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REAPPRAISAL OF MESOZOIC FISHES AND ASSOCIATED INVERTEBRATES AND FLORA FROM TALBRAGAR AND KOONWARRA, EASTERN AUSTRALIA

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ABSTRACT: Eastern Australia has two major Mesozoic fossil localities. The Talbragar Fish Bed in central west New South Wales contains an assemblage of Upper Jurassic fishes, plants and insects. The Koonwarra Fossil Bed, in South Gippsland, Victoria, has an assemblage of Lower Cretaceous fishes, plants and insects. The geological settings of these localities are described. Each locality has a common genus of fish that was originally described as *Leptolepis*. The names of both these fish have been changed, the Talbragar one to *Cavenderichthys talbragarensis* and the Koonwarra one to *Waldmanichthys koonwarri*. Both of these fish have been placed into the Family Luisiellidae, together with a Patagonian fish, *Luisiella feruglioi*. Each locality also has a member of the family Archaeomenidae: *Archaeomene tenuis* from Talbragar and *Wadeichthys oxyops* from Koonwarra. The relationships of these and other fish have been discussed by various authors over the last 20 years and a summary of these comments is presented, as well as a brief comparison between the plants of both localities. The localities of Talbragar, Koonwarra and the Argentinian fishes during the Mesozoic appear to have similar palaeo-environmental settings, which may explain the similarities in the assemblages. The Australian localities contain well-preserved specimens which shed light on the diversity and extent of fishes in southern Gondwana, a region otherwise poorly represented in the fossil record.

Keywords: Talbragar, Koonwarra, Luisiellidae, Archaeomenidae, Mesozoic, *Cavenderichthys*, *Waldmanichthys*

IMPORTANCE TO SCIENCE

Mesozoic fishes include some of the earliest forms of teleosts, which are advanced forms of the ray-finned fishes (Actinopterygians) and are the most abundant and diverse fishes in marine and fresh waters today. Studying these fossils provides an important insight into the evolutionary history of life. The Southern Hemisphere has limited exposures of Mesozoic fish-bearing strata, and in comparison with the Northern Hemisphere very little is known about them. Recent discoveries in China (Rich et al. 2012) have exposed sites with similar lithologies and assemblages of fossils to the two Australian sites described here, but no detailed comparisons could be made because more work needs to be done on the Australian localities.

The Talbragar Fish Bed, located in central New South Wales, 125 km east of the regional city of Dubbo and 26 km northeast of the village of Gulgong, is one of the best fossil sites for studying Jurassic fishes in Australia (Figure 1). It contains well-preserved external moulds of at least eight fish genera, many plant fragments and, due to recent discoveries, an increasing number of insects. The site was discovered in 1889 and its importance was recognised immediately, to the extent that several bullock-dray loads of rock were removed and taken to Mudgee railway station (about 57 km away), then to Sydney, where the best specimens were selected and shipped to London for identification by A.S. Woodward at the British Museum. The most common fish was named *Leptolepis talbragarensis* and specimens became widely distributed among research institutions in Australia and beyond.

Little work has been done on these fishes, especially the non-leptolepid fish, over the years since Woodward published in 1895. Between 2000 and 2007, the author organised several digs and collected many more specimens, as well as located about 250 additional specimens in the curated collections of the NSW Department of Mines (now Department of Industry, Resources and Energy), the Australian Museum in Sydney and Museums Victoria in Melbourne.

At the International Conference on Mesozoic Fishes in Madrid in 2005, the author's presentation on *Cavenderichthys talbragarensis* and the other Talbragar fishes that were not so well known raised considerable interest among researchers from the Northern Hemisphere, many of whom had not seen these taxa before. Mesozoic fish expert Gloria Arratia (pers. comm. 2005) stressed the importance to workers outside Australia of more detailed descriptions and analyses of Australian examples of fish so that their phylogenetic relationships could be determined. She also supported a comparison of the Talbragar assemblage with that from Koonwarra in Victoria.

Fossils have been known from the Koonwarra fossil fish site, which is located about 145 km southeast of Melbourne, since the 1960s. According to Waldman (1971), fossils were discovered by workmen straightening

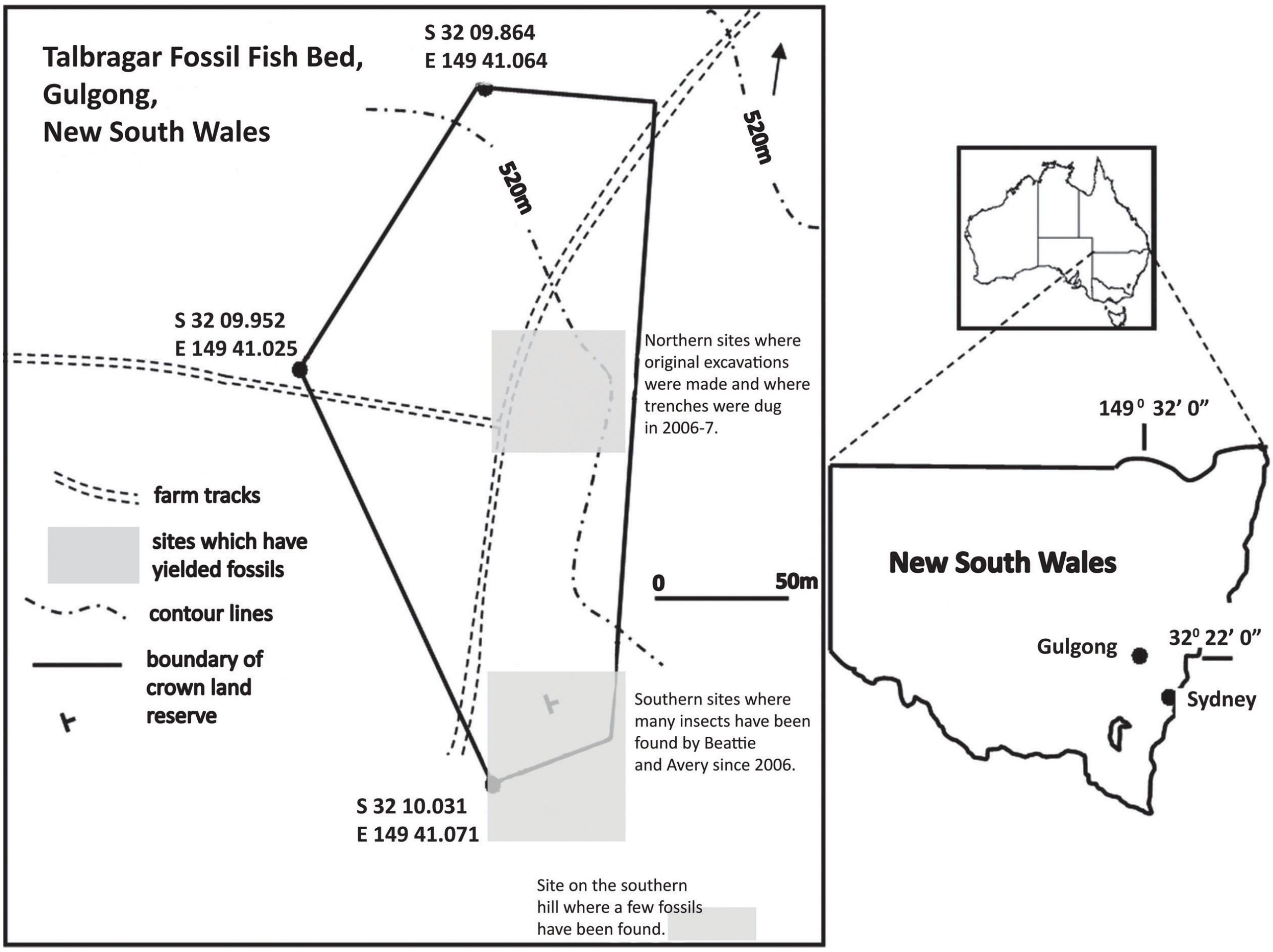

Figure 1: Location map of the Talbragar Fish Bed, modified from Beattie and Avery (2012).

out a bend in the South Gippsland Highway in 1962. The University of Melbourne, National Museum of Victoria (now Museums Victoria), and the Victorian Mines Department then made collections primarily from the north side of the highway. Excavations on the south side of the highway were commenced by Monash University staff and students early in 1966, and extended by staff from the University of Melbourne and the National Museum of Victoria in February 1981. Tom Rich, Curator of Vertebrate Palaeontology at Museums Victoria, has been lobbying to reopen the site for many years, but funding for it has yet to be arranged. In 2013 he arranged a small dig to gauge the parameters needed to open an area suitable to make a comparison with the Jehol Biota in China. He has observed that 'An abundance of exquisitely preserved birds, mammals and feathered dinosaurs, among other fossils, has been recovered from the Early Cretaceous Jehol Biota of north-eastern China (Li et al 2011). The similarities both in the nature of those deposits and the plant, arthropod and fish fossils they contain to those from the lacustrine (lake) facies of the Strzelecki Group of south-western Gippsland in Victoria, Australia, suggests that a prolonged, systematic search of the latter could yield tetrapods of similar quality.' (T. Rich, pers. comm. 2016).

GEOLOGICAL SETTING

The Talbragar Fish Bed

The geology of the Talbragar Fish Bed was first described in a foreword to the paper by Woodward (1895) in which he described six fish taxa. T.W. Edgeworth David and Edward Pittman, in a foreword entitled 'A note on the stratigraphy of the fish-bearing beds of the Talbragar River', first summarised the geology of the local area as follows: 'The Fish Beds proper form the lowest of the three members into which, on lithological grounds, the deposit to which they belong may be divided. They consist of laminated, hard, siliceous shales, cherty in places, rendered ochreous by ferruginous infiltrations, and traversed by joints. Their bedding is almost horizontal, as far as can be judged from their line of outcrop, which can be traced for about ten chains. Their exact thickness was not observable, but appeared to be about ten feet. Fish and plants are so abundant that it is difficult to find even a small fragment of the shale devoid of them. The plants are preserved in the form of siliceous impressions, their pure white colour contrasting with the ochreous tint of the enclosing shale.'

The stratigraphy and physiography of the Talbragar Fish Bed have been outlined by several authors (Dulhunty

1937; Dulhunty & Eadie 1969; Hind & Helby 1969; Percival 1979; Pogson & Cameron 1999). More recently, a detailed description of the palaeoenvironment was published by Beattie & Avery (2012). Their map provides information about the location of the original or northern site and the insect-rich southern site, where the most recent excavations have taken place (Figure 1). The location of the Talbragar Fish Bed is within a few kilometres of the northwestern extent of outcrops of the Triassic rocks of the Sydney Basin. Sandstone cliffs, equivalent to Hawkesbury Sandstone, which are exposed nearby, are a feature of the upper strata of this basin, whose depositional history extended from the late Carboniferous through to the Jurassic. (http://www.environment.nsw.gov.au/bioregions/SydneyBasin-Landform.htp). It is assumed that all the Jurassic deposits have been eroded, leaving the Talbragar Fish Bed as an isolated remnant of a north-flowing fluvial system. Despite some searching in the local area, no other outcrop of a comparable rock has yet been documented.

The Talbragar Fish Bed is largely a fine-grained mudstone with well-defined thin bedding preserved in sub-horizontal layers. Evidence from the fauna and flora suggest it is a freshwater lacustrine deposit (Bean 2006; Beattie & Avery 2012).

The northern site. During two digs in April and October 2006 three trenches were excavated running east–west across the site. For the first trench, a stratigraphic column was constructed by Robert Jones and Yong-Yi Zhen from the Australian Museum. This showed an upper layer of fossil-bearing rock that was finely bedded, deeply iron-stained and about 30–40 cm thick, above a layer of more massive material, still fine-grained and highly fossiliferous, but generally paler in colour, and underlain by clay. During the second dig, another trench dug 10 m to the north of the first trench and parallel to it revealed essentially identical stratigraphy. A third trench dug about 20 m to the west of the second trench, on the other side of a farm access track (see Figure 1), necessitated the removal of more than 1 m of topsoil before the fossil-bearing layers were encountered. In the western extent of this trench the first rocks encountered were only iron-stained along joint cracks, with little penetration of iron-staining into the body of the joint blocks, which are white with extremely fine bedding. Fossils are still abundant, but without the iron-staining and the subsequent cementing by weathering processes they are harder to see, and very difficult to work with, due to the rock's softness and absence of fossil replacement. There are still two discernible layers, the upper about 30–40 cm thick and the lower about 50–60 cm thick, both essentially white.

The rock exposed became more iron-stained towards the eastern end of the trench, like the material in the other two trenches. This pattern of iron-staining may be evidence of the depth of weathering, rather than the presence of overlying Tertiary basalt as was previously postulated (Bean 2006). Plant fossils do not generally take up the iron oxide, so in the clear majority of cases they remain white, replaced with siliceous material, while the fish are often brown. Black manganese oxides may coat some fossils that are close to joint planes. Only by spending some time on the site and examining many samples is it possible to develop a more accurate picture of what the environment of deposition might have been. Rock samples without fossils that are commonly discarded by palaeontologists looking for good specimens often show evidence of slumped bedding, coarser grain-size, higher velocity currents, and even ripple marks. In a few samples, mud cracks or sand infilling can be seen, which indicates that at some time the lake dried up. The presence of two large (>40 cm) and so far unidentified fish, which were found in the central part of the first dig in 2006, is evidence that this area was, at certain times, covered by relatively deep water. A specimen of the deep-bodied fish *Aetheolepis* was found nearby. The former two fish were found near the top of the lower layer, suggesting that it represents a slightly different environment of deposition from the top layer. Bean (2006) suggested that a volcanic eruption depositing tuffaceous material may have filled in a billabong and ended deposition. However, a thorough sedimentological assessment is required to determine the most likely palaeoenvironment.

The southern site. Only a few insects and one arachnid were found in the northern site by palaeontologists before 2000, but recent exploration in the southern part of the site has been more productive (Figure 2). During the first dig in 2006, most of the searching was carried out in the northern section of the excavation and on that occasion only a few insects were unearthed. During the second dig, in October 2006, an area about 400 m south of the main excavation was explored by entomologists Robert Beattie, Sarah Martin and Steven Avery. This yielded about ten specimens, which is a relatively rich haul for insects. Since then more than 20 weekend collecting trips have been undertaken by Beattie and Avery, and other colleagues who have been trained in insect-searching techniques. More than 400 insects have been found, as well as a few spectacular fish. The environment of deposition seems to be rather different from the northern site. While the sediments are much the same, namely mudstone with deep iron-rich weathering, the bedding is not so well defined and the plant material is quite different. There is an aquatic macrophyte, tentatively considered a filamentous alga, which probably made up the base of the food web, and was previously incorrectly ascribed to *Selaginella* (White 1981; Beattie and Avery 2012). In the insect locality, molluscs have also

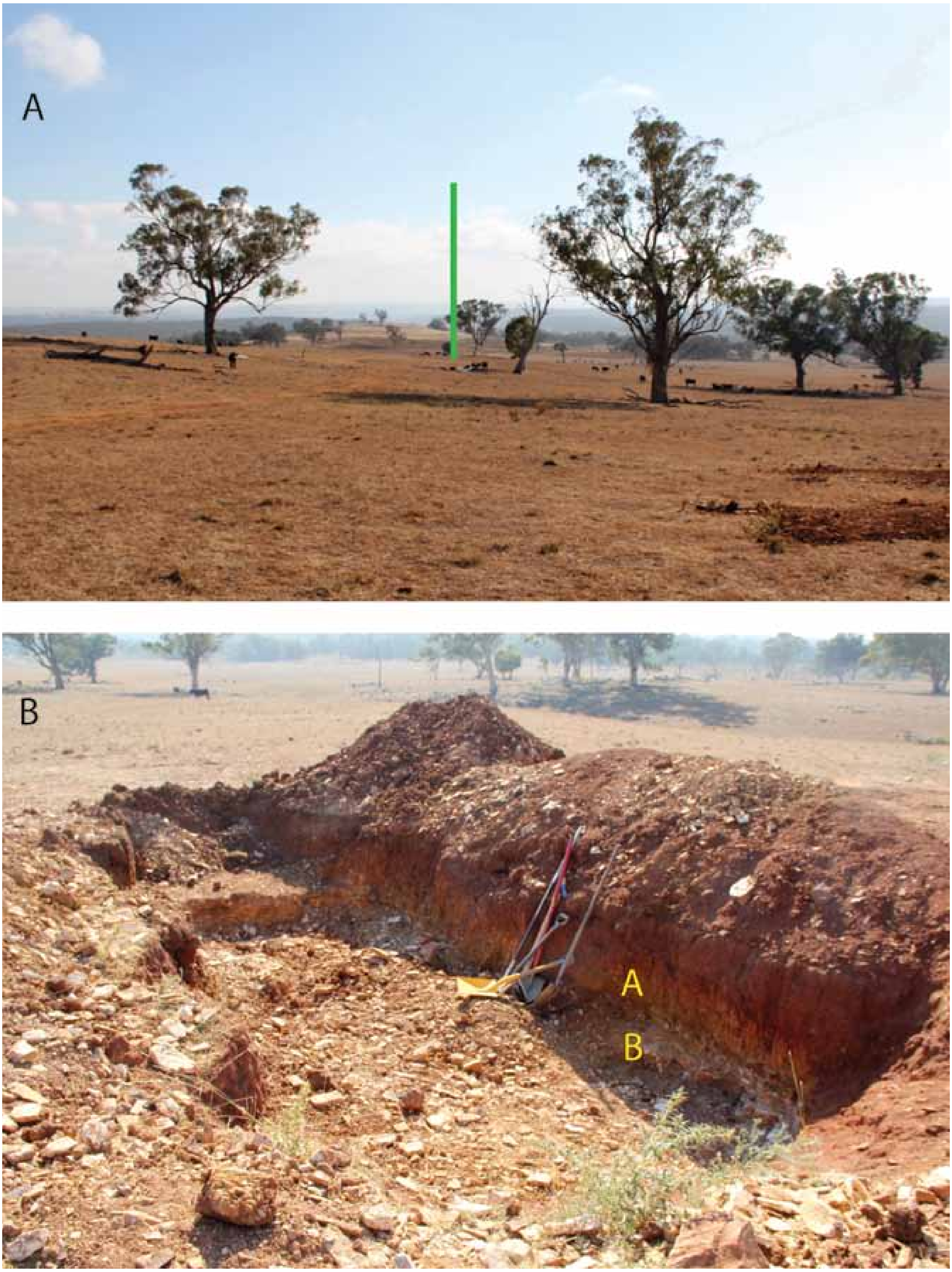

Figure 2: A. Talbragar site, looking north from the southern site. The base of the green line indicates the location of the original northern site. B. Excavation at the southern site. Yellow letters show positions of layers A and B.

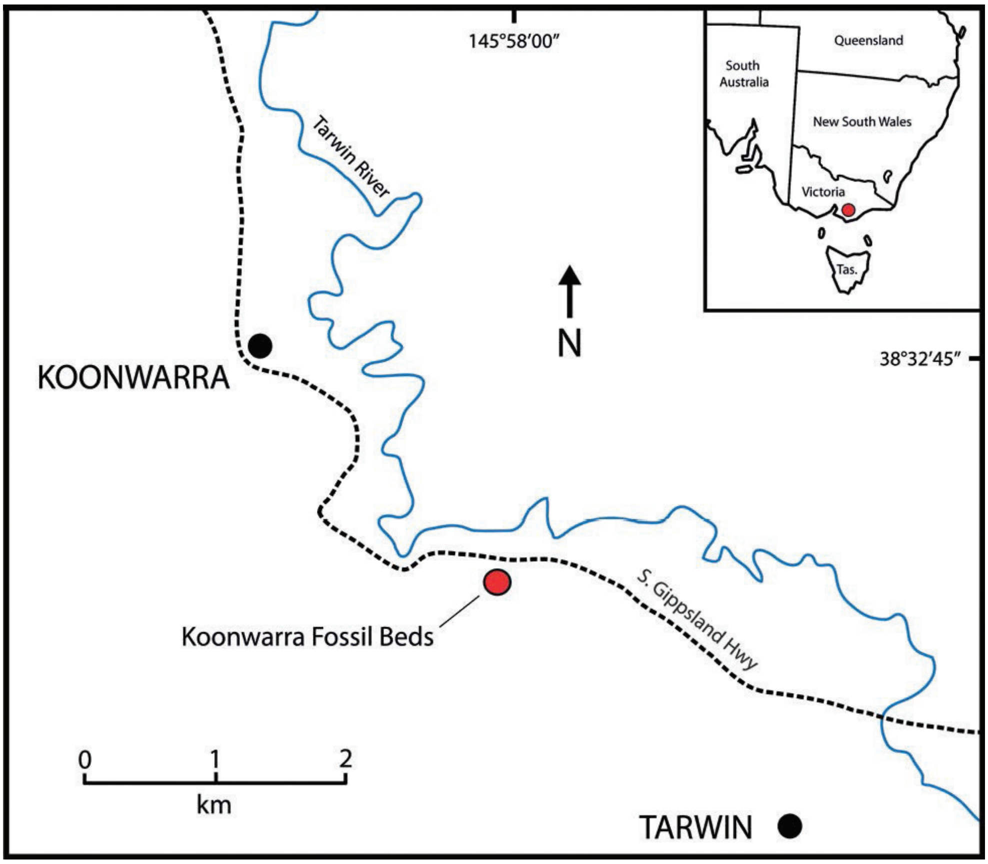

Figure 3: Locality map for the Koonwarra Fossil Bed. From Tuite et al. (2016) with permission.

been found, both bivalves and gastropods. Interestingly several large coprolites were found in the main northern excavation which consisted almost entirely of bivalves and gastropods. The molluscs in the coprolites are small, less than 0.5 cm, but obviously enough to provide a meal for a fish. The most common fish found so far in the southern site is *Cavenderichthys,* although in 2016 a good specimen of *Aphnelepis australis* was found. The insects found in this site include gelastocorids (shoreline predatory toad bugs), a spider, weevils and numerous other terrestrial beetles (Beattie & Avery 2012). All these factors seem to indicate a shallow-water environment, which may represent the edge of the lake.

The Koonwarra Fossil Bed

The geology of the Koonwarra Fossil Bed (Figure 3) was first described by Waldman (1971), who observed a stratigraphic succession consisting of an upper arkose layer ~34.5 m thick, then a fossiliferous mudstone sequence ~7m thick, and a lower arkose ~11.5 m thick. Within the mudstone succession, clay layers alternate with siltstone/claystone layers, interpreted as an accumulation of varved sediments in a cold-water lake with seasonal anoxia related to ice formation and thawing. The idea of seasonal freezing during the Early Cretaceous in this high-latitude location was supported by Frakes & Francis (1988), based on the presence of outsized exotic blocks of glacial origin in strata of a similar age in Central Australia. Drinnan & Chambers (1986), noted that the fossiliferous layers comprised ‘8 m of fine-grained mudstone interbedded between two fluvial arkosic sandstones. The mudstones consist of graded laminae of various thicknesses composed of alternate layers of claystone and siltstone and strike 230–235^0 with a dip of 35–40^0 S; they represent a lacustrine environment in the predominantly fluviatile sediments of the Victorian Lower Cretaceous’.

The February 1981 excavation was mainly to collect plant material, but also yielded two samples for radiometric dating. Apatite assumed to be volcanogenic and obtained from 7 m above the fossiliferous layers yielded a fission-track age of 115+/-6 Ma, while a second sample from immediately below the fossil-bearing layers gave an age of 118+/-5 Ma (Lindsay 1982).

Some of the significant plants described by Drinnan & Chambers (1986) from Koonwarra include the liverworts, *Dendroceros victoriensis* and *Riccardia koonwarriensis;* a horsetail, *Phyllotheca wonthaggiensis*; the fern-like *Sphenopteris warragulensis*; ferns, *Cladophlebis biformis, Thinfeldia* sp.; pentoxylate *Taeniopteris daintreei; Ginkgo australis.* There are also conifers, including Podocarpaceae (*Brachyphyllum gippslandicum)* and Araucariaceae.

The most comparable Mesozoic flora with the

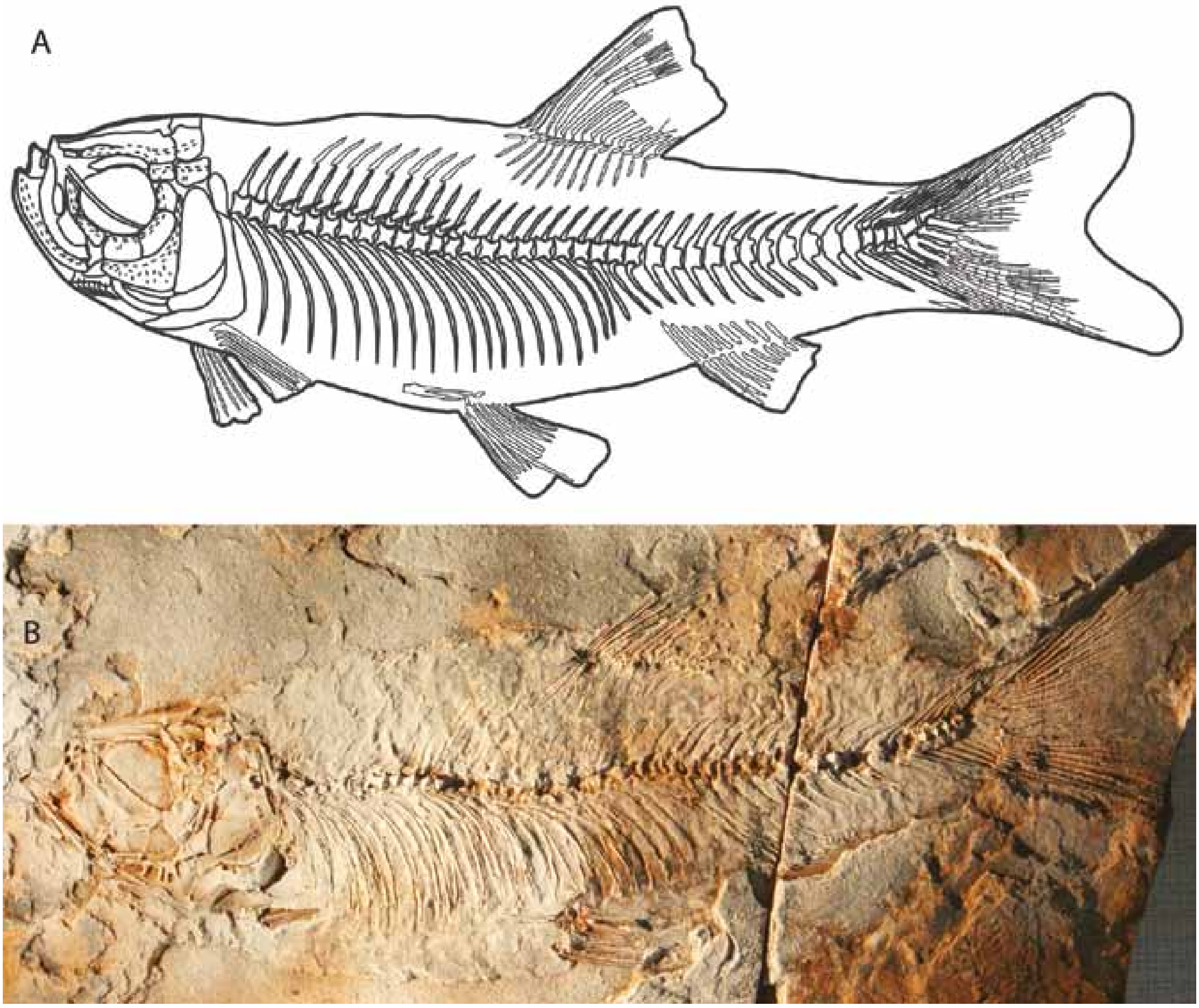

Figure 4: A. Reconstruction of *Cavenderichthys talbragarensis* (Woodward) by Bean (2006). B. Specimen of *C. talbragarensis* supporting original reconstruction. Photo by the author; fossil in the private collection of Rodney Berrell.

Koonwarra flora is that of the Rajmahal Series of India. The comparable species are *Sphenopteris hislopi; Cladophlebis indica; Thinfeldia indica; Nipaniophyllum raoi (cf Taeniopteris daintreei); Ginkgo rajmahalensis;* and *Brachiphyllum mammilare.*

The Talbragar flora contains four comparable species: *Coniopteris hymenophylloides (*cf. *Sphenopteris travisi); Thinfeldia talbragarensis; Taeniopteris spatulata; Brachyphyllum* sp. (Drinnan & Chambers 1986). The similarity between the Talbragar and Koonwarra flora suggests that the two sites shared a similar palaeoenvironment. It also shows that some of these plants existed for a considerable time without much change.

The insects from Koonwarra have been studied by Jell & Duncan (1986) and are diverse. Some were lacustrine, such as larvae and immature forms of mayflies, dragonflies, scorpion-flies, stoneflies, caddis flies and dytiscid and hydrophilid beetles. The terrestrial fauna included adult dragonflies, scorpion-flies, carabid and staphylinid beetles, which scavenged the leaf litter, parasitic wasps which attacked wood-boring beetle larvae, and a few pulicid fleas which might indicate marsupials were in the vicinity (Jell & Duncan 1986).

A few feathers found at Koonwarra were thought to be from a small bird, but since small feathered dinosaurs were discovered in the Jehol Biota in China, their origin is less certain (T. Rich, pers. comm. 2016).

TAXONOMIC HISTORY OF THE FAMILY LUISIELLIDAE

A.S. Woodward (1895) was the first to describe the Talbragar fishes, naming *Coccolepis australis*, *Aphnelepis australis*, *Aetheolepis mirabilis*, *Archaeomaene tenuis*, *Leptolepis talbragarensis, Leptolepis lowei* and *Leptolepis gregarious*. Wade (1941) concluded that '*Leptolepis lowei*' and '*Leptolepis gregarious'* were actually members of the species *Leptolepis talbragarensis*, being variants due to ontogeny and state of preservation.

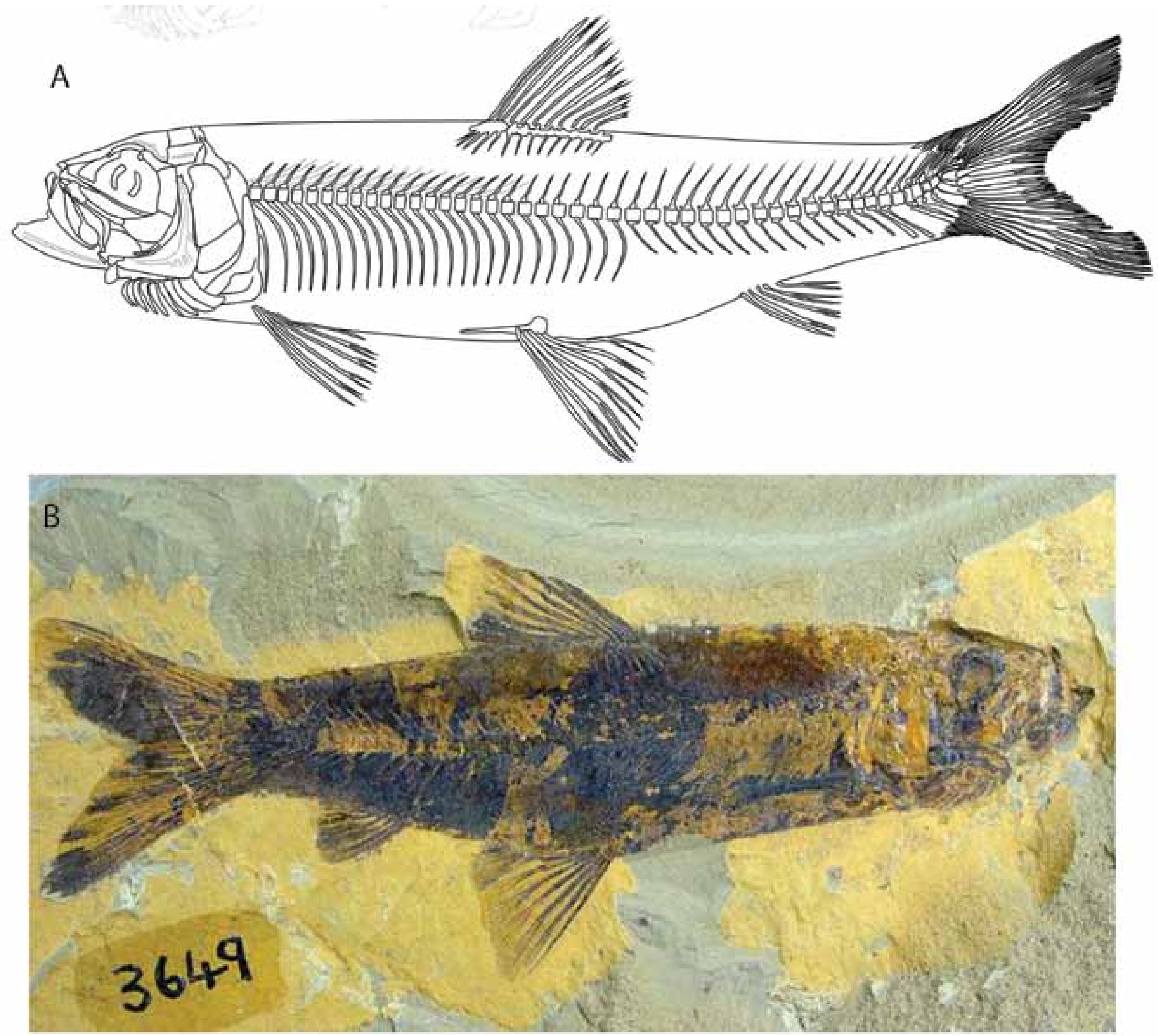

Figure 5: A. Reconstruction of *Waldmanichthys koonwarri* by Lionel Cavin (pers. comm. 2016). B. New photograph by the author of *W. koonwarri*, one of several used to check characters. Museums Victoria P197819 holotype.

Cavender (1970) published a comparison between coregonines and other salmonids and the earliest known teleostean fishes, in which he partly redescribed and re-drew *Leptolepis talbragarensis* and concluded that it was probably not a member of the genus *Leptolepis*. Arratia (1997) renamed the fish *Cavenderichthys talbragarensis*, but did not include a full description as Cavender indicated he was still working on it. The author redescribed *Cavenderichthys* based on new material collected from Talbragar and investigated its relations with other fish, but did not carry out a phylogenetic analysis (Bean 2006). It was concluded that the species *L. lowei* and *L. gregarious* both belonged to *Cavenderichthys talbragarensis* (Figure 4).

Waldman (1971) described *Ceratodus* sp. from Koonwarra, as well as four new species which he named *Coccolepis woodwardi*, *Koonwarria manifrons*, *Leptolepis koonwarri* and *Wadeichthys oxyops,* a member of the Archaeomenidae. It is now obvious that *Leptolepis* cannot be the genus for *L. koonwarri*, any more than it can be for *L. talbragarensis.* Sferco et al. (2015a) included an anatomical description of *Luisiella feruglioi* that highlighted its many similarities to *Cavenderichthys talbragarensis* and *Waldmanichthys koonwarri* (Figure 5). Sferco et al. (2015b) published a phylogenetic analysis and erected a new clade of freshwater teleosts from the Jurassic of Gondwana, Luisiellidae, which contains *Luisiella feruglioi* from Patagonia and *Cavenderichthys talbragarensis* from New South Wales, together with the newly named *Waldmanichthys koonwarri* from Victoria (Figure 6). Sferco et al. (2015a) included an anatomical description of *Luisiella feruglioi* that highlighted its many similarities to *Cavenderichthys talbragarensis* and *Waldmanichthys koonwarri* (Figure 5). Cavin has reviewed the characters of *Waldmanichthys* (L. Cavin, pers. comm. 2016), and the author has reviewed characters of *Cavenderichthys* used in the phylogenetic analysis of Sferco 2015b. The details of these reviews will be published subsequently.

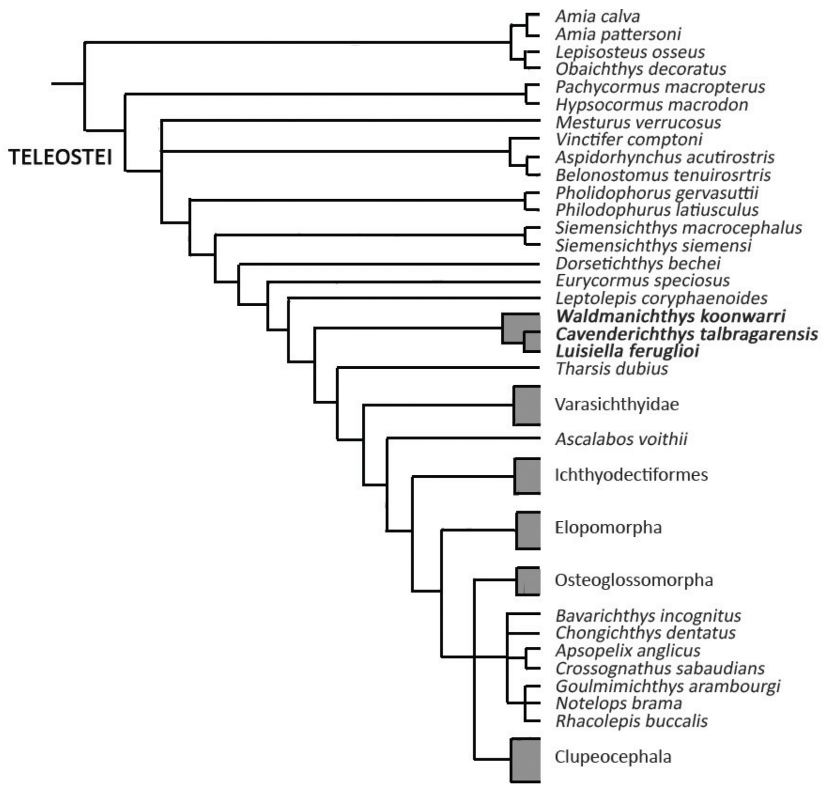

Figure 6: Simplified strict consensus tree modified after Sferco et al. (2015b). The clade with bold species names is Luisiellidae, including two Australian forms. The Archaeomenidae were not included in their analysis due to lack of data.

TAXONOMIC HISTORY OF THE FAMILY ARCHAEOMENIDAE

When Woodward (1895) described the fish from Talbragar, he placed *Aphnelepis australis* and *Aetheolepis mirabilis* in the Family Semionotidae, because of the presence of enamelled rhombic scales. He placed *Archaeomene* into the Family Pholidophoridae Woodward 1890, describing two species, *Archaeomene tenuis* and *A. robustus*. Boulenger (1904) erected the Family Archaeomaenidae to include the genus *Archaeomene*, but his only description was 'Vertebral centra not more than rings; fins with fulcra; scales cycloid'. Wade (1941) believed that *Aphnelepis*, *Aetheolepis* and *Archaeomene* were all closely related because of the similarity of the structure of the cheek, each having a large suborbital, an extensive preoperculum and a greatly expanded circumorbital 3. He placed them in the Sub-order Cenogenoidei, and erected three families, using Archaeomenidae (Boulenger 1904) for *Archaeomene,* and two new families, Aphnelepidae and Aetheolepidae for the other two genera. Wade also erected *Madariscus* gen. nov. (to contain Woodward's *Archaeomene robustus*) and assigned it to the Archaeomenidae. The phylogenetic relationship of these three families has not so far been tested. In his paper on the Upper Jurassic Pycnodontidae, Ebert (2013) expressed his opinion that *Aetheolepis mirabilis* was a pycnodontiform because it has fringing fulcra on all unpaired fins. Ebert has now seen more detailed pictures of *Aetheolepis*, including the one in this paper (Figure 7), and based on photographs supplied by the author, now believes that *Aetheolepis* is not a pycnodontiform fish, as it lacks the characteristic dentition (M. Ebert, pers. comm., Sep. 2016).

Schaeffer (1972) described another member of the family Archaeomenidae, *Oreochima ellioti* from the Lower Jurassic of Antarctica. This taxon is under study by the author and will be redescribed and its phylogenetic position investigated. *Wadeichthys oxyops* from Koonwarra has

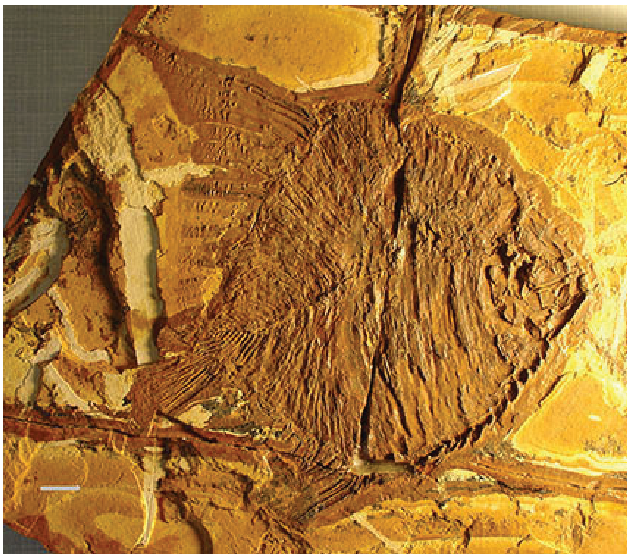

Figure 7: *Aetheolepis mirabilis*. Photo by the author; scale bar = 10 mm. ANU61121.

Figure 8: *Aphnelepis australis*. Photo by the author; scale bar = 10 mm. AMF141883.

also been placed in Archaeomenidae (Waldman 1971) and will be redescribed by the author.

Taverne (2011) listed five members of the family Archaeomenidae; *Archaeomene* Woodward 1895; *Madariscus* Wade 1941; *Oreochima* Scheaffer 1972; *Wadeichthys* Waldman 1971; and *Zaxilepis* Su 1994. He described some of the differences between members of the family Archaeomenidae and recognised that they are closely related. Working from the literature, he stated that *Aphnelepis* should be in a family Aphnelepidae and *Aetheolepis* in a family Aetheolepidae. Arratia (2013) commented on this validation by Taverne, but also stated that none of the genera included have been revised since their original descriptions. *Zaxilepis quinglongensis* occurs in the freshwater Lower Jurassic deposits of Yunnan, southwest China (Su 1994). It will be interesting to see the results of a phylogenetic analysis of all these fossils, which the author plans to carry out when redescriptions have been completed.

A new specimen of *Aphnelepis australis* found at the insect-collecting site at Talbragar shows an extraordinarily well-preserved dorsal fin with a long principal ray on its leading edge (Figure 8). This is the first example of this ray to be found so well preserved and is unusual because it is so delicate. Most of the specimens so far described have a broken surface on the dorsal fin. There are fringing fulcra on all the unpaired fins, and several small precurrent rays anterior to the leading edges. This new specimen suggests that more exceptionally well-preserved fish might be found in the same area, which was not worked on until recently since considerable excavation is required to reach the bed at that location.

Archaeomene tenuis was described by Woodward (1895) and revised by Wade (1941). Wade also described a new genus, *Madariscus*, to contain Woodward's *Archaeomene robustus,* which was described by Woodward as 'a more robust species of *Archaeomene'*. He based the division on a large, but imperfect specimen; however, specimens collected since 2002 show an ontogenetic series of individuals ranging from about 5 cm to about 15 cm, all having the same bone structure and belonging to the species *Archaeomene tenuis*. In the author's view, probably *Madariscus* is a junior synonym for *Archaeomene*; also, *Archaeomene robustus* is a synonym for *Archaeomene tenuis* (Figure 9) (work in progress by the author).

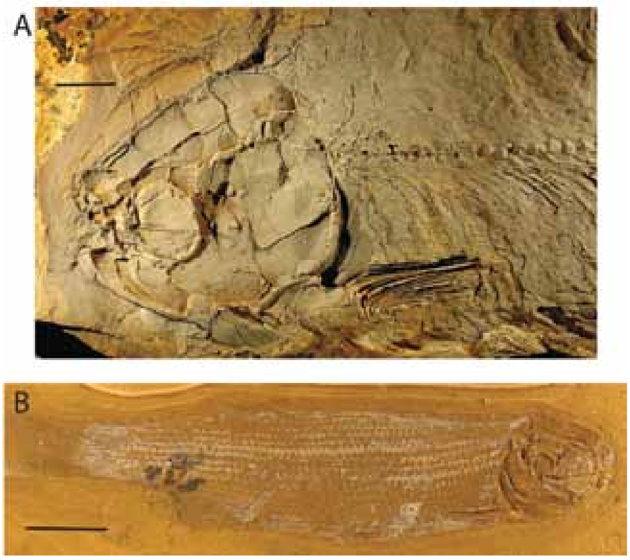

Figure 9: *Archaeomene tenuis*. A. Adult individual formerly identified as *Madariscus robustus*. AMF104686. B. Juvenile individual. ANU54988. Scale bars = 10 mm.

TAXONOMIC HISTORY OF THE OTHER TALBRAGAR FISHES

The first description of the taxon *Coccolepis bucklandi* was by Agassiz in 1843 and came from Upper Jurassic Solnhofen Limestone in Bavaria. It is still awaiting a strict phylogenetic analysis, but Lopez-Arbarello et al. (2013) renamed a fish from Argentinian Patagonia, previously known as *Coccolepis groeberi* (Cione & Pereira 1987) and *Oligopleurus groeberi* (Bordas 1943), as *Condorlepis groeberi.* This fish occurs in the same beds as *Luisiella feruglioi*. Lopez-Arbarello et al. (2013) compared the Patagonian fish *Luisiella feruglioi* to *Cavenderichthys talbragarensis* and *Condorlepis groeberi* to *Coccolepis australis.* They suggested that 'a thorough revision of the latter species might suggest that it is closely related to the Almada coccolepidid', but this is yet to be tested and it may be that the Australian fish belongs to a new genus. There is also a coccolepid in the Koonwarra bed, *Coccolepis woodwardi* (Waldman 1971)*,* which will be included in the revision.

Wade (1953) wrote a preliminary note on *Uarbryichthys latus*, a rare Talbragar fish which he ascribed to the Family Macrosemiidae. Bartram (1977) cast doubt on the affiliations of *Uarbryichthys* to this family, but the issue is yet to be resolved. Murray & Wilson (2009) placed *Uarbryichthys* as a sister group to the Family Macrosemiidae as a result of their phylogenetic analysis, which confirms it is a macrosemiiform.

There is another fish found in the Talbragar beds that has not yet been described. Of three individuals known so far, one specimen in the Australian Museum has the whole body and the lower part of the head in part and counterpart. During the 2006 dig two more specimens of the same large fish were found, >40 cm long, but both individuals are missing their heads. A separate partial head also exists, with well-preserved jaws and preoperculum that appear to match this taxon, but the chance of it belonging to either of the headless individuals is remote. These fish have some similarities with the genus *Furo* found in Solnhofen, Germany, and other European localities. A revision of *Furo*

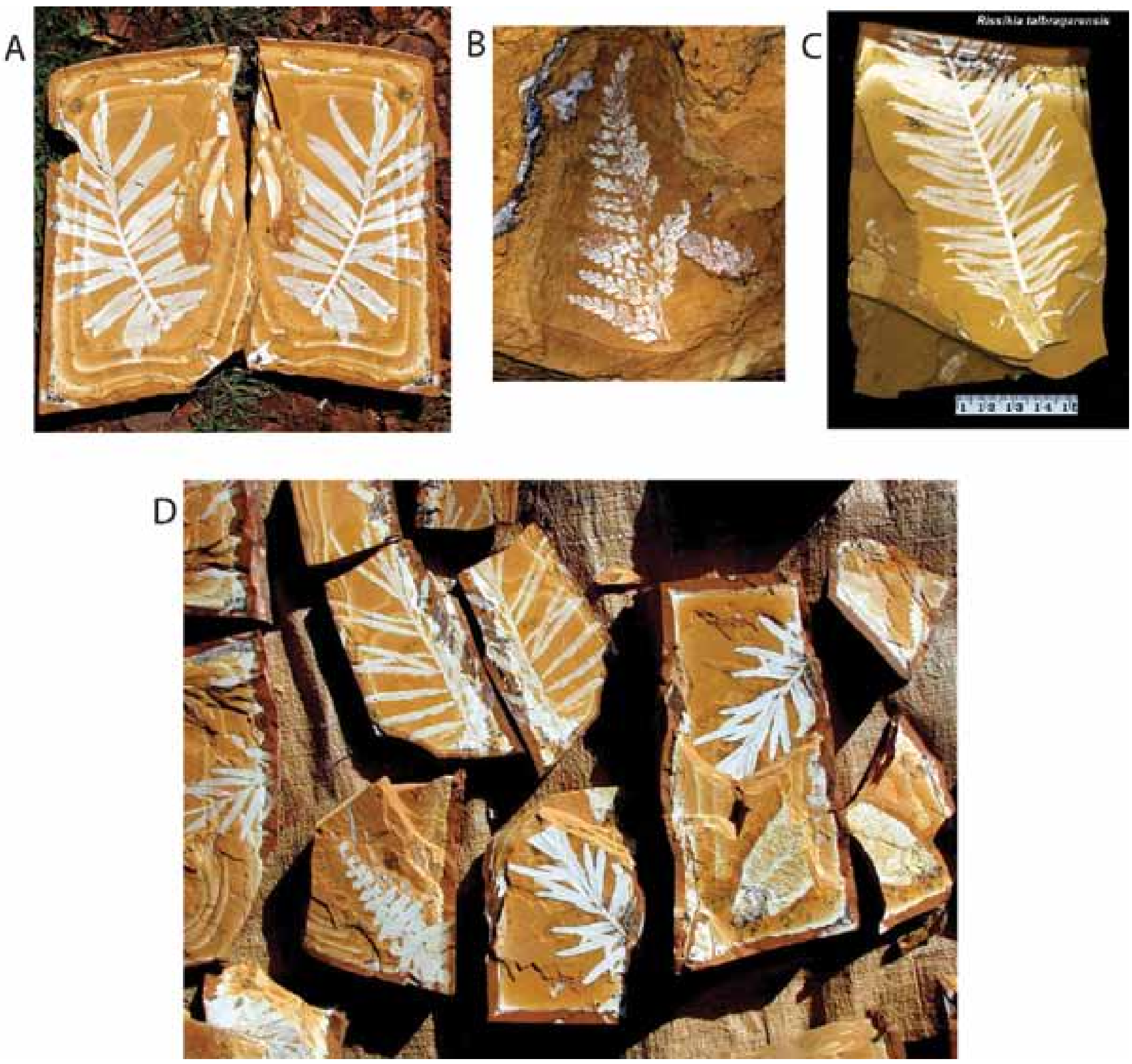

Figure 10: A. *Podozamites jurassica* and *Cavenderichthys talbragarensis*. B. Unidentified Jurassic fern. C. *?Rissikia talbragarensis*. D. Various plants from Talbragar.

muensteri by Lane and Ebert (2012) has indicated that the genus *Furo* and its family Ophiopsidae need revision, so the large fish found at Talbragar will need to be described and named.

Turner and Avery (2017) have published a description of the first-known Jurassic chondrichthyan ('shark') from Australasia. This is based on a partial specimen found at Talbragar by Steve Avery in the early 1990s and now housed in the Australian Museum. The partial preservation has meant that it is impossible to be certain about which chondrichthyan group is represented; however, examination of the fin and scales suggests it might be a non-marine hybodontiform, synechodontiform or neoselachian (Turner & Avery 2017).

TALBRAGAR PLANTS

The plants in the Talbragar Fish Bed are truly spectacular. First described by Walkom (1921) then White (1981), they include conifers (*Podozamites jurassica*, ?*Rissikia talbragarensis*, '*Brachyphyllum sp.*', '?*Pagiophyllum peregrinum*', *Elatocladus australis*, *Allocladus cribbii*, *Allocladus milneanus*), pentoxylaleans (*Taeniopteris*, *Carnoconites* and *Sahnia* spp.), ?cycadophytes (*Nilssonia compta*), some enigmatic seed ferns (*Rintoulia* sp.) and fern fragments (Turner et al. 2009). One of the most common plants was named *Podozamites jurassica* by Walkom (1921) but renamed *Agathis jurassica* by White (1981) (Figure 10). This name has come into common usage, but the affiliation is not accurate and the original name should be used. This is significant because of reports in the media that this plant is related to the Wollemi pine (*Wollemia nobilis*), suggesting that the Wollemi pine might be a 'living fossil'. McLoughlin, in Turner et al. (2009), stated '*Podozamites jurassica* does not provide a close match in venation pattern, leaf shape or phyllotaxy to either *Wollemia* or other extant araucariacean genera. Convincing evidence for *Wollemia* extends back only to the Late Cretaceous.' (Figure 10).

THE SIGNIFICANCE OF LATITUDE

During the Mesozoic, the southern part of Gondwana was straddling the south geographic pole. The commonly used map projections do not make it easy to see the relationships between localities such as Talbragar, Koonwarra, and the Patagonian location of the Canadon Calcareo Formation, which is the origin of many specimens of *Luisiella feruglioi*. The EarthByte group from the University of Sydney produce reconstructions based around the South Pole at specific times that illustrate the relationships clearly (Figure 11) (Seton et al. 2012). The palaeolatitudes generated for the localities are as follows:

150 +/- 4 Ma: Upper Jurassic (Bean 2006)
-66.95 Talbragar Fish Bed (approximate time of deposition)
-71.77 Koonwarra Fossil Beds
-50.73 Canadon Calcareo Formation (approximate time of deposition)
118 +/- 6 Ma: Lower Cretaceous (Lindsay 1982)
-62.13 Talbragar Fish Bed
-68.32 Koonwarra Fossil Beds (approximate time of deposition)
-48.40 Canadon Calcareo Formation

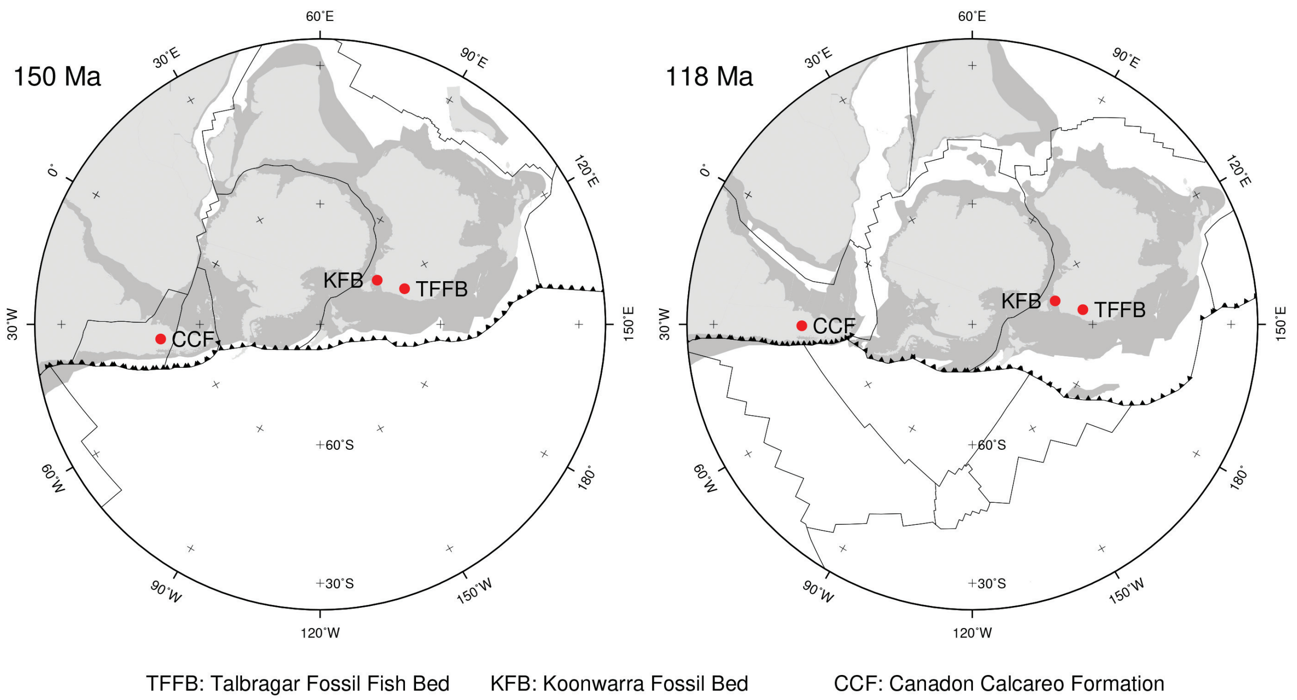

Figure 11: South Pole centred projections of Southern Gondwana, showing the locations of the fossil beds during the Late Jurassic (left) and Early Cretaceous (right), based on Seton et al. (2012).

These figures for latitude of Talbragar and Koonwarra use the most recent palaeomagnetic data and are not as high as some earlier predictions (Seton et al. 2012). This result will need to be factored into the discussion about the validity of the idea put forward by Waldman (1971) that a covering of ice over the lake in winter was responsible for the cyclic nature of deposition, or to the suggestion by Jell and Duncan (1986) that wet and dry seasons were a factor. The facts that all three localities appear to have been located along a continuous palaeo-coastline, and all assemblages are freshwater, lacustrine or marginally fluvial, go some way to explaining the similarities of the assemblages.

CONCLUSIONS AND FUTURE WORK

This study has resulted in some significant changes being made to the taxonomy of two Australian Mesozoic fishes.

1 *Leptolepis talbragarensis* Woodward, 1895 is now known as *Cavenderichthys talbragarensis* (Woodward, 1895) by Arratia (1997).
2. *Leptolepis koonwarri* Waldman, 1971, is now known as *Waldmanichthys koonwarri* (Waldman, 1971) by Sferco et al. (2015b).
3. Both these fishes are currently interpreted as members of the Family Luisiellidae, a freshwater Gondwanan clade, together with *Luisiella feruglioi* from Patagonia (Sferco et al. 2015b).
4. Members of the family Archaeomenidae are now undergoing a detailed re-description and analysis of their phylogenetic relationships in order to accurately record their evolutionary history. This family includes *Archaeomene tenuis, Wadeichthys oxyops, Oreochima ellioti* and *Zaxilepis quinglongensis.* The affinities of *Aetheolepis mirabilis* and *Aphnelepis australis* also need revision.
5. Other fishes from Talbragar and Koonwarra need to be re-described and their phylogenetic relationships determined. This should add significantly to the current fragmentary knowledge of Mesozoic fishes in Australia, and add to the understanding of their places in the evolutionary history of fishes around the world.

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References

Arratia, G., 1997. Basal teleosts and teleosteans phylogeny. *Paleo Icthyologica* 7: 5–168.

Arratia, G., 2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii, Teleostei). *Journal of Vertebrate Paleontology Memoir* 33: 1-138.

