggests that locomotor ability was not significantly different between juveniles and adults; however, the change in the mouth position suggests a significant ontogenetic shift in feeding, particularly the position of the prey in the water column. A similar condition occurs in *Amia,* which also demonstrates small changes in the cleithrum but exhibits ontogenetic niche separation. The extant *Amia calva* from the 5th week of hatching already possesses characteristics of the adult form, including essential fin characters, scales, and teeth (Bashford, 1897). It appears that this is also the case for *P. formosa* in that fin shape, full scale complement, and teeth develop early in ontogeny and are perhaps a developmental characteristic of many halecomorphs.

As with other actinopterygians and sarcopterygians, both extant and extinct, the total number of fin rays per fin is fixed early in ontogeny (Cloutier, 2010). This feature is also observed within *P. formosa.*

Fin rays from adult specimens of other fossil actinopterygians (e.g., *Vidalamia catalunica*) show an increase in the number of distal fin ray bifurcations along with an increase of lepidotrichia showing segmentations (Wenz & Poyato-Ariza, 1994). This feature is also observed in *P. formosa* whereby the distal lengths of the main fin rays bifurcate into multiple branched bundles of lepidotrichia (e.g., Fig. 3.7). Adults of *P. formosa* show fin rays which are more strongly ossified and have more distal bifurcations than in juveniles.

Furthermore, Wenz & Poyato-Ariza (1994), also described fringing fulcra developing later in ontogeny for *Vidalamia catalunica.* The fringing fulcra also develops late in ontogeny in the extant spotted gar *Lepisosteus oculatus* (Desvignes et al., 2018). This late development of fringing fulcra is also observed in *P. formosa.* Fringing fulcra and an increase in distal bifurcations of fin rays, at least for basal actinopterygians and more specifically halecomorphs, can be used to identify ontogenetic stages within these extinct fish.

The repositioning of the mouth from a superior position in juveniles (Fig. 3.8B, C) to a terminal position in adults (Fig. 3.8D) indicates a change in feeding strategy and diet through ontogeny, as is the case with extant fishes (Deary et al., 2017). The terminal mouth position is considered more conducive to prey capture in the water column, whereas an upturned mouth is associated with ambush predation or surface feeding (Essner et al., 2014). Coupled with the positional change in the mouth is a size difference, which suggests that there was some size sorting of prey items between adults and juveniles. However, as all ontogenetic stages in *P. formosa* have sharp conical teeth, it is suggested that both adults and juveniles exhibited predatory behaviour. A similar condition is seen in the predatory fish *Xiphactinus* (King & Super, 2021) and *Promecosomina,* with both being toothed through all ontogenetic stages.

The geographically separate locations and different depositional environments of these locations in which juvenile and adult fishes are found indicate that spatial niche partitioning occurs in *P. formosa*. Spatial niche partitioning between juveniles and adults is thought to reduce competition for food, decrease predation of juveniles (from the same or other species), and therefore lead to more juveniles being recruited into adult populations (Deary et al., 2017). The extinct ichthyodectid fish *Xiphactinus audax* from the Niobrara Chalk Formation, United States of America, also shows spatial niche partitioning, with juveniles being extremely rare in the fossil record (King & Super, 2021). Spatial niche partitioning in the fossil record is nothing new and has also been recognised in dinosaurs (Lyson & Longrich, 2011), and mammals (Shabani et al., 2019).

The early ontogenetic stages of basal actinopterygians are easy to identify based on the completeness of scale cover. Schultze & Bardack (1987) identified an ontogenetic series in *Elonichthys hypsilepis* and *Elonichthys peltigerus* from the Mazon Creek Fauna of Illinois, U.S.A. Wade (1935) also recognised an ontogenetic sequence in the palaeonisciform fish *Brookvalia gracilis,* based on differences in squamation from the Beacon Hill locality, indicating that it too represents a nursery site for palaeonisciform fishes. The presence of *P. formosa* juveniles in an estuarine environment and adults in a lacustrine environment indicate that these fishes exhibited ontogenetic niche separations with migration from the nursery site to lakes and rivers as adults, indicating a catadromous lifestyle.

8 Phylogeny

8.1. Taxon Selection

A phylogenetic analysis using 46 taxa of which 43 comprised the ingroup and three, *Atractosteus spatula* (Ginglymodi), *Pachycormus macropterus* (Neopterygii) and *Dorsetichthys bechei* (Teleostei) comprised the outgroup, was undertaken (Supplementary Material – Appendix II and Appendix III). Fossil Parasemionotiformes from Madagascar, with the exception of *Watsonulus eugnathoides* and *Parasemionotus labordei,* were not included in this analysis, because ontogeny was not recognised resulting in juveniles and adults been placed in separate genera (Ebert, 2018). Although the Madagascan taxa are currently undergoing revision, the taxonomic attributions of *Watsonulus eugnathoides* and *Parasemionotus labordei* are considered robust (Ebert, 2018).

8.2 Tree Computing Method

A data matrix using 75 unordered and unweighted characters (Ebert, 2018) were analysed using PAUP (Swofford, 2019, v. 4.0 test version for Mac) (Supplementary Material – Appendix II, III and IV). A stepwise heuristic search algorithm and ACTRAN optimization, utilising one thousand replications with random taxon addition sequences was undertaken.

8.3. General Results

The heuristic search resulted in 10 equally parsimonious trees with 457 steps, a consistency index of 0.2801, homoplasy index of 0.7199 and a retention index of 0.5782 (Supplementary Material – Appendices S4 and S5). These results, although not robust, are consistent with the values obtained by Ebert (2018). A strict consensus tree was computed (Fig. 3.11).

Fig. 3.11.

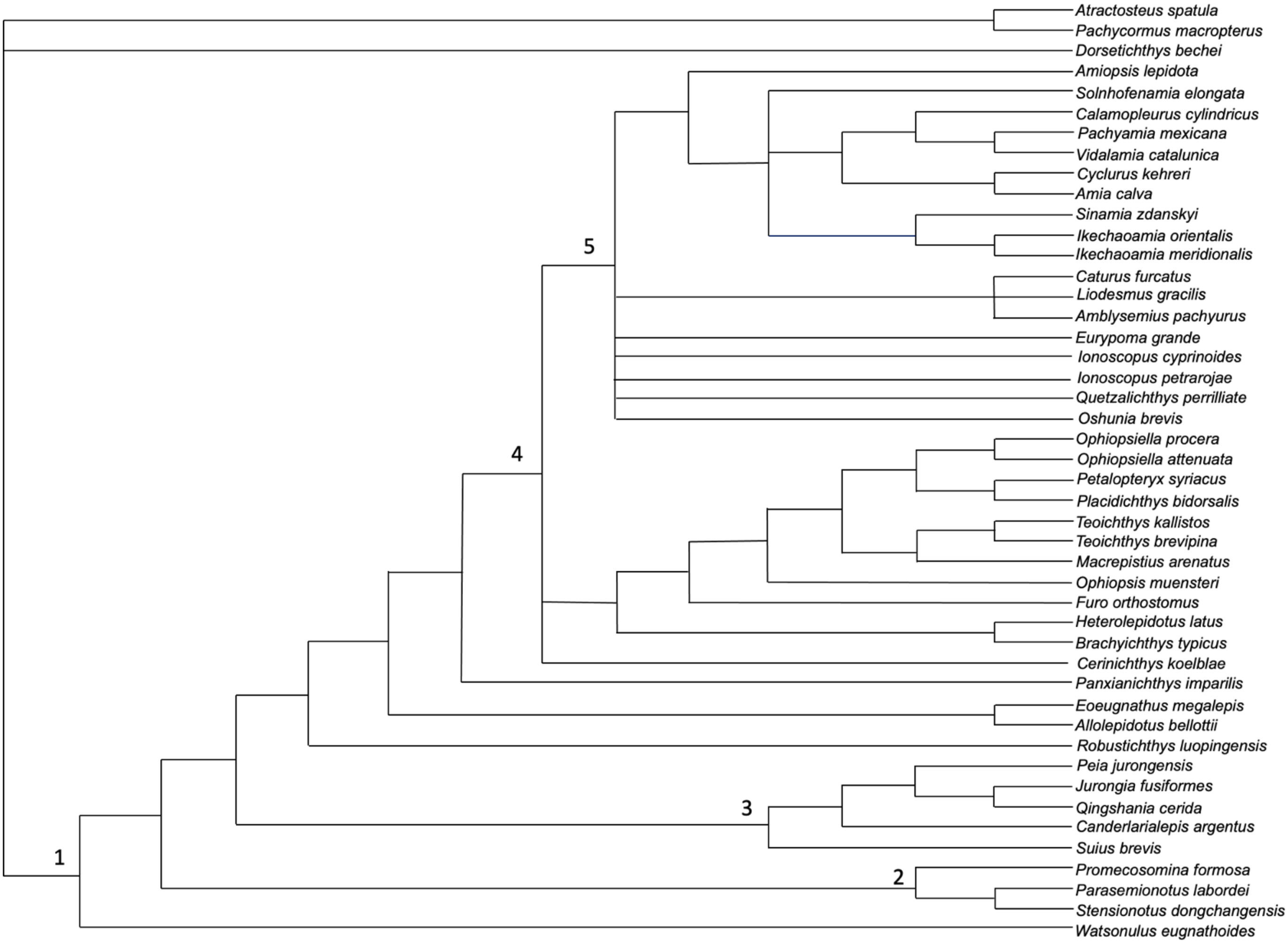

Fig. 3.10. Phylogenetic relationships of *Promecosomina formosa*. Strict consensus tree of 10 most-parsimonious trees (length 457, CI, 0.2801, RI, 0.5782, HI, 0.7199).

Clade 1 (Fig. 3.11)

The monophyly of the Halecomorphi is supported by all trees, a result that is consistent with recent phylogenetic analyses; however, the relationships of the ingroup differ (e.g., Ebert, 2018).

In all trees (Fig. 3.11 and Supplementary Material – Appendix IV) *Watsonulus eugnathoides* is placed as the most basal member of the Halecomorphi on the basis of five unambiguous characters and one reversal: presence of 4-10 suborbital bones (character 5; 0 ==> 2); parietal length, relatively short, width to length ratio not exceeding 0.90 (character 12; 0 --> 1); long, very thin, tube-like (four times longer than deep or more) anterior subinfraorbital bone (character 23; 0 ==> 2); 12 or more epaxial caudal basal fulcra (character 24; 1 ==> 0); infraorbital bones enlarged and reaching the preopercle (character 49; 0 --> 2); and shape of posterior margin of maxilla, concave or with a posterior maxillary notch present (character 68; 0 ==> 1).

Clade 2

Clade 2 is resolved as the sister group to all other taxa, except *Watsonulus* and comprises *Promecosmina formosa*, *Parasemionotus labordei* and *Stensionotus dongchangensis*. The monophyly of the clade is supported by: a straight, nearly vertical or slightly forked caudal fin with long medial fin rays (character 16; 0 ==> 2); 4-6 epaxial caudal basal fulcra (character 24; 1 --> 2); a moderately long maxilla that extends below the orbit (character 32; 0 ==> 1); the upper postinfraorbital is approximately the same length as the lower postinfraorbital (character 35; 0 ==> 1); and by the reversals of character 57 (1 ==> 0) with the maxillary length approximating the mandibular length, absent dorsal lateral line pores (character 58; 1 --> 0); Proportions; standard length (SL)/head length (HL) greater than 3.5x (character 65; 0 --> 1).

Promecosomina formosa is resolved as the basal member of the clade based on possessing a long and narrow preopercle that is crescent shaped (character 13, [1]); a predorsal length of 41.8 % (calculated from AM F.101712), (character 40 [2]); vertical scale rows containing 50 scales (character 41 [1]); principal caudal fin rays of 21 rays (character 51 [2]) and a maximum standard length of 28.5 cm (AM F.101749) (character 73 [0]).

Clade 3

The monophyletic clade comprising *Peia jurongensis*, *Jurongia fusiformes, Qingshania cerida*, *Candelarialepis argentus* and *Suius brevis* is defined by lateral edge of post temporal elongate, about equal to or greater than width of anterior edge (character 15; 0 ==> 1), frontal width sub rectangular, not substantially tapered anteriorly or widened posteriorly (character 20; 0 --> 1), shape of anterior subinfraorbital bone (infraorbital two), long, very thin, tube-like (four times longer than deep or more) (character 23; 0 --> 2), ventral surface of lower circumorbital bones intensely pitted (character 38; 0 --> 1), a small first supraorbital bone (character 56; 1 --> 0) and no fringing fulcra on the ventral lobe of the caudal fin (character 71; 0 ==> 1). This clade is basal to the Panxianichthyformes which had previously been resolved as the sister taxon to the Parasemionotiformes.

The remainder of the taxa are largely in agreement with the results of Ebert (2018) apart from a polytomy at clade 5 possibly because of the inclusion of additional basal taxa. Further discussion of taxa within clades 4-5 is outside the scope of this research.

9 DISCUSSION

The four clades of the Halecomorphi (Parasemionotiformes, Panxianichthyformes, Ophiopsiformes and Amiiformes) as resolved by Ebert (2018), are largely supported here, although the members and relationships within these families differ (Fig. 3.11). The most notable difference is *W. eugnathoides* which, unlike previous analyses, is not placed within the Parasemionotidae (Piveteau, 1934) or even the Parasemionotiformes (Lehman, 1966; Neuman, 1986; Ebert, 2018) but is resolved at the base of the Halecomorphi.

The Parasemionotiformes were previously considered to comprise three families: Parasemionotidae Stensiö 1932, the monospecific Promecosominidae Wade 1941 comprising *Promecosomina formosa,* and an unnamed family, also monospecific, comprising *Peia jurongensis* Li 2009. Here, the separation of the Promecosomidae, as a monotypic family, from the Parasemionotidae (Wade, 1941; Neuman, 1986) is not supported; however, the Parasemionotidae and the other unnamed family (now comprising multiple genera) are supported (Fig. 3.11).

Previous cladistic analyses (Lambers, 1995; Grande & Bemis, 1998; Ebert, 2018; Feng et al., 2023), have used *Watsonulus eugnathoides* as the sole representative of the Parasemionotidae, and so the hypotheses of relationships obtained must be questioned. Grande and Bemis (1998) noted that *W. eugnathoides* had a large and distinct ovoid preopercular and that this characteristic was diagnostic of the Parasemionotiformes. However, Grand and Bemis (1998) questions the validity of this character because it was noted that in some taxa post mortem the crescent-shaped preopercle can become fused to the suborbital plates, giving the appearance of this same ovoid outline. Here we determine that the Parasemionotiformes lack an ovoid preopercle and suggest that the previous inclusion of *W. eugnathoides* in the Parasemionotiformes was based on a single character that in fact the other members of this group lack. However, because the Madagascan fauna, of which *W. eugnathoides* is a member, have not been included in this analysis these results must be taken as preliminary and cannot be confirmed until the current review of the taxa Madagascar is completed.

The Parasemionotidae were recognised as “a bucket group of Early Triassic, scale-covered halecomorph fishes” by Beltan (1968), and Patterson (1973) also recognising that there was no particular relationship between the taxa placed within the Parasemionotidae, considering instead it represented a basal halecostome grade. Patterson (1973) suggested that taxa that did not show synapomorphies to other groups should be placed within the Parasemionotidae, which added to the problem of determining relationships. In order to remedy the growing number of taxa with no synapomorphies placed within the Parasemionotidae, Neuman (1986) revised a number of the halecomorph taxa and provided a formal diagnosis of the family Parasemionotidae; however, he noted that there was no single defining character but instead a combination of characters that establish monophyly of the group. The phylogenetic analysis presented here indicates that the Parasemionotidae can be defined by the 5 synapomorphies (listed above), with only one (character 16 and character 23 of Grande & Bemis (1998)), abbreviated heterocercal tail, body lobe reduced, outer principal rays of upper lobe equal to those on lower lobe) in common with the characters presented by Neuman (1986).

Neuman (1986) supported Wade’s (1941) placement of *P. formosa* in its own family based on a single character: a crescent-shaped preopercle that extended laterally towards the dentary, more so than that seen in other Parasemionotiformes. However, additional specimens recovered and described here demonstrate that *Promecosomina formosa* does possess a crescent shaped preopercle. In many of the original specimens collected by Wade (1941), the preopercle was crushed and the shape distorted, resulting in the true preopercle shape not being recognised supporting the observations of Grande and Bemis (1998). Gardiner (1960: fig. 64) interpreted two suborbitals that completely onlap and overlap the preopercle; however, again this has been shown to also be a taphonomic artefact and better-preserved fossils, clearly do not support either this relationship or that *Promecosomina formosa* had two suborbitals.

Previously, Wade (1941) indicated that *P. formosa* could be defined by its small fusiform shape; however, the larger sample size examined here has enabled the determination that a small fusiform shape is a juvenile trait. Other characters presented as diagnostic by Neuman (1986) that should be considered juvenile traits include: body small to large and fusiform; maxilla small, not extending to the preopercle; lepidotrichia of fins unbranched for long proximal portion of length; and abbreviated heterocercal tail, body lobe reduced, and outer principal rays of upper lobe equal to those on lower lobe (Neuman, 1986).

Neuman (1986) resolved fishes with a preopercle having a ventral limb located vertically beneath the dorsal limb within the Parasemionotidae. However, four out of the five "parasemiontidae" fishes (Neuman, 1986: fig. 21) are shown to have an oval-shaped preopercle with the ventral limb placed vertically beneath the dorsal limb. In addition, specimens of *Thomasinotus* possess a preopercle that is elongate and almost crescent shaped. This suggests that, even among taxa referred to the Parasemionotiformes, there is considerable intraspecific variation of the preopercle. Further investigation of multiple specimens is required to determine if the differences noted in opercle shape are taphonomic or natural variations between individuals.

Peia jurongensis, *Jurongia fusiformes*, *Qingshania cerida*, *Candelarialepis argentus* and *Suius brevis* have previously been considered members of the order Parasemionotiformes (Romano et al., 2019; Liu et al., 2002). However, inclusion of *Peia jurongensis* was based on several plesiomorphic characters that include the presence of a fenestra in the rostral region; absence of dermal ossification in the neurocranium; roughly square shaped parietals, and the absence of ossified vertebral centra (Li, 2009). *Jurongia* *fusiformes* and *Suius brevis* were assigned to the Parasemionotiformes based on their similarity to other Parasemionotiformes, including being small and fusiform, a trait noted herein to be a juvenile characteristic, and body being covered by scales (Liu et al., 2002). Assignment of *Qingshania cerida* to the Parasemionotiformes and the Parasemionotidae is based on the character of an ovoid preopercle, small anal, paired fins with fewer rays, and a hemiheterocercal tail (Liu et al., 2002). *Candelarialepis argentus* has been assigned to the Parasemionotiformes and the Parasemionotidae on the basis of an overall similarity with other members of this group (Romano et al., 2019). Although previous phylogenetic analyses have not included all these taxa, the hypothesis of relationship obtained here supports the unnamed family indicated by Li (2009) as the monophyletic sister group to the Parasemionotidae based on six synapomorphies (clade 4) however, it differs from Li (2009) in that this family (*inserta sedis*) is placed more crownward. In addition, our results exclude *J. fusiformes*, *Q. cerida*, *C. argentus* and *S. brevis* from the Parasemionotidae, resolving them instead as Family *insertae sedis* (Li, 2009).

10 CONCLUSION

Based on additional larger specimens found in the 1980s and better preserved specimens, we redescribe the morphology of *Promecosomina formosa* and conclude that there is only one species of *Promecosomina* from the Middle Triassic, Sydney Basin, New South Wales, Australia. Utilising the newly recognised adult morphology a phylogenetic analysis was undertaken. This showed strong support for the inclusion of *Promecosomina* within the Parasemionotidae forming a monophyletic clade consisting of *Promecosmina formosa*, *Parasemionotus labordei* and *Stensionotus dongchangensis.* The phylogenetic analysis further supports the erection of the Family *insertae sedis* Li (2009) and expands the taxa within this family. This study also highlights potential issues associated with using only one taxon to represent a group, as the current study indicates that *Watsonulus eugnathoides* is the most basal halecomorph fish, residing outside of the Parasemionotidae. However, until redescription of the Madagascan taxa can be undertaken and other fauna re-examined to determine if adult and juveniles have been correctly identified these results must be taken as preliminary.

Credit Attribution Statement

Rodney W. Berrell: Conceptualization, Methodology, Writing – original draft, Writing-review and editing, all figures. **Kate Trinajstic:** Methodology, Investigation, Project Administration, Software, Supervision, Writing – original draft, Writing-review and editing.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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List of supplementary information

Appendix I – Standard fish measurements (Mous et al., 1995) were used for measuring specimens of *Promecosomina*. Measurements are in centimeters.

Appendix II - Nexus File

Appendix III – Phylogenetic Characters Scores

Appendix IV - Phylogenetic Character List

Appendix V – Ten Most Parsimonious Trees

Appendix VI– Apomorphy list

Supplemental Information to:

New morphological information on and a redescription of the basal halecomorph fish, *Promecosomina formosa* Woodward 1908 from the Middle Triassic of the Sydney Basin, New South Wales, Australia

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Outline of contents:

Appendix 1: Fish Measurements

Dimensions	AM F.38905 P. formosa holotype	AM F.66968 P. beaconensis holotype	AM F.101712	AM F.101729	AM F.101728	AM F.101338	AM F.119022	AM F.119004	AM F.119028	AM F.119055	AM F.101368
Total length	16.7	12.1		25.5	24.6	18.5	21.5	19.6	23.5	27	23.5
Fork length	N/A	11.8		24.9	23.5	N/A	N/A	19.2	22.3	N/A	21.4
Standard length (SL)	14.1	10.5	21.6	19	18.2	14.5	17.8	17	20	22	18
Head length	4.1	2.7	5.9	5.5	5.4	4	6	6	4.8	6.5	5.4
Head length / SL ratio %	29.078	25.71428571	27.31481481	28.94736842	29.67032967	27.586	33.70786517	35.29411765	24	29.54545455	30
Head depth	3.2	1.9	4.3	4.7	4.3	3.5	3.5	4.1	3.8	5.9	4.7
head length / head depth Ratio	1.2813	1.421052632	1.372093023	1.170212766	1.255813953	1.1429	1.714285714	1.463414634	1.263157895	1.101694915	1.14893617
Max. body depth	4.2	3.3	8.1	7.5	6.6	5.8	6	6	7	9.1	7
Predorsal length	9	N/A	14.1	13	12.5	9.4	12.5	N/A	14	14	12.5
Prepelvic length	7.5	5.4		N/A	11.5	7.5	9.5	8.8	12	N/A	11
Preanal length	11.3	7.8		15.5	14.4	N/A	13.6	12.7	15	18.9	14.1
Elongation ratio	3.3571	3.181818182	2.666666667	2.533333333	2.757575758	2.5	2.966666667	2.833333333	2.857142857	2.417582418	2.571428571
Anterior depth		3		7	5.5	5.5	5.7	5.5	6	8	6.5
Posterior depth		1.9		7	6.4	5.5	6	N/A	6.5	9	6.9
Dosal fin height		N/A		4	4	3	N/A	N/A	3.5	3.5	3
Distance between plv and pect fins	N/A	2		N/A	4.5	3	N/A	3.5	4.5	N/A	4.5

Dimensions	AM F.101376	AM F.101374	AM F.101760	AM F.101770	AM F.101318	AM F.101302	AM F.101297	AM F.100941	AM F.135153
Total length	20.2	23.9	25.5	22.3	23	23.9	20.5	25.7	25
Fork length	19.5	23.2	25	21.5	22.4	22.6	19.5	24	21.4
Standard length (SL)	15	19.5	21.5	18.5	20	20.4	16.4	21.6	20.9
Head length	4.5	5	5.4	5	5.5	6	4.8	6	5.5

Head length / SL ratio %	30	25.64102564	25.11627907	27.02702703	27.5	29.41176471	29.26829268	27.77777778	26.31578947
Head depth	2.6	2.6	3.8	4	N/A	3.1	3.8	N/A	4.6
head length / head depth Ratio	1.730769231	1.923076923	1.421052632	1.25	N/A	1.935483871	1.263157895	N/A	1.195652174
Max. body depth	5.5	7	9	6	7.1	6.7	5.5	8.4	7.4
Predorsal length	9.5	12.5	14.5	11.4	11.4	12.4	10.5	13.5	13.9
Prepelvic length	N/A	10.2	12.9	9.5	N/A	10.1	9.4	11.5	10.7
Preanal length	11.3	15	18	14.5	14.2	15.8	13	16.5	15.7
Elongation ratio	2.727272727	2.785714286	2.388888889	3.083333333	2.816901408	3.044776119	2.981818182	2.571428571	2.824324324
Anterior depth	4.6	4.6	7.5	5	7.4	6	5.5	7.5	7.3
Posterior depth	5.3	5.3	7.9	6	3.7	3	2.1	3.3	3.5
Dosal fin height	3	3	4	2.8	2	2	1.2	3	3
Distance between plv and pect fins	N/A	N/A	5	4	N/A	5	4	4.2	4

Dimensions	AM F.135094	AM F.135093	AM F.101772	AM F.101442	AM F.101660	AM F.101672	AM F101682	AM F.101677	AM F.101679
Total length	29.5	20.5	30	20	22.5	21	24.4	25.5	24.5
Fork length	28.6	19.2	25.4	19.4	22	20.5	22.2	24.9	24
Standard length (SL)	24.7	17.1	24.8	16.8	19	16.4	20.4	20.7	20
Head length	6.3	5	6	4.5	5.6	4.9	5	7	5.4
Head length / SL ratio %	25.5061	29.2398	24.1935484	26.7857143	29.4736842	29.8780488	24.5098039	33.8164251	27
Head depth	4.2	4.1	4.9	4.1	4.6	3.5	3.6	3.9	5.1
head length / head depth Ratio	1.5	1.21951	1.2244898	1.09756098	1.2173913	1.4	1.38888889	1.79487179	1.05882353
Max. body depth	8.8	6	9.8	5.9	6.5	4.7	7	7.4	7.5
Predorsal length	16	10.4	14.5	11	11	10.1	14.5	13	N/A
Prepelvic length	14.2	9.6	12.9	N/A	N/A	8.4	10.7	11	11.5
Preanal length	16.6	13	17.6	12.6	15	12	15.7	15.3	15.6
Elongation ratio	2.80682	2.85	2.53061224	2.84745763	2.92307692	3.4893617	2.91428571	2.7972973	2.66666667
Anterior depth	8.9	5.4	9	5.5	6.2	5.3	7	N/A	6.6
Posterior depth	4	2.4	3.8	2.4	3	2.4	3	3.2	N/A
Dosal fin height	3.1	2.8	3.5	2.5	3.5	2.5	N/A	3	N/A
Distance between plv and pect fins	7.6	4.2	9	N/A	N/A	3	5	4.8	N/A

Dimensions	AM F.101749	AM F.101673	AM F.135068	AM F.17954	AM F.142858	AM F.142859	AM F.142857	AM F. 29731	AM F.101671	AM F.101306	AM F.101310	AM F.3196
Total length	29	21.9	31.8	18	6.4	6.7	6.5	N/A	24.8	N/A	23.9	N/A
Fork length	26.6	22.9	31.3	17.2	6	6.5	6.4	11.6	22.5	N/A	20.7	N/A
Standard length (SL)	24	18.6	26	15.1	5.6	5.8	5.5	10.5	21.2	N/A	19.8	N/A
Head length	6.3	5.1	7	2.5	1.2	1.2	1.1	3.2	6.5	N/A	6.7	1.4
Head length / SL ratio %	26.25	27.4193548	26.92307692	16.5562914	21.4285714	20.6896552	20	30.4761905	30.6603774	N/A	33.8384	N/A
Head depth	N/A	4.3	4.9	2.3	0.8	1.2	N/A	1.5	4.6	N/A	4.4	0.9
head length / head depth Ratio	N/A	1.18604651	1.428571429	1.08695652	1.5	1	N/A	2.13333333	1.41304348	N/A	1.52273	1.55556
Max. body depth	8.2	6.5	9	4.8	1.4	1.4	1.2	2.6	7.2	8	N/A	1.3
Predorsal length	14.7	11.8	15.8	7.4	3.4	3.7	N/A	6.2	13.3	N/A	N/A	N/A
Prepelvic length	12.7	9.5	15	6.5	N/A	N/A	N/A	5.6	12.1	N/A	11	N/A
Preanal length	17.5	14	19.6	9.5	4.3	N/A	4.3	7.9	16.6	N/A	15.5	N/A
Elongation ratio	2.92682927	2.86153846	2.888888889	3.14583333	4	4.14285714	4.58333333	4.03846154	2.94444444	#VALUE!	#VALUE!	#VALUE!
Anterior depth	7.5	5.9	9.5	4.4	1.2	1.4	N/A	2.7	7	7.4	6.3	0.9
Posterior depth	3.5	N/A	4.2	2	0.7	0.7	0.6	1.5	4	3.4	2.9	1
Dosal fin height	3.6	3.5	4	2	N/A	0.5	N/A	N/A	N/A	N/A	N/A	N/A
Distance between plv and pect fins	6.9	5	8	3.5	N/A	N/A	N/A	2.3	5.3	5	4.8	N/A

Supplemental Information to:

New morphological information on and a redescription of the basal halecomorph fish, *Promecosomina formosa* Woodward 1908 from the Middle Triassic of the Sydney Basin, New South Wales, Australia

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Outline of contents:

Appendix 2: Nexus files

Supplemental Information to:

New morphological information on and a redescription of the basal halecomorph fish, *Promecosomina formosa* Woodward 1908 from the Middle Triassic of the Sydney Basin, New South Wales, Australia

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Outline of contents:

Appendix 3: Characters are coded as conditions 1-5 with polymorphic conditions as ‘A’.

Atractosteus spatula 1 1 0 0 4 1 0 1 2 1 0 0 0 1 0 1
0 - 0 0 1 0 1 3 0 1 0 2 0 0 - 2 0 0 0
0 0 0 3 1 2 - 0 1 0 0 0 0 0 0 3 1 0 0
1 1 ? 1 1 2 3 0 1 1 1 0 0 0 1 0 0 2 0
1 1

Dorsetichthys bechei 0 4 ? 0 0 0 0 1 0 0 1 1 0 0 1 0 0
- 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
0 0 1 0 1 2 2 0 1 1 0 1 2 0 1 1 0 0 0
0 0 ? 1 2 1 0 0 1 1 0 0 0 0 0 0 0 0 0
2

Pachycormus macropterus ? 0 ? 0 1 0 0 - ? 0 2 - 2 0 - 0
0 0 0 - 0 0 1 ? 1 1 1 1 1 0 0 0 0 0 1
? 0 - 0 ? ? 1 1 0 1 - 0 - 0 0 ? 2 1 0
0 2 1 0 1 ? 1 0 0 ? ? 0 0 0 1 0 0 1 0
? ?

Amiopsis lepidota ? 2 1 0 0 0 0 0 0 0 1 0 1 0 0 1
3 0 0 0 0 0 0 1 0 0 0 0 1 1 1 0 0 1 0
2 1 0 2 0 2 2 1 1 1 0 1 1 1 1 2 2 0 0
0 1 1 0 1 2 0 0 0 ? ? 0 1 1 0 0 1 2 0
0 2

Solnhofenamia elongata 1 3 1 0 0 0 0 1 0 0 2 1 1 0 0
1 3 0 ? 0 0 1 2 0 1 0 0 0 1 1 0 0 0 1
0 2 1 0 2 0 2 1 1 1 1 A 1 1 1 1 2 2 0

0 0 1 1 0 1 2 0 0 0 ? ? 0 0 1 0 0 1 2
0 0 2

Calamopleurus cylindricus 1 3 1 1 3 1 0 3 0 0 1 0 2 1 1
1 3 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 1
0 1 1 0 2 0 2 1 1 0 2 0 1 1 1 1 3 2 0
0 2 1 1 0 1 2 0 0 0 1 1 0 0 1 1 0 1 2
0 0 2

Pachyamia mexicana 1 3 2 1 3 1 0 1 0 0 3 0 2 1 1 1
3 1 1 1 1 1 0 1 1 0 0 0 1 1 0 0 0 1 0
0 1 0 2 2 ? 1 1 1 1 0 1 1 1 0 2 2 ? 0
3 0 1 0 1 2 0 0 0 1 1 0 0 1 1 0 1 2 0
0 2

Vidalamia catalunica ? 3 2 ? 3 1 0 1 0 0 2 0 2 1 1 1
3 1 1 1 1 1 0 1 1 0 0 0 1 1 0 0 0 1 0
0 1 0 2 2 ? 1 1 1 0 0 1 1 1 0 3 2 ? 0
3 ? 1 0 1 2 0 0 0 1 1 0 0 1 1 0 1 2 0
0 2

Cyclurus kehreri 1 3 2 1 3 1 1 2 1 1 3 1 1 0 0 1
3 0 0 0 0 0 0 3 1 0 0 0 1 1 0 0 0 1 1
0 1 0 2 0 0 1 1 1 1 2 0 1 1 2 1 2 2 0
0 3 2 0 1 2 0 0 0 1 0 0 1 1 1 0 1 2 0
0 2

Amia calva 1 3 2 1 3 1 1 2 1 1 5 0 1 0 0 1 3 0
0 0 0 0 0 3 1 0 0 0 1 1 2 0 0 1 1 2 1

0	2	2	2	2	1	1	0	A	1	1	2	0	2	2	0	0	3	2
1	0	1	2	0	0	0	1	1	0	0	1	1	0	1	2	0	0	2

Sinamia	*zdanskyi*		0	2	?	0	?	0	0	1	2	1	2	?	1	0	1	1
3	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0
0	0	0	3	0	2	0	1	0	0	0	1	1	0	0	3	0	0	0
3	0	1	?	1	?	2	0	1	1	1	1	0	1	?	0	1	2	0
0	2																	

Ikechaoamia	*orientalis*		?	2	?	?	?	0	0	?	0	1	1	?	1	0	0	1
?	?	?	0	?	0	?	1	1	1	0	0	1	1	0	1	0	1	0
0	3	0	3	0	?	0	1	?	?	?	1	?	?	?	3	2	0	0
3	?	?	?	0	?	0	?	?	1	1	1	?	1	?	0	1	1	1
0	2																	

Ikechaoamia	*meridionalis*		?	2	1	?	?	0	0	1	0	1	2	?	1	?	?	1
3	0	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0	1	0
0	3	0	3	0	?	0	1	0	2	0	1	1	1	0	3	2	0	0
3	0	2	?	0	?	0	0	1	1	1	1	0	1	0	0	1	1	1
0	2																	

Caturus	*furcatus*		0	4	0	0	1	0	0	0	0	0	1	1	1	1	0	0
1	0	0	0	0	0	2	1	0	0	1	1	1	1	0	0	0	1	0
0	1	0	1	0	2	1	1	1	1	0	0	1	1	1	0	2	0	0
0	0	1	1	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0
0	2																	

Liodesmus	*gracilis*			?	4	0	?	?	0	?	0	0	0	1	1	1	1	0
0	3	0	0	0	0	0	?	1	0	0	1	1	1	1	?	0	0	1

0	0	1	0	0	0	?	2	1	?	?	?	1	?	?	1	0	2	0
0	0	1	1	0	1	2	0	0	0	1	0	0	0	1	?	0	1	0
1	0	2																
Amblysemius	*pachyurus*		?	4	0	?	1	0	0	0	0	0	1	1	1	1	0	0
0	0	0	0	0	0	2	1	0	0	1	1	1	1	0	0	0	1	0
0	1	0	1	0	2	0	1	1	1	0	1	1	1	1	1	2	0	0
0	1	1	0	1	2	0	0	0	1	1	0	0	0	0	0	0	0	0
0	2																	
Eurypoma	*grande*		?	4	0	?	1	0	?	?	0	1	1	?	1	0	?	0
?	0	0	?	0	0	2	0	0	?	0	?	1	1	0	0	0	1	0
?	1	0	2	0	?	2	1	0	1	1	?	1	1	1	?	2	0	0
0	?	0	0	?	2	0	0	0	1	0	0	0	1	?	0	0	1	0
0	?																	
Ionoscopus	*cyprinoides*		1	1	0	0	2	0	0	0	0	0	2	0	1	0	0	0
3	0	0	0	?	0	0	1	0	0	0	0	1	1	0	0	0	1	0
0	1	1	3	0	1	1	1	0	1	1	1	1	1	1	2	2	0	0
0	0	1	0	1	2	0	0	0	0	1	0	0	1	1	0	0	1	0
0	?																	
Ionoscopus	*petrarojae*		?	3	0	0	1	0	?	?	0	?	1	1	1	0	0	0
?	?	0	?	0	0	?	0	0	0	0	?	1	1	?	1	1	1	0
0	1	0	3	1	?	?	1	1	?	?	1	1	1	0	1	2	0	0
0	?	?	0	?	2	0	0	0	0	1	0	0	1	?	0	0	1	0
0	?																	

Quetzalichthys perrilliatae ? 1 0 0 1 0 ? 1 2 ? 2 0 1 0 0
0 3 ? 0 0 0 0 0 1 0 0 0 0 1 1 2 0 1 1
0 0 1 1 3 0 ? 2 1 1 1 1 1 1 1 0 1 2 0
0 0 ? 1 0 0 2 0 1 0 0 0 0 0 1 1 0 0 1
0 0 2

Oshunia brevis 0 1 ? 0 ? 0 0 2 0 ? 1 0 1 0 0 0 ?
0 0 0 ? 0 1 ? 0 0 0 0 1 1 ? 0 1 1 0 0
1 1 3 1 1 ? 1 0 1 0 1 1 1 0 ? 2 0 0 0
? 1 0 0 2 0 0 0 0 0 0 0 1 0 0 0 1 0 0
2

Ophiopsiella procera 0 4 2 0 2 0 0 0 2 1 2 ? 1 0 0
0 1 ? 0 0 0 0 1 1 0 1 0 0 1 1 1 1 1 1
0 2 0 0 2 2 1 0 1 0 1 0 0 1 1 1 2 1 0
0 3 1 1 1 0 1 2 1 0 1 1 0 0 1 1 0 0 0
0 0 2

Ophiopsiella attenuata 0 4 2 0 2 0 ? 3 2 1 2 1 1 0 0 0
1 ? 0 0 0 0 0 1 0 0 0 0 1 1 1 1 1 1 0
2 0 0 2 2 1 0 1 0 1 0 0 0 1 1 3 1 0 0
3 1 1 1 0 1 2 1 0 1 1 0 0 1 1 0 0 0 0
0 2

Teoichthys kallistos 0 4 2 ? 4 1 ? 3 2 1 5 0 1 0 0 0
0 ? 0 0 0 0 ? 1 0 1 0 0 1 1 1 1 1 1 0
1 0 0 ? 2 1 0 1 1 1 1 1 1 0 0 3 0 0 0
3 1 1 1 2 1 3 0 0 1 1 0 0 1 1 0 0 1 0
0 2

Teoichthys	*brevipina*		0	1	?	0	4	0	0	3	2	1	1	0	1	0	0	0
0	?	0	0	1	0	0	2	0	1	0	0	1	1	2	1	1	1	0
1	0	0	2	0	1	0	1	1	1	0	?	1	0	0	3	0	0	0
2	1	2	?	2	1	2	0	0	1	1	0	0	0	1	0	0	1	1
0	2																	
Macrepistius	*arenatus*		0	4	?	?	2	1	?	3	2	?	?	?	1	0	?	0
0	0	0	0	?	0	1	1	0	1	0	0	1	1	1	1	1	1	0
1	0	0	2	2	?	?	1	?	1	0	?	1	1	1	2	0	0	0
?	?	1	?	?	1	3	0	0	?	?	0	0	?	1	0	0	2	0
0	2																	
Petalopteryx	*syriacus*		0	?	2	?	?	0	?	?	2	?	4	0	1	0	0	0
?	?	0	?	?	0	?	1	?	1	0	0	1	?	?	1	1	1	0
?	0	0	?	2	1	0	1	0	?	?	1	?	?	0	2	1	0	0
3	1	1	1	0	1	2	0	0	1	1	0	0	1	1	1	0	1	0
0	2																	
Placidichthys	*bidorsalis*		0	3	2	?	?	0	?	?	2	0	3	0	1	0	0	?
1	?	?	?	0	0	0	2	?	?	0	0	1	?	0	1	1	1	0
?	0	?	?	2	0	0	1	0	?	?	1	?	?	0	2	1	0	0
3	1	1	?	0	1	2	0	0	1	1	0	0	1	1	1	0	1	1
0	2																	
Ophiopsis	*muensteri*		0	4	0	0	1	0	?	3	2	1	1	0	1	0	0	0
3	0	0	?	0	0	0	2	0	0	0	0	1	1	2	1	1	1	0
0	0	0	1	1	2	0	1	1	1	0	1	1	1	1	2	1	0	0

0 1 1 1 3 2 3 0 0 1 1 0 0 1 0 0 0 1 0
0 2

Furo orthostomus 0 4 0 0 1 0 0 1 2 1 1 0 1 0 0 0 3
0 0 1 0 0 0 1 0 1 0 0 1 1 2 1 1 1 0 0
0 0 1 1 2 1 1 1 1 0 0 1 1 1 0 1 0 0 0
1 1 ? 2 2 3 0 0 1 1 0 0 1 0 0 0 1 0 0
2

Heterolepidotus latus 0 4 0 0 1 0 0 0 2 1 1 1 1 0 0 0
0 ? 0 0 0 0 0 1 0 0 0 0 1 1 2 1 1 1 0
? 0 1 1 1 2 1 1 1 1 0 ? 0 1 0 0 0 0 0
0 1 2 1 2 ? 2 0 0 0 0 0 0 1 1 0 0 2 0
0 2

Brachyichthys typicus 0 4 0 0 2 1 ? 1 2 1 1 1 1 0 0
0 1 0 0 0 0 0 0 ? 0 0 0 0 1 1 ? 1 1 1
0 ? 0 1 1 1 2 0 1 1 0 0 0 1 1 0 0 0 1
1 0 1 2 1 2 1 3 0 0 0 0 0 0 1 0 0 0 2
0 0 2

Cerinichthys koelblae 0 0 0 0 0 0 0 1 2 0 1 1 1 0 0 0
1 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 1 1 0
0 0 0 0 1 2 0 1 0 0 0 0 1 2 0 0 1 1 1
0 ? 1 0 0 3 3 0 0 0 0 0 0 1 0 0 0 1 0
0 2

Robustichthys luopingensis 0 ? ? 0 2 1 ? 1 2 1 2 0 1 0 0 2
0 0 0 0 1 0 0 1 0 0 0 0 1 ? 2 1 1 1 0

0 0 0 ? 1 1 ? 1 0 1 1 ? 1 1 0 0 0 0 0
0 1 1 1 0 2 2 0 0 0 0 0 1 0 0 0 0 1 1
1 0

Eoeugnathus megalepis 0 0 ? 0 ? 1 0 0 2 0 1 1 1 0 0 0
1 ? 0 0 1 0 0 1 0 0 0 0 0 1 0 0 1 1 0
0 0 1 0 1 0 2 1 0 1 ? 1 1 1 1 2 1 0 0
0 1 0 ? 1 2 2 0 0 0 0 0 0 1 ? 0 0 1 1
1 0

Allolepidotus bellottii 0 0 ? 0 0 1 ? 1 2 0 1 0 1 0 0 0
0 ? 0 0 1 0 0 1 0 0 0 0 0 1 0 0 ? 1 0
0 0 0 0 1 0 1 1 1 1 0 0 1 2 1 2 1 0 0
0 1 1 1 1 2 2 0 0 0 0 0 0 1 0 0 0 1 1
1 0

Panxianichthys imparilis 0 0 ? 0 1 1 ? 1 2 0 1 0 1 0 0
0 3 ? 0 0 1 0 0 1 0 0 0 0 0 1 0 0 1 1
0 0 0 1 0 1 0 0 1 0 1 1 0 1 1 0 1 1 0
0 0 1 1 ? 0 2 2 0 0 0 0 0 1 1 0 0 0 1
0 1 0

Watsonulus eugnathoides 0 4 0 0 2 0 0 1 2 0 1 1 3 0 0 0
0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 1 2 2 1 0 1 0 0 1 2 0 1 0 0 0
0 1 1 1 0 2 2 0 0 1 0 0 0 1 0 0 0 2 0
1 0

Promecosomina formosa 0 4 ? 0 0 0 0 1 2 ? 1 ? 1 0 0
2 0 1 0 1 1 0 0 2 0 ? 0 0 ? 0 0 1 0 ?
1 0 0 0 ? 2 1 ? 1 0 1 0 0 ? 0 0 2 0 0
0 0 1 0 0 0 2 2 0 0 0 1 0 ? ? 0 0 0 2
0 ? ?

Peia jurongensis ? ? ? ? ? 0 0 2 ? 0 1 0 2 0 1 ? ?
1 0 1 1 0 2 ? 1 ? 0 0 1 1 0 0 0 1 0 0
0 - ? 1 0 ? 1 ? 1 0 1 1 0 1 2 0 0 ? 0
2 0 ? ? 2 2 ? 0 1 1 0 ? 0 0 0 ? ? 1 ?
?

Parasemionotus labordei 0 ? ? 0 1 ? 0 1 ? ? 1 ? 3 ? 0
2 ? ? 0 ? 0 0 0 ? 0 0 0 ? 0 ? 0 1 0 ?
1 ? 0 ? ? 1 0 ? 1 ? 0 1 0 1 2 0 1 0 0
0 0 0 0 ? 0 2 2 ? 1 0 1 0 ? 0 0 0 0 ?
1 ? ?

Candelarialepis argentus ? ? ? 0 0 1 0 1 ? ? ? ? 2 0 1
? ? 1 0 1 0 0 ? ? 0 ? 0 0 1 0 ? 2 0 ?
? ? 0 1 ? 1 1 ? 1 ? ? ? 1 ? ? 0 ? 0 ?
? 0 0 1 ? ? ? 2 ? 0 0 0 ? ? ? ? 0 ? ?
0 ? 0

Stensionotus dongchangensis 0 ? ? 0 0 0 0 0 ? ? ? 0 2 0 1
? ? ? 0 0 ? 0 1 ? ? ? 0 0 ? ? 0 1 0 ?
1 ? ? 0 ? ? ? ? 1 ? ? 1 ? 0 2 0 ? ? ?
? ? 0 0 ? ? ? ? ? 0 ? ? ? 0 0 0 ? ? ?
? ? ?

Jurongia fusiformes 0 ? ? 0 ? ? 0 ? ? ? ? ? 3 ? 1 ?
? ? ? ? ? 1 ? ? ? ? 0 0 ? ? ? 0 0 0 ?
? 0 ? ? ? ? ? 1 ? ? ? 1 ? ? 0 ? ? ? ?
? ? 0 ? ? ? ? ? ? ? ? ? ? 0 ? ? ? 1 ?
? ?

Qingshania cerida 0 ? ? ? 1 0 0 ? ? ? ? 0 2 0 0 0 ?
1 0 1 ? 1 ? ? 1 ? 0 0 ? ? ? 0 ? ? ? 0
0 ? ? 1 0 ? 1 ? ? ? 1 ? ? 0 2 0 0 0 0
? 0 ? 0 ? 2 ? ? 1 0 0 ? 0 ? 0 1 ? 1 ?
?

Suius brevis? ? ? 0 ? 0 0 ? ? ? ? ? 3 ? 1 0 ? 1

0 ? ? 0 ? ? 0 ? 0 0 ? ? ? 0 0 ? ? ?

0 ? ? 1 0 ? 0 ? ? ? 0 ? ? 0 0 ? 0 0

0 ? ? ? 0 ? 2 ? ? 0 0 ? ? ? ? 0 1

Supplemental Information to:

New morphological information on and a redescription of the basal halecomorph fish, *Promecosomina formosa* Woodward 1908 from the Middle Triassic of the Sydney Basin, New South Wales, Australia

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Outline of contents:

Appendix 4: List of Characters.

1: Posterior extent of exoccipitals (from Grande & Bemis 1998: character 2): reaches posterior margin of occiput [0]; does not reach posterior margin of occiput [1].

2: Solid vertebral centra (modified from Sun et al. 2016a: character 3): centra absent [0]; present, with two lateral fossae on each side of most centra [1]; present, with three or more lateral fossae on each side of most of the centra [2]; present, centra smooth-sided [3]; vertebrae not fully ossified [4].

3: Number of supraneurals (modified from Grande & Bemis 1998: character 5): 19 or more [0]; 12 to 18 [1]; 11 or less [2].

4: Articular ossification of lower jaw (from Grande & Bemis 1998: character 6): a single element, or two elements tightly sutured to each other [0]; two separate elements not in contact with each other [1].

5: Suborbital bones (modified from Grande & Bemis 1998: character 7): one [0]; two to three [1]; four to ten [2]; absent [3]; more than ten [4].

6: Strength of ornamentation on dermal bones of skull (from Grande & Bemis 1998: character 8): weak and/or fine [0]; strong, coarse [1].

7: Presence/absence of substantial scapulocoracoid ossification (from Grande & Bemis 1998: character 11): one or more elements present in the shoulder girdle [0]; absent [1].

8: Number of supraorbital bones (from Alvarado-Ortega & Espinosa-Arrubarrena 2008: character 22): 3-4 [0]; 2 [1]; 0 [2]; more than 4 [3].

9: Urodermals in the caudal skeleton (modified from Grande & Bemis 1998: character 13): present [0]; absent [1]; presence of a complete ganoin scaled caudal lobe [2].

10: Presence/absence of sclerotic ring ossification (from Grande & Bemis 1998: character 14): present [0]; absent [1].

11: Number of segmented dorsal fin rays or dorsal proximal radials (modified from Grande & Bemis 1998: character 15): 11 or less segmented rays and 11 or less proximal radials [0]; 12 to 20 segmented rays and 12 to 20 proximal radials [1]; 21 to 29 segmented rays and 21 to 29 proximal radials [2]; 30 to 38 segmented rays and 30 to 38 proximal radials [3]; 39 to 47 segmented rays and 39 to 47 proximal radials [4]; 48 and more segmented rays and 48 and more proximal radials [5].

12: Parietal length (from Grande & Bemis 1998: character 18): relatively long, with a width- to-length ratio not exceeding 0.90 [0]; relatively short, with a width-to-length ratio well exceeding 0.90 [1].

13: Shape of preoperculum (from Grande & Bemis 1998: character 20): L-shaped [0]; crescent-shaped, long and narrow [1]; crescent-shaped, wide in middle tapering dorsally and ventrally [2]; ovoid [3].

14: Morphology of caps of the jaw teeth in (from Grande & Bemis 1998: character 21): round in cross-section, not sharply carinate [0]; labiolingually compressed, sharply carinate (keeled) [1].

15: Lateral edge of posttemporal in (from Grande & Bemis 1998: character 22): shorter than length of anterior edge [0]; elongate, about equal to or greater than width of anterior edge [1].

16: Shape of posterior margin of caudal fin (modified from Grande & Bemis 1998: character 23): forked (median fin rays less than two thirds the length of the leading rays) [0]; convexly

rounded [1]; straight and nearly vertical or slightly forked, with long median fin rays (more than two third the length of the leading rays) [2].

17: Postmaxillary process under postmaxillary notch (modified from Grande & Bemis 1998: characters 30 and 62): absent [0]; present and small (without teeth) [1]; present and thick and elongate (without teeth) [2]; present and small (with teeth) [3].

18: Shape of gular (from Grande & Bemis 1998: character 32): subtriangular or subrectangular with acute rounded anterior apex [0]; broad, oval, without acute anterior apex [1].

19: Peculiar ornamentation pattern of strongly defined, converging lines on opercles in (from Grande & Bemis 1998: character 33): absent [0]; present [1].

20: Frontal width in (modified from Grande & Bemis 1998: character 34): relatively wide, with a width-to-length ratio of 0.26 to 0.65 [0]; relatively narrow, with a width-to-length ratio of 0.13 to 0.25 [1].

21: Shape of dermopterotic (from Grande & Bemis 1998: character 35): greatly widened posteriorly and tapered anteriorly [0]; subrectangular, not substantially tapered anteriorly or widened posteriorly [1].

22: Width of operculum (modified from Grande & Bemis 1998: character 36): narrow, with width-to-height ratio of 0.48 to 1.06 [0]; wide, with width-to-height ratio in range of 1.07 to 1.39 [1].

23: Shape of anterior subinfraorbital bone (infraorbital two) (modified from Grande & Bemis 1998: character 43): subrectangular, longer than deep [0]; subrectangular, deeper than long (or as long as deep) [1]; long, very thin, tube-like (four times longer than deep or more) [2].

24: Number of epaxial caudal basal fulcra or unsegmented procurrent rays (modified from Grande and Bemis 1998: character 44): 12 or more [0]; 7 to 11 [1]; 4 to 6 [2]; 0 to 3 [3].

25: Presence/absence of fringing fulcra on median fins (from Grande & Bemis 1998: character 45): present [0]; absent [1].

26: Dermopterotic length to parietal length (from Grande & Bemis 1998: character 50): dermopterotic significantly longer [0]; lengths about equivalent [1].

27: Shape of maxilla extremely slender and rod-like (from Grande & Bemis 1998: character 53): no [0]; yes [1].

28: Number of branchiostegal rays (modified from Grande & Bemis 1998: character 54): 20 or fewer [0]; 21 or more [1]; absent [2].

29: Dermosphenotic attachment to skull roof (from Grande & Bemis 1998: character 56): loosely attached on the skull roof or hinged to the side of skull roof [0]; firmly sutured into skull roof, forming part of it [1].

30: Shape of rostral bone (from Grande & Bemis 1998: character 57): plate-like or short tube-like, without lateral horns [0]; roughly V-shaped, with lateral horns [1].

31: Lacrimal shape (modified from Grande & Bemis 1998: character 58): longer than deep, and smaller than orbit [0]; deeper than long, or at least as long as deep, and massive (about size of orbit) [1]; longer than deep and about the size of the orbit or longer [2].

32: Maxilla (from Arratia 2013: character 56): elongate, extending behind orbit [0]; moderately long, extending below the orbit [1]; very short, anterior to orbit [2].

33: Presence/absence of lateral line canal in maxilla (from Grande & Bemis 1998: character 60): absent [0]; present [1].

34: Symplectic involvement in jaw joint (from Grande & Bemis 1998: character 61): does not articulate with lower jaw [0]; distal end articulates with articular bone of lower jaw [1].

35: Relative size of uppermost postinfraorbital (from Grande & Bemis 1998: character 66): short, much shorter than lowermost postinfraorbital [0]; long, about equal in length to lowermost postinfraorbital [1].

36: Lateral line ossicles between caudal fin rays (modified from Gardiner et al. 1996: character 21): absent [0]; one to three [1]; more than three [2].

37: Type of scales (modified from Alvarado-Ortega & Espinosa- Arrubarrena 2008: character 15): rhomboid [0]; amioid [1]; body naked [2]; [3] rhomboid and amioid.

38: Ventral surface of lower circumorbital bones (from Alvarado-Ortega & Espinosa- Arrubarrena 2008: character 18): smooth [0]; intensely pitted [1].

39: Vertebral centra (modified from López-Arbarello et al. 2013: character 57): unossified [0]; hemichordacentra [1]; solid perichordally ossified, diplospondylous [2]; solid perichordally ossified, monospondylous [3].

40: Predorsal length (modified from Grande 2010: character 34): 46–53% of standard length [0]; 54% or more of standard length [1]; 45% or less of standard length [2].

41: Vertical scale rows (from postcleithra to hinge line): 42 or less [0]; 43 to 50 [1]; 51 or more [2].

42: Maxillary teeth: 22 or less [0]; 23 to 40 [1]; 41 or more [2].

43: Number of supramaxillae (from Sun et al. 2016a: character 67): none [0]; one [1]; two [2].

44: Teeth of dentary: same size or slightly larger (longer) as maxillary teeth [0]; twice the size of the maxillary teeth or larger [1]. Ebert 2018 character 44.

45: Number of subinfraorbitals: two [0]; one [1]; three or four [2]. Ebert 2018 character 45.

46: Number of postinfraorbitals: two [0]; three [1]. Ebert 2018 character 46.

47: Fringing fulcra on pectoral fin: present [0]; absent [1]. Ebert 2018 character 47.

48: Circumorbital ring (modified from Lòpez-Arbarello 2012: character 29): Supraorbitals contact infraorbitals, closing the orbit [0]; Supraorbitals do not contact infraorbitals at the anterior rim of the orbit [1].

49: Relative size of the infraorbital bone (or bones) at the posteroventral corner of the orbit (ventral postinfraorbital). (from Lòpez-Arbarello 2012: character 36): not enlarged [0]; enlarged, but do not reach the preoperculum [1]; enlarged and reach the preoperculum [2].

50: Mandibular length as a percentage of head length (modified from Grande 2010: character 50): less than 56% [0]; 56% and more [1].

51: Principal caudal fin rays (modified from Grande 2010: character 88): 27 and more [0]; 23 to 26 [1]; 18 to 22 [2]; 17 or less [3].

52: Scales in the anterior part of the body: unserrated [0]; serrated (all scales, or at least the larger scales in the anterior part of the body) [1]; amioid scales [2]; with a strong posteriorly directed spine [3]. Ebert 2018 character 52.

53: Multiple tiny scales in caudal area: absent [0]; present [1]. Ebert 2018 character 53.

54: Broadened ray segments: absent [0]; present [1]. Ebert 2018 character 54.

55: Relative position of the dorsal fin (modified from Lòpez-Arbarello 2012: character 1): between pelvic and anal fins (can begin slightly anterior of pelvic) [0]; opposite to anal fin [1]; opposite to pelvic fins (more than 1⁄4 of the dorsal fin anterior of pelvic fin) [2]; originates much anterior to pelvic fins and extends opposite to anal fin [3].

56: First supraorbital bone (modified from Lòpez-Arbarello 2012: character 31): small [0]; large [1]; supraorbitals absent [2].

57: Maxillary length: nearly as long as mandible [0]; clearly shorter than mandible [1]; much shorter than mandible (about halve the size of the mandible) [2]. Ebert 2018 character 57.

58: Dorsal lateral line pores: absent [0]; present [1]. Ebert 2018 character 58.

59: Scales in the area of the ventral margin, from the branchial arche to the anal fin: normal body scales (slightly smaller), scales between branchiostegals and the pectoral fin absent [0]; normal body scales (slightly smaller), scales between branchiostegals and the pectoral fin present [1]; normal body scales (slightly smaller), tiny ganoin scales between branchiostegals and the pectoral fin present [2]; tiny ganoin scales between branchiostegals and anal fin [3]; tiny ganoin scales anterior to the dorsal and ventral margin of the caudal fin [4]. Ebert 2018 character 59.

60: Lateral line scales: absent [0]; present, with pit-organ pore (‘Grübchenorgan’; Schultze 1966) and lateral line pore near the centre of the scale [1]; present, with pit-organ pore and lateral line scale pore at the posterior end of the scale forming an indentation [2]; without visible pore in the centre or indentation at the posterior end [3]. Ebert 2018 character 60.

61: Ganoin scales between the postcleitral scales and the posterior end of the dorsal fin: absent [0]; all broader than long [1]; scales only in the stomacal area longer than broad [2]; scales in the stomacal area and in the region of the insertion of the dorsal fin longer than broad [3]; all longer than broad [4]. Ebert 2018 character 61.

62: Serrations at posterior margin of extrascalula: absent [0]; present [1]. Ebert 2018 character 62.

63: Number of pairs of extrascapular bones (modified from Sun et al. 2016a: character 47): only one pair present [0]; more than one [1].

64; Proportions; standard length (SL)/body depth (BD): less than 3,5x [0]; 3.5x and more [1]. Ebert 2018 character 64.

65: Proportions; standard length (SL)/head length (HL): less than 3.5x [0]; 3.5x and more [1]. Ebert 2018 character 65.

66: Number of parietal bones (from Sun et al. 2016a: character 46): paired parietals normally present [0]; only a single median parietal present [1].

67: Distinct supramaxillary notch of maxilla (from Sun et al. 2016a: character 60): absent [0]; present [1].

68: Shape of posterior margin of maxilla (Grande & Bemis 1998: character 62): convexly rounded or straight [0]; [1] excavated (concave or with a posterior maxillary notch present).

69: Antorbital contributing to orbital margin (Sun et al. 2016a: character 76): present [0]; absent [1].

70: Dorsal fin: one single dorsal fin [0]; two dorsal fins [1]. Ebert 2018 character 70.

71: Fringing fulcra on ventral lobe of caudal fin: present [0]; absent [1]. Ebert 2018 character 71.

72: Segmentation of caudal rays (anterior segments of the dorsal lobe): much longer than broad (2/1 or more) [0]; nearly the same length and width [1]; much broader than long (2/1 or more) [2]. Ebert 2018 character 72.

73: Maximum standard length: more than 15 cm [0]; 15 cm and less [1]. Ebert 2018 character 73.

74: Symplectic/quadrate contact (Grande 2010: character 69 and Sun et al. 2016a: character 90): present [0]; absent, symplectic separated from quadrate by quadratojugal [1].

75: Quadratojugal (Grande 2010: character 70; Sun et al. 2016a: character 93): somewhat plate-like, placed lateral to the quadrate [0]; splint-like [1]; absent [2].

Supplemental Information to:

New morphological information on and a redescription of the basal halecomorph fish, *Promecosomina formosa* Woodward 1908 from the Middle Triassic of the Sydney Basin, New South Wales, Australia

Rodney W. Berrell[1,]* and Kate Trinajstic[2]

[1]*School of Earth and Planetary Sciences, Curtin University, Kent Street, Bentley, Western Australia, 6102, Australia, r.berrell@postgrad.curtin.edu.au*

[2]*School of Molecular and Life Sciences (MLS), Curtin University, Kent Street, Bentley, Western Australia, 6102, Australia, K.Trinajstic@curtin.edu.au*

*Corresponding author.

Outline of contents:

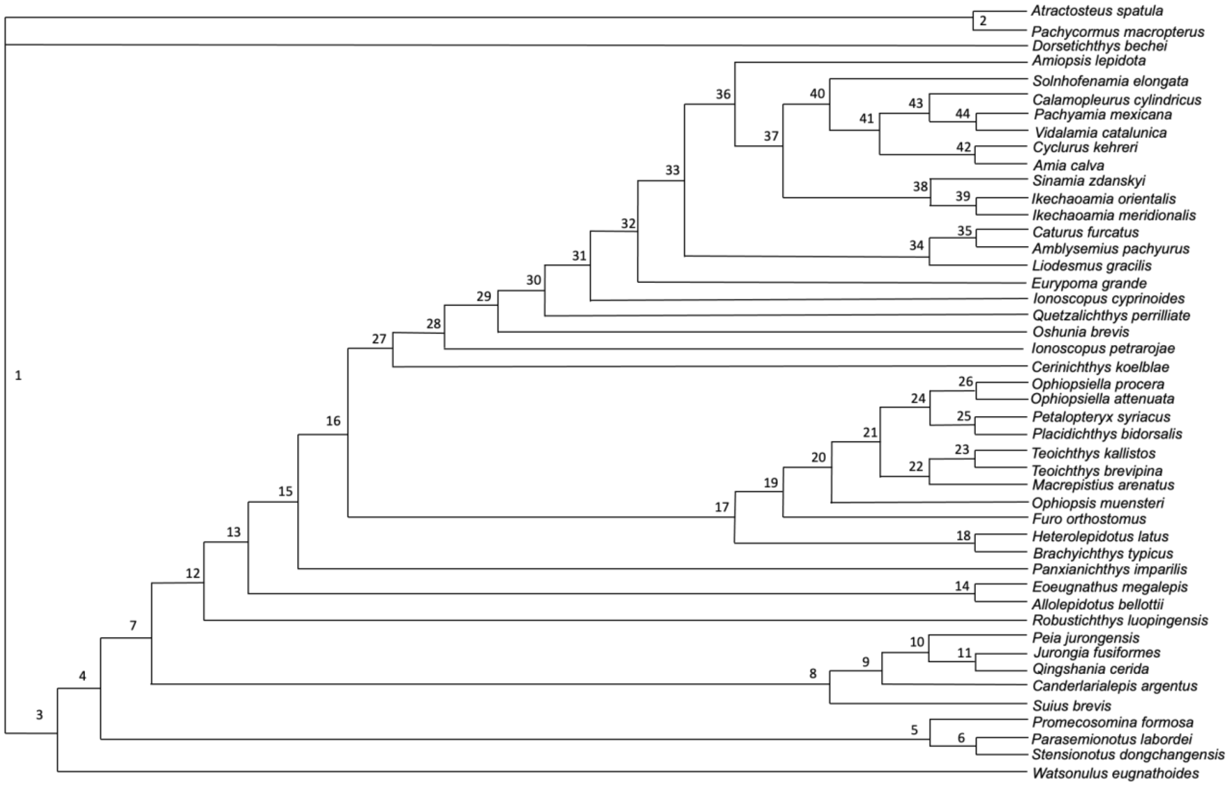
Appendix 5. Summary of ten most parsimonious trees. For relationships of Parasemionotiformes taxa, see Figure 10.

Heuristic search settings:
Optimality criterion = parsimony
Character-status summary:
Of 75 total characters:
All characters are of type 'unord'
All characters have equal weight
All characters are parsimony-informative
Gaps are treated as "missing"
Starting tree(s) obtained via stepwise addition
Addition sequence: random

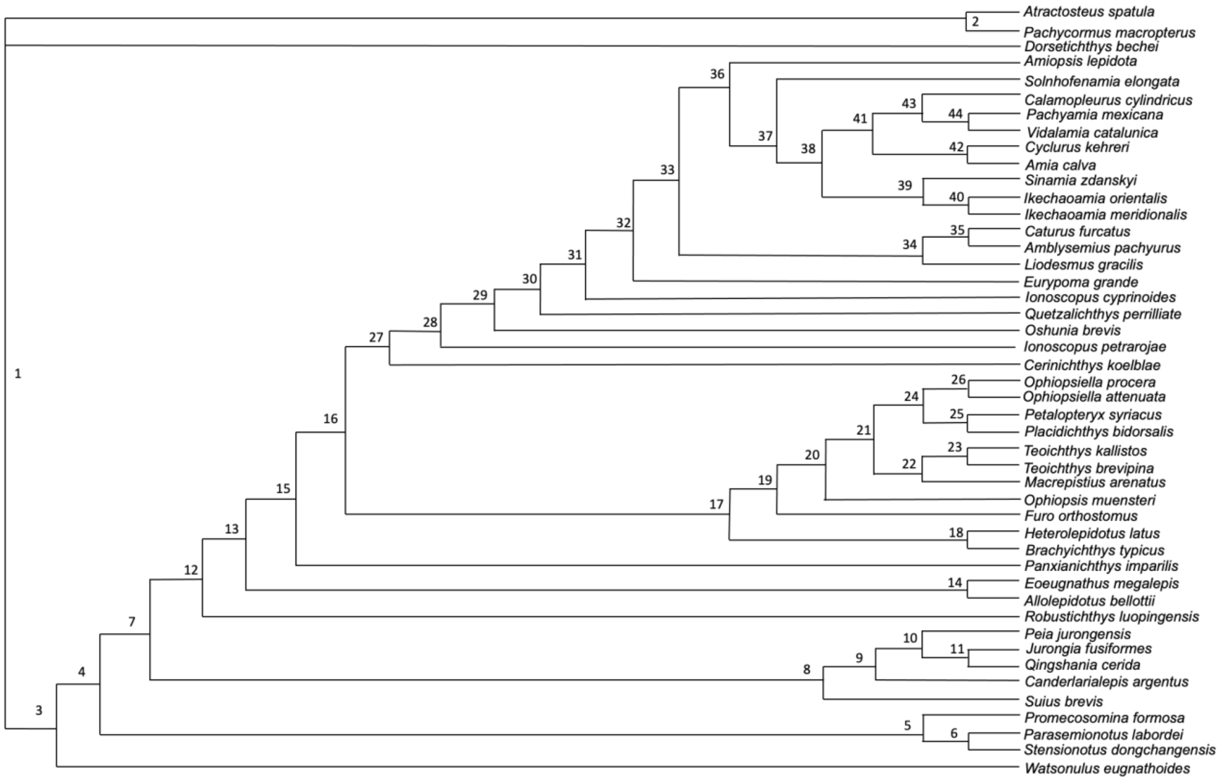
Tree description
Tree length = 458
Consistency index (CI) = 0.2795
Homoplasy index (HI) = 0.7205

Retention index (RI) = 0.5775
Rescaled consistency index (RC) = 0.1614

Tree 1



Tree 2



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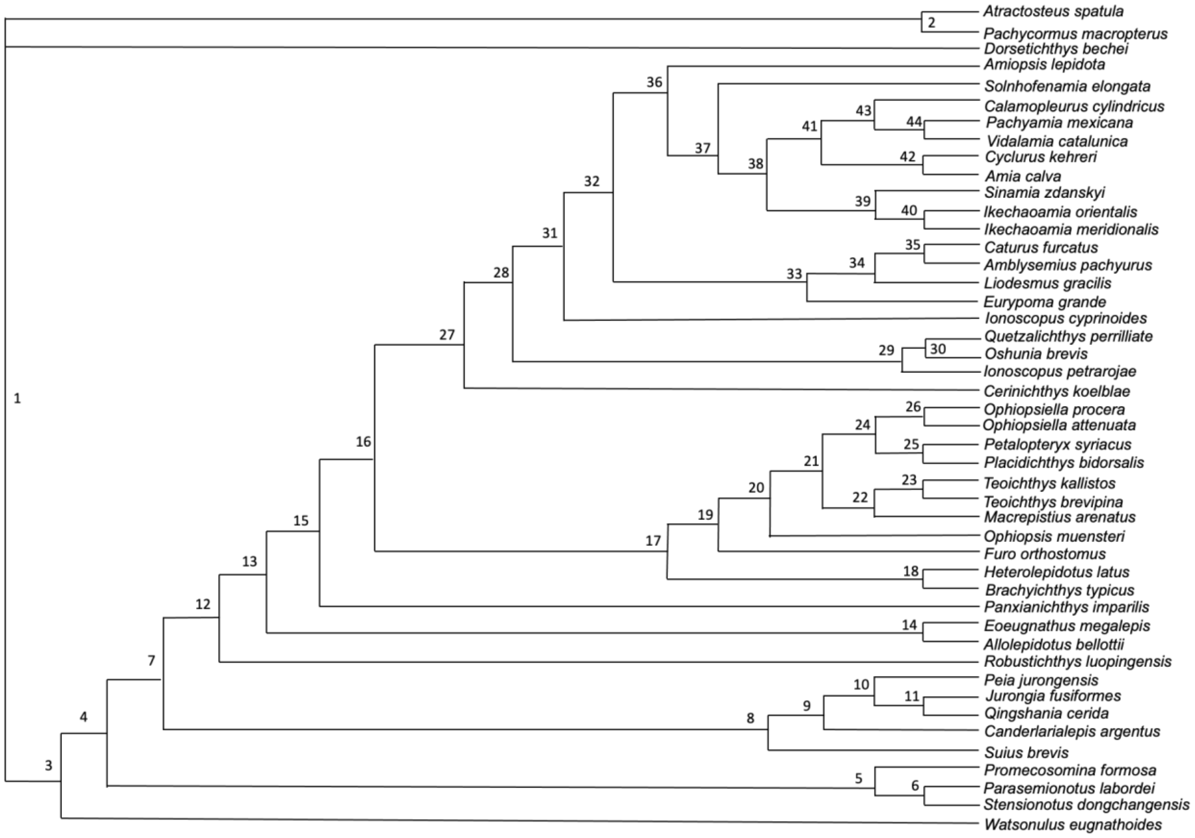
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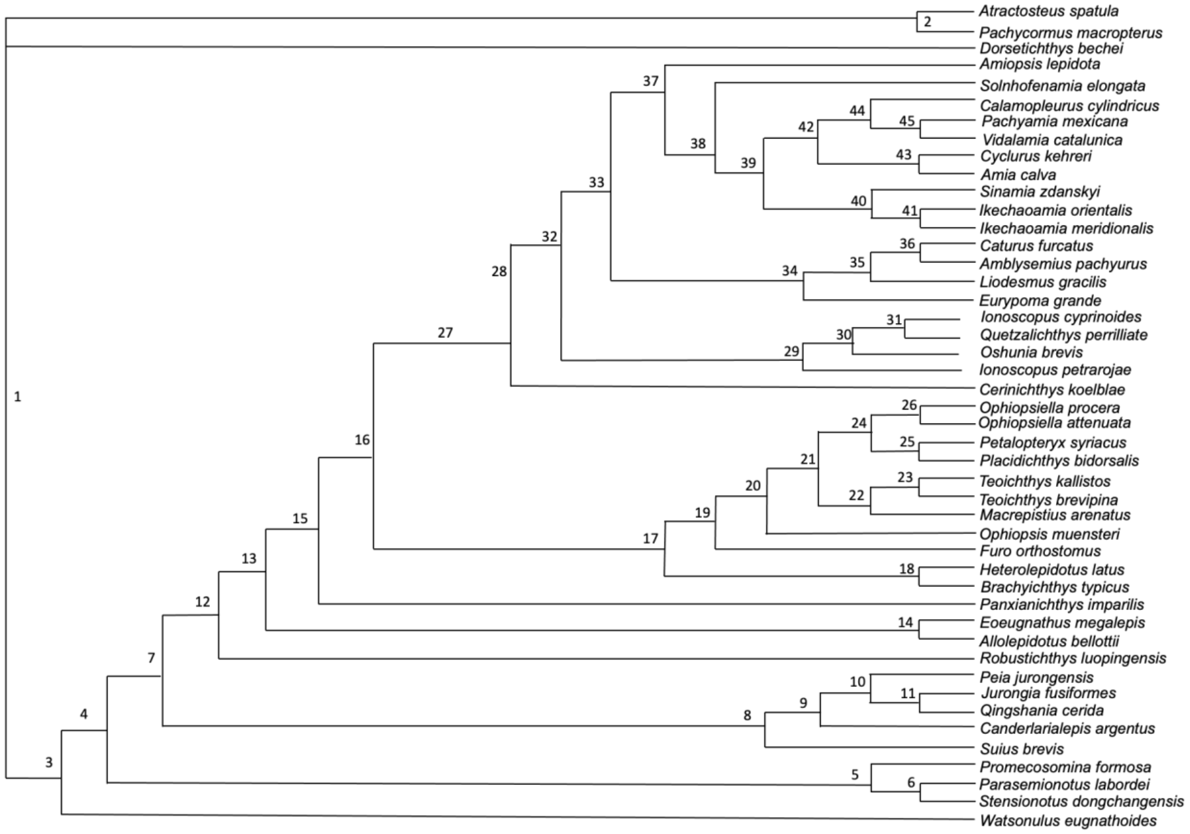
Dorsetichthys bechei
Amiopsis lepidota
36
Solnhofenamia elongata
43
Calamopleurus cylindricus
44
41
Pachyamia mexicana
Vidalamia catalunica
37
42
Cyclurus kehreri
38
Amia calva
32
Sinamia zdanskyi
39
40
Ikechaoamia orientalis
Ikechaoamia meridionalis
31
35
Caturus furcatus
34
Amblysemius pachyurus
28
33
Liodesmus gracilis
Eurypoma grande
Ionoscopus cyprinoides
29
30
Quetzalichthys perrilliate
Oshunia brevis
27
Ionoscopus petrarojae
Cerinichthys koelblae
1
26
Ophiopsiella procera
Ophiopsiella attenuata
24
25
Petalopteryx syriacus
16
Placidichthys bidorsalis
21
23
Teoichthys kallistos
20
22
Teoichthys brevipina
19
Macrepistius arenatus
15
Ophiopsis muensteri
17
Furo orthostomus
13
18
Heterolepidotus latus
Brachyichthys typicus
12
Panxianichthys imparilis
14
Eoeugnathus megalepis
Allolepidotus bellottii
7
Robustichthys luopingensis
10
Peia jurongensis
11
Jurongia fusiformes
4
9
Qingshania cerida
8
Canderlarialepis argentus
Suius brevis
3
Promecosomina formosa
5
6
Parasemionotus labordei
Stensionotus dongchangensis
Watsonulus eugnathoides

Tree 4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Solnhofenamia elongata
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Calamopleurus cylindricus
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Pachyamia mexicana
Vidalamia catalunica
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Cyclurus kehreri
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Amia calva
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Sinamia zdanskyi
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Ikechaoamia orientalis
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Caturus furcatus
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Amblysemius pachyurus
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Liodesmus gracilis
Eurypoma grande
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Ionoscopus cyprinoides
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Quetzalichthys perrilliate
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Oshunia brevis
Ionoscopus petrarojae
Cerinichthys koelblae
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Ophiopsiella procera
Ophiopsiella attenuata
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Petalopteryx syriacus
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Placidichthys bidorsalis
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Teoichthys kallistos
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Teoichthys brevipina
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Macrepistius arenatus
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Ophiopsis muensteri
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Furo orthostomus
13
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Heterolepidotus latus
Brachyichthys typicus
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Panxianichthys imparilis
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Eoeugnathus megalepis
Allolepidotus bellottii
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Robustichthys luopingensis
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Peia jurongensis
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Jurongia fusiformes
4
9
Qingshania cerida
8
Canderlarialepis argentus
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Promecosomina formosa
5
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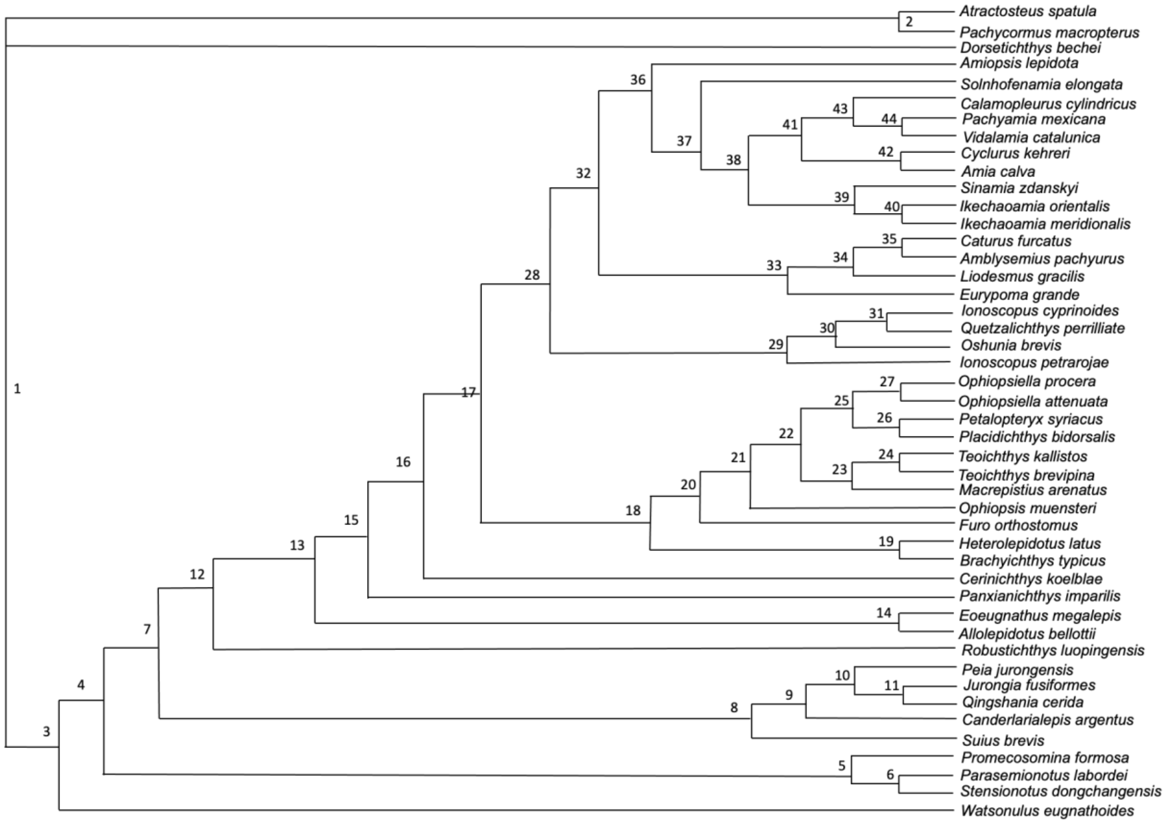
Parasemionotus labordei
Stensionotus dongchangensis
Watsonulus eugnathoides

Tree 5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Amblysemius pachyurus
33
28
Liodesmus gracilis
Eurypoma grande
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Ionoscopus cyprinoides
30
Quetzalichthys perrilliate
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Oshunia brevis
Ionoscopus petrarojae
27
Ophiopsiella procera
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17
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Ophiopsiella attenuata
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Petalopteryx syriacus
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Teoichthys kallistos
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Teoichthys brevipina
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Furo orthostomus
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Brachyichthys typicus
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Cerinichthys koelblae
Panxianichthys imparilis
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Eoeugnathus megalepis
7
Allolepidotus bellottii
Robustichthys luopingensis
Peia jurongensis
10
4
Jurongia fusiformes
11
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Qingshania cerida
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Canderlarialepis argentus
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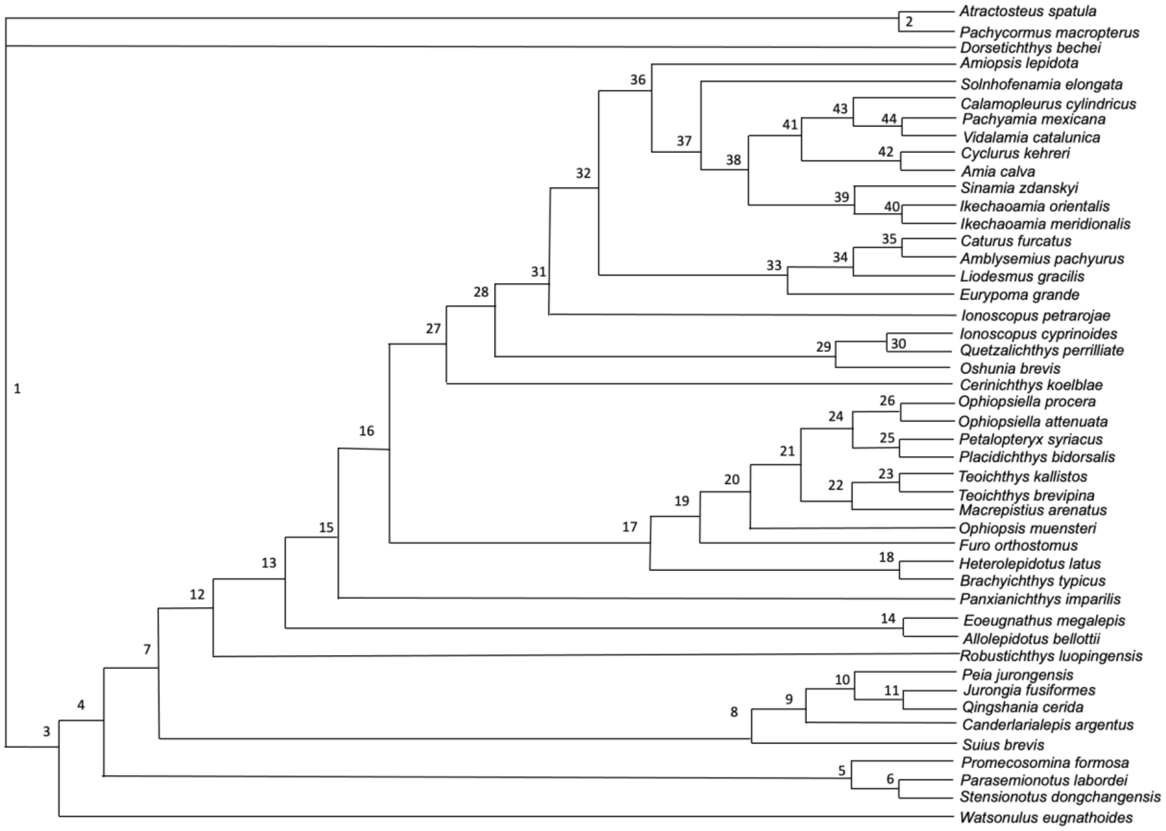
Parasemionotus labordei
Stensionotus dongchangensis
Watsonulus eugnathoides

Tree 6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Promecosomina formosa
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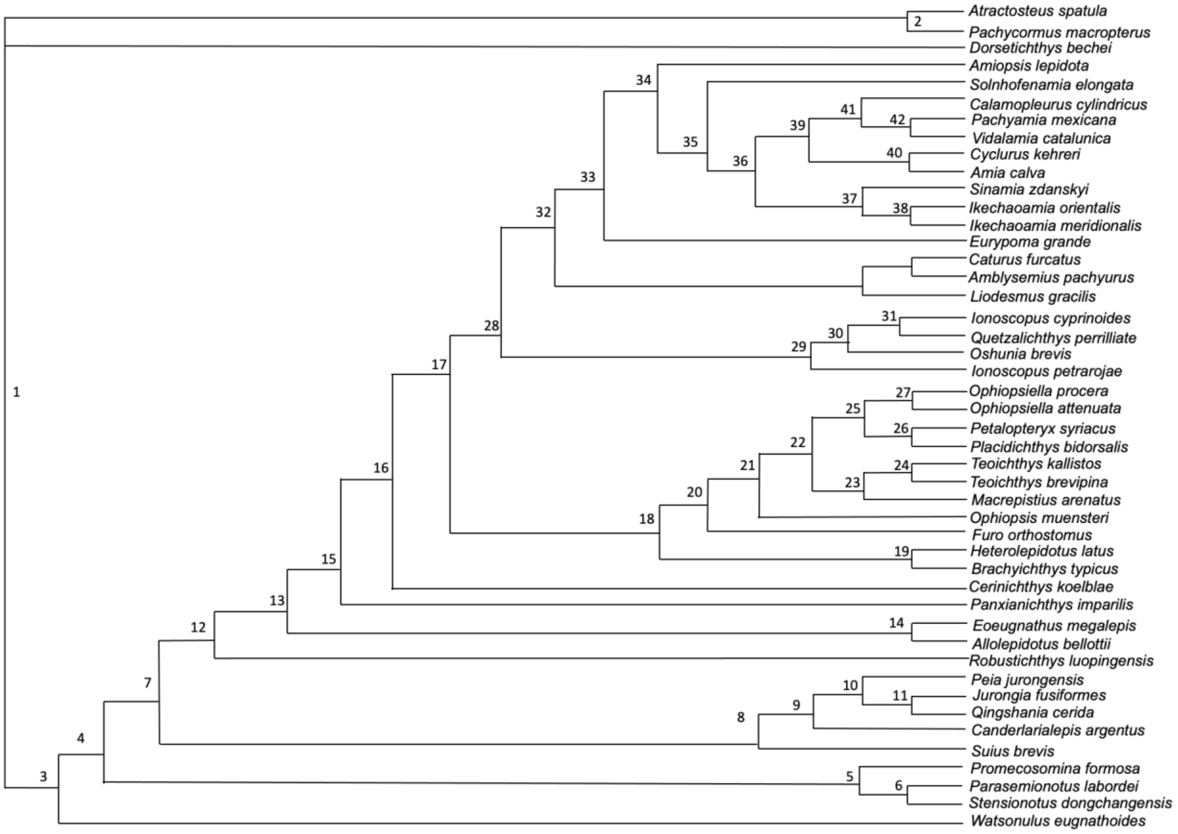
Parasemionotus labordei
Stensionotus dongchangensis
Watsonulus eugnathoides

Tree 7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Amiopsis lepidota
Solnhofenamia elongata
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Calamopleurus cylindricus
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Cyclurus kehreri
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Canderlarialepis argentus
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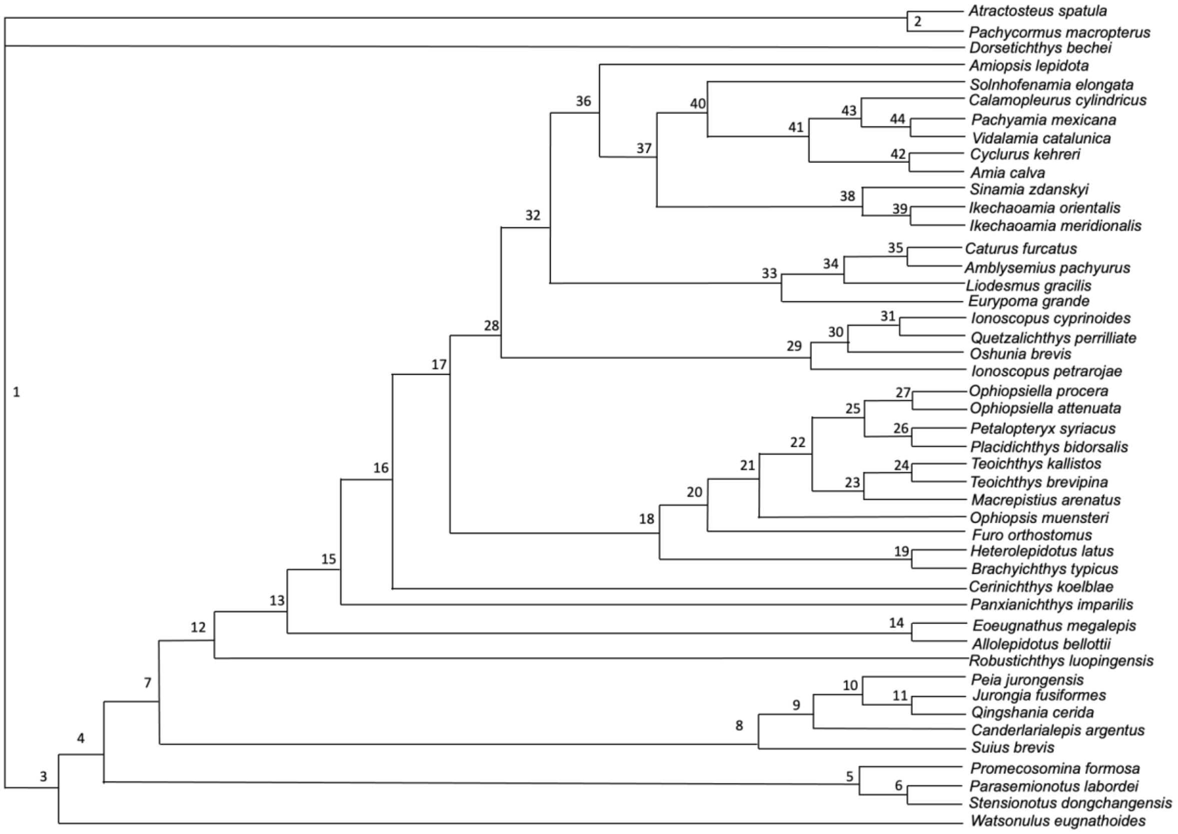
Stensionotus dongchangensis
Watsonulus eugnathoides

Tree 8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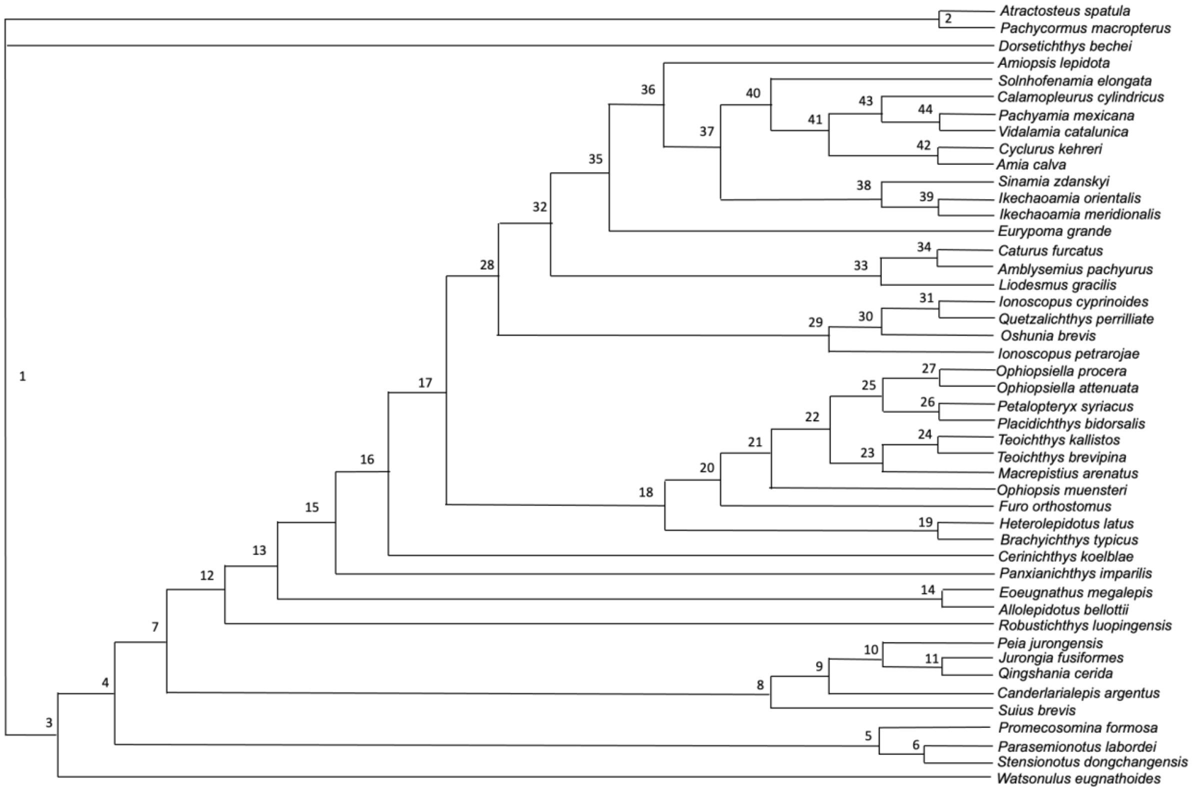
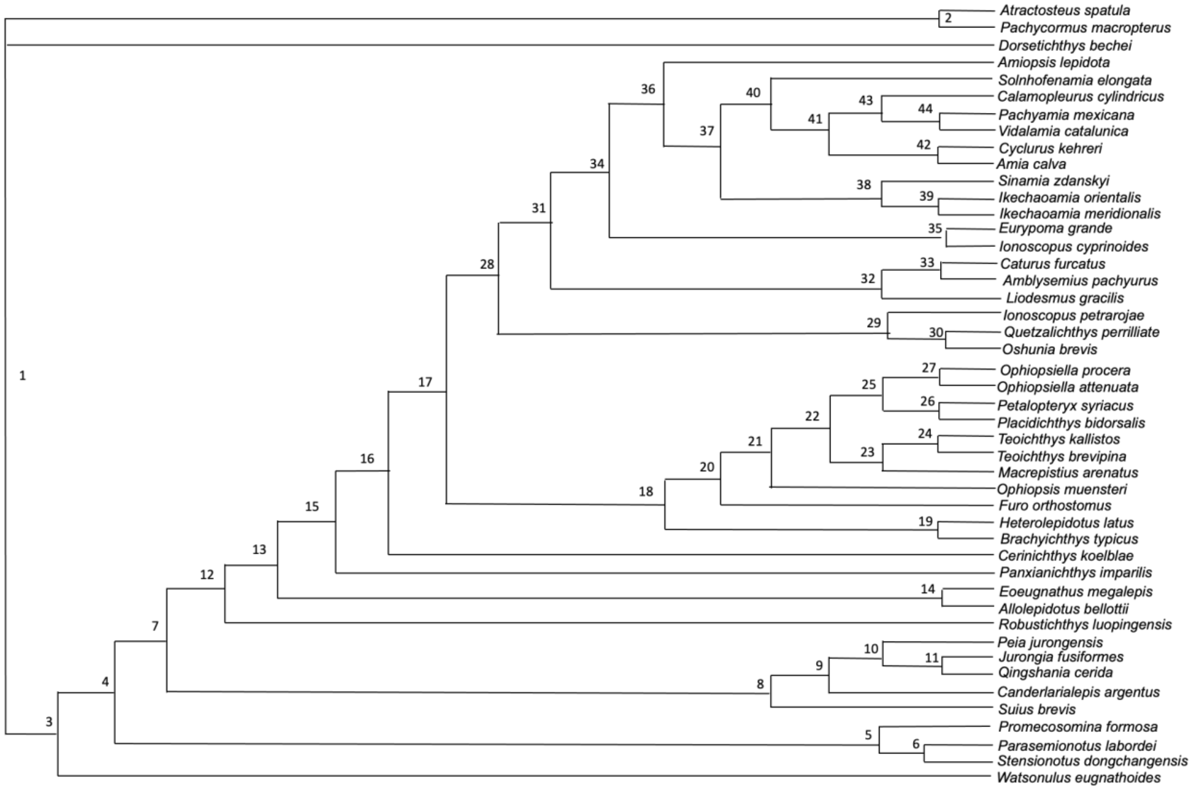
Stensionotus dongchangensis
Watsonulus eugnathoides

Tree 9



Tree 10



Supplemental Information to:

New morphological information on and a redescription of the basal halecomorph fish, *Promecosomina formosa* Woodward 1908 from the Middle Triassic of the Sydney Basin, New South Wales, Australia

Rodney W. Berrell[1,]* and Kate Trinajstic[2]

[1] *School of Earth and Planetary Sciences, Curtin University, Kent Street, Bentley, Western Australia, 6102, Australia, r.berrell@postgrad.curtin.edu.au*

[2] *School of Molecular and Life Sciences (MLS), Curtin University, Kent Street, Bentley, Western Australia, 6102, Australia, K.Trinajstic@curtin.edu.au*

* Corresponding author.

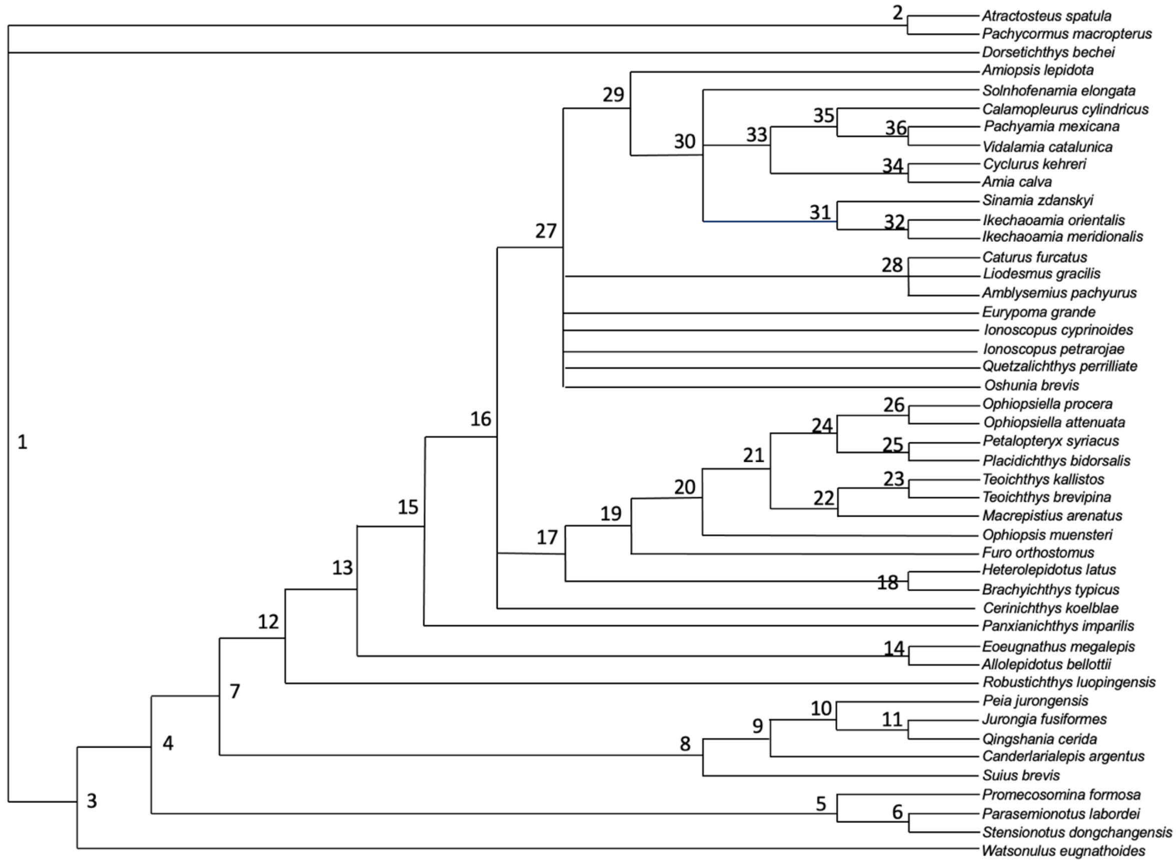
Outline of contents:

Appendix 6. List of character state transformations for taxa below node 16, due to polytomy results and typology of parsimonious trees does not match strict consensus, based on the strict consensus of 10 most parsimonious trees. For relationships of parasemionotiformes taxa, see Figure 10.

Heuristic search settings:
Optimality criterion = parsimony
Character-status summary:
Of 75 total characters:
All characters are of type 'unord'
All characters have equal weight

```
All characters are parsimony-informative
Gaps are treated as "missing"
Starting tree(s) obtained via stepwise addition
 Addition sequence: random

Strict consensus tree of 10 most parsimonious trees
Tree length = 458
Consistency index (CI) = 0.2795
Homoplasy index (HI) = 0.7205
Retention index (RI) = 0.5775
Rescaled consistency index (RC) = 0.1614
```



```
Apomorphy lists:

Branch                    Character                          Steps   CI        Change
----------------------------------------------------------------------------------------------
------------------------------------
node_1 --> node_2
                1 (Posterior extent of exoccipitals)         1                 0.333   0 -
        -> 1
                2 (Solid vertebral centra)                   1                 0.333   4 -
        -> 0
                5 (Suborbital bones)                         1                 0.286   0 -
        -> 1
```

```
          11 (Number of segmented dorsal fin rays)    1              0.333   1 -
      -> 0
          23 (Shape of anterior subinfraorbital bone)  1             0.182   0
      ==> 1
          24 (Number of epaxial caudal basal fulcra)   1             0.300   1 -
      -> 3
          26 (Dermopterotic length to parietal length) 1             0.200   0
      ==> 1
          28 (Number of branchiostegal rays)           1             0.667   0 -
      -> 1
          42 (Maxillary teeth)                         1             0.167   2 -
      -> 1
          48 (Circumorbital ring)                      1             0.250   1 -
      -> 0
          51 (Principal caudal fin rays)               1             0.188   1 -
          -> 3
          69 (Antorbital)                              1             0.143   0
      ==> 1
          75 (Quadratojugal)                           1             0.667   0 -
      -> 1

node_2 --> Atractosteus spatula
          2 (Solid vertebral centra)                   1             0.333   0 -
      -> 1
          5 (Suborbital bones)                         1             0.286   1 -
      -> 4
          6 (Strength of ornamentation on dermal bones of skull)
                                                       1             0.125   0
                                                ==> 1
          10 (Presence absence of sclerotic ring ossification)
                                                       1             0.143   0
                                                ==> 1
          14 (Morphology of caps of the jaw teeth)     1             0.333   0
      ==> 1
          16 (Shape of posterior margin of caudal fin) 1             0.500   0
      ==> 1
          21 (Shape of dermopterotic)                  1             0.143   0
      ==> 1
          28 (Number of branchiostegal rays)           1             0.667   1 -
          -> 2
          32 (Maxilla)                                 1             0.286   0
          ==> 2
          39 (Vertebral centra)                        1             0.333   0
          ==> 3
          43 (Number of supramaxillae)                 1             0.667   1
      ==> 0
          44 (Teeth in dentary)                        1             0.125   0
      ==> 1
          45 (Number of subinfraorbitals)              1             0.222   1
      ==> 0
```

```
          55 (Relative position of the dorsal fin)        1              0.500   0
==> 1
          61 (Ganoin scales between the postcleitral scales and the posterior end
          of the dorsal fin)                                      1
                0.333   1 ==> 3
          63 (Number of pairs of extrascapular bones) 1              0.333   0
==> 1

node_2 --> Pachycormus macropterus
          11 (Number of segmented dorsal fin rays)     1              0.333   0 -
->  2
          13 (shape of preoperculum)                   1              0.429   0
==> 2
          25 (Presence/absence of fringing fulcra on median fins)
                                                       1              0.333   0
                                                   ==> 1
          27 (Shape of maxilla)                        1              0.500   0
==> 1
          29 (Dermosphenotic attachment)               1              0.200   0
==> 1
          35 (Relative size of uppermost postinfraorbital)      1     0.333   0
==> 1
          52 (Scales in the anterior part of the body) 1              0.286   1
==> 2
          53 (Multiple tiny scales in caudal area)     1              0.500   0
==> 1
          56 (First supraorbital bone)                 1              0.273   1
==> 2
          58 (Dorsal lateral line pores)               1              0.200   1
          ==> 0
          72 (Segmentation of caudal rays)             1              0.222   2
==> 1

node_1 --> Dorsetichthys bechei
          9 (Urodermals in the caudal skeleton)        1              0.400   2
==> 0
          12 (Parietal length)                         1              0.100   0 -
-> 1
          15 (Lateral edge of posttemporal)            1              0.167   0
==> 1
          39 (Vertebral centra)                        1              0.333   0
==> 1
          40 (Predorsal length)                        1              0.250   1
==> 0
          41 (Vertical scale rows)                     1              0.182   2
==> 1
          43 (Number of supramaxillae)                 1              0.667   1
==> 2
          46 (Number of postinfraorbitals)             1              0.300   0
==> 1
```

```
          49 (Relative size of the infraorbital bone)     1          0.222   0 -
    -> 2
          56 (First supraorbital bone)                    1          0.273   1
    ==> 0
          57 (Maxillary length)                           1          0.222   1
    ==> 0
          72 (Segmentation of caudal rays)                1          0.222   2
    ==> 0
          74 (Symplectic/quadrate contact)                1          0.500   1
    ==> 0
          75 (Quadratojugal)                              1          0.667   0 -
    -> 2

node_1 --> node_3
          13 (shape of preoperculum)                      1          0.429   0
    ==> 3
          34 (Symplectic involvement in jaw joint)        1          0.500   0
    ==> 1
          52 (Scales in the anterior part of the body)    1          0.286   1
    ==> 0
          59 (Scales in the area of the ventral margin)   1          0.375   1
    ==> 0
          61 (Ganoin scales between the postcleitral scales and the posterior end
          of the dorsal fin)                                   1
              0.333   1 ==> 2
          65 (Proportions; standard length (SL)/head length (HL))
                                                          1          0.111   1 -
                                                        -> 0

node_3 --> node_4
          18 (Shape of gular)                             1          0.333   0 -
    -> 1
          21 (Shape of dermopterotic)                     1          0.143   0 -
    -> 1
          41 (Vertical scale rows)                        1          0.182   2
    ==> 0
          64 (Proportions; standard length (SL)/body depth (BD))
                                                          1          0.167   1
                                                        ==> 0
          73 (Maximum standard length)                    1          0.125   0 -
    -> 1

node_4--> node_7
          2 (Solid vertebral centra)                      1          0.333   4 -
    -> 0
          29 (Dermosphenotic attachment to skull roof)1              0.200   0 -
    -> 1
          30 (Shape of rostral bone)                      1          0.500   0 -
          -> 1
```

51 (Principal caudal fin rays) 1 0.188 1 ==> 0
72 (Segmentation of caudal rays) 1 0.222 2 ==> 1

node_7 --> node_12
6 (Strength of ornamentation on dermal bones of skull) 1 0.125 0 ==> 1
13 (shape of preoperculum) 1 0.429 3 ==> 1
18 (Shape of gular) 1 0.333 1 --> 0
33 (Presence/absence of lateral line canal in maxilla) 1 0.500 0 ==> 1
49 (Relative size of the infraorbital bone) 1 0.222 0 --> 1

node_12 --> node_13
29 (Dermosphenotic attachment to skull roof) 1 0.200 1 --> 0
52 (Scales in the anterior part of the body) 1 0.286 0 ==> 1
68 (Shape of posterior margin of maxilla) 1 0.250 0 ==> 1

node_13-->node_15
5 (Suborbital bones) 1 0.286 0-->1
17 (Postmaxillary process under postmaxillary notch) 1 0.222 0 ==> 3
42 (Maxillary teeth) 1 0.167 2==>0
58 (Dorsal lateral line pores) 1 0.200 1-->0
73 (Maximum standard length) 1 0.125 1==>0

node_15 --> *Panxianichthys imparilis*
38 (Ventral surface of lower circumorbital bones) 1 0.167 0 ==> 1
46 (Number of postinfraorbitals) 1 0.300 0 ==> 1
51 (Principal caudal fin rays) 1 0.188 0 ==> 1
67 (Distinct supramaxillary notch of maxilla) 1 0.250 0 ==> 1

node_13 --> node_14
50 (Mandibular length as a percentage of head length) 1 0.222 0 ==> 1
51 (Principal caudal fin rays) 1 0.188 0 ==> 2
59 (Scales in the area of the ventral margin) 1 0.375 0 ==> 1

node_14 --> *Eoeugnathus megalepis*
8 (Number of supraorbital bones) 1 0.273 1 ==> 0
12 (Parietal length) 1 0.100 0 ==> 1
17 (Postmaxillary process under postmaxillary notch) 1 0.222 0 ==> 1
38 (Ventral surface of lower circumorbital bones) 1 0.167 0 ==> 1
47 (Fringing fulcra on pectoral fin) 1 0.143 0 ==> 1
57 (Maxillary length) 1 0.222 1 ==> 0

node_14 --> *Allolepidotus bellottii*
42 (Maxillary teeth) 1 0.167 2 ==> 1
44 (Teeth of dentary) 1 0.125 0==>1
49(Relative size of the infraorbital bone) 1 0.222 1 ==> 2

node_12 --> *Robustichthys luopingensis*
5 (Suborbital bones) 1 0.286 0 ==> 2
10 (Presence absence of sclerotic ring ossification) 1 0.143 0 ==> 1
11 (Number of segmented dorsal fin rays or …) 1 0.333 1 ==> 2
16 (Shape of posterior margin of caudal fin) 1 0.500 0 ==> 2
31 (Lacrimal shape) 1 0.250 0 ==> 2
32 (Maxilla) 1 0.286 0 ==> 1
41 (Vertical scale rows) 1 0.182 0 ==> 1
46 (Number of postinfraorbitals) 1 0.300 0 ==> 1
67 (Distinct supramaxillary notch of maxilla) 1 0.250 0 ==> 1

```
node_7 --> node_8
          15 (Lateral edge of posttemporal)            1          0.167   0
     ==> 1
          20 (Frontal width)                           1          0.250   0 -
     -> 1
          23 (Shape of anterior subinfraorbital bone)  1          0.182   0 -
     -> 2
          38 (Ventral surface of lower circumorbital bones) 1     0.167   0 -
     -> 1
          56 (First supraorbital bone)                 1          0.273   1 -
     -> 0
          71 (Fringing fulcra on ventral lobe of caudal fin)  1   0.333   0
     ==> 1

node_8 --> node_9
          13 (shape of preoperculum)                   1          0.429   3
     ==> 2
          47 (Fringing fulcra on pectoral fin)         1          0.143   0
     ==> 1
          51 (Principal caudal fin rays)               1          0.188   0 -
     -> 2

node_9 --> node_10
          5 (Suborbital bones)                         1          0.286   0 -
     -> 1
          8 (Number of supraorbital bones)             1          0.273   1 -
     -> 2
          25 (Presence/absence of fringing fulcra on median fins) 1  0.333   0
     ==> 1
          56 (First supraorbital bone)                 1          0.273   0 -
     -> 2
          57 (Maxillary length)                        1          0.222   1
     ==> 0
          64 (Proportions; standard length (SL)/body depth (BD)) 1   0.167  0
     ==> 1

node_10 --> Peia jurongensis
          50 (Mandibular length as a percentage of head length) 1   0.222   0
     ==> 1
          65 (Proportions; standard length (SL)/head length (HL)) 1  0.111   0
     ==> 1

node_10 --> node_11
          22 (Width of operculum)                      1          0.333   0
     ==> 1
          34 (Symplectic involvement in jaw joint)     1          0.500   1 -
     -> 0

node_11 --> Jurongia fusiformes
```

```
                 13 (shape of preoperculum)                  1             0.429   2
          ==> 3

node_11 --> Qingshania cerida
                 15 (Lateral edge of posttemporal)           1             0.167   1
          ==> 0

node_9 --> Candelarialepis argentus
                 6 (Strength of ornamentation on dermal bones of skull) 1  0.125   0
          ==> 1
                 21 (Shape of dermopterotic)                 1             0.143   1 -
          -> 0
                 30 (Shape of rostral bone)                  1             0.500   1 -
          -> 0
                 32 (Maxilla)                                1             0.286   0
          ==> 2
                 41 (Vertical scale rows)                    1             0.182   0
          ==> 1
                 73 (Maximum standard length)                1             0.125   1
          ==> 0

node_8 --> Suius brevis
                 43 (Number of supramaxillae)                        1     0.667   1
          ==> 0

node_4 --> node_5
                 16 (Shape of posterior margin of caudal fin) 1            0.500   0
          ==> 2
                 24 (Number of epaxial caudal basal fulcra)  1             0.300   1 -
          -> 2
                 32 (Maxilla)                                1             0.286   0
          ==> 1
                 35 (Relative size of uppermost postinfraorbital) 1        0.333   0
          ==> 1
                 57 (Maxillary length)                       1             0.222   1
          ==> 0
                 58 (Dorsal lateral line pores)              1             0.200   1 -
          -> 0
                 65 (Proportions; standard length (SL)/head length (HL))
                                                             1             0.111   0 -
                                                      -> 1

node_5 --> Promecosomina formosa
                 20 (Frontal width)                          1             0.250   0
          ==> 1
                 40 (Predorsal length)                       1             0.250   1
          ==> 2
                 41 (Vertical scale rows)                    1             0.182   0
          ==> 1
```

```
                51 (Principal caudal fin rays)               1          0.188   1
        ==> 2
                73 (Maximum standard length)                 1          0.125   1 -
        -> 0

node_5 --> node_6
                21 (Shape of dermopterotic)                  1          0.143   1 -
        -> 0
                45 (Number of subinfraorbitals)              1          0.222   1 -
        -> 0
                46 (Number of postinfraorbitals)             1          0.300   0
        ==> 1
                49 (Relative size of the infraorbital bone)  1          0.222   0 -
        -> 2
                56 (First supraorbital bone)                 1          0.273   1
                ==> 0

node_6 --> Parasemionotus labordei
                5 (Suborbital bones)                         1          0.286   0
        ==> 1
                63 (Number of pairs of extrascapular bones)  1          0.333   0
        ==> 1

node_6 --> Stensionotus dongchangensis
                8 (Number of supraorbital bones)             1          0.273   1
        ==> 0
                13 (shape of preoperculum)                   1          0.429   3
                ==> 2
                15 (Lateral edge of posttemporal)            1          0.167   0
        ==> 1
                23 (Shape of anterior subinfraorbital bone)  1          0.182   0
        ==> 1
                48 (Circumorbital ring)                      1          0.250   1
        ==> 0

node_3 --> Watsonulus eugnathoides
                5 (Suborbital bones)                         1          0.286   0
        ==> 2
                12 (Parietal length)                         1          0.100   0 -
        -> 1
                23 (Shape of anterior subinfraorbital bone)  1          0.182   0
        ==> 2
                24 (Number of epaxial caudal basal fulcra)   1          0.300   1
        ==> 0
                49 (Relative size of the infraorbital bone)  1          0.222   0 -
        -> 2
                68 (Shape of posterior margin of maxilla)    1          0.250
                0==>1
```

Chapter 4. The first record of amiid fishes (Halecomorphi, Amiiformes, Amiidae, Calamopleurini) from Eastern Gondwana.

Chapter 4 was accepted to be published in the peer-reviewed journal '*Cretaceous Research*' on the 16th March 2023.

Berrell, R.W., Cavin, L., Trinajstic, K., Boisvert, C., Smith, E. T. 2023. The first record of amiid fishes (Halecomorphi, Amiiformes, amiidae, Calamopleurini?) from Eastern Gondwana. Cretaceous Research.

4.1 ABSTRACT

The extant Amiiformes are represented by a single living freshwater genus *Amia* (bowfin) with recent phylogenomic analysis indicating the presence of multiple species. However, they have a more extensive fossil record, first appearing in the Early Jurassic and are recorded as occurring on all continents, except Antarctica and Australia. Here, we describe fossil amiid fishes Calamopleurini? (Halecomorphi, Amiiformes) from the Cretaceous (Albian—Cenomanian) Griman Creek Formation, Lightning Ridge, New South Wales, Australia, representing the first record, extinct or extant, of the amiids in Australia. The material comprises jaw elements that have been replaced by opal. This new record from Australia adds to previously documented Cretaceous Western Gondwanan occurrences from South America and Africa and further supports a distinct southern "Gondwanan" fish population in the seas surrounding the fragmenting Gondwanan landmasses during the 'mid' — Late Cretaceous.

Keywords: Amiidae, Calamopleurini, Gondwana, Griman Creek Formation, Lightning Ridge, Australia

4.2 Introduction

Amiiformes are an order of halecomorph fish, exemplified by a single extant genus, *Amia* (Grande and Bemis, 1998) containing at least two living species (Wright et al., 2022; Brownstein et al. 2022) which is confined to freshwater habitats in the United States and Canada (Grande and Bemis, 1998). The Amiiformes diversified during the Mesozoic occurring globally except for areas with a paleolatitude below 30°S. This includes the southern tips of South America, South Africa and eastern Gondwana (Antarctica, India and Australia, New Zealand, and Papua New Guinea) (Grande and

Bemis, 1998). Their oldest occurrence is from Early Jurassic marine strata which indicates that a habitat transition from exclusively marine to exclusively freshwater occurred between the ancestral and extant taxa (Grande and Bemis, 1998).

The Amiiformes order is divided into the Caturoidea (Caturidae + Liodesmidae) and the Amioidea (Amiidae + Sinamiidae) (Martin-Abad and Poyato-Ariza, 2013). The Amiidae comprises four subfamilies, one of which, the Vidalamiinae is further divided into two tribes: the Calamopleurini, and the Vidalamiini. The former is an entirely Gondwanan tribe, and the latter is a dominantly Laurasian tribe with some rare relict Gondwanan taxa (Martin-Abad and Poyato-Ariza, 2013).

The group currently shows the greatest diversity during the Late Jurassic (Martin-Abad and Poyato-Ariza, 2013), however, this diversity, might be a bias due to the number of lagerstätten localities that are dated as Late Jurassic (e.g., Solnhofen Formation Germany, Torleite Formation Germany, Cerin lithographic limestones, France) (Flannery Sutherland et al., 2019). By the Late Cretaceous, the Amiiformes are represented only by members of the Vidalamiinae and Amiinae (Martin-Abad and Poyato-Ariza, 2013, Figure 2), with all other clades being extinct by the K-Pg boundary. The only extant subfamily are the Amiinae.

Throughout east Gondwana (Australia, Antarctica, New Zealand, and Papua New Guinea), the record of Amiiformes is absent despite fossiliferous rock packages of the right age (Late Jurassic — Late Cretaceous) and right depositional environments (marine, estuarial and lacustrine) (Berrell et al., 2020). Whilst Australia lacks lithographic limestones or lagerstätten (formed largely in marine depositional environments) from which many European and South American Amiiformes have been described, Australia does present numerous isolated opalised fish elements, including jaw fragments and vertebrae. These have been found by opal miners, in the Griman Creek Formation at Lightning Ridge, New South Wales, Australia (Fig. 4.1).

In this paper, we discuss specimens in public collections that were excavated early last century, in the late 1980s, mid 1990s and 2019. The specimens consist of isolated actinopterygian jaw bones from the 'mid' Cretaceous, Griman Creek Formation of Lightning Ridge, New South Wales, Australia. Although there is not a wealth of material, preservation is excellent including a number of morphological landmarks which aid in the identification of the material. These specimens are here described for the first time and placed into a taxonomic context expanding knowledge on fish diversity and biogeography from Gondwana.

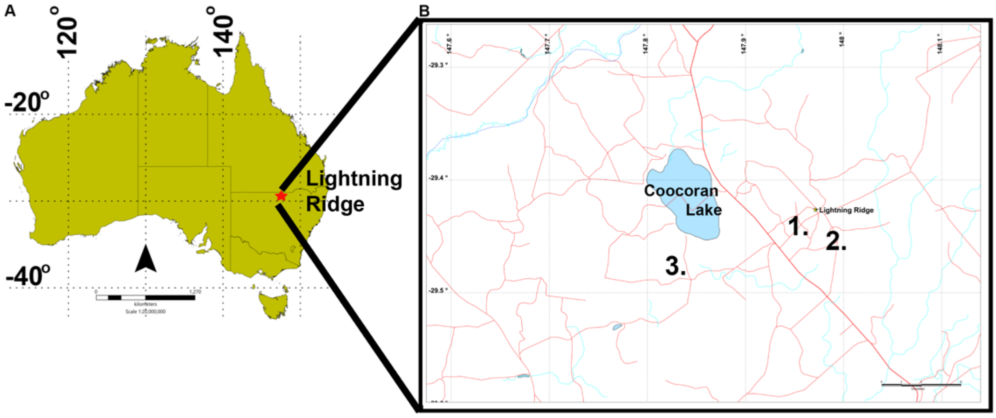


Fig. 4.1. A. Map of Australia, showing the opal mining town of Lightning Ridge in north-western, New South Wales, Australia, and B. Close-up of the opal mining fields that have produced Calamopleurini? Material. Red linework = Roads, Blue linework = water drainages and lakes. Abbreviations. 1. Four Mile Field, Lightning Ridge; 2. Three Mile Field, Lighting Ridge; 3. Allah's Field, Coocoran, Lightning

Ridge. Scale bar for A. Australia is 1,270 km (1:20, 000, 000). Scale bar for B. Insert is 8 km. Grid lines are in latitude and longitude.

4.3 Geological Setting, Locality and Fauna

The Great Artesian Basin is a hydrological basin comprising three geological basins: the Eromanga, the Surat and the Cooper basins separated from each other by buried basement ridges (Henderson, 2004). These basins contain the majority of Mesozoic strata in eastern Australia.

The Eromanga and Surat Basins occupy most of Queensland (QLD), northern New South Wales and part of northeast South Australia (SA), Australia. The rocks that crop out in each basin are attributed to the Rolling Downs Group – a package of stratigraphy that is Lower Cretaceous in age and records a marine transgression – regression event of the epeiric Eromanga Sea (Henderson, 2004) (Fig. 4.2). The Eromanga Sea was shallow, poorly connected to the open ocean, due to the buried basement ridges, muddy, stagnant, and anoxic in parts (Rey, 2013).

The basins developed as a flexural foreland basin associated with the Cordillera Orogen, acting as depocenters for the eroding arc (Rey, 2013), and eventually sediment oversupply and hinterland uplift replaced the marine setting with a thick package of continental sandstones (Winton and Griman Creek Formations). The Winton Formation is located within the Eromanga Basin, whilst the Griman Creek Formation is located within the Surat Basin (Rey, 2013). The Griman Creek Formation is up to 400 m thick (Bell et al., 2019 and references therein), whilst the Winton Formation is over 1200 m thick (Fielding, 1992). Based on age detrital zircon dating, and biostratigraphy, the lower parts of the Winton and Griman Creek Formations appear to be contemporaneous (Tucker et al., 2013; Bell et al., 2019).

The Griman Creek Formation crops out within the Surat Basin in north-central New South Wales and southern Queensland, Australia, between the townships of Lightning Ridge (NSW) and Surat (Queensland) (Bell et al., 2019). It contains the Wallangulla Sandstone and the Coocoran Claystone member (Bell et al., 2019) with the fossils and commercial opal found within the Finch Claystone facies of the Wallangulla Sandstone (Fig. 2). The Finch Claystone facies represent channel deposits with sharp erosive contacts (Bell et al., 2019). The depositional environment at Lightning Ridge is interpreted as freshwater, based on sedimentary features such as crossbedding, rip-up clasts, sediment size (sandstone and claystone), and the fining upwards sequences (Bell et al., 2019).

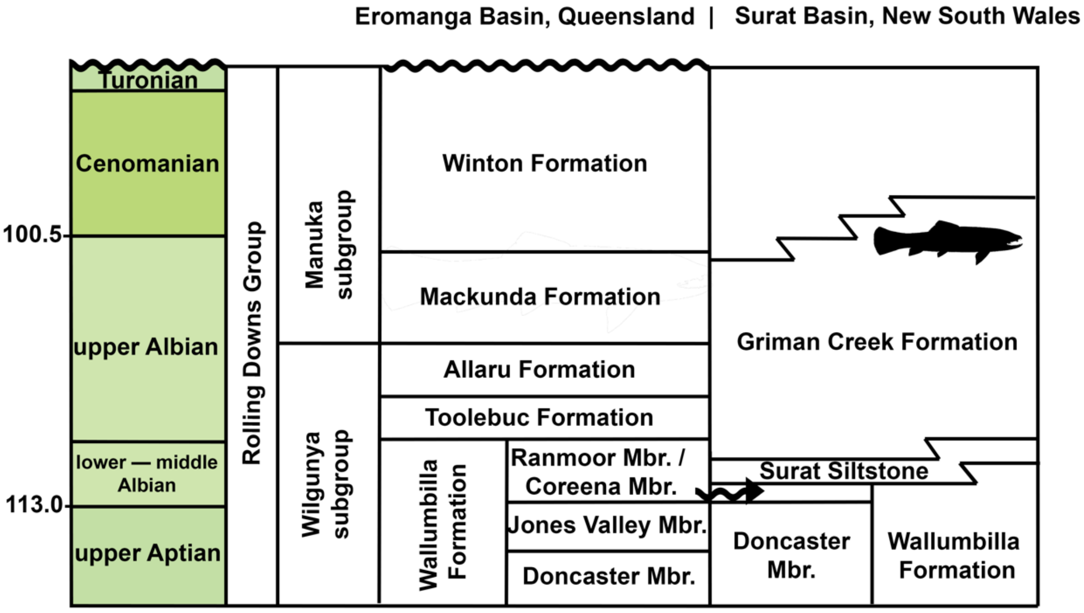


Fig. 4.2. The stratigraphy of the Eromanga Basin of Queensland and the Surat Basin of New South Wales, Australia. Approximate stratigraphic position of *Calamopleurus*? Sp. is indicated by the fish silhouette. Abbreviation: Mbr. Member.

Opal mining fields at Lightning Ridge are divided into several areas. Specimens discussed here are from old fields around the township of Lightning Ridge, informally known as the Lightning Ridge Opal Fields; and from an area 30kms west of the township collectively known as the Coocoran Opal Fields (Smith, 1999; Burton, 2004) (Fig. 4.1.).

Opal mining fields at Lightning Ridge are divided into several areas. Specimens discussed here are from old fields around the township of Lightning Ridge, informally known as the Lightning Ridge Opal Fields; and from an area 30kms west of the township collectively known as the Coocoran Opal Fields (Smith, 1999; Burton, 2004) (Fig. 4.1.).

In this paper, the names of fossil localities refer to mining fields. Specimens discussed here were collected by miners across multiple levels at depths between 1-30 metres. Precise stratigraphic context and potential differences in fossil biota between horizons are not yet determined. Specimens discussed here were recovered from Allah’s Field, Coocoran (LRF0028), the Three Mile Field (LRF1469) and Four Mile Field (LRF3367) closer to the township of Lightning Ridge (Fig. 4.1.). Location for AM F.18593 is uncertain, however, this specimen from 1925 probably originated from an old field near the Lightning Ridge township, as more distant fields such as the Coocoran were yet to be found. The fossils were collected from Finch Claystone horizons that are 0.1 – 2.0 metres thick and sit between 12-20 metres deep, however, the exact age and depth of the horizons are unknown. However, fossils of marine bivalves and glauconite pellets are known to occur at the base of the Griman Creek

Formation indicating a change from marine to freshwater conditions as the sequence gets younger (Exon, 1976).

The Surat Basin is shallower than the adjacent Eromanga Basin and was isolated from the inland sea earlier than the Winton Formation. New zircon dating puts opal sediments near Lightning Ridge at 100.2 — 96.6 Ma (Bell et al., 2019), an interval that spans inland sea regression, and aberrant hydrological conditions in the Surat Basin (anoxic, turbid water; high organic load, volcaniclastic silt) are regarded as crucial to opal/fossil formation (Rey, 2013). Previously the age assigned was middle — late Albian (Hamilton-Bruce et al., 2004) based on palynology. The new-age data suggest that, for at least parts of the Griman Creek Formation, deposition was coeval to lower parts of the Winton Formation (Bell et al., 2019; Tucker et al., 2013), i.e., early Cenomanian.

The fauna described below is from Griman Creek Formation, from deposits within a 100 km radius of the opal mining township of Lightning Ridge, New South Wales. The fossils recovered to date include freshwater gastropods (Hamilton-Bruce et al., 2004) and freshwater bivalves (Hocknull, 2000), fishes (actinopterygian, sarcopterygian (limited to three species of ceratodont lungfishes) and chondrichthyan (lamniform (Smith, 1999) and Chimaeriform) fishes (Berrell et al., 2020, Table 1), amniotes including turtles (Smith, 2010; Smith and Kear, 2013), crocodylians (Molnar and Willis, 2001; Hart et al., 2020), pliosaurs and elasmosaurs, pterosaurs and dinosaurs (Molnar and Galton, 1986; Smith, 1999; Bell et al., 2019), birds (Bell et al., 2019) and mammals (Archer et al., 1985, Flannery et al., 1995 and Rich et al., 2020).

4.4 Material and methods

Fossil Recovery — Opalised fossils at Lightning Ridge are generally recovered as a by-product of opal mining, either by manual collection (direct from the mine-face; or from surface mullock) or during mechanised mining (air hammers, 'diggers', 'blowers'). Mining sediment is washed in 'agitators' resulting in disarticulation, breakage and abrasion of fossil materials. In addition, the exact horizon in which the fossils were recovered is lost, as is most taphonomic data.

In opalised bones, the biogenic components of the vertebrate skeleton have been replaced by either common or precious opal (Smith, 1999; Rey, 2013). Opal is generally thought to form from silica-rich colloidal liquid that has filled pore space, cracks, fractures, and cavities resulting from the dissolution of mineralised fossils and primary minerals (Rey, 2013).

The fossils discussed herein were found in the 1920s and between the mid 1990s and late 2000s. AM F.18593 was part of the collections of George Smith NSW Inspector of Mines from (1904-1925) purchased by the Australian Museum in 1925, but remained undescribed. LRF0028 was donated to the Australian Opal Centre through the Australian Government’s Cultural Gifts Program by Stephen George Turner and LRF1469 was donated through the Australian Government’s Cultural Gifts Program by David Joseph Barclay. LRF3367 was donated by Glenn Roddenby and Yvonne Willis.

Measurements — Elements were measured using digital calipers with a tolerance of 1 mm. The angle of mid maxillary notch was measured using an angle/linear ruler (Table 4.1).

Comparative Material — To determine angles of the posterior maxilla notch of the Cretaceous Vidalamiinae, taxa from Grande and Bemis (1998) and Forey and Grande (1998) were used. The mid maxillary notch of *Vidalamia catalunica, Pachyamia latimaxillaris, Pachyamia Mexicana,* and *Calamopleurus cylindricus* was measured using an angle/linear ruler from drawings of specimens in Grande and Bemis (1998) Figure 243 and from Forey and Grande (1998) for *C. africanus* and recorded in Table 4.1 below.

Institutional Abbreviations — **AM F.**, Australian Museum, Sydney, New South Wales, Australia; **LRF**, Australian Opal Centre, Lightning Ridge, New South Wales, Australia.

Anatomical Abbreviations — anatomical abbreviations follow Grande and Bemis 1998. **Ac.** Acrodin cap; **Ap.** Autopalatine; **Dp1.** dermopalatine; **Mx**. maxilla; **Mxn**. maxillary notch; **cnV**. maxillary branch of the cranial nerve V; **Pc.** pulp cavity; **t**. jaw teeth; **tn.** tooth notch; **ts**. tooth socket; **tu**. unerupted tooth.

4.5 Systematic Paleontology

Subclass Actinopterygii Cope, 1887

Division Halecostomi Regan, 1923

Order Amiiformes Hay, 1929

Superfamily Amioidea Bonaparte, 1838

Family Amiidae Bonaparte, 1838

Subfamily Vidalamiinae Grande and Bemis, 1998

Tribe Calamopleurini? Grande and Bemis, 1998

Genus *Calamopleurus*? Agassiz, 1841

Calamopleurus? sp. (Fig. 4.3.- Fig. 4.4)

Type Species. *Calamopleurus cylindricus* Agassiz, 1841:84, Early Cretaceous of Brazil.

Remarks. Based on the material recovered, only comprising jaw elements, the ability to compare morphology with known taxa is limited. However, those features which are present indicate that Calamopleurini? Shows the greatest morphological similarity and therefore the material is tentatively referred to this tribe.

Material. LRF3367 is an isolated left maxilla, broken into three pieces with four teeth (Fig 3A-D). LRF0028, an isolated right maxilla broken into two non-contiguous pieces bearing five teeth (Fig. 3E-H); LRF1469, an isolated anterior dermopalatine bearing three teeth and an incomplete autopalatine (Fig. 3I-K);. AM F.18593, is an isolated ectopterygoid, missing both the anterior and posterior portions although bearing three teeth (Fig. 3L-N). LRF0028 and LRF3367 were retrieved after processing through mining machinery and showed signs of mechanical abrasion. AM F.18593 and LRF1469 were collected directly from the mine face and the tooth apices retain their sharp points. All specimens are considered to represent one species and have been reconstructed as such in order to describe maxillary and dermopalatine features.

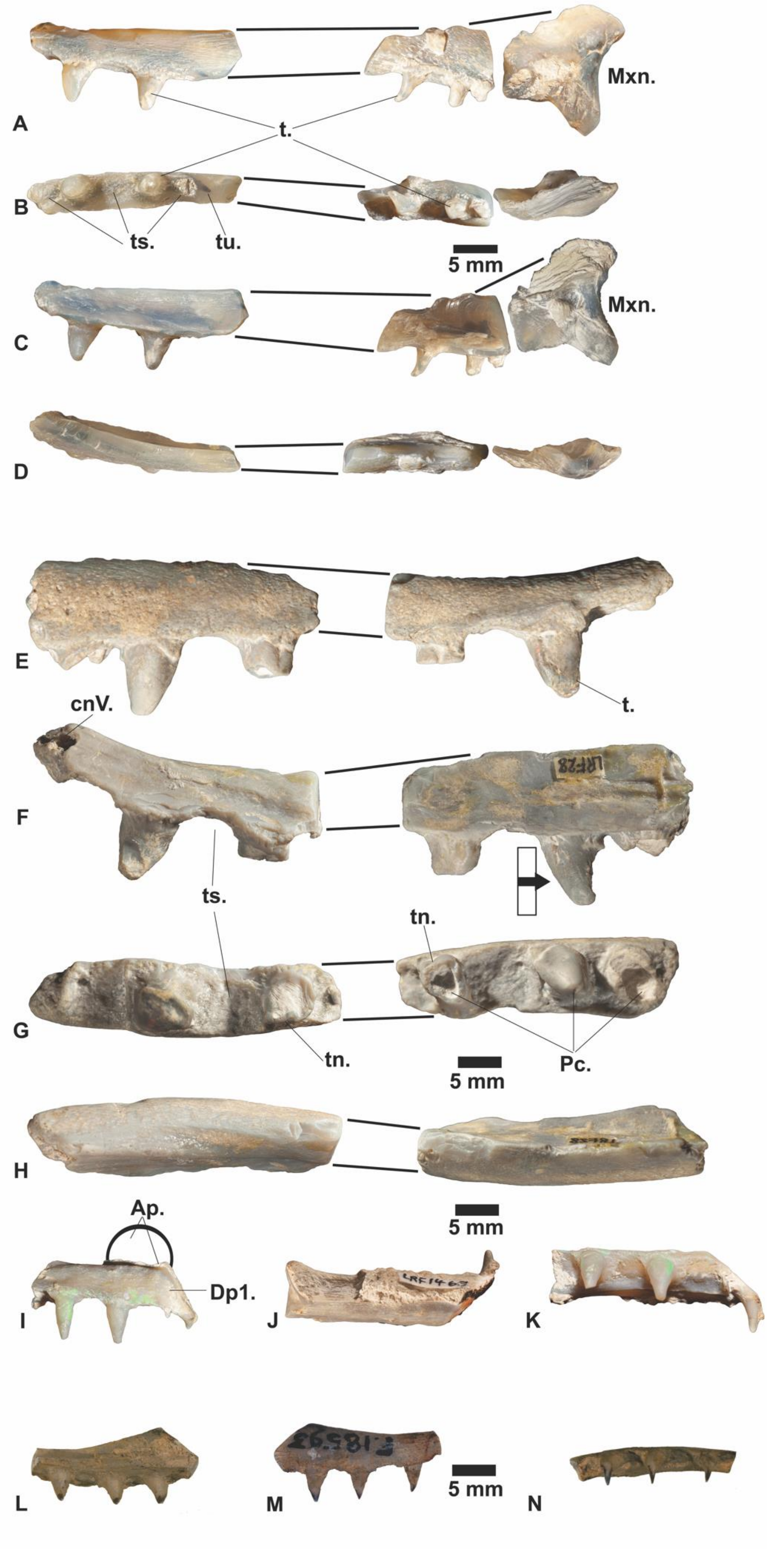

A
Mxn.
t.
B
ts.
tu.
5 mm
C
Mxn.
D
E
t.
cnV.
F
LRF28
ts.
tn.
G
tn.
Pc.
5 mm
H
Ap.
Dp1.
5 mm
I
J
LRF1463
K
L
M
5 mm
N

Fig. 4.3. Specimens referred to *Calamopleurus*? sp. LRF3367. A. Left maxilla, broken into three pieces with four teeth and one unerupted tooth, ~ 50mm in length, external view (labial); B. Occlusal view; C. Internal view (lingual); D. dorsal view. LRF0028. E. Right maxilla broken into two sections bearing 6 teeth (in various degrees of completeness), ~70mm in length, external view (labial); F. Internal view (lingual); Box with arrow indicate view presented in Fig. 4. G. Occlusal view; H. dorsal view. LRF1469. I. Anterior dermopalatine bearing three teeth and an incomplete autopalatine preserved as a single section, 22mm in length, internal view (lingual); J. Dorsal view; K. Occlusal view. AM F.18593. L. Left ectopterygoid bearing three teeth, ~19mm in length, internal view (lingual); M. Occlusal view; N. dorsal view. Scale bars 5 mm, different views of the same bone are scaled to the same scale as the scale bar. Lengths are given in mm for preserved bone only. Thick black lines represent the approximate contours of missing parts. Anatomical abbreviations: Ap. Autopalatine; cnV. maxillary branch of the cranial nerve V; Dp1. dermopalatine; Mx. maxilla; Mxn. maxillary notch; Pc. Pulp cavity; t. jaw teeth; tn. tooth notch; ts. tooth socket; tu. unerupted tooth. Photography by Robert A. Smith for images A-K.

4.6 Description

The maxilla is generally narrow and thin–rectangular in shape, tapers slightly anteriorly, is rounded in cross-section and has an attenuated and shallow anterior portion (LRF3367: Fig. 3A-D, LRF0028; Fig. 3E-H). The posterior portion of the maxilla has a mid-line, C-shaped postmaxillary notch with the maxilla expanded on either side of the notch (LRF3367; Fig 4.3A, C). The anterior articular process is not preserved on any of the specimens.

There are fine striations and vermiculation over the surface of the maxillary bone, sub-parallel to the long axis of the bone (Fig. 4.3E). Posteriorly there are large circular pores on the exterior (labial) surface which probably represent the site of vascular structures (LRF0028; Fig. 4.3E). A slight groove on the labial surface of the maxilla, located just above the tooth bases, extends the entire length of the bone (LRF0028; Fig. 4.3E). Anteriorly in the maxilla, at the end of the bone, is a 2mm foramen for the maxillary branch of the cranial nerve V (LRF0028; Fig. 4.3F).

Teeth form a single row, teeth are unequal sizes with the two anterior teeth equal in size and the last two posterior teeth reduced in size, have rounded apices and wide, collared ovoid bases (LRF0028) and where teeth are complete the tips have an acrodin cap (Fig. 4.4.). The teeth are recurved. In cross-section, the teeth are oval to circular in shape, and some have a V-shaped notch on one side (LRF0028; Fig. 4.3G). The pulp canal can be determined in teeth that are broken (LRF0028) and is large and hollow towards the base of the teeth and becomes narrower towards the tooth tip.

There are tooth sockets between the preserved teeth, and these are deep and concave, giving the maxilla a scalloped outline (LRF0028; Fig. 4.3E). When LRF3367 is viewed in transmitted light, an unerupted tooth is visible inside the translucent opal (Fig. 4.3B).

The anterior portion of a left dermopalatine (LRF1469; Fig. 4.3I-K) is rectangular in shape, tapers anteriorly and bears three teeth, although due to the bone being incomplete, more teeth may have been present in life (LRF1469). Dorsally there is a flat broken piece of bone that corresponds to a fragment of an adjacent bone, either the autopalatine or endopterygoid (Fig. 4.3I).

The left ectopterygoid (AM F.18593; Fig. 4.3L-N):

The mid-section of the ectopterygoid is elongate and narrow, expands posteriorly and tapers anteriorly, and is t-shaped in cross-section (Fig. 4.4B). There are deep striations, vermiculation, and small circular depressions on the internal surface. There are four tooth sockets and three preserved teeth (Fig. 4.3L-N) along a single row. The sockets are deep and concave, giving the ectopterygoid a scalloped outline (Fig. 4.3M). Along the length of the bone, above the teeth, there is a gutter as presented in Grande and Bemis (1998) Figure 304. The teeth are conical, recurved and slightly elongated at the apex, with acrodin caps and sharp pointed tips (Fig. 4.4B). At the tooth base, deep troughs, which extend and taper approximately 1/3 the way up the tooth surface producing a scalloped margin where they flare at the point they connect with the tooth base. Teeth lack carinae.

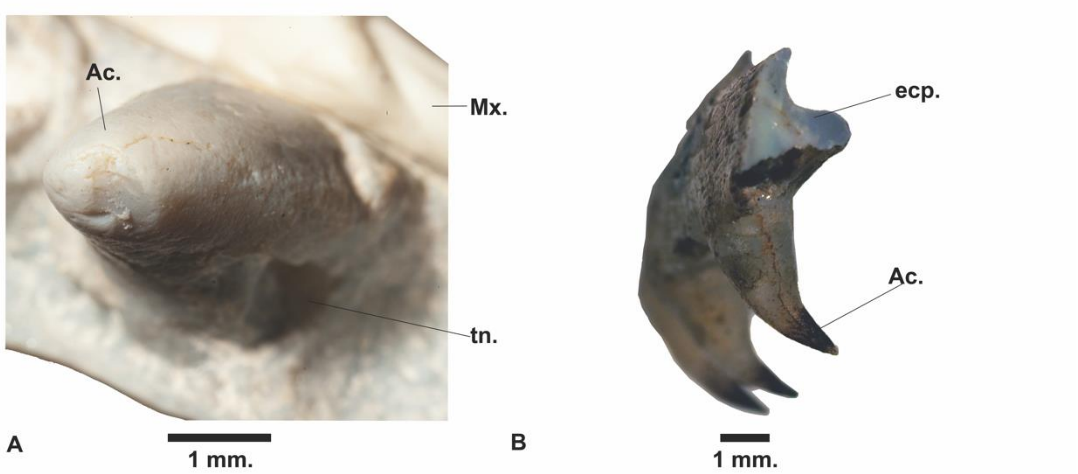


Fig. 4.4. A. LRF0028. Oblique dorso-posterior view of maxillary tooth. Scale = 1. B. AM F.18593. Oblique dorso-posterior view of ectopterygoid tooth. Scale = 1 mm.

Anatomical abbreviations: Ac. Acrodin cap; ecp. ectopterygoid; Mx. maxilla; tn. tooth notch. Photography by Robert A. Smith for image A.

4.6 Taxonomy

Although no individual bone is complete, there are enough isolated pieces to reconstruct a complete maxilla. The studied material shows characters typical of halecomorphs, such as a large pulp cavity, teeth in a single row with acrodin caps, and the posterior end of the maxilla expanded with a mid-line notch.

The outline of the maxilla of halecomorphs varies among members of this clade (Grande and Bemis, 1998: fig. 243). In the Caturidae the maxilla is very long and thin for its whole length: although in some species there can be a slight posterior expansion (Lambers, 1994), while in *Amia* and *Cyclurus* the maxilla is more complex, being triangular and widest posteriorly. In the Vidalamiinae the anterior portion of the maxilla is long and thin, expanded posteriorly with a 'C' shaped mid-line posterior notch. The depth of the notch and angles between the bone on either side of the notch varies between halecomorphs (Fig. 4.5 and Table 4.1). In the basal member of the halecomorphs, *Watsonulus eugnathoides* the notch is very shallow and is positioned medially within the maxilla. The bone on either side of the notch in *Watsonulus eugnathoides* is angled at 135°. Within members of the Calamopleurini the notch is gentle (Fig. 4.5 and Table 4.1), and 'C' shaped forming an angle of between 145° in *Calamopleurus*? sp. (Fig. 4.5A), 130 ° in *Calamopleurus africanus* (Fig. 4.5B) and 95° in *Calamopleurus cylindricus* (Fig. 4.5C). In other members of the Vidalamiinae particularly the Vidalamiini the notch is 'L' shaped being very open with a 50° angle between the bones appearing to form 2 separate rami of the maxilla (Fig. 4.5D.) In the extant halecomorph species *Amia calva* the notch is very sharp and incised forming a 'V' shape (with a 50^{o} angle) that is located ventrally on the maxilla (Fig.4.5E).

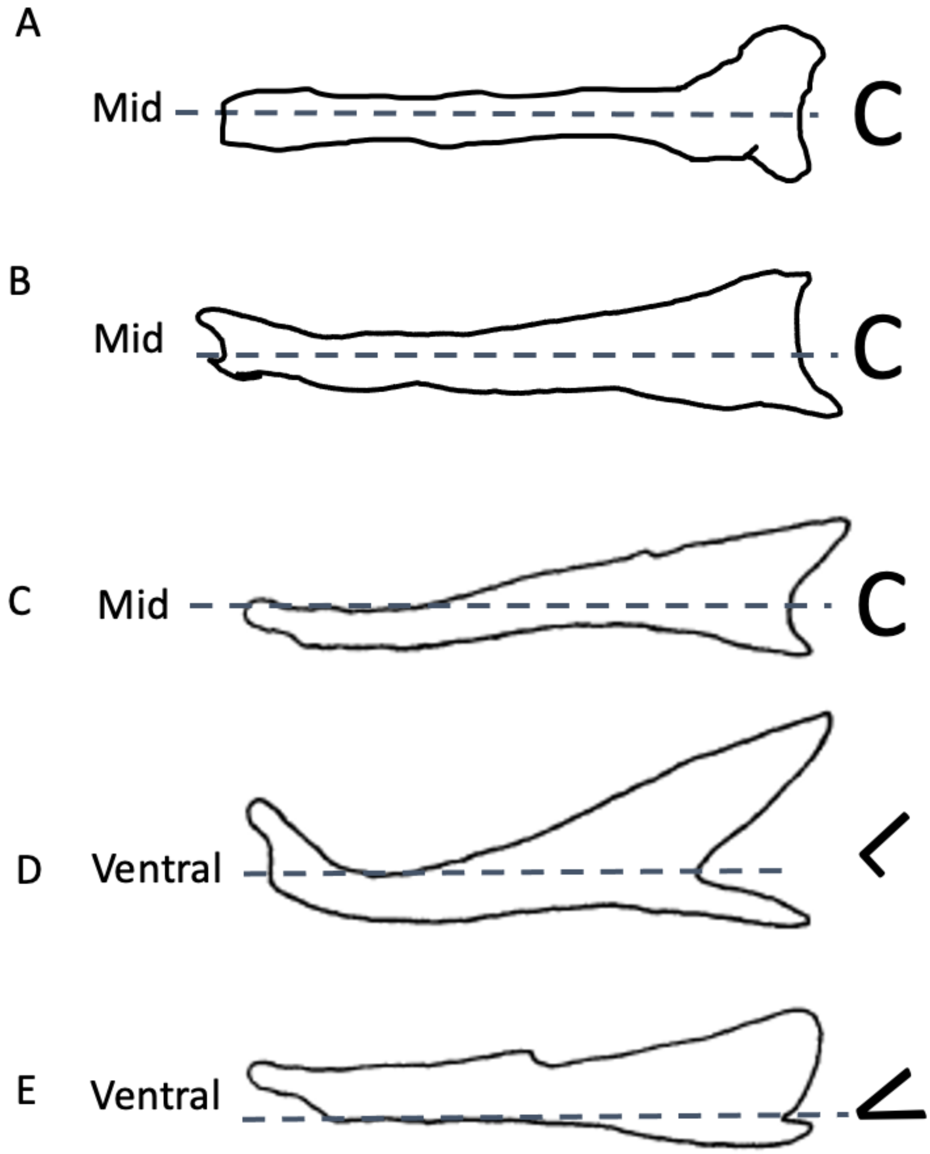


Fig. 4.5. Postmaxillary notch of the Vidalamiinae maxilla (A – C), A. *Calamopleurus*? Sp., B. *Calamopleurus africanus, C. Calamopleurus cylindricus*, D. *Pachyamia latimaxillaris*, and a halecormorph E. *Amia calva*. Outlines are not to scale. Lettering on the right-hand side of the postmaxillary notch indicates a description of shape in the text e.g., 'C' shaped and in (Table 1).

In LRF3367 the anterior portion of the maxilla is narrow and widens to form a deep posterior margin. There is a wide shallow notch on its posterior margin that is similar to some Vidalamiinae, such as *Calamopleurus* (Grande and Bemis, 1998), but also similar to some Sinamiidae, such as *Sinamia liaoningensis* (Zhang, 2012) or *Siamamia naga* (Cavin et al., 2007).

The lateral outline of the maxilla indicates that the present material more likely belongs to the Vidalamiinae. This subfamily comprises two tribes, the Calamopleurini and the Vidalamiini. The latter is characterized by a greatly enlarged maxillary notch, which gives the posterior part of the bone a unique shape among amiids (Grande and Bemis, 1998).

Maxilla or dentary teeth with carinae are present among halecomorphs in the Caturidae and Vidalamiinae, although the shape slightly varies between both clades (Grande and Bemis, 1998: 579). Furthermore, the maxillary teeth in *Calamopleurus* reduce in size posteriorly (Grande and Bemis, 1998).

The number of teeth along the maxilla increases in age within halecomorphs (Grande and Bemis, 1998), and therefore the number of teeth cannot be used for taxonomic purposes. The ontogeny of the Vidalamiinae is not very well understood, so the development and morphology of the maxilla and the posterior border notch between younger and older individuals is currently unknown, therefore using the angle and depth of the notch (Table 4.1) is not advised for determining species. One aspect of vidalamiines ontogeny, particularly in *Vidalamia catalunica* is that in juveniles, the dentary and maxillary teeth lack carinae, and the carinae develop in older (considered adult) fish (Grande and Bemis1998). This could account for differences observed between the teeth of different-sized specimens from the Griman Creek Formation.

Table 4.1. Comparison between the angles of the posterior maxilla notch of the Vidalamiinae.

Taxa	**Angle of notch (degrees)**	**Shape of notch**	**Location of notch**
Vidalamia catalunica	60	L shaped	ventral
Pachyamia latimaxillaris	60	L shaped	ventral
Pachyamia mexicana	60	L shaped	ventral
Calamopleurus cylindricus	95	C shaped	Entire (midline)
Calamopleurus africanus	130	Gently c shaped	Entire (midline)
Calamopleurus? sp.	145	Gently c shaped	Entire (midline)

Furthermore, the anterior left dermopalatine shows a single marginal tooth row whereby teeth are approximately all equal in size and lacking carinae. In *Amia* the anterior dermopalatine, or dermopalatine 1, frequently has a single row of sharply pointed teeth with a group of blunter teeth medially to the primary tooth row (Grande and Bemis, 1998). The dominant row of teeth (on the maxilla or dentary) increases in size anteriorly in *Amia* (Grande and Bemis, 1998). All other Amiidae have multiple tooth rows on the dermopalatine except for the Calamopleurini (Grande and Bemis, 1998).

We provisionally refer this material to *Calamopleurus?* based on the above features. *Calamopleurus* is currently the only known genus of this tribe in the Cretaceous.

4.7 Discussion

Based on the current fossil records, the Amiiformes originated in the Early Jurassic seas in what is now western-central Europe (Martín-Abad and Poyato-Ariza, 2013). These marine fishes are restricted by the configuration of the continental landmasses and remain in the northern hemisphere, at least until the Late Jurassic. The distribution pattern of the Amiiformes throughout the Cretaceous is also restricted to shallow marine environments. Deep marine oceans and the location of continental landmasses restricted their distribution (Martín-Abad and Poyato-Ariza, 2013).

The Vidalamiinae (which include *Calamopleurus*? sp.) are the only amiid subfamily known from Gondwana (Grande and Bemis, 1999). The Vidalamiinae shows the strongest vicariant pattern among the amiidae (Grande and Bemis, 1999) as further evident in this study. The Vidalamiinae is split into two tribes: a generally northern hemisphere tribe and a southern hemisphere tribe, both restricted to shallow marine continental shelf environments. They are separated from each other by the equator and the configuration of the supercontinents restricting dispersal. This is currently the only amiid fish known from the fossil deposits of Australia. Potential for older occurrences of amiid fishes in Australia is not thought possible, due to deep ocean basins and continental land masses restricting their dispersal (within the Northern Hemisphere) any earlier than the Late Cretaceous because of the split of South America and Africa to form the Proto – Atlantic Ocean creating dispersal routes southwards. By the time amiid fishes did reach Australia, the group was already in decline.

Previously confirmed occurrences of *Calamopleurus* are restricted to the type species *Calamopleurus cylindricus* Agassiz, (1841) in the Aptian–Albian of north-eastern Brazil, *Calamopleurus mawsoni* from Lower Cretaceous Ilhas Formation of the

Bahia Supergroup, Brazil, and the Albian – Cenomanian *Calamopleurus africanus* (Forey and Grande, 1998) of Morocco. Although the age of 100.2 — 96.6 Ma falls within the currently known temporal range for *Calamopleurus*, this description represents the first occurrence in east Gondwana. Based on the occurrence of the type species, *Calamopleurus* was probably euryhaline as the paleoenvironment of *C. cylindricus* (Santana Formation, Brazil) varied from lacustrine to lagoonal (Maisey, 1994). *C. mawsoni* is known only from the freshwater Ilhas Formation, Brazil, (Grande and Bemis, 1998) and *C. africanus* from the freshwater fluvial environments of the Kem Kem Group, Morocco (Cavin et al., 2015) (Fig. 6).

The Australian Mesozoic fish record currently indicates that Australia has a large number of endemic species. However, recent studies are showing an increasing representation of taxa from Proto-Atlantic localities (Berrell et al., 2014, 2020). Currently, the majority of the fish from the Griman Creek Formation are not described or identified. This has limited our ability to fully ascertain if there are any links between other Gondwanan localities. The Winton Formation, located further to the north of the Griman Creek Formation and considered coeval, does contain *Cladocyclus geddesi* – an ichthyodectiform fish resolved as the sister taxon to the Brazilian taxa *Cladocyclus gardneri* (Berrell et al., 2014). Despite *Cladocyclus* not currently being recognised from the Griman Creek Formation, the distribution pattern at the generic level repeats that of *Calamopleurus*, showing greater connectivity than the Australian fossil record suggests.

Berrell et al. (2014) proposed two dispersal scenarios to explain the presence of *Cladocyclus geddesi* within the Winton Formation of central-western Queensland, Australia, presented again here to explain the presence of *Calamopleurus?* in the Cretaceous of Australia.

The first scenario suggested that at least some freshwater fish taxa were widespread throughout Gondwana in freshwater environments prior to its eventual breakup. Maisey (2000) put forward a similar hypothesis, where freshwater cladocyclids existed in small, interconnected rift lakes (Crato Formation) between South America and Africa prior to the development of an equatorial seaway resulting from the breakup of South America and Africa (Maisey, 2000; Berrell et al., 2014). The biogeography of the Australian Cretaceous dinosaur fauna also shows strong connections with the South American dinosaur fauna and those of other Gondwanan continents with connections via South America (Kubo, 2020; Poropat et al., 2016) and at least in some part, the same scenario can be seen for the fishes.

The second scenario put forward by Berrell et al., (2014) involved the marine dispersal of fish taxa along the coastlines of the fragmenting continents of Gondwana potentially aided by marine currents with subsequent invasion of estuarial–freshwater environments. In this scenario, the currents that developed as a result of Africa and South America splitting and forming the proto-Atlantic would have aided in fish dispersion throughout eastern Gondwana via shallow seas and their currents drawing from the equatorial regions in a southern direction (Luyendyk et al., 1972) to the south pole with fauna potentially restricted to continental shelf environments (Fig. 4.6).

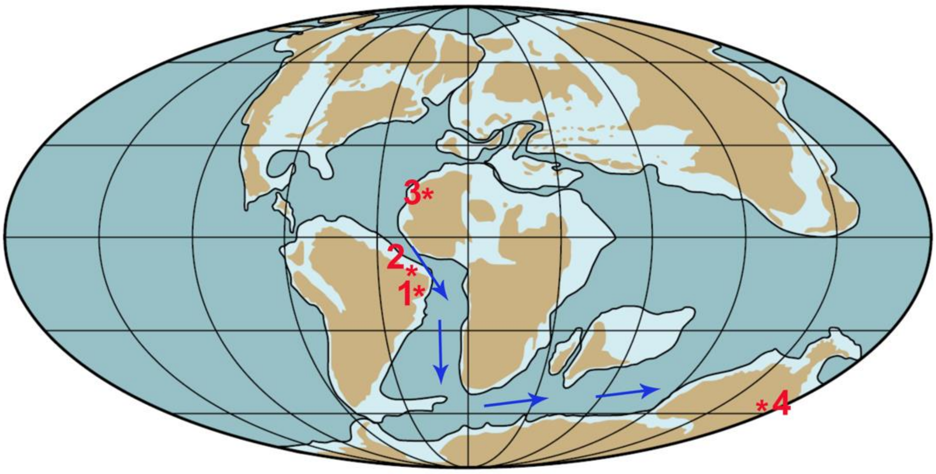


Fig. 4.6. Cenomanian (~94 Ma) paleographic world map showing localities that have produced *Calamopleurus* (map after Scotese, 2002, da Silva and Gallo, 2007 and Hey, 2009).

Abbreviations 1. Ilhas Formation, Brazil (Neocomian) *Calamopleurus mawsoni;* 2. Santana Formation, Brazil (Albian – Cenomanian) *Calamopleurus cylindricus*; 3. Kem Kem Beds, Morocco (Cenomanian ~ 94 Ma) *Calamopleurus africanus*; 4. Griman Creek Formation, New South Wales Australia (Cenomanian – Turonian 100.2 – 96 Ma) *Calamopleurus*? sp. Blue arrows represent possible colonizing routes, taking into account oceanic circulation in the 'mid'-Cretaceous (Luyendyk et al. (1972) analogue model and analogy with modern ocean circulation (after Roth, 1986). Note not all currents are shown, only those considered as a potential colonizing route. Arrows represent direction only and not the velocity of currents or speed of colonizing. Grids are in latitude and longitude.

We favour the marine dispersal scenario as Africa and South America split because the large, laminated limestones equivalent to the Crato Formation (lacustrine lakes) are not found extending south along the proto-coast lines of Mesozoic Africa and South America. Furthermore, fish faunas are distinct enough between regions and time zones in Gondwana, that a single cosmopolitan fauna did not exist.

The discovery of *Calamopleurus?* within the Griman Creek Formation at Lightning Ridge NSW, Australia also further supports faunal interchange between west and east Gondwana and indicates that this fish could tolerate conditions associated with high palaeolatitudes, with Lightning Ridge placed at palaeolatitude of ~60°S (Bell et al., 2019).

4.8 Conclusions

The described material represents the first record of amiid fishes from the Early-Late Cretaceous of Eastern Gondwana (Australia, New Zealand, Antarctica and Papua New Guinea) and is the youngest occurrence of the Calamopleurini within Gondwana. The designation of these fossils extends both the paleogeographic distribution and time range of amiid fishes in Gondwana and provides evidence of a previously unrecognized vicariant event. These fossils increase the known fish diversity from the Griman Creek Formation, which until now, consisted of three species of lungfish (*Metaceratodus wollastoni, Ceratodus diutinus* and *Neoceratodus potkooroki*), and undetermined lamniformes and Chimaeriformes (Bell et al., 2019; Berrell et al, 2020 Table 1). The specimens from the Griman Creek Formation of Lightning Ridge indicate that the Calamopleurini? were widespread constituents of Gondwana, particularly South America, Africa, and now Australia. The presence of the Calamopleurini potentially on three continents indicates that marine dispersal is an important biogeographical mechanism for this genus.

The fragmentary nature of the specimens precludes a definitive referral to a species but can be assigned to the tribe Calamopleurini? on the basis of an enlarged pulp cavity (hollow teeth), acrodin caps with carinate (for maxillary teeth, condition absent on dermopalatine teeth), constricted waist and rounded tooth base and a mid-maxillary notch.

4.9 Declaration and competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Chapter 5. Revision of *Dugaldia emmilta* (Teleostei, Ichthyodectiformes) from the Toolebuc Formation, Albian of Australia, with comments on the jaw mechanics

Part of the study presented in Chapter 5 was accepted in the peer-reviewed journal '*Journal of Vertebrate Paleontology*' on the 28th of May 2019 and presented at the Society for Vertebrate Paleontology conference on the 5-8th November 2014.

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5.1 Abstract

Dugaldia emmilta is a teleostean fish found in the late Albian Toolebuc Formation in Queensland, Australia. In the original description, *D. emmilta* was attributed to the Neoteleostei because of the presence of a tripartite occipital condyle, and the species was postulated to have a basal position among neoteleosteans because of the presence of several plesiomorphic characters. A re-examination of the holotype, together with the description of two new specimens, indicates that *D. emmilta* is an ichthyodectiform fish. A phylogenetic analysis resolves this species as the sister to *Ogunichthys* + Ichthyodectoidei. This species shows unusual features for an ichthyodectiform, in particular the shape of the mandible and the arrangement of the teeth on the lower jaw. Jaw mechanics in ichthyodectiforms are peculiar because they allow a significant lateral enlargement. In *Dugaldia*, a similar disposition is present but is exaggerated by specific features of the maxilla and the mandible. Comparisons with the sarcastic fringehead (*Neoclinus blanchardi*), a living blenny that shows a 'gaping display,' reveal that *Dugaldia* was likely able to exhibit extreme lateral mouth enlargement.

5.2 Introduction

Ichthyodectiformes are an extinct clade of basal teleosts discovered in dominantly marine and, to a lesser extent, freshwater deposits from all continents, in strata of Middle Jurassic to Late Cretaceous age (Patterson and Rosen, 1977; Cavin et al., 2013; Kim et al., 2014). The group contains at least 20 genera and about double that number of species.

The current Australian record of Ichthyodectiformes is restricted to the Early Cretaceous marine-brackish deposits of the Eromanga Basin of central west and northwest Queensland (Figure 5.1.). *Cooyoo australis* is arguably Australia's best-known ichthyodectiform and is found in both the Toolebuc Formation and the Allaru Mudstone in northwest Queensland (Lees and Bartholomai, 1987). The other ichthyodectiform known from the Eromanga Basin is *Cladocyclus geddesi* from the upper Albian portion of the Winton Formation, central-western Queensland (Berrell et al., 2014).

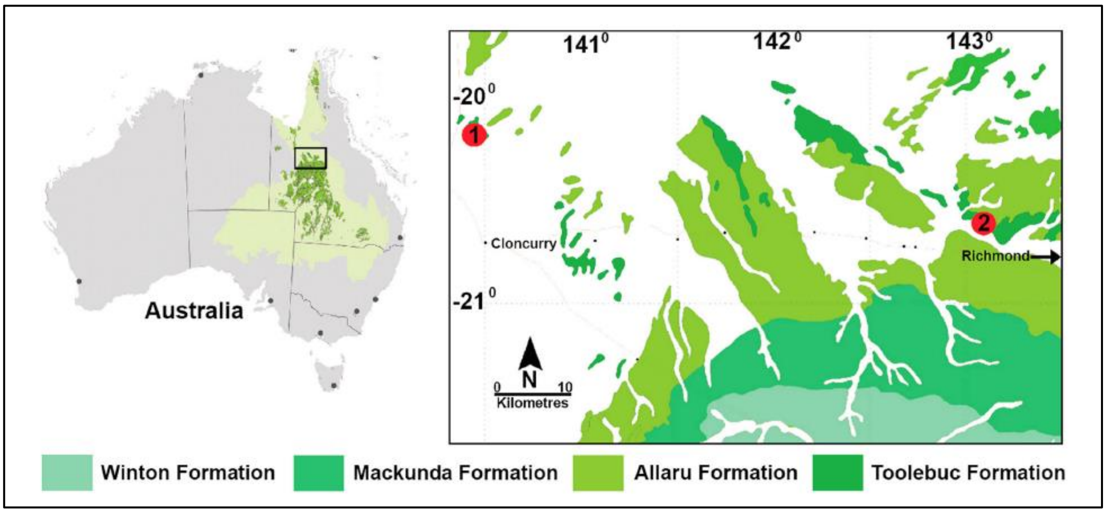

Figure 5.1. Map showing the discovery sites of *Dugaldia emmilta*. The holotype GSQ 9242 was discovered near the town of Cloncurry northwest Queensland, and the referred specimens KKF714 and KKF715 were discovered near the town of Richmond, northwest Queensland, Australia.

Here, we revise the fish *Dugaldia emmilta* from the Lower Cretaceous Toolebuc Formation of Cloncurry and describe new specimens discovered from the same formation near Richmond, Queensland, Australia. A combination of features, including teeth within a single series in the jaw, well-developed coronoid process, and an ethmopalatine, supports the placement of this fish within Ichthyodectiformes, and not as a basal neoteleost as suggested in the original study (Lees, 1990).

5.3 Geological setting

The Toolebuc Formation is a relatively thin unit (~65 m at its thickest point) that comprises a beige- to cream-colored unit containing calcareous, carbonaceous mudstone with abundant coquinite formed dominantly by the bivalve *Inoceramus sutherlandi* McCoy and *Aucellina hughendenensis* Etheridge, interbedded with bituminous shale and minor labile sandstone; in part the unit contains nodular limestone (Henderson, 2004; Cook et al., 2013). The unit crops out in a broad arc that stretches from Hughenden in the east through to Cloncurry in the west and to Boulia in the southwest of northwest and central-western Queensland, Australia (Cook et al., 2013) (Figure 5.1.).

The Toolebuc Formation is part of the stratigraphic package known as the Rolling Downs Group (Figure 5.2.), which consists of conformable strata that date from the upper Aptian to the early Turonian (Gray et al., 2002; Tucker et al., 2013), corresponding to the *Coptospora paradoxa* spore-pollen zone and the *Pseudoceratium ludbrookiae* dinoflagellate zone (McMinn and Burger, 1986; Moore et al., 1986).

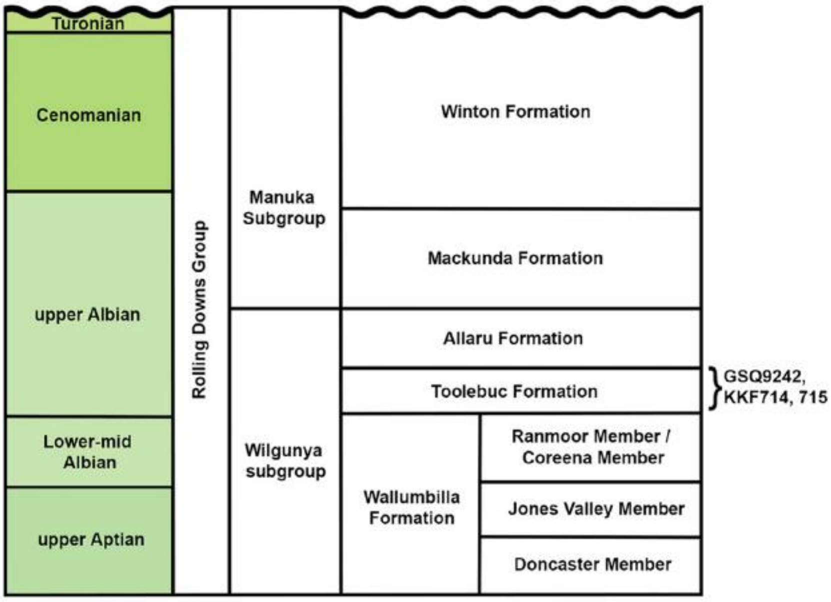

Figure 5.2. Stratigraphy of the Rolling Downs Group of the Eromanga Basin, Queensland, after Gray et al. (2002) and Tucker et al. (2013). *Dugaldia emmilta* (GSQ 9242, KKF714, and KKF715) comes from the Toolebuc Formation, late Albian in age.

The Rolling Downs Group contains a record of extensive marine inundation during a time when approximately 60% of Australia’s current land surface was covered by shallow seas (Frakes et al., 1987; Campbell and Haig, 1999). The geological units basal to the Toolebuc Formation represent a transgressive phase with maximum flooding occurring at the deposition of the Toolebuc (Campbell and Haig, 1999). The depositional environment for the Toolebuc was considered to be below wave base and beyond the reach of wind-generated currents because of a lack of ripple marks and rare local alignment of *Inoceramus* shell prisms (Henderson, 2004). This lack of disturbance of the sea floor and apparent anoxia may explain the completeness and preservation of fossil vertebrate specimens from the Toolebuc Formation.

Vertebrate fossils found within the Toolebuc Formation include a titanosauriform sauropod (QM F6142) (Poropat et al., 2017); pterodactyloid pterosaurs (Kellner et al., 2010); marine reptiles, including the ichthyosaur *Platypterygius australis* (Kear, 2016), the plesiosaurs *Eromangasaurus carinognathus* and *Kronosaurus queenslandicus* (Longman, 1930; Kear, 2005); and protostegid turtles *Bouliachelys suteri*, *Notochelone costata*, and *Cratochelone berneyi* (Owen, 1882; Longman, 1915; Kear and Lee, 2006). The formation also preserves a diverse chondrichthyan (Kemp, 1991) and osteichthyan fish fauna comprising a pachycormiform (Kear, 2007), an aspidorhynchid (Bartholomai, 2004), two pachyrhizodontids (Bartholomai, 1969, 2012), several probable elopomorphs (Bartholomai, 2010a, 2010b), a possible ionoscopiform (Bartholomai, 2015), an ichthyodectiform (Lees and Bartholomai, 1987), and undescribed aulopiforms.

5.4 Material and methods

Institutional abbreviations: GSQ, Geological Survey of Queensland (specimens now housed at The Queensland Museum), Hendra, Brisbane, Queensland, Australia; KKF, Kronosaurus Korner, Richmond, Queensland, Australia; QM, The Queensland Museum, Brisbane, Queensland, Australia.

Preparation of Material: Specimen KKF714 was discovered ca. 12 km northwest of the township of Richmond, Queensland, Australia, on August 1, 2008 (Michelle Johnston, pers. comm.). The specimen was found exposed at surface in fossil collecting quarry number 1 and has had minimal preparation. Localized mud and fragments of coquina were removed from the specimen with the use of needles and pins with the matrix moistened with water (Michelle Johnston, pers. comm.). Specimen KKF715 was found at the same locality by Karen Corkill on June 1, 2015, and had a similar preparation as described for KKF714.

Comparative Material Examined: *Cooyoo australis* Lees and Bartholomai, 1987: QM F12711, QMF12327, QMF6346, complete skulls and associated vertebrae from the Allaru Mudstone, Hughenden area, north-central Queensland, Australia.

5.5 Systematic Palaeontology

Teleostei Müller, 1845

Ichthyodectiformes, Bardack and Sprinkle, 1969

Dugaldia emmita Lees, 1990

Emended Diagnosis - Ichthyodectiform with a proportionally large head, contained 3.2 times in standard length; saber-shaped edentulous maxilla; mandible with few recurved teeth at its anterior extremity, with a series of horizontally held teeth on the anterior margin of the well-developed coronoid process; ca. 57 vertebrae, 33 abdominal and 24 caudal.

Stratigraphic and Geographic Range - Toolebuc Formation, Upper Cretaceous, late Albian of Australia.

Holotype - GSQ 9242, partially disarticulated skull and 11 associated vertebrae.

Type Locality – The specimen was discovered from the Dugald River, Granada Station, north of Cloncurry, northwest Queensland.

Type Horizon – Toolebuc Formation, Rolling Downs Group, Lower Cretaceous (late Albian), Eromanga Basin, Queensland, Australia.

Referred Specimens - KKF714, a disarticulated skeleton; KKF715, a complete skeleton. Both specimens are from fossil collecting quarry number 1 (ca. 20°38′49.7″S, 143°05′57.8″E), near Richmond, northwest Queensland, Australia.

5.6 Description

In the following description, we sum up the descriptive parts of the osteology of *Dugaldia emmilta* (GSQ 9242) that have been described by Lees (1990) and for which no further comments are needed. We focus the description on anatomical structures that were not available during the original study and/or on characters of particular systematic value.

The single complete specimen (KKF715) measures 512 mm of standard length and 625 mm of total length. The head length is comprised 3.2× the standard length, which makes it the ichthyodectiform with the proportionally largest head (generally 4× or more, except *Mesoclupea* with 3.9× [Chang, 1963], and up to 7× in *Ichthyodectes* [Bardack, 1965]).

Braincase - As described by Lees, the skull roof (Figs. 5.3–5.8) is formed by large, paired frontals, almost as wide anteriorly as posteriorly, that are sutured to a wide and short rostrodermethmoid anteriorly. Specimen KKF714 shows a well-developed arched ridge on the frontal (Fig. 5.7) corresponding to the path of the supraorbital sensory canal. Posterolaterally, the frontal is sutured to the autosphenotic at the level of the posterior margin of the orbit and forms the anterior portion of a spine. More posteriorly, the frontal sutures with the pterotic. The posterior part of the skull roof is poorly preserved on the holotype and, unfortunately, also on the other available specimens. Lees (1990) was uncertain about the parietal pattern, but they favoured a medioparietal condition (contact between both parietals) and even figured an unpaired parietal in their reconstruction (Lees, 1990: fig. 5b), which is the condition found in derived ichthyodectiforms. We also observe an unpaired ossification posterior to the frontals (Fig. 5.8A), but it is unclear whether this bone is an anterior extension of the supraoccipital, in which case the skull roof would have been lateroparietal and the median extension of the pterotic figured by Lees would correspond to the parietal, or whether the unpaired bone corresponds to fused parietals, as in Lees's (1990) reconstruction. Specimen KKF715 shows a poorly preserved piece of the supraoccipital and a small bone located anterolaterally with unprecise margin, which likely corresponds to the parietal (Fig. 5.6). We consider the arrangement of this posterior part of the skull roof as uncertain for the moment and coded this feature as unknown in our phylogenetic analysis.

In posterior view (Fig. 5.5C, D), the supraoccipital is squarish in shape and bears the base of a supraoccipital crest along the posterior face, but its total expansion, in particular its dorsal development on the skull roof, is unknown. Based on what is still present, the crest was certainly not very large. The pterotic and autosphenotic, as visible on the holotype and on KKF715, correspond to the description made by Lees (1990), i.e., a large, striated pterotic extending posteriorly as a spine and forming the lateral wall of the posttemporal fossa and an autosphenotic forming a ventrolaterally oriented well-developed spine. Both ossifications are dug by an elongated and uniformly wide articular facet for the hyomandibular. The only difference we noticed with Lees's figure 4 in this region is a slightly more posterior extension of the autosphenotic at the level of the articular facet. The epioccipitals are large bones forming the posterolateral corner of the skull roof, with an articular surface for the posttemporal. Although this part of the skull roof is poorly preserved in all specimens, it is unlikely that well-developed crests were present on the epioccipitals. The posterior face of the epioccipital is large. Laterally the bone forms the medial wall and dorsally the roof of the posttemporal fossa (Fig. 5.5C, D). The intercalar is large and extends as a posterolaterally blunt spine. The exact shape of this bone is difficult to reconstruct, but it appears, as Lees's reconstruction shows (1990: fig. 6b), that it forms a groove together with the pterotic. The groove probably accommodated the jugular vein, and possibly also cranial nerves IX and X, because no separate foramina are visible on the exoccipital. The basioccipital participates in the ventral part of the occipital condyle and prevents the parasphenoid from reaching the posterior margin of the braincase. The exoccipitals are large, paired bones that meet above the foramen magnum and probably also below the foramen magnum, although this area is difficult to observe. The left exoccipital shows a process located on the ventrolateral corner of the foramen magnum, which articulates with the first vertebral centrum. On the holotype, the prootic is separated by a gap from the parasphenoid because the bone has shifted (Fig. 5.3). As described by Lees (1990), the basisphenoid is visible as a vertical shaft of bone. It is close to the ascending process of the parasphenoid because it has shifted from its original median position separating the posterior myodome. The parasphenoid was described in detail by Lees (1990): its main feature is that the bone does not posteriorly reach the occipital condyle. It is edentulous, a large foramen for the internal carotid opens at the level of the well-developed ascending process, and in lateral view the bone forms an angle of ca. 120 at the level of the ascending process (Fig. 5.3). An important character that can be added is the absence of a basipterygoid process. Anterior to the parasphenoid is the vomer (Fig. 5.5A, B), which bears paired tooth patches separated medially by a ridge. Each patch bears a lateral row of five proportionally large, recurved teeth and a medial row of four smaller teeth. The ethmoid massif is visible on both sides of the holotype (Fig. 5.5A, B). Our interpretation of the ossification forming this complex differs from Lees's (1990) interpretation. This difference rests on the fact that she regarded *Dugaldia* as a neoteleosts, whereas we consider it to be an ichthyodectiform (see below).

More specifically, Lees (1990) suggested, based on comparison with the ethmoid of neoteleosts, that a large mesethmoid forms the anterior part of the complex wedged between a dorsal rostrodermethmoid and a ventral vomer. The latter anteriorly shows an articular facet for articulation with the head of the maxilla and premaxilla, and a posterior wing, which forms with the 'lateral rostrodermethmoid' (here: lateral ethmoid) an articular facet for the palatine. We here consider that the structure is more like the ethmoid complex of ichthyodectiforms. Consequently, we identify the main ventral part of the ethmoid massif as the ethmopalatine, a neoformation found in ichthyodectiforms (Patterson and Rosen, 1977). Although the exact limit of this bone is difficult to detect, it seems posteriorly to form most of the articular facet for the palatine, with a possible participation of the lateral ethmoid, and anteriorly most of the articular facet for the maxilla, with a probable participation of the vomer and possibly of the rostrodermethmoid. This deep socket for the maxilla allowed wide range of movement of the maxilla (see below). Furthermore, the vomer anteriorly bears a small articular surface for the articulation with the premaxilla.

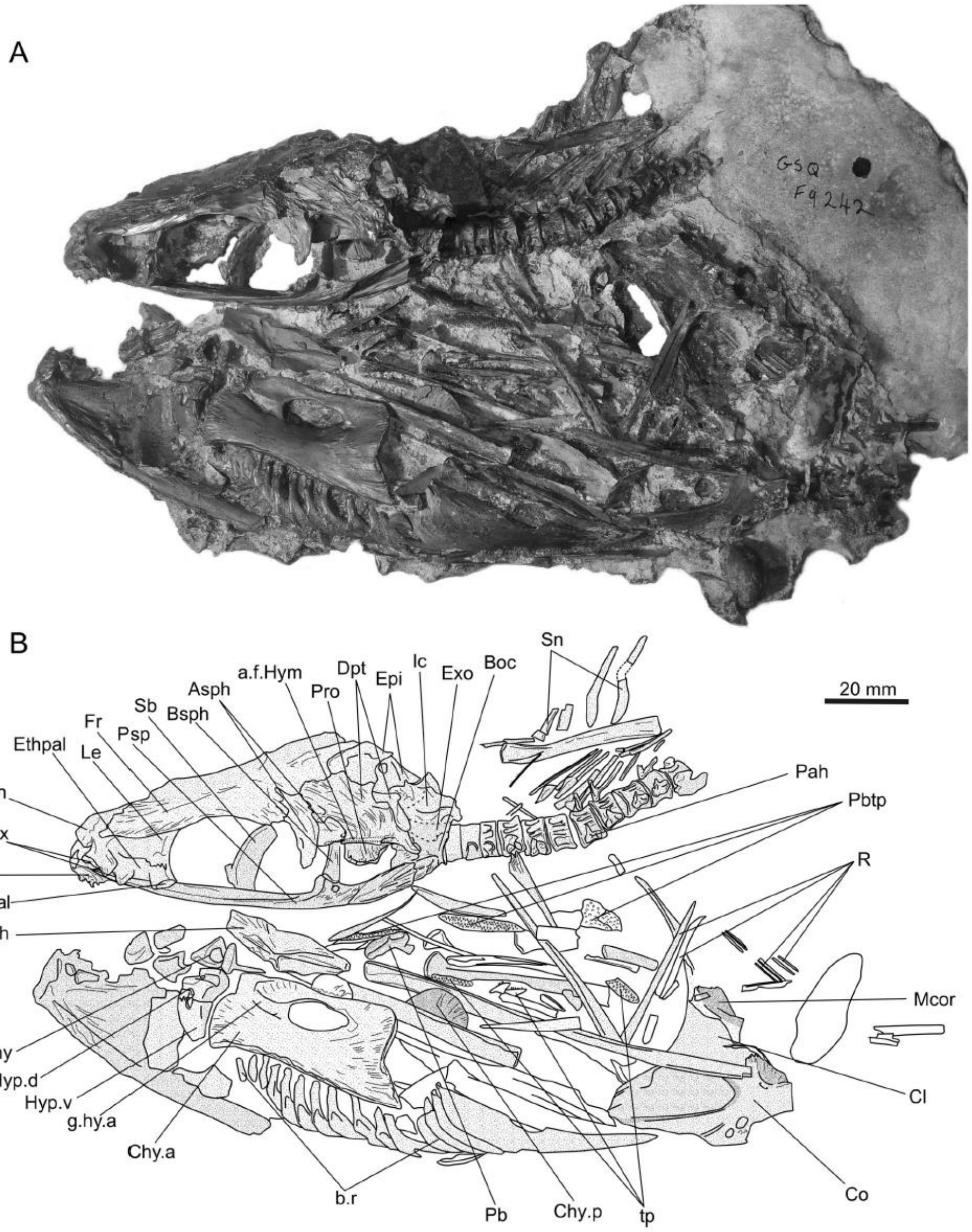

Figure 5.3. *Dugaldia emmilta*, holotype (GSQ 9242). A, photograph and B, interpretive line drawing in left lateral view. Abbreviations: a.f.Hm, articular facet for the hyomandibula; a.f.Mx, articular facet for the maxilla; a.f.Pal, articular facet

for the autopalatine; Asph, autosphenotic; Bhy, basihyal; Boc, basioccipital; b.r, branchiostegal ray; Bsph, basisphenoid; Chy.a, ceratohyal anterior; Chy.p, ceratohyal posterior; Cl, cleithrum; Co, Coracoid; Deth, dermethmoid; Dpt, dermopterotic; Dsph, dermosphenotic; Epi, epioccipital; Ethpal, ethmopalatine; Exo, exoccipital; Fr, frontal; g.hy.a, groove for the hyoid artery; Hyp.d, hypohyal dorsal; Hyp.v, hypohyal ventral; Ic, intercalar; Le, lateral ethmoid; Mcor, mesocoracoid; Pah, parapophysis; Pb, pharyngobranchial; Pbtp, pharyngobranchial tooth plate; Pro, prootic; Psp, parasphenoid; R, rib; Sb, sclerotic bone; Sn, supraneural; tp, tooth plate; V, vomer.

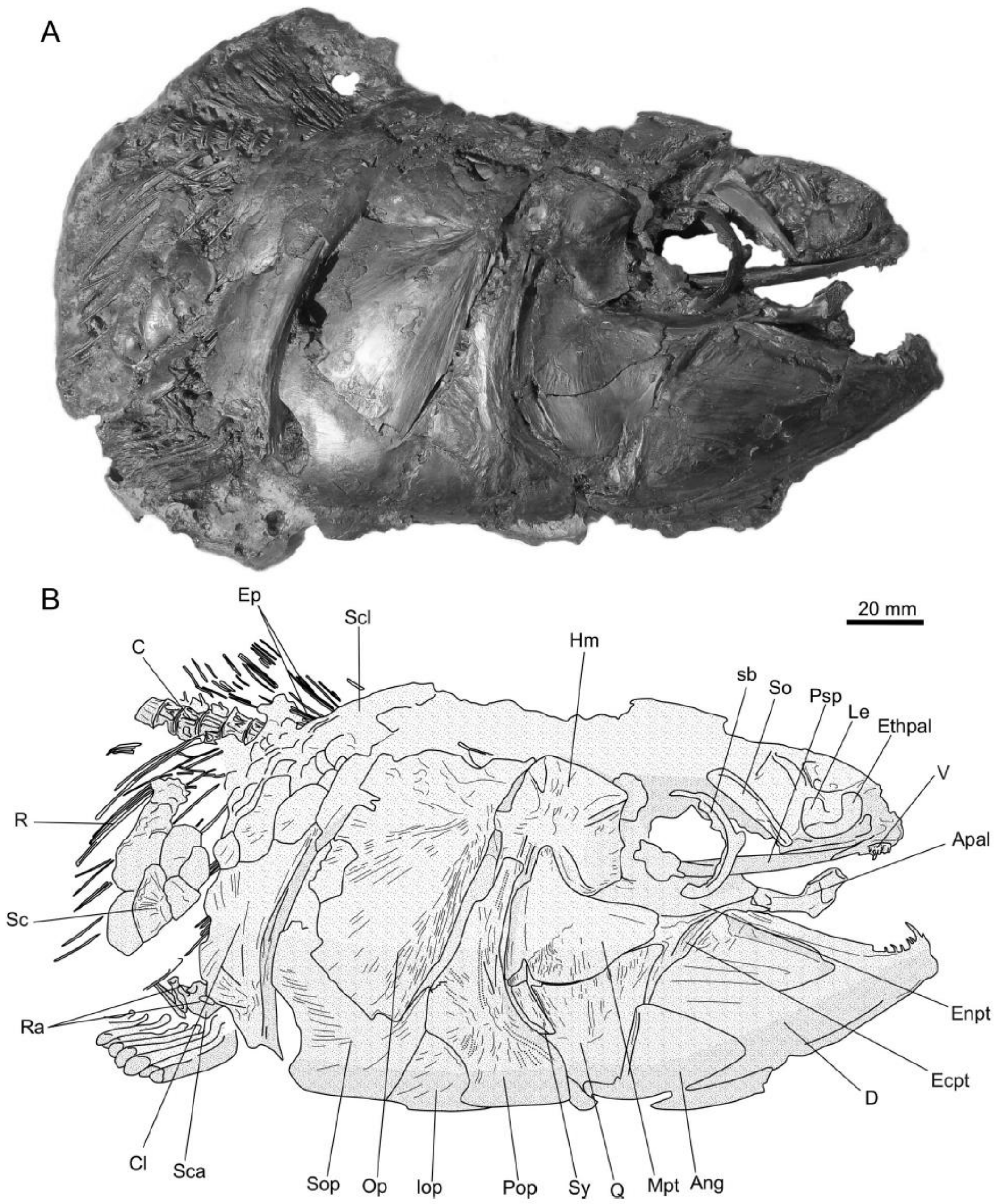

Figure 5.4. *Dugaldia emmilta*, holotype (GSQ 9242). A, photograph and B, interpretive line drawing in right lateral view. Abbreviations: Ang, angular, Apal, autopalatine; C, centrum; Cl, cleithrum; D, dentary; Ecpt, ectopterygoid; Enpt, entopterygoid; Ep, epineural; Ethpal, ethmopalatine; Hm, hyomandibula; Iop, interopercle; Le, lateral ethmoid; Mpt, metapterygoid; Op, opercle; Pop, preopercle; Psp, parasphenoid; Q, quadrate; R, rib; Ra, radial; sb, sclerotic bone; Sc, scale; Sca, scapula; Scl, supracleithrum; So, supraorbital; Sop, subopercle; Sy, symplectic; V, vomer.

The new interpretation is furthermore supported by the occurrence on the right side of the holotype of the anterior extremity of the palatine (Fig. 5.4), which is formed by the typical ichthyodectiform double articular surfaces for articulation with the ethmosphenoid dorsally and the maxilla ventrally. A supraethmoid, usually present in ichthyodectiforms, is not discernible, but this may be due to the strong state of ossification of the ethmoid region obscuring the sutures. Interpretation of the ethmoid region of *Dugaldia* based on the ichthyodectiform Bauplan is reinforced by the morphology of KKF715. In this individual (Fig. 5.6B, C), the palatine head is still in anatomical connection and articulates with both the ethmopalatine and the maxilla. The latter bone articulates anteriorly through a broad, medially recurved articular head, with the anterior compound facet of the ethmoid massif. The lateral ethmoid forms the dorsal and part of the posterior pillar that supports the articular facet for the palatine. A large fragment of a sclerotic ring is preserved on the holotype (Fig. 5.4), but the basal sclerotic has not been observed, possibly due to the compressed nature of the preservation of KKF714 and KKF715.

Suspensorium—The suspensorium is relatively well preserved on the right side of the holotype (Fig. 5.4), and Lees described its major features, which are consequently not detailed here. The only supplement we add to this description is the shape of the articular head of the quadrate, which was described as a ‘blunt apex’ (Lees, 1990) in the holotype, but which corresponds to a distinct articular head protruding from the main triangular body of the bone on KKF714 and KKF715 (Figs. 5.6, 5.7). Part of the ectopterygoid is visible on the holotype (contra Lees, 1990) and on KKF715. It is an edentulous, boomerang-shaped bone, which contacts the quadrate posteriorly and the palatine anteriorly.

Jaws—Only the lower jaw is preserved on the holotype (GSQ 9242), but specimens KKF714 and KKF715 have the upper jaw preserved (Figs. 5.6–5.8), excluding the premaxilla (except possibly a fragment on KKF715 (Fig. 5.6C). The maxilla is an elongated, saber-shaped, and edentulous ossification, with parallel margins and a regularly convex oral border. The anterior extremity forms an internally recurved arm ending anterodorsally in a process (Fig. 5.6B, C), that articulates with the deep articular socket of the ethmoid massif. Dorsally, at the base of the recurved arm is another articular facet for the palatine. Two deep supramaxillae are present. The posterior one has a dorsal arm extending above the anterior one, which is approximately oval (Figs. 5.6B, C, 8). The mandible is clearly visible on the holotype (GSQ 9242) and on KKF715 (Figs. 5.4, 5.5E–G, 5.6B, C). The coronoid process is very large, deep, and triangular. It is formed mostly by the dentary, with a participation of the angular posteriorly.

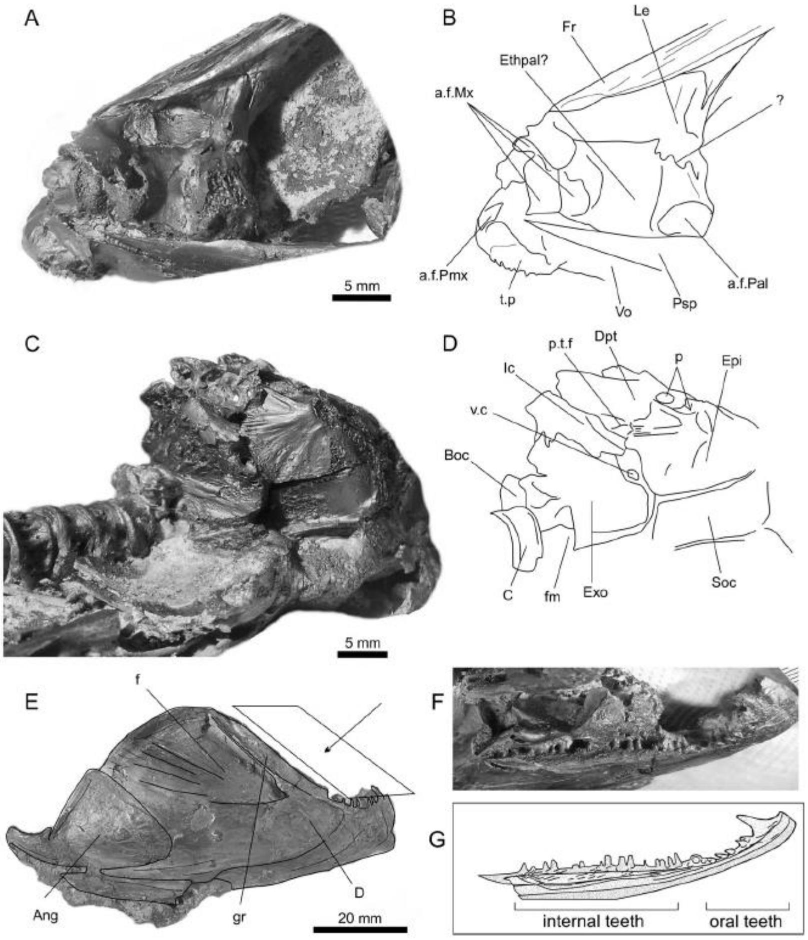

Figure 5.5. *Dugaldia emmilta*, holotype (GSQ 9242). A, B, detail of the ethmoid region; C, D, detail of the occipital region; E–G, detail of mandible; E, right lateral view of the mandible; F, photograph and G, interpretive drawing of the teeth in view perpendicular to the oral border (arrow and parallelogram in E). Abbreviations: a.f.Mx, articular facet for the maxilla; a.f.Pal, articular facet for the autopalatine; a.f.Pmx, articular facet for the premaxilla; Ang, angular; Boc, basioccipital; C, centrum; D, dentary; Dpt, dermopterotic; Epi, epioccipital; Ethpal, ethmopalatine; Exo, exoccipital; f, fossa; fm, foramen magnum; Fr, frontal; gr, groove; Ic, intercalar; Le, lateral ethmoid; p, pore; Psp, parasphenoid; p.t.f, posttemporal fossa; Soc, supraoccipital; t.p, tooth patch of the vomer; Vo, vomer; v.c, vertical semicircular canal.

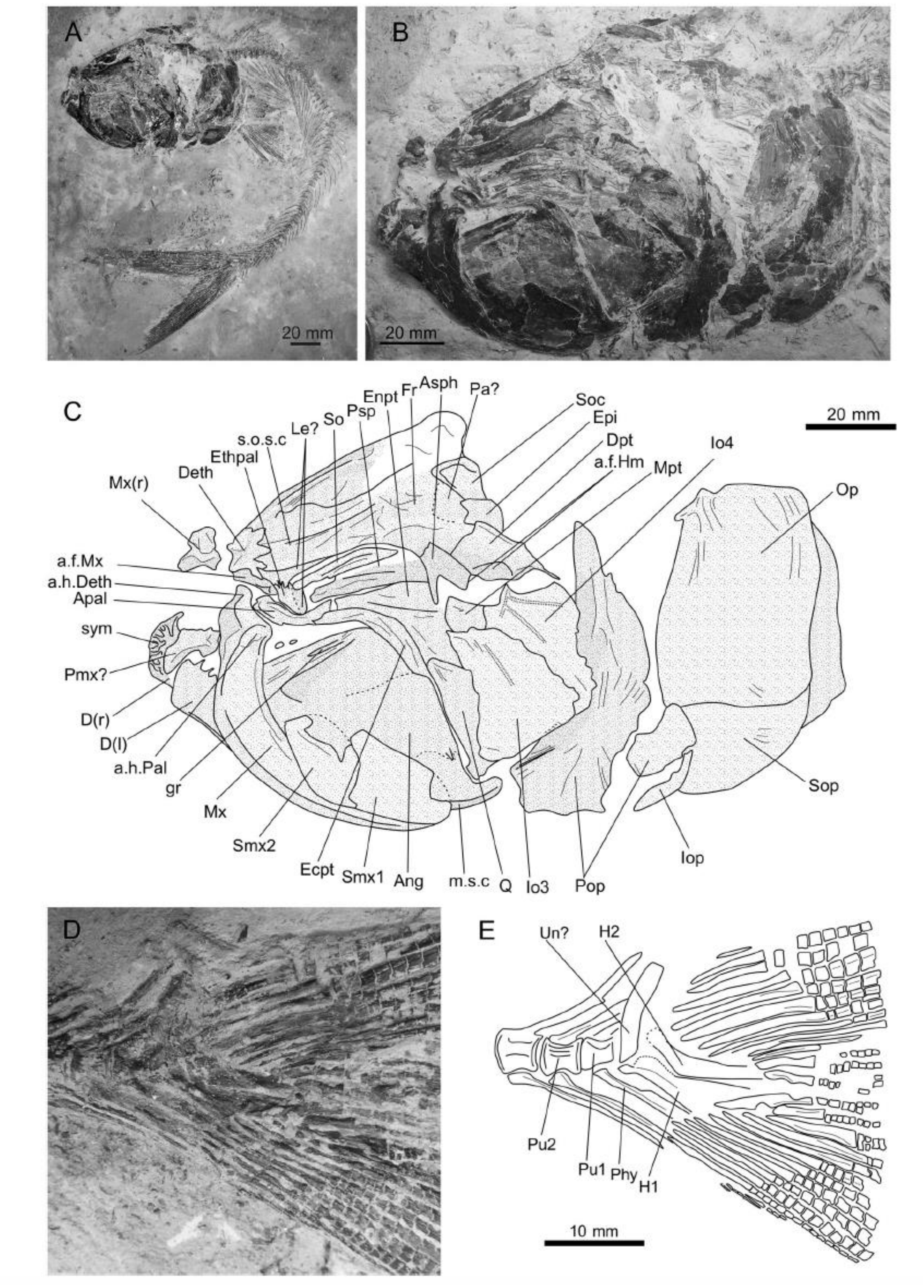

Figure 5.6. *Dugaldia emmilta*, KKF715. A. Photograph of a complete specimen in left lateral view; B, photograph of head region; C, interpretive drawing of the head; D, photograph and E, interpretive drawing of the caudal skeleton. Abbreviations: a.f.Hm, articular facet for the hyomandibula; a.f.Mx, articular facet for the maxilla;

a.h.Deth, articular head with the dermethmoid; a.h.Pal, articular head with the autopalatine; Ang, angular; Apal, autopalatine; Asph, autosphenotic; D, dentary; Deth, dermethmoid; Dpt, dermopterotic; Ecpt, ectopterygoid; Enpt, entopterygoid; Epi, epioccipital; Ethpal, ethmopalatine; Fr, frontal; gr, groove; H, hypural (numbered); Io, infraorbital (numbered); Iop, interopercle; (l), left; Le, lateral ethmoid; Mpt, metapterygoid; m.s.c, mandibular sensory canal; Mx, maxilla; Op, opercle; Pa, parietal; Phy, parhypural; Pmx, premaxilla; Pop, preopercle; Psp, parasphenoid; Pu, preural centrum (numbered); Q, quadrate; (r), right; Smx, supramaxilla (numbered); So, supraorbital; Soc, supraoccipital; Sop, subopercle; s.o.s.c, supraorbital sensory canal; sym, symphysis; Un, uroneural (numbered).

Anterior to the coronoid process, the dentary has parallel margins and ends abruptly with a vertical margin. The symphysis is deep compared with those of generalized teleosts, but it is proportionally shallow compared with the more derived ichthyodectiforms. On KKF715, the symphysis shows a pattern of crests and grooves (Fig. 5.6B, C), indicating that the two hemimandibles were loosely attached to each other, probably through a ligament. The anterior portion of the dentary bears three medium-sized teeth on KKF715 (Fig. 5.6B, C), and five relatively small teeth plus a larger anterior tooth on the holotype (Fig. 5.4), as observed in *Cladocyclus* among other ichthyodectiforms (Maisey, 1991). All teeth are pointed and posteriorly recurved without sculpting. The anterior margin of the coronoid process formed by the dentary shows unusual features (Fig. 5.5E–G). A thickened ridge runs along the lateral side of this margin, with a groove along its length. This ridge marks the upper margin of a large triangular fossa that covers most of the coronoid process. This fossa is not related to the jaw adductor muscle complex because these muscles attached to the inner side of the mandible, but it is likely the site of attachment of the infralabial ligament (Datovo and Vari, 2013). The most striking feature of the dentary is the occurrence of a series of teeth held horizontally on the internal side, along the anterior margin of the coronoid process (Fig. 5.5F, G). These teeth, difficult to see on the holotype, were not observed by Lees. Because no suture is visible between these teeth and the more anterior series of dentary teeth, and because of the general arrangement of the lower jaw in ichthyodectiforms (Bardack, 1965; Patterson and Rosen, 1977), we are confident that these horizontal teeth are borne by the dentary.

About 14 teeth are observed, but probably three to four more were originally present. Because this part of the specimen is not altered in the holotype, and also because KKF714 shows no trace of these teeth in lateral view, we suggest that they are held in their original position. A ventrally oriented groove runs along the whole ventral margin of the mandible. The mandibular sensory canal, whose posterior entry is visible on the angular of KKF714 (Fig. 5.7), probably runs parallel to the groove. A large angular forms the posterior margin of the coronoid process and the articular facet in lateral view and apparently extends anteriorly ventral to the dentary. No other bones of the mandible (articular and retroarticular) are visible.

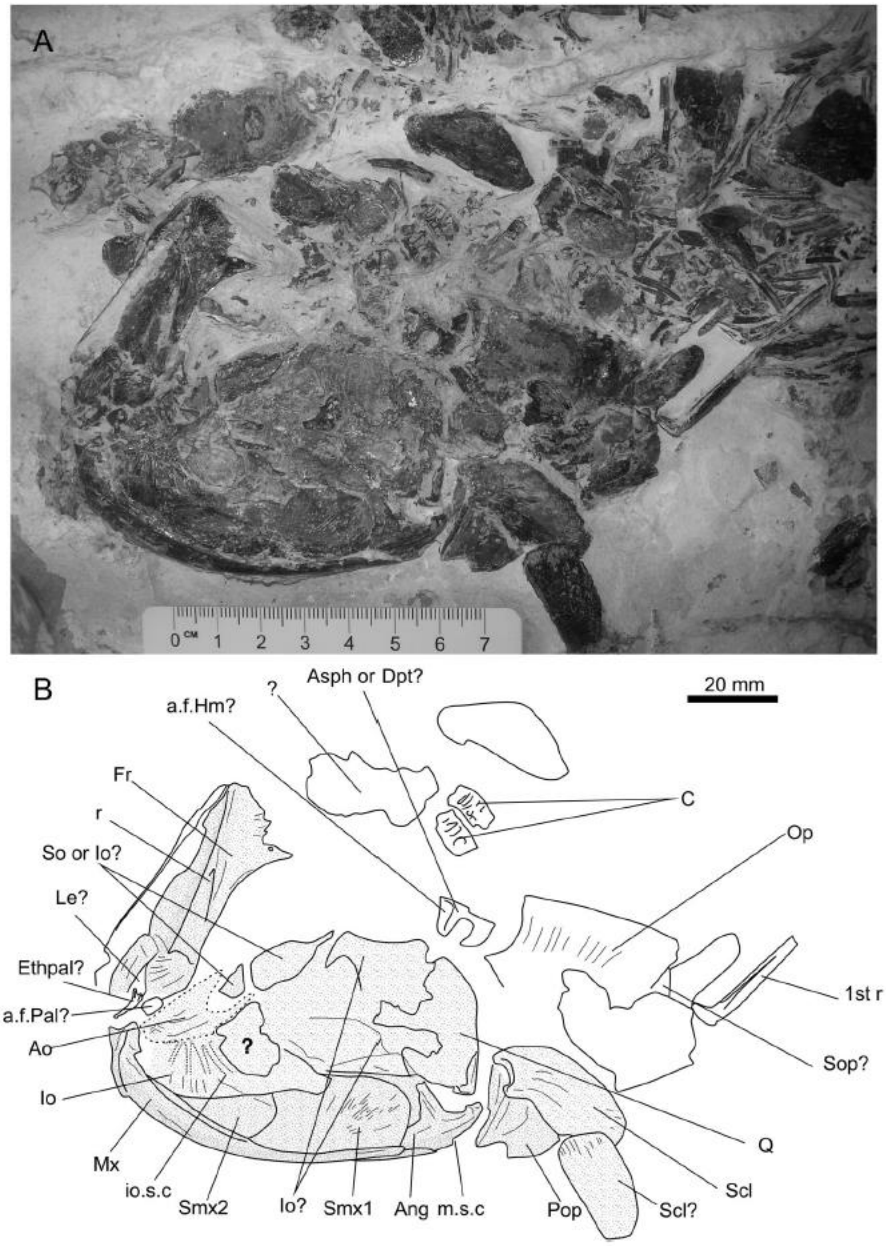

Figure 5.7. *Dugaldia emmilta*, KKF714, A, photograph and B, interpretive line drawing in left lateral view. Abbreviations: a.f.Hm, articular facet for the hyomandibula; a.f.Pal, articular facet for the autopalatine; Ang, angular; Ao, antorbital; Asph, autosphenotic; C, centrum; Ethpal, ethmopalatine; Fr, frontal; Io, infraorbital (numbered); i.o.s.c, infraorbital sensory canal; Le, lateral ethmoid; m.s.c, mandibular sensory canal; Mx, maxilla; Op, opercle; Pop, preopercle; Q, quadrate; r, ridge; Scl, supracleithrum; Smx, supramaxilla (numbered); So, supraorbital; Sop, subopercle; 1st r, first radial.

Circumorbital Series—As mentioned by Lees (1990), from this series only a supraorbital is preserved on the right side of the holotype (Fig. 5.4). The new specimens, however, provide more information that allows reconstructing in large part the circumorbital series (Fig. 5.8). A large infraorbital posterior to the orbit and a second one in the ventroposterior corner of the orbit fill the whole space between the orbit and the preopercle (KKF714). In KKF715, another large and trapezoidal infraorbital is located anteroventrally to the orbit. This specimen also shows a poorly preserved bone located anterodorsally to the large infraorbital interpreted as the antorbital (Fig. 5.7). An elongated, irregularly shaped bone present below the parasphenoid of the holotype and visible in internal view shows a connection between three sensory canals (Fig. 5.3). It likely corresponds to a shifted dermosphenotic.

We hypothesize that the circumorbital ring was composed of a single long supraorbital, a dermosphenotic, and three large infraorbitals, which filled the whole cheek, and an antorbital. These bones are very thin. The circumorbital sensory canal is preserved as fragments, which allow reconstructing the pattern as a canal surrounding the orbit with at least two long diverticula in the posterior infraorbital, one long diverticulum in the ventroposterior infraorbital, and four diverging diverticula in the anterior-most infraorbital.

Opercular Series—The opercular series is better preserved on the holotype (Fig. 5.4) described by Lees, and only a little information can be added from the new specimens. The posteroventral corner of the preopercle is truncated on the holotype, but KKF715 (Fig. 5.6B, C) shows that this corner was more expanded, although its exact shape is unknown. The preopercular sensory canal is visible as faint ridges. The precise pattern is difficult to detect, but several diverticula are present, some apparently oriented posterodorsally on the vertical limb and some oriented anteroventrally on the horizontal limb. The opercle is rectangular in shape rather than semi-circular. A large subopercle, with only a very small anterior dorsal process is visible in lateral view. The interopercle (Figs. 5.4, 6B, C) appears to be large, but it is mostly hidden by the ventral limb of the preopercle.

Hyoid and Branchial Arches—Lees (1990) considered that this part of the skeleton is not well preserved, but the holotype preserves anatomical structures with a lot of information (Fig. 5.3). The large anterior ceratohyal, with a beryciform foramen, the dorsal and ventral hypohyals with a foramen for the hyoidean artery, and branchiostegal rays (11 articulating with the anterior ceratohyals and four with the posterior ceratohyals at least) are present and described by Lees (1990). We add to this description the occurrence of a fragment of the posterior ceratohyal. A small element, with a deep socket, located just above the hypohyal, is regarded as the basihyal. Numerous fragments of the branchial arches are preserved, but a detailed reconstruction is difficult. The hypobranchials and ceratobranchials are very elongated. Several small tooth plates, with pointed and closely spaced teeth, are apparently associated with these ventral elements. Epibranchials are also present, but their count and arrangement could not be reconstructed. An elongated tooth plate is apparently associated with an epibranchial. A pharyngobranchial is recognized. It is formed by a rounded body with a distinctive process, which likely articulated with the next anterior branchial arch. A tooth plate is associated with it.

Pectoral Girdle and Fin—The pectoral girdle is only preserved on the holotype (Figs. 5.3, 5.4), but the dorsal part is poorly preserved, with only a fragment of the supracleithrum preserved.

On KKF714, a probable shifted supracleithrum is preserved (Fig. 5.7). It is ovoid in shape, with a slightly curved dorsal extremity dug by a large concave articular facet. The cleithrum is broad and has a gently curved anterior margin, but not well-defined horizontal limb. An ossification, which is partly visible in medial view and shows a dorsal fan-shaped contact with the cleithrum, is regarded as a mesocoracoid (this bone is apparently interpreted as the scapular by Lees, 1990). A mesocoracoid has been described in this position in the ichthyodectiform *Eubiodectes libanicus* (Cavin et al., 2013). In external view, the scapular bears three saddle-shaped condyles that probably articulated directly with the rays. Posterior to the scapular is an independent element with two articular facets that we identified as a radial. We recognize in the holotype (Fig. 5.4) the base of eight rays (contra 11 by Lees, 1990) and about 13 rays in KKF715 (Fig. 5.6A). On the latter, the rays appear to be undivided along most of their length and divided and branched distally. The first ray is distinctly broader than the others.

Vertebral Column—In the complete KKF715, we count 52 vertebrae, and we estimate that five centra are hidden by the opercular series and pectoral girdle (Fig. 5.6A). Among these 57 vertebrae, approximately 33 are abdominal and 24 are caudal, plus an indeterminate number of ural centra. As noted by Lees (1990), the first vertebrae of the holotype are deeper than long (Fig. 5.3). The first two centra are not ornamented and bear apparently fused small parapophyses ventrolaterally. From the third centrum backward, the centra bear deep grooves on their lateral sides. The lateral grooves are few in the anterior-most vertebrae (ca. three), then they are more abundant in the abdominal region and toward the caudal peduncle (ca. six). From approximately the sixth centrum backward, autogenous parapophyses complex in shape are present (Fig. 5.3). Each parapophysis, which articulates with the rib, is composed of a pair of rounded processes situated anteriorly and posteriorly and a spiny process extending dorsally. The neural elements on the abdominal vertebrae are better visible on the holotype. The neural arches are autogenous and occupy most of the length of the centrum. Each neural spine is thin and elongated and forms an angle of about 45 with the axis of the vertebral column. In the anterior part of the abdominal series at least, the elongated epineurals are fused to their neural arches. The holotype and KKF715 show that the ribs are proportionally very wide proximally, elongated, and probably reach the ventral part of the belly. Each rib has a well-marked groove (Figs. 5.3, 5.6A). Four supraneurals are visible on the holotype, but more were probably present originally. The posterior two are complete: they are arched and present a lamina of bone more developed proximally.

Pelvic Girdle and Pelvic, Dorsal, and Anal Fins—Although almost complete and articulated, KKF715 shows no traces of a pelvic girdle and pelvic, dorsal, and anal fins (Fig. 5.6A). We consider that these fins have been destroyed or shifted before fossilization rather than that they were absent in the living fish.

Caudal Skeleton and Fin—The caudal skeleton and fin are preserved on KKF715 only, but few details can be observed (Fig. 5.6D, E). The caudal fin is supported by the first two preural centra and by an indeterminate number of ural centra. The centrum of Pu2 is slightly smaller than the last caudal centra and ornamented by at least two deep grooves. It bears long autogenous neural and hemal spines. The centrum of Pu1 is unornamented. It has a posterior extremity smaller than the anterior extremity and is slightly upturned. The autogenous parhypural has a narrow proximal part, which forms a broader blade distally. The first hypural shows a rounded articulated head along its anterior margin, followed by a narrow ‘neck’ that extends distally as a broad triangular plate. Bony material is present above its proximal end and may correspond to a thinner posterior plate of the first hypural, because it is present in some ichthyodectiforms (see, e.g., Patterson and Rosen, 1977). A broad hypural is visible close to the first hypural and is angled, as is often the case for the second hypural of ichthyodectiforms. Its connection with the ural centra is unclear. A broad, arched, and elongated plate covers the ural centra. It is possibly a shifted large uroneural. The hypurostegy is important. The caudal fin is deeply forked. The count of the rays is uncertain: There are at least four dorsal procurrent rays, one simple and eight branched principal rays in the upper lobe, and at least two procurrent, one simple, and eight branched principal rays in the ventral lobe. The sutures between the lepidotrichia are step-like, except the proximal ones.

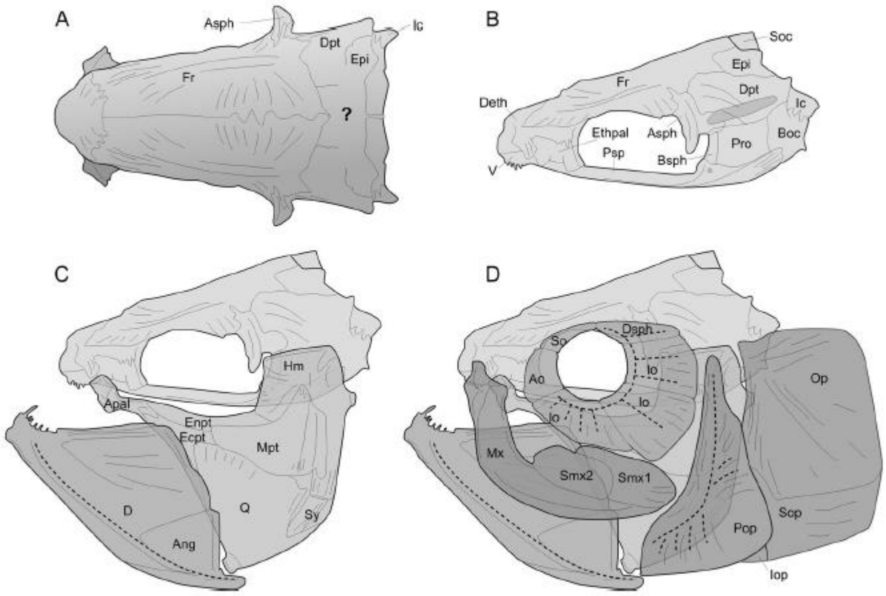

Figure 5.8. *Dugaldia emmilta*. A, dorsal view, reconstruction of the skull roof; B, reconstruction of the braincase in left lateral view; C, with addition of the mandible and suspensorium; D, with addition of the upper jaw, circumorbital, and opercular series. Abbreviations: Ang, angular; Ao, antorbital; Apal, autopalatine; Asph, autosphenotic; Boc, basioccipital; Bsph, basisphenoid;D, dentary; Deth, dermethmoid; Dpt, dermopterotic; Dsph, dermosphenotic; Ecpt, ectopterygoid; Enpt,

entopterygoid; Epi, epioccipital; Ethpal, ethmopalatine; Fr, frontal; Hm, hyomandibula; Ic, intercalar; Io, infraorbital; Iop, interopercle; Mpt, metapterygoid; Mx, maxilla; Op, opercle; Pop, preopercle; Pro, prootic; Q, quadrate; Smx, supramaxilla (numbered); So, supraorbital; Soc, supraoccipital; Sop, subopercle; Sy, symplectic; V, vomer.

Scales—The scales are deeper than long, cycloid, and bear concentric radii (Fig. 5.4).

5.7 Systematic affinities

Dugaldia presents several characters that are regarded as diagnostic for ichthyodectiforms: a well-ossified ethmoid massif with a probable ethmopalatine ossification; a disc-like articular head of the autopalatine; a saber-shaped maxilla with two deep supramaxillae; large infraorbitals with elongated diverticula of the infraorbital sensory canal; a participation of the exoccipital in the occipital condyle; the coronoid probably in contact with its counterpart; wide and elongated ribs, with a groove along their length and articulating with their corresponding centrum via a complex parapophysis; elongated epineurals; and deeper than long ovoid scales. Structure of the occipital condyle, i.e., a tripartite occipital condyle formed by the basioccipital and both exoccipital processes, was regarded by Lees (1990) as evidence of neoteleostean affinities following a proposition by Patterson (1964). Lees noticed that a similar structure might be present in the salmonids, although it might be convergent in this group. Stewart (1999), however, showed that a similar pattern is also present in several ichthyodectiforms. Other characters of *Dugaldia* are present in most ichthyodectiforms but are also widespread in other teleostean clades: the general shape of the preopercle, frontal, and vertebral centra; and the hypurostegy and step-like sutures between the lepidotrichia. However, *Dugaldia* also shows characters absent in ichthyodectiforms, at least in the more derived Cretaceous taxa: absence of basipterygoid process on the parasphenoid; probable absence of the typical denticulated basal sclerotic bone; and, although poorly preserved, the posterior part of the skull roof apparently has no strong crests on the supraoccipital and epiotics. The lower jaw appears to be very different from the typical lower jaw of Ichthyodectiformes, at least from the derived Cretaceous taxa in which it is generally rectangular in shape, with a poorly developed coronoid process. The mandible recalls that of *Ogunichthys triangularis*, from the Aptian–Albian of Brazil, although in the latter the coronoid process is less developed and there is no internal row of teeth (Alvarado-Ortega and Brito, 2010).

5.8 Phylogenetic analysis

We coded the characters of *Dugaldia* in the data matrix of Cavin et al. (2013), with the additions and corrections from Berrell et al. (2014). To this data matrix we added the following recently described taxa: *Ogunichthys triangularis* Alvarado- Ortega and Brito, 2010; *Verraesichthys bloti* Taverne, 2010 (but see Cavin et al., 2013, for comments about this species); *Jinjuichthys cheongi* Kim et al. (2014); *Cladocyclus geddesi* Berrell et al. (2014); and *Amakusaichthys goshouraensis* Yabumoto et al. (2018). We also added *Mesoclupea showchangensis*, based mostly on the description of Chang (1963).

The inclusion of these new taxa, as well as the corrections of miscoded characters in previous studies, led us to alter the data matrix as follows. (1) Stewart (1999) pointed out that the pterotic in some ichthyodectiforms extends anteriorly to the autosphenotic bone, and not simply anteriorly to the autosphenotic spine. This feature allows a better definition of character 5, which was consequently slightly altered (‘bone’ instead of ‘spine’). According to this definition, the character was recoded for some taxa (*Heckelichthys, Chiromystus mawsoni, Cooyoo australis*, *Eubiodectes libanicus*, and *Thrissops* sp. from Kimmeridge). (2) The relationships of the premaxilla with the ethmoid complex and with the maxilla are very peculiar in ichthyodectiforms due to their special jaw mechanics (see below). Cavin et al. (2013) recognized four states characterizing the arrangement of the premaxilla (character 18). However, during the scoring of characters of the new taxa included in this analysis, it appeared that two of these states were hardly distinguishable on some of the taxa (premaxilla with a dorsal process, articulating with the maxilla = 1; with no dorsal process, articulating with the maxilla = 2). We redefine these character states as follows: premaxilla with a well-developed dorsal process, articulating with the maxilla = 1; with a poorly developed or no dorsal process, articulating with the maxilla = 2. As a consequence of this change, scoring of this character was modified for *Chiromystus*, *Cladocyclus*, *Occithrissops*, *Thrissops* from Kimmeridge, and *Unamichthys*. (3) We corrected errors of scorings of character 15 for *Allothrissops*, *Ghrisichthys*, and *Xiphactinus*. (4) The scoring of characters for *Cooyoo* by Cavin et al. (2013) was based exclusively on the paper by Lees and Bartholomai (1987). Examination of material of *Cooyoo* housed in the Queensland Museum, Brisbane (especially specimen QM F1016), allowed us to score more characters (4, 5, 10, 11, 14, 15, 18, 24, 26, 32, 36, 56, and 69). (5) In order to better use the phylogenetic signal attached to the number of vertebrae, we divided character 69 into five distinct states, rather than two defined in Cavin et al. (2013). Rescoring of this character for each terminal taxon has been made. The character definitions and the data matrix are available in Appendices 1 and 2, respectively. The outgroups used in the analyses are *Amia calva*, *Leptolepis coryphaenoides*, and *Elops hawaiensis*. The data were analyzed using PAUP*4.0b10 (Swofford, 2001). A heuristic search (using random addition sequence, replicated 1,000 times, 10 trees held at each iteration, and tree bisection and reconnection branch swapping) was carried out to try to avoid the ‘islands of trees’ problem (Maddison, 1991). In a first analysis, we obtained six most parsimonious trees (length = 240 steps, consistency index [CI] = 0.4333, retention index [RI] = 0.6477, rescaled CI = 0.2807). The strict consensus tree is shown in Figure 5.9. Character changes in one of the most parsimonious trees are presented in Supplemental Data. The general pattern is somewhat similar to the patterns obtained by Cavin et al. (2013), Berrell et al. (2014), and Yabumoto et al. (2018), in particular in the recognition of three families, Cladocyclidae, Ichthyodectidae, and Saurodontidae, that are nested in the Ichthyodectoidei. The first two families are poorly supported, but Saurodontidae and Ichthyodectoidei are slightly better supported, each with a Bremer support value of 2. The main difference with the previous studies is that the cladocyclids are here resolved as the sister group of the saurodontids, whereas in previous analyses this position was occupied by the ichthyodectids. Another difference from the patterns by Cavin et al. (2013) and Berrell et al. (2014), but partly similar to the pattern by Yabumoto et al. (2018), is the resolution of a clade grouping the Tethyan *Heckelichthys* with the Japanese *Amakusaichthys*. In the Yabumoto et al. (2018) study, this clade is grouped with the pair *Cooyoo* + *Unamichthys*, the whole clade being the sister group of ichthyodectids plus saurodontids.

In the present analysis, the *Heckelichthys* + *Amakusaichthys* clade is deeply nested within the saurodontids, together with *Unamichthys*, whereas *Cooyoo* is positioned in Ichthyodectidae as the sister to Ichthyodectes. We suggest that the differences observed between Yabumoto et al.’s (2018) results and the topology obtained here are mostly due to the more complete scoring of *Cooyoo*. The sister clade of the Ichthyodectoidei is *Ogunichthys*, and the sister clade taxon of this pair is *Dugaldia*.

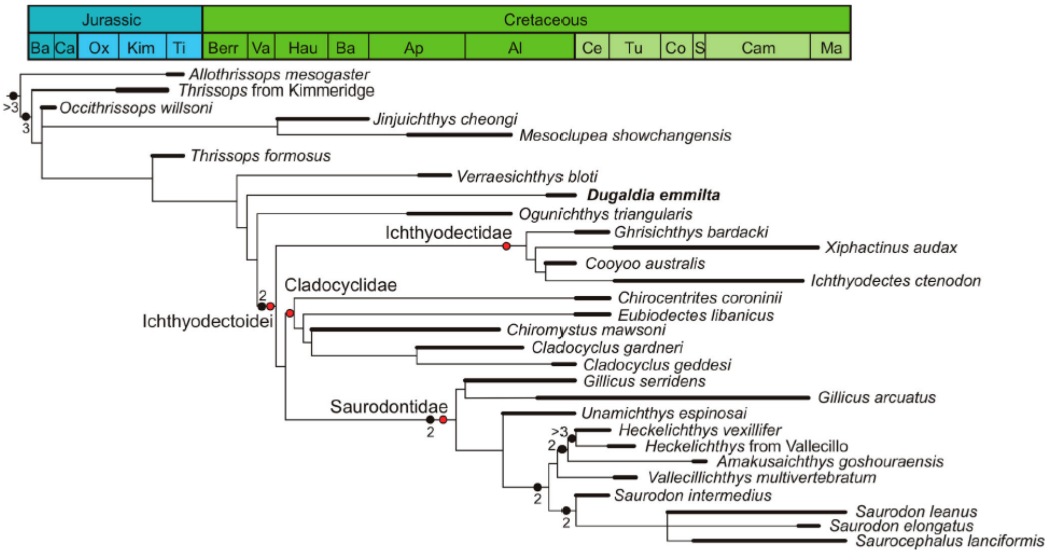

Figure 5.9. Time-scaled strict consensus tree of the ichthyodectiforms of six most parsimonious trees. See text for tree statistics. Bremer support values greater than 1 are indicated in association to nodes with black spots.

It is noteworthy that both *Ogunichthys* and *Dugaldia* possess a triangular lower jaw, differing from the rectangular mandible of most ichthyodectoids. This analysis resolves the position of two of the freshwater Ichthyodectiforms (*Jinijuichthys* and *Mesoclupea*) and supports their divergence from their marine counterparts during the Early Jurassic. This appears to suggest a rapid radiation into new niches and suggests a long ghost lineage for the freshwater ichthyodectiformes. The basal position of *Thrissops* from the Kimmeridge in this phylogenetic analysis supports conclusions by Cavin et al. (2013) that differences in the skull are not observed in any other species of *Thrissops*. Although this specimen has not been formally described, *Thrissops* from Kimmeridge should currently be considered more primitive than other species of *Thrissops* and the sister to *Allothrissops*.

5.9 Jaw Mechanics

It has been shown that jaw mechanics of ichthyodectiforms are very specialized and differ from the jaw mechanics in most other actinopterygians (Giersch et al., 2010; Cavin et al., 2013). In these fishes, the jaws are always massive and incapable of protrusion but adapted to a significant enlargement of the oral cavity by lateral jaw and suspensorium movement. In derived ichthyodectiforms, the anterior process articulating with the facet formed by the ethmopalatine, the dermethmoid, and the vomer is poorly developed, and the articulation is centered on the palatine process. In these forms, the palatine head has a typical shape with two parallel facets articulating dorsally with the ethmopalatine bone and ventrally with the maxilla. This arrangement allows weak anteroposterior motion, but a more important lateral motion owing to the lateral sliding of the palatine head against the massive ethmoid. The lateral enlargement of the mouth gape is indicated also by the loose symphysis of the lower jaw allowing the hemimandibles to move apart, and by the well-developed spine of the autosphenotic for anchorage of the levator arcus palatini muscle, which moves the suspensorium laterally.

In *Dugaldia*, most of these features are present (Fig. 5.10), i.e., freely movable head of the palatine, strong autosphenotic spine, and loose symphysis, but, in addition, it shows specific characters: (1) the anterior articular process of the maxilla is still well developed and articulates in a deep socket of the ethmoid, which allows the maxilla to move dorsally and laterally and to switch into an almost horizontal position; (2) the lateral face of the mandible bears a large triangular fossa, which likely accommodated the infralabial ligament; and (3) a row of teeth is oriented horizontally along the oral margin of the mandible.

The sarcastic fringehead (*Neoclinus blanchardi*) is a living blenny that shows a ‘gaping display’ for territorial defense based on a lateral flaring of its extremely long maxillae. Interestingly, anatomical specializations in this species, recently studied by Hongjamrassilp et al. (2018), are partly shared with *Dugaldia*. These features include (1) great mobility of the maxilla due to the freedom of motion of the articular head of the maxilla in its fossa; the mobility of the maxilla is greater in *Dugaldia* than in other ichthyodectiforms owing to the conical shape of the articular head and of the deep socket that receives it; (2) enlargement in size and shape of the posterior portion of the maxilla. In *N. blanchardi*, this portion of the maxilla is less calcified than the anterior portion of the bone, a feature that we cannot assess on *Dugaldia*; and (3) the buccopalatal membrane, connecting the maxilla to the lower jaw, is very large in *N. blanchardi* and allows the jaws to open wide and permits significant lateral movement of the maxillae. This membrane is not preserved in *Dugaldia*, but the deep triangular fossa present on the coronoid process of the mandible may indicate the attachment of the membrane, and/or of the infralabial ligament, which connects the dentary to the posterior end of the maxilla, and which stretches the membrane anteriorly (Datovo and Vari, 2013).

In the sarcastic fringehead, the gaping display is a behaviour for territorial defence toward intruders. During the display, the well-developed oral dentition and the large adductor mandibulae muscles are revealed as a potential signal of biting performance (Hongjamrassilp et al., 2018). In *Dugaldia*, the adductor mandibulae muscles were also likely visible when the mouth was wide open. Moreover, the internally oriented row of teeth was likely visible inside the mouth. However, it is not possible to determine whether this ability to widen the mouth was used for social interactions or for food grasping. We favour the second hypothesis.

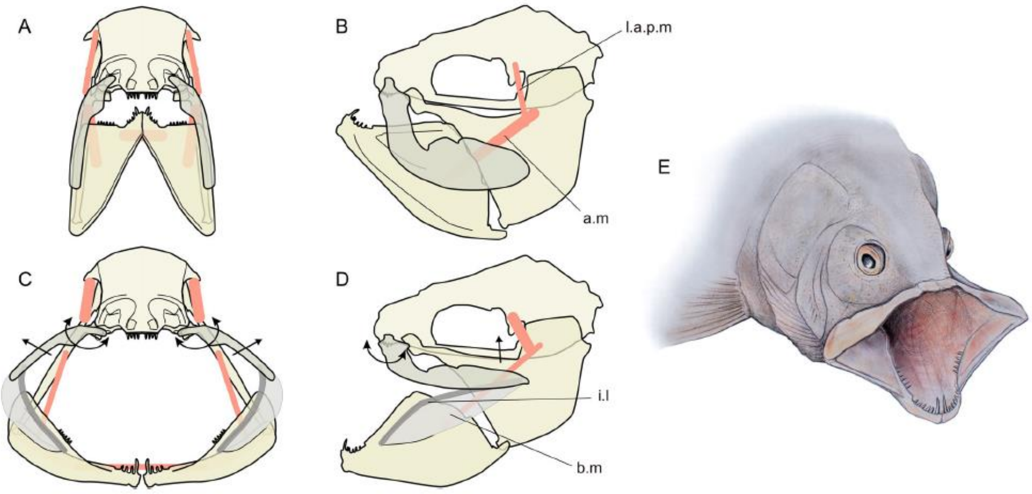

Figure 5.10. Jaw mechanics of *Dugaldia emmilta*. A, B, reconstruction of the skull, mouth closed, C, D, mouth open. A, C, anterior views; B, D, lateral views; E, reconstruction of the head with open mouth. Abbreviations: a.m, adductor mandibulae; b.m, buccopalatal membrane; i.l, infralabial ligament; l.a.p.m, levator arcus palatini muscle.

5.9 Conclusions

The actinopterygian marine assemblage of the Toolebuc Formation is relatively diversified, but the description of several taxa is still pending. It contains a pachycormiform (*Australopachycormus*), an aspidorhynchid (*Richmondichthys*), two species of pachyrhizodontids (*Pachyrhizodus marathonensis* and P. grawi), several probable elopomorphs (*Flindersichthys*, *Euroka*, and *Stewartichthys*), a possible ionoscopiformes (*Canaryichthys*), undescribed aulopiforms, and the ichthyodectiform *Cooyoo*. *Cooyoo* needs to be revised, because it is too incompletely known. In previous phylogenetic analyses (Cavin et al., 2013; Berrell et al., 2014), *Cooyoo* was resolved as the sister genus of *Unamichthys*, a contemporaneous ichthyodectiform from Mexico. In our analysis, *Unamichthys* is located close to *Dugaldia*, thereby indicating a possible phylogenetic proximity between *Dugaldia* and *Cooyoo*. However, this part of the cladogram is still poorly supported by characters and a better knowledge of these genera is necessary before drawing firm conclusions. In the younger, late Albian to early Turonian continental Winton Formation of Queensland, another ichthyodectiform, *Cladocyclus geddesi*, was described by Berrell et al. (2014). This genus, otherwise known in shallow marine, brackish, and freshwater environments of South America and Africa during the late Early and early Late Cretaceous, belongs to a family, the cladocyclids, that is quite distinct from *Dugaldia*. But in all instances, the Australian ichthyodectiforms (*Cooyoo*, *Dugaldia*, and *Cladocyclus*) trace a puzzling paleogeographic scenario connecting mainly Australia with the South Atlantic and western Tethys regions.

The lower jaw of *Dugaldia* shares some features with the possibly closely related *Ogunichthys* from the Lower Cretaceous (? Aptian) Marizal Formation, Brazil (Alvarado-Ortega and Brito, 2010). In the Australian species, however, these features are exaggerated and, together with the peculiar features of the upper jaw, indicate very special jaw mechanics. It is likely that the fish was able to greatly enlarge its gape by a lateral motion of the jaws.

This characteristic was possibly related to its mode of feeding— a possible ram feeder on plankton—or for social interactions, as in the sarcastic fringehead.

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Supplemental information 5.1

Description of characters used in phylogenetic analyses. All characters are treated as unordered.

1: Epioccipital crest: absent (0); present (1).

2: Supraoccipital crest: absent or small (0); large, extending over occipital region only (1); large, extending over first few vertebrae (1).

3: Parietals: paired (0); fused in midline (1).

4: Notch in frontal to receive nasal: absent (0); present (1).

5: Anterior extent of the pterotic: not reaching level of the autosphenotic bone (0); extending anteriorly beyond level of autosphenotic bone (1).

6: Intercalar: normal in size (0); enlarged, forming part of the hyomandibular facet and enclosing a canal for the jugular vein (1).

7: Occiptal condyle: simple condyle formed entirely by basiocciptal (0); compound condyle formed by both basiocciptal and exoccipitals (1).

8: Basipterygoid process: small or absent (0); prominent, angled downward (1); prominent, angled upward (2).

9: Parasphenoid dentition: present (0); absent (1).

10: Parasphenoid profile: almost straight in lateral view or forming only a slight angle beneath the posterior margin of the orbit (0); forming a pronounced angle beneath the posterior margin of the orbit (1).

11: Parasphenoid extent: extends posteriorly to the occipital condyle (0); fails to reach the occipital condyle (1).

12: Vomer: with teeth (0); without teeth (1).

13: Ethmopalatine: absent (0); small, no membanous outgrowth, articular facet simple, and ventrally orientated (1); large, no membranous outgrowth (2); large, with membranous outgrowths separating and suturing with the rostrodermethmoid and lateral ethmoid, articular facet complex (3).

14: Rostrodermethmoid: absent (0); with a considerable constriction behind the initial extension in dorsal view (1); only slight constriction behind the initial extension (1).

15: Suborbital: present (0); absent (1).

16: Perichondral basal sclerotic bone with serrated margin: absent (0); present (1).

17: Supramaxillae: one supramaxilla (0); two, the posterior one with a long and thin anterodorsal process extending over the anterior supramaxilla (1); two, the posterior one without a long process (2); two, the posterior one with a long and thin anteroventral process extending under the anterior supramaxilla (3); supramaxilla absent (4).

18: Premaxilla articulations: firmly attached to the skull roof (0); with a well-developed dorsal process, articulating with the maxilla (1); with a poorly developed or no dorsal process, articulating with the maxilla (2); firmly attached posteriorly to maxilla (3).

19: Oral margin of the maxilla: regularly convex (0); straight or slightly concave (1); sinusoidal (2).

20: Maxillary margins: converge to the anterior extremity (0); parallel (1); converge to the posterior extremity (2).

21: Teeth in jaws: in several series (0); in single series (1); absent (2).

22: Maxillary teeth: uniform in size (0); irregular in size (1); absent (2).

23: Maxillary and dentary teeth: conical (0); laterally compressed (1); conical, with anterior and posterior carinae (2).

24: Premaxillary teeth: regular in size (0); irregular in size (1).

25: Symphyseal teeth on premaxilla: absent (0); present (1).

26: Dentary lateral teeth: regular in size (0); irregular in size (1).

27: Dentary teeth, orientation: perpendicular to the oral margin (0); anteriorly inclined (1).

27: Replacement tooth alveoli: absent (0); present (1).

28: Coronoid process reduced, oral and ventral margin of the mandible almost parallel and mandibular symphysis deep: absent (0); present (1).

29: Predentary: absent (0); present, isosceles triangle in shape (1); present, right triangle in shape, with right angle at the posteroventral corner (2).

30: Fossa well defined on the medial side of the mandible near its anterior extremity: absent (0); present (1).

31: Retroarticular contributes to the articular facet: present (0); absent (1); unknown because retroarticular fused (2).

32: Angular contributing to articular facet for quadrate: absent (0); present (1); unknown because fused with another bone (2).

33: Head proportion index (hpi): hpi > 0.8 below posterior half of the orbit or posterior to the orbit (0); 0.4 < hpi < 0.7 below the anterior margin of the orbit (1); hpi < 0.2 below the lateral ethmoid (2).

34: Mouth cleft orientation: directed anteriorly (0); directed upward (1).

35: Hyomandibular: with no fossae (0); with fossae both sides of hyomandibular ridge (1); with single fossa (2).

36: Opercular process on the hyomandibula: well defined and rounded (0); prominent vertical ridge (1).

37: Preopercular process on the hyomandibula: present (0); absent (1).

38: Metapterygoid contact with palatine: absent (0); present (1).

39: Anterior ceratohyal with a foramen: absent (0); present (1).

40: Parietal branch of the supraorbital sensory canal: present (0); present as an anterior pit line only (1).

41:Otic sensory canal: bone-enclosed throughout its path (0); in a groove (at least in the anterior part) (1).

42: Canaliculi in infraorbital canal: few (0); many (1).

43: Infraorbital canal: extends into antorbital bone (0); ends blindly in the first infraorbital (1).

44: Mandibular sensory canal runs above a ventrally oriented groove: absent (0); present (1).

45: Extrascapular: normal size (0); large, covering the lateral face of the supraoccipital crest (1).

46: Coracoid: normal (0); enlarged, broadly meeting antimere in ventral midline (1).

47: First pectoral ray width: 1.5 times the breadth of the second pectoral ray (0); 2 or more times the breadth of the second ray (1).

48: Interdigitating suture uniting paired pelvic bones: absent (0); present (1).

49: Anterior process of the pelvic bone: broad (0); rod-like (1).

50: Parapophyses: separate (0); co-ossified with centra (1).

51: Rib shape: tapers regularly from the proximal to the distal extremities (0); with an anterior wing along the proximal quarter (1).

52: Anal and dorsal fins: anal not falcate, moderate in size, with a long or short dorsal fin, the origin of which is positioned well anterior to level of anal fin (0); anal long, falcate, opposed by a short remote dorsal fin (1); both short and remote (2); anal long, opposed by a dorsal deeper than body depth (3).

53: First anal and dorsal pterygiophores: not reaching the hemal spine or tip-to-tip contact with the hemal spine (0); elongated, arranged in clusters that extend into the inter–hemal spine spaces (1).

54: Shape of proximal radial of first dorsal fin pterygiophore: simple (0); basally forked (1).

55: Elongated epineural bones: absent (0); present (1).

56: Anterior supraneurals: simple rod-like structure (0); with an anterior membranous blade (1).

57: Ventral lobe of the caudal fin in adult-sized individuals: undifferentiated from the dorsal lobe (rounded tail) (0); as long as the dorsal lobe (1); longer than the dorsal lobe (2).

58: Lateral sides of the abdominal vertebral centra: smooth (0); with several (at least 3) shallow longitudinal grooves or elongated pits (1); with a longitudinal lateral ridge separating two deep elongated pits (2); with a single pit (3).

59: Hemal arches of the caudal region: not fused to centra (0); fused with centra (1).

60: First hypural inserts into ural centrum by a ball-and-socket joint: absent (0); present (1).

61: Epurals: three or more (0); two (1); one (2).

62: Number of hypurals: nine or more (0); eight (1); seven (2).

63: Uroneurals: absent (0); present, lie on the dorsal lateral side of the centra (1); the first three or four extend anteroventrally to cover the entire lateral surface of the first, second, or third preural centrum (2).

64: Uroneurals: absent (0); present, first uroneural extends forwards to preural (Pu) 4 (1); present, first uroneural extends forwards to Pu3 (2); present, first uroneural extends forwards to Pu2 (3); present, first uroneural extends forwards to Pu1 (4).

65: Number of urodermals: two (0); one (1); none (2).

66: Sutures between segments of the caudal fin: straight or sigmoidal (0); step-like (1).

67: Scales with pits on the posterior exposed part: pits absent (0); pits present (1).

68: Number of vertebrae: less than 61 (0); between 61 and 70 (1); between 71 and 80 (2); between 81 and 90 (3); more than 91 (4).

69: Cleithrum: long axes of vertical and horizontal arms aligned at an obtuse angle (0); long axes of vertical and horizontal arms aligned approximately perpendicular to each other (1).

Supplemental information 5.2

	1111111111222222222233333333334444444444555555555566666666667 1234567890123456789012345678901234567890123456789012345678901234567890
Amia calva	0- 00000000000010001010000100000000000010010000000000100000100000000000020030
Leptolepis coryphaenoides	0000000100000100110010000000000022000000?001?000000000010?100000120000?
Elops hawaiensis	0000000000000110110100000000000022000010000000000000000000011000213100P0
Allothrissops mesogaster	0000100100101100110010000000000?010000?0100011010?1001110021?00122010P0
Chirocentrites coroninii	11???1???1??????232111010100100??01???????1?1110110011111120???23?1?1?
Heckelichthys ‘vallecillo’	121?0??111??21?1230222- ?0- - 010???2101?0??00101?011003101?12?11?24????1?
Heckelichthys vexillifer	12100??11???21?1230222- ?0- - 010???210100???0?01?0????3111?12?????????01?
Amakusaichthys goshouraensis	????1???????32??2?02100??12?1??1121???????111??1??103111022111?2421101
Chiromystus mawsoni	1?1??11?11??2????2211001?10010???0120?0???1?1?10???101?11120???2??110?
Eubiodectes libanicus	12100??2111?2??123211001110010???11?0?0?00??1110?1001101122011?23?1010
Cladocyclus gardneri	121011121110310122111000?100100010120001110111001011101?1201212321111
Cladocyclus geddesi	121011?????31?122?11000?10010001?120???????1???????????????????????????1
Ghrisichthys bardacki	111111?1101?3?112311100??000100??112010??0101?11??00???1??20???21???10
Gillicus arcuatus	111111211?132?12321100000001011111111111?11?10?100111?1201?222?112?
Gillicus serridens	111?11???1??320?2321100101??10??111?????11??1110??0?????1?2???????????
Ichthyodectes ctenodon	1111111101?31?123111000000010?1101?11?1??????10????2??????01?222?11P0
Occithrissops willsoni	0000?1??11??2??01200???0000?00???0100?0110??1?10010111??2201011210?00
Thrissops formosus	120011?110?12?11121010000000000??0100?0010??1110010111111111011111000
Thrissops from Kimmeridge	1201?1??001?210?1200100010000000?010000???0?0?1???0111???1????????10??
Xiphactinus audax	1111111110003111231111010100100110121111?01?0111110021?111201?222?1130
Unamichthys espinosai	110011?111??320123011000010?10?1101???????1?0110??0011?1?220?0?222?120
Vallecillichthys multivertebratum	121111?111?132?133021021010012111112111????00101100110101201?222?1141
Dugaldia emmilta	???001101110321?1?01120??10?00??11100101??1?1?10??01???11110??????1?0?
Ogunichthys triangularis	?100?1?111??31?113P11001110?00?11110??0???1?1110?10011?10?2??0?222?100
Jinjuichthys cheongi	1?0001?211??????1?00122?000?00???110??0?????10???1?111??01100021310??0
Mesoclupea showchangensis	?0010????1?????012001000000?00???11???1???????10???011110110?221220?0?
Cooyoo australis	11110112111?31112311100 0?10?10?1?012??0?????0??0??01???1??2??????????1?
Saurocephalus lanciformis	1111111??????2???31210100011111?????????0?????????????????????????????
Saurodon leanus	11111111111132?03312101000111111111?1?01????0?1????????????201?221??140
Saurodon intermedius	11101????????2??2312101110101????11???0?00??0?????????????????????????
Saurodon elongatus	?????1???1???????32210??00111P?1??1??10???????1??110110101201?222?114?
Verraesichthys bloti	121011??1???31??13101000100?00???110010???????11??0?11?1??20??21????00

Conclusion

This study presents a comprehensive analysis of the taxonomy and stratigraphy of Australian Mesozoic fishes and determined that the Australian Mesozoic localities have a huge potential to add to the diversity of fossil fish knowledge from the Southern Hemisphere. Within Australia, research has gained pace with regards to taxonomy of Mesozoic vertebrate taxa, in particular the dinosaurs (Poropat et al., 2023 and references therein) but many fossil fish that have been co-recovered await study. Likewise, Mesozoic sharks are well documented from Western Australia (Berrell et al., 2020 and references therein; Siversson 1996) and there is increased work on the co-occurring marine reptiles (Poropat et al., 2023 and references therein); however, the actinopterygian fish fauna remains undescribed.

Vertebrate microfossils from the Toolebuc Formation (Eromanga Basin), whilst small and easily missed, constitute an important part of the fauna from the Eromanga Sea during the Early Cretaceous. Until now (Berrell et al., 2020), these microfossils were undescribed. Isolated elements from an actinopterygian were described using terminology in Arratia (1997) and shark teeth were described using the terminology of Cappetta (2012), both of which demonstrated the ability to identify taxa from micro-remains, thereby increasing the known diversity for the fauna. The microvertebrate assemblage was dominated by mostly benthic taxa (*Echinorhinus australis* and the lizardfish taxon *Apateodus* sp.), with occasional appearances from taxa that existed within the epipelagic zone (e.g., *Pachyrhizodus* sp.). This thesis highlights the necessity of detailing the microvertebrate fauna in addition to the macrovertebrate fauna when determining faunal diversity.

The Triassic Kockatea Shale (Perth Basin) had limited documented fossils, with those known recovered primarily from oil and gas drill cores. These fossils were mostly described as ‘fish mash,’ containing partially articulated osteichthyan skeletal elements (Dickins and McTavish, 1963; Metcalfe et al., 2008). It was possible to use terminology in Yabumoto and Neuman (2004) to describe coelacanth scales, and to use terminology from Marramà et al. (2017) to describe isolated actinopterygian scales and jaw elements with an unpaired gular attached. Based on the fossils retrieved, at least two marine fish taxa were documented: a coelacanth and an actinopterygian with similarities to *Teffichthys*. In addition, it was determined that the fishes from the Kockatea Shale were more closely related to fossils from co-eval faunas of Madagascar than to similar-aged faunas of eastern Australia. This could be partly explained by similar depositional environments, with both the Madagascan localities and the Kockatea Shale representing marine settings. Palynomorphs, which were used to date the Kockatea Shale, demonstrated that the age of the Blina Shale, which shares the temnospondyl taxon *Deltasaurus,* could be revised in age from Induan to Olenekian.

The investigation of historical collections of multiple fish of the genus *Promecosomina*, recovered from the Triassic of the Sydney Basin and housed in the Australian Museum, revealed individuals across multiple size ranges and, although previously attributed to different species (Wade 1935), this thesis indicates they instead represented an ontogenetic series. The type specimen, with a standard length of < 15 cm, is interpreted here as a juvenile, and additional fossils recovered in the 1980s showed the presence of larger fish with a standard length up to ~26 cm. It was confirmed that only one species (*P. formosa*) is present and that specimens previously attributed to *P. beaconensis* are the juveniles of *Promecosomina formosa*. Therefore *P. beaconensis* is a junior synonym of *P. formosa* (Chapter 3 submitted).

Using the phylogenetic analysis of Ebert (2018) for the Halecomorphi, an additional seven taxa of Parasemionotiformes were coded, with *Promecosomina formosa* being coded for the first time. This study altered the previous hypothesis of relationships within the Parasemionotiformes (Ebert 2018), resolving *Promecosomina* within the Parasemionotidae. Because of this, the family Promecosominidae erected to contain *Promecosomina,*is left with no members, Promecosominidae is therefore considered invalid (Chapter 3). *Watsonulus* which had previously been used in phylogenetic analyses (Feng et al., 2023; Ebert 2018; Grande and Bemis 1998; Lambers 1995; among others) to represent the Parasemionotidae, is resolved basal to this family. This demonstrates the need to use more than one genus to represent a family in phylogenetic analyses. The phylogenetic analysis presented here indicates that the Parasemionotidae originated in Gondwana, with an unnamed sister group containing fishes from Laurasia.

Isolated toothed elements from the Late Cretaceous Griman Creek Formation, Lightning Ridge, New South Wales have previously been referred to as “teleosts”. Further description of these elements using terminology and taxonomy from Grande and Bemis (1998) refutes this assignment and instead, they are identified as the genus *Calamopleurus* that had its origins from the Early Cretaceous of Brazil and Late Cretaceous of Africa. This is significant as it suggests that there was faunal interchange between west and east Gondwana during the Early–Late Cretaceous.

Early actinopterygians of the Mesozoic were highly mobile, with some taxa showing wide distribution across both, freshwater and marine environments. The general assumption (e.g., Cavin 2008) that some fossil forms were restricted by geographic barriers such as deep marine basins and continental configurations can no longer be sustained (Berrell et al. 2014 and Berrell et al. 2023). During the Cretaceous, shallow marine–estuarine conditions existed between South America and Africa as they split. The new north-south seaway is thought to have aided migration through linking multiple shallow marine environs, allowing for distribution of typically Brazilian/African taxa (i.e., *Cladocyclus* and *Calamopleurus*). The currents that developed as a result of Africa and South America rifting apart are thought to have aided dispersion southwards (see Chapter 4). The Australian record contains Gondwanan colonizers from Africa / South America with some endemics. This indicates that there was faunal interchange from west to east Gondwana and that this was not only restricted to the terrestrial fauna such as the dinosaurs (Poropat et al. 2016).

The actinopterygian *Dugaldia* was originally described from a single isolated specimen discovered from the Toolebuc Formation near Cloncurry in Queensland (Lees 1990) and assigned as a neoteleost based on several plesiomorphic characters and a tripartite occipital condyle. Additional specimens recovered from the Toolebuc Formation near Richmond, Queensland have allowed the description of morphological features not present in the original specimen, and the reinterpretation of the skull shows the presence of an ethmopalatine, a bone exclusive to the Ichthyodectiformes, found in the floor of the nasal cavity (Patterson and Rosen 1977). In addition, *Dugaldia* exhibits several characters (a well-ossified ethmoid massif, with ethmopalatine ossification; disk-like articular head of the autopalatine, sickle-shaped maxilla with two supra maxillae; large infraorbitals; participation of the exoccipitals in the occipital condyle; coronoid in contact with its counterpart; elongated ribs with groove; elongated epineurals and deeper than long ovoid scales) which indicate it is an ichthyodectiform and this is confirmed by a phylogenetic analysis. However, it resides outside the Ichthyodectidae and is united as a sister group to *Ogunichthys triangularis*.

The objective of this thesis was to determine if the view that the modern depauperate freshwater actinopterygian fauna in Australian was the result of a lack of diversity in the Mesozoic fish fauna or the result of a lack of knowledge pertaining to the fossil record. The increased number of taxa described herein, the large amount of material that remains undescribed, and the existence of underexplored Mesozoic sites indicate that the fossil record of Australian Mesozoic fishes is understudied. Determining if the diversity of extant fishes is correlated with Mesozoic diversity cannot be determined until further paleontological work is undertaken across the Australian continent.

Future research

Future work is required in three main areas: the first is that currently described taxa need to be redescribed (many descriptions are over 100 years old) and undescribed taxa in museum collections require description. The second is that, following re-description or primary description, taxa need to be placed within a phylogenetic context to test the hypotheses of relationships. The third area of research is that underexplored or unexplored strata must be surveyed for fossil fish remains.

Most of the fishes from the Triassic Sydney Basin require revision considering updated taxonomic nomenclature. For example, fish previously attributed to Perleididae include several Australian taxa: *Manlietta crassa* and *Procheirichthys ferox* (Wade 1935), although the Triassic Perleididae have recently been redefined (Marramà et al. 2017) following the discovery of additional specimens of the type genus *Perleidus* from Italy that show a different caudal fin morphology than that of other "*Perleidus*" described from Africa, Canada, China, Greenland and Madagascar (Marramà et al. 2017). Because the Madagascan specimens exhibit a unique combination of skull dermal bone pattern along with the structure of the caudal fin, they have been excluded (Marramà et al. 2017) from the Perleidiformes with Marramà et al. (2017) erecting a new genus (*Teffichthys*). This suggests that the Perleidiformes may represent a paraphyletic group, similar to that noted for the Parasemiontiformes in Chapter 3 (and discussed above).

The fishes from the Eromanga Basin have typically been referred to the same taxon (Bartholomai 2004; Bartholomai 2012), despite a 35-million-year time span from the base of the section to the top of the section (Tucker et al., 2013). A detailed taxonomic review is required to determine if the taxa are the same and thus long-ranging, or if instead there are morphological differences indicating the presence of multiple taxa with a more constrained time ranges.

There are many specimens within museum collections across Australia that remain undescribed. Examples include chimaerid tooth plates and teleost (?Elopomorpha) tooth plates from the Griman Creek Formation, actinopterygians from the Giralia

Formation in Western Australia and new specimens recently collected from the Winton Formation. There is much work still to be undertaken within current collections and this is compounded by the large amount of material currently being added through extensive collecting of dinosaurs around Winton (Poropat et al., 2023 and references therein).

Work is ongoing regarding the descriptions and taxonomic placement of undescribed halecomorph fish from the Jurassic Talbragar Fish Beds by Dr Lynne Bean from ANU an undescribed halecomorph from the Toolebuc Formation.

The above summary shows the magnitude of work still to be undertaken in Australia in all aspects of Mesozoic osteichthyan research and the opportunities that remain in the area of palaeoichthyology in Australia.

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Appendix 1 - Attributions of work

Chapter 1 – Mesozoic Fishes of Australia

To Whom It May Concern

I, *Rodney William Berrell* contributed *(conceived the idea, wrote the manuscript, liaised with co-authors, created the majority figures, submitted the paper for peer review)* to the paper/publication entitled *Mesozoic Fishes of Australia: localities, taxonomy taphonomy and biogeography* submitted for consideration to be published in An *Australasian Journal of Palaeontology: Alcheringa.*

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Chapter 2 – Early Triassic (early Olenekian) Marine fishes of East Gondwana (Kockatea Shale) Western Australia

To Whom It May Concern

I, *Rodney William Berrell* contributed (identification of Osteichthyan remains, *Writing - Original draft preparation for peer review)* to the paper/publication entitled: Early Triassic (early Olenekian) life in the interior of East Gondwana: mixed marine–terrestrial biota from the Kockatea Shale, Western Australia. Submitted and published in *Palaeogeography, Palaeoclimatology, Palaeoecology*.

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Chapter 3 - A redescription of the basal halecomorph fish *Promecosomina formosa* Woodward 1908 from the Early Triassic of the Sydney Basin, New South Wales, Australia

To Whom It May Concern

I, *Rodney William Berrell* contributed *(Conceptualization, Methodology, Writing - Original draft preparation submitted the paper for peer review)* to the paper/publication entitled: A redescription of the basal halecomorph fish *Promecosomina formosa* Woodward 1908 from the Early Triassic of the Sydney Basin, New South Wales, Australia. Submitted for consideration to be published in Journal of Systematic Palaeontology.

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I, as a Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate.

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Chapter 4 – The first record of amiid fishes (Halecomorphi, Amiiformes, Amiidae, Calamopleurini) from Eastern Gondwana

To Whom It May Concern

I, *Rodney William Berrell* contributed *(Conceptualization, Methodology, Writing - Original draft preparation submitted the paper for peer review)* to the paper/publication entitled: *The first record of amiid fishes (Halecomorphi, Amiiformes, Amiidae, Calamopleurini) from Eastern Gondwana*. submitted for consideration to be published in Cretaceous Research.

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Chapter 5 – Revision of *Dugaldia emmilta* (Teleostei, Ichthyodectiformes) from the Toolebuc Formation, Albian of Australia, with comments on the jaw mechanics

To Whom It May Concern

I, *Rodney William Berrell* contributed *(Contributed to the introduction, wrote the geological setting, constructed figures 1 & 2, contributed to materials and methods, provided edits and comments to text as required)* to the paper/publication entitled *Revision of Dugaldia emmilta (Teleostei, Ichthyodectiformes) from the Toolebuc Formation, Albian of Australia, with comments on the jaw mechanics* submitted for publication in the *Journal of Vertebrate Paleontology*.

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Appendix 2 – Copyright statements

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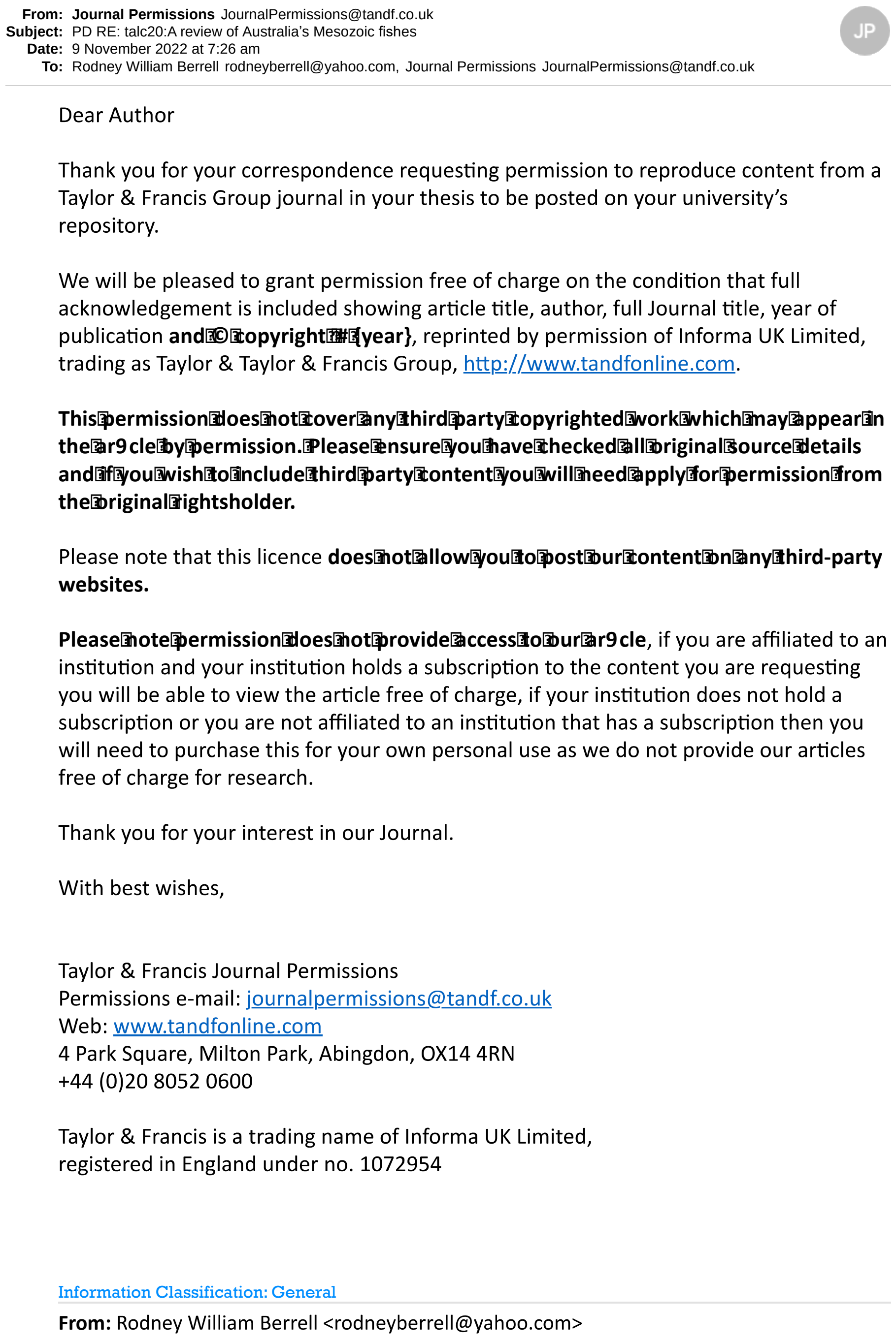

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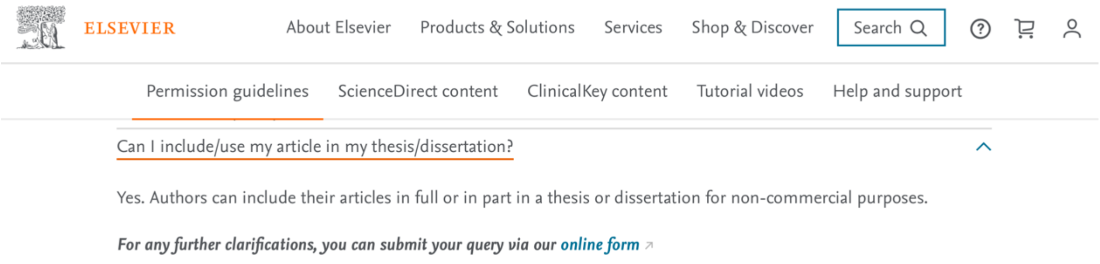

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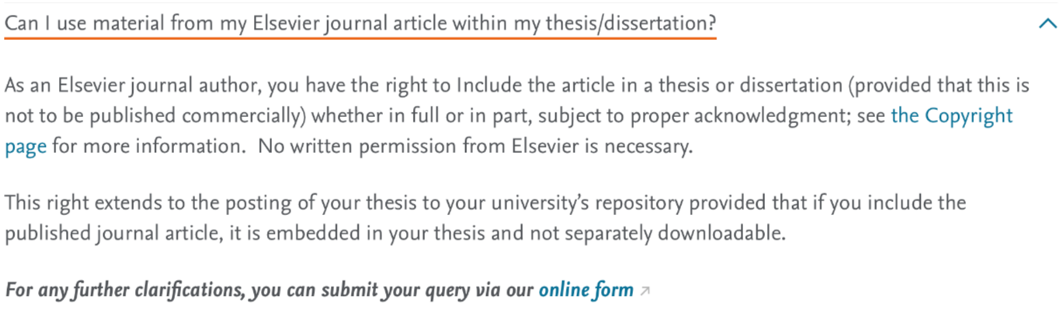

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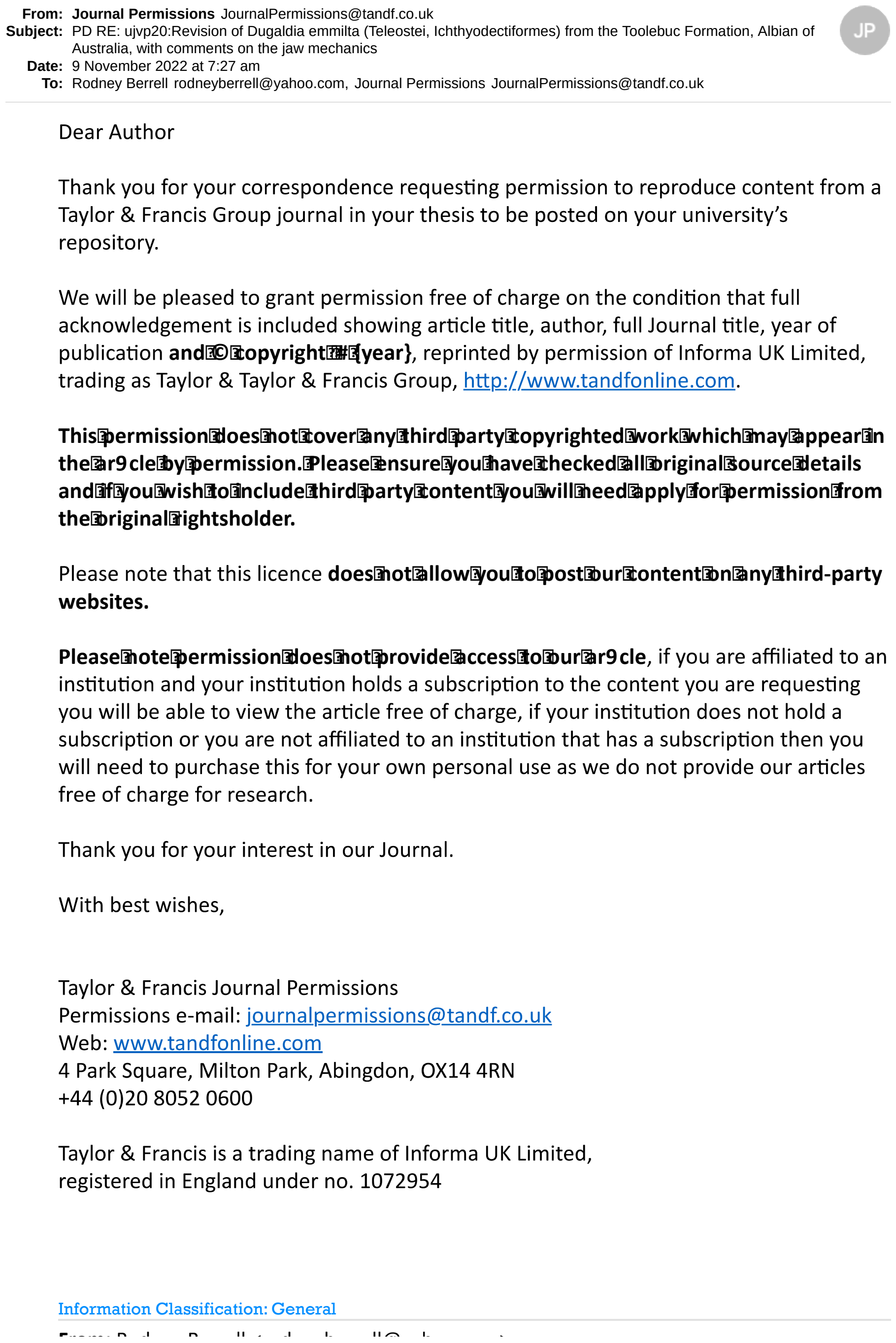

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