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Upper Devonian osteichthyan remains from the Genoa River, Victoria, Australia

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The Genoa River Trackway site in the Upper Devonian Combyingbar Formation represents one of the earliest records of tetrapods (land vertebrates) from Australia. However, the osteichthyan assemblage from the site is poorly known compared to other Devonian tetrapod localities. New information from a tetrapodomorph fish lower jaw possibly indicates the first record of a tristichopterid from the Genoa River Beds. The specimen shares a posteroventral embayment in the profile of lower jaw with *Eusthenopteron foordi*, *Platycephalichthys bischoffi*, and Moroccan tristichopterid material, as well an isolated specimen of the 'osteolepidid' *Gyroptychius*. Polyplocodont and dendrodont teeth are also described from the Genoa River, with the latter indicating the presence of a large, porolepiform taxon. The antiarch placoderm *Remigolepis* represents the most abundant fossil fish taxon recorded from the Genoa River. The possible presence of phyllolepid placoderm material may support previous suggestions of a pre-Famennian age for the Genoa River Beds.

Keywords tristichopterid, Tetrapodomorpha, Genoa River, Devonian, polyplocodont, dendrodont

Introduction

The fine-grained sandstone of the Genoa River Beds (=Combyingbar Formation [Vandenberg *et al*., 1992]) along the Genoa River, southeastern Victoria, is renowned for preserving the first record of Devonian tetrapods from Australia and Gondwana (Warren and Wakefield, 1972). Discovered by Norman A. Wakefield in 1971, this material was described as three distinct tetrapod trackways by Warren and Wakefield (1972) and Clack (1997), with subsequent work focusing mainly on the two better preserved footprint sets, believed to be distinct in form (Clack, 2002; Young, 2006; 2007). Biostratigraphic and lithological indicators summarised by Young (2006) suggested a Frasnian age for the locality, but did not describe any fossils to support this. Dunn (1897), Hall (1959) and Douglass (1974) recorded Upper Devonian plant material from the Genoa River, with the strata broadly corresponding to the Merrimbula Group of the New South Wales south coast (Lewis *et al*., 1994), more specifically, lithofacies 1–3 of the Early to Mid-Frasnian, Twofold Bay Formation (Simpson *et al*., 1997; Young, 2007). The age of the Genoa River trackways are notable for being '…probably contemporary with *Obruchevichthys* and *Elginerpeton*' (Clack, 2002; p. 92), previously considered to be the oldest known tetrapods (Ahlberg, 1995). However, the recent discovery of a tetrapod trackway site from the Eifelian Northern Holy Cross Mountains, Poland (Niedźwiedzki *et al*., 2010) is significantly older than this aforementioned material.

In contrast to the importance of the Genoa site, none of the vertebrate assemblage has been described. Such details have been published regarding the fauna from Northern Hemisphere tetrapod localities, such as those from East Greenland (summarised by Blom *et al*., 2007). The record of the Devonian fish fauna from the Genoa River includes the placoderm taxa *Bothriolepis*, *Remigolepis* and *Groenlandaspis* (Young, 1988) and a phyllolepid taxon (recorded in the field notes of Anne Warren [Anne Warren, La Trobe University, pers. comm., 2009]). Isolated 'crossopterygian skull elements' have also been reported from the site (Young, 1988; p. 192), along with bone elements and scales from the porolepiform fish *Holoptychius* (Young, 1993), although this record has since been questioned (Young, 2007). A large, poorly preserved partial lower jaw of an 'osteolepiform' fish was identified by Ahlberg and Clack (1998), based on a broad distribution of denticles on the prearticular and a posterodorsally directed glenoid surface of the articular. New descriptive work on this specimen, NMV P198470, is presented here following further preparation. Several similarities to tristichopterid specimens from the Frasnian of Canada, Russia and the Famennian of Tafilalt, Morocco, are suggested. Two distinct sarcopterygian fish tooth morphologies from the Genoa River fauna are also described in detail for the first time. This includes a small polyplocodont tooth and a large dendrodont tusk. The former morphology is known from tetrapodomorph fishes and lower tetrapods, while the latter is unique to the Porolepiformes

(Schultze, 1970). A list is presented of the fossil fish specimens collected from the Genoa River and stored in Museum Victoria. The biostratigraphic implications of the Genoa River fauna are discussed, including the possible presence of phyllolepid material.

Material and methods

The aforementioned specimens were collected in 1973 by Ian Stewart on a field trip led by James W. Warren along the bank of the Genoa River, Victoria, Australia. Preliminary work on the jaw (NMV P198470) was carried out by Alec L. Panchen and Anne Warren, but was never published (Anne Warren, La Trobe University pers. comm., 2009). Manual surface preparation was undertaken by Per E. Ahlberg and Jennifer A. Clack (Ahlberg and Clack, 1998), with bone material being dissolved in hydrochloric acid by T.H in 2008. A black latex peel of the specimen was then dusted with sublimate of ammonium chloride and photographed with a Nikon D80 camera using a Nikon DX 18–135 mm lens. The polyplocodont (NMV P229479) and dendrodont (NMV P229477) teeth were sectioned by Ian Stewart, and photographed with a Leica DFC500 camera using a Leica M205C microscope. Anatomical terminology follows that of Jeffery (2003).