Bartram, A.W.H., 1977. The Macrosemiidae, a Mesozoic family of holostean fishes. *Bulletin of the British Museum (Natural History)* 29(2): 137–234.

Bean, L.B., 2006. The leptolepid fish Cavenderichthys talbragarensis (Woodward, 1895) from the Talbragar Fish Bed (Late Jurassic) near Gulgong, New South Wales. *Records of the Western Australian Museum* 23: 43–76.

Beattie, R.G., & Avery, S., 2012. Palaeoecology and palaeoenvironment of the Jurassic Talbragar Fish Bed, Gulgong, New South Wales, Australia. *Alcheringa* 36(4): 451–465.

Bordas, A.F., 1943. Peces del Cretacio del Rio Chubut (Patagonia). *Physis* 19.

Boulenger, G.A., 1904. A synopsis of the suborders and families of teleostean fishes. *Annals and Magazine of Natural History Series* 7, 13: 161–190. Retrieved from biostor.org/reference/66427

Cavender, T.M., 1970. A comparison of coregonines and other salmonids with the earliest known teleostean fishes. In *Biology of the Coregonid Fishes,* C.C. Lindsey & C.S. Woods, eds. University of Manitoba, Winnipeg, Canada, pp. 1–32.

Cione, A.L. and Pereira, S.M. 1987. Los peces del Jurásico de Argentina. El Jurásico anterior a los movimientos intermálmicos, p. 287-298. In *Bioestratigrafía de los sistemas Regionales del Jurásico y Cretácico de América del Sur*, W. Volkheimer, ed. Centro Regional de Investigaciones Científicas y Técnicas, Mendoza.

Drinnan, A.N. & Chambers, T.C., 1986. Flora of the Lower Cretaceous Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. In *Plants and Invertebrates from the Lower Cretaceous Koonwarra Fossil Bed,* *South Gippsland, Victoria*, P.A. Jell and J. Roberts, eds. *Association of Australasian Palaeontologists Memoir* 3, 1–75.

Dulhunty, J.A., 1937. Notes on the stratigraphy and physiography of the Talbragar “fish-bed” area. *Journal and Proceedings of the Royal Society of New South Wales* 71: 350–356.

Dulhunty, J.A. & Eadie, J., 1969. Geology of the Talbragar Fish Bed area. Journal and Proceedings of the Royal Society of New South Wales 102: 1–4.

Ebert, M., 2013. The Pycnodontidae (Actinopterygii) in the late Jurassic: 1) The genus Proscinetes GISTEL, 1848 in the Solnhofen Archipelago (Germany) and Cerin (France). Archaeopteryx 31: 22–43.

Frakes, L.A. & Francis, J.E., 1988. A guide to Phanerozoic cold polar climates from high-latitiude ice-rafting in the Cretaceous. *Nature* 333: 547–549.

Hind, M.C. & Helby, R.J., 1969. The Great Artesian Basin in New South Wales, (918619437). http://doi.org/10.1080/14400956908527970

Jell, P.A. & Duncan, P.M., 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. In Jell P.A. & Roberts J. (Eds) *Plants and invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria*. *Association of Australasian Palaeontologists Memoir* 3: 111–205

Lane, J.A. & Ebert, M., 2012. Revision of Furo muensteri (Halecomorphi, Ophiopsidae) from the Upper Jurassic of Western Europe, with comments on the genus. *Journal of Vertebrate Paleontology* 32(4): 799–819.

Li, X-B., Zhang, M-S. & Wang Y-N. 2011. Two early Cretaceous fishes discovered from the most northern area of China: implications for the palaeonbiogeography of the Jehol Biota. *Geographical Journal.* 46: 323–332.

Lindsay, N.M., 1982. The burial history of the Strzeleki Group Sandstones, S.E. Australia: a petrographic and fission track study. M.Sc. Thesis, University of Melbourne (unpublished).

López-Arbarello, A., Sferco, E. & Rauhut, O.W.M., 2013. A new genus of coccolepidid fishes (Actinopterygii, Chondrostei) from the continental Jurassic of Patagonia. 1. *Palaeontologia Electronica* 16(1): 1–23.

Murray, A.M. & Wilson, M.V.H., 2009. A new Late Cretaceous macrosemiid fish (Neopterygii, Halecostomi) from Morocco, with temporal and geographical range extensions for the family. Palaeontology 52(2): 429–440. http://doi.org/10.1111/j.1475-4983.2009.00851.x

Percival, I.G., 1979. *The Geological Heritage of New South Wales*. Vol. 1., New South Wales Government National Parks and Wildlife Service, 1979.

Pogson, D.J. & Cameron, R.G., 1999. Surat Basin. Explanatory Notes, Dubbo Geological Sheet 1:250000 S1/55-4. Geological Survey of New South Wales, Mineral Resources of NSW, pp. 330–332.

Rich, T.H., Li, X-B. & Vickers-Rich, P., 2012. Assessment of the Potential Jehol biota-like Cretaceous polar fossil assemblage in Victoria, Australia, pp. 505–516. In *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*, P. Godefroit, ed. *Indiana University Press,* Bloomingham, 692 pp.

Schaeffer, B., 1972. A Jurassic fish from Antarctica. *American Museum Novitate*, 2495.

Seton, M., Müller, R.D., Zahirovic, S., Gaina, C., Torsvik, T., Shephard, G., Talsma, A., Gurnis, M., Turner, M., Maus, S. & Chandler, M., (2012), Global continental and ocean basin reconstructions since 200 Ma, *Earth Sci. Rev.*, 113(3–4), 212–270.

Sferco, E., López-Arbarello, A. & Báez, A.M., 2015a. Anatomical description and taxonomy of *Luisiella feruglioi* (Bordas), new combination, a freshwater teleost (Actinopterygii, Teleostei) from the Upper Jurassic of Patagonia. *Journal of Vertebrate Paleontology* 35: 3 e924958-1-20.

Sferco, E., López-Arbarello, A. & Báez, A.M., 2015b. Phylogenetic relationships of *Luisiella feruglioi* (Bordas) and the recognition of a new clade of freshwater teleosts from the Jurassic of Gondwana. BMC Evolutionary Biology 15(1): 268. http://doi.org/10.1186/s12862-015-0551-6

Su, D., 1994. New Early Jurassic actinopterygians from Weixin, Yunnan. *Vertébrala PalAsiatica,* 32(3): 151–165 (in Chinese with English summary).

Taverne, L., 2011. Osteologie et relations phylogenetiques de *Steurbautichthys* (‘Pholodophophorus’) aequatorialis gen. nov. (Teleostie, ‘Pholodophoriformes’) du Jurassique moyen de Kisangani, en Republique Democratique du Congo. *Bulletin de l’Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 81, 129–173.

Tuite, M.L., Flannery, D.T. & Williford, K.H., 2016. Organic geochemistry of a high-latitude Lower Cretaceous lacustrine sediment sample from the Koonwarra Fossil Beds, South Gippsland, Victoria, Australia. *Memoirs of Museum Victoria* 74: 73–79. http://museumvictoria.com.au/about/books-and-journals/journals/memoirs-of-museum-victoria/

Turner S., Bean L., Dettmann, M., McKellar, J.L., McLoughlin, S. & Thulborn, T., 2009. Australian Jurassic sedimentary and fossil successions: current work and future prospects for marine and non-marine correlation. GFF; FF131:49–70.

Turner, S. & Avery, S., 2017. A Jurassic non-marine chondrichthyan in Australia and its palaeogeographic significance. Palaeoworld. http://dx.doi.org/10.1016/j.palwor.2017.01.001

Wade, R.T., 1941. The Jurassic Fishes of New South Wales. *Journal and Proceedings of the Royal Society of New South Wales* 75: 71–84.

Wade, R.T., 1953. Jurassic Fishes of New South Wales (Macrosemiidae) with a note on the Triassic genus *Promecosomina*. *Journal and Proceedings of the Royal Society of New South Wales* 87(2): 63–72.

Waldman, M., 1971. Fish from the freshwater Lower Cretaceous of Victoria, Australia, with comments on the palaeo-environment. *Special Papers in Palaeontology* 9(1): 1–124.

Walkom, A.B., 1921. Mesozoic floras of New South Wales. Part 1 – Fossil plants from Cockabutta Mountain and Talbragar. *Geological Survey of New South Wales, Palaeontology. Memoir* 12: 1–12.

White, M.E., 1981. Revision of the Talbragar fish bed flora (Jurassic) of New South Wales. *Records of the Australian Museum* 33: 695–721.

Woodward, A.S., 1895. The fossil fishes of the Talbragar Beds (Jurassic?). *Geological Survey of New South Wales, Palaeontology*. *Memoir* 9: 1–27.