Institutional abbreviations

NMV, Museum Victoria, Melbourne; MNHN, Muséum national d'Histoire naturelle, Paris, France; NRM, Naturhistoriska riksmuseet (Natural History Museum of Sweden).

Systematic descriptions

Superclass Osteichthyes Huxley, 1880

Class Sarcopterygii Romer, 1955

Horizon. Combyingbar Formation (Vandenberg *et al*., 1992)

Order Tetrapodomorpha Ahlberg, 1991

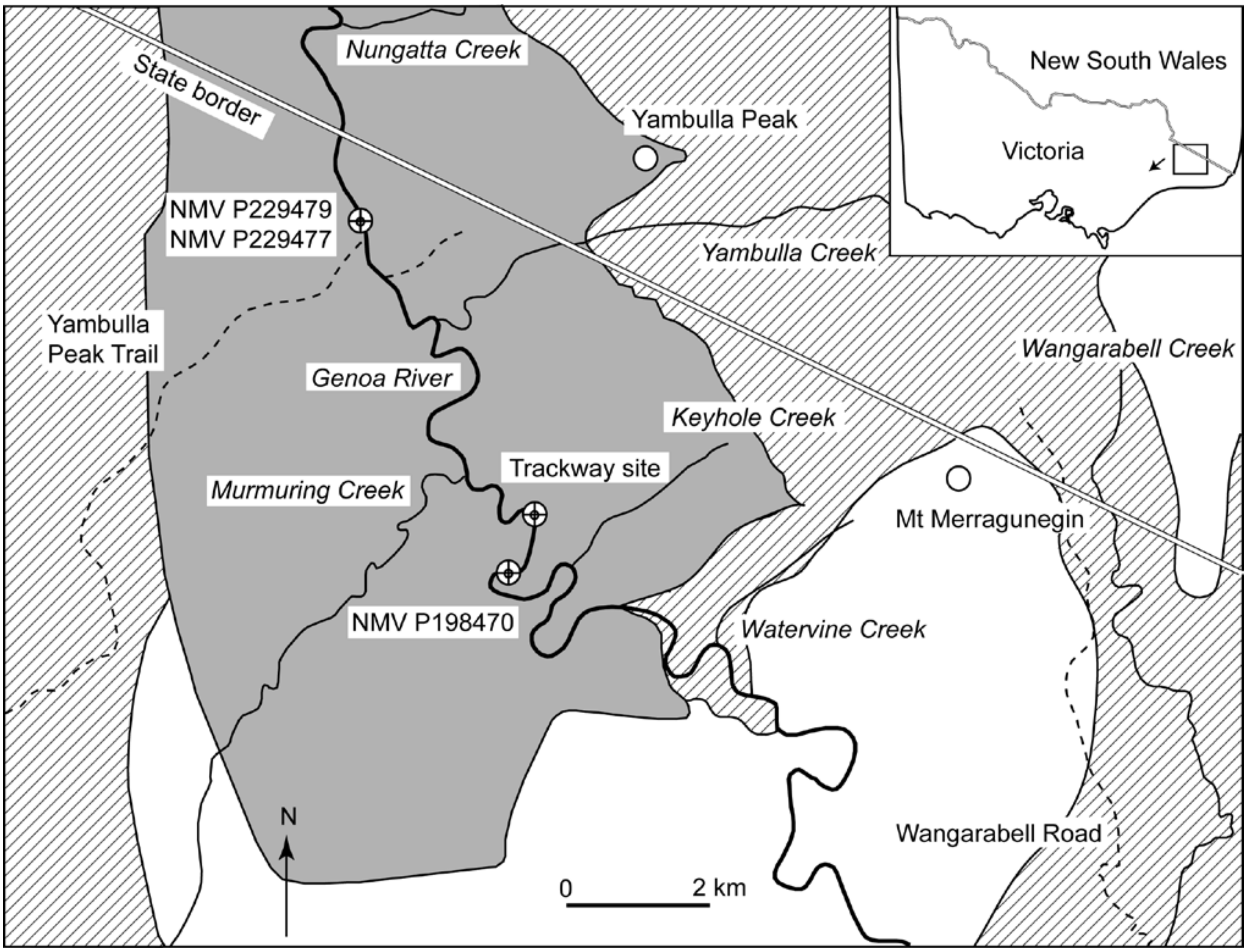

Figure 1. Geological map of Genoa River area, Genoa, Victoria, Australia (modified from Marsden, 1976; Simpson et al., 1997); grey = Late Devonian, Combyingbar Formation; diagonal lines = Early Devonian, Maramingo Granite; white = Ordovician slate, sandstone.

tetrapodomorph gen. et sp. indet.

Large incomplete lower jaw (Ahlberg and Clack, 1998; p. 35)

Poorly preserved lower jaw; belonged to an osteolepiform fish (Young, 2006; p. 413)

Poorly preserved osteolepiform sarcopterygian lower jaw (Young, 2007; p. 1003)

Referred specimen. NMV P198470, an incomplete lower jaw, including infradentaries, prearticular, articular, and possible dentary and coronoid elements.

Locality. Along the Genoa River, between the branches of Murmuring Creek and Keyhole Creek (fig. 1).

Description. Only the lingual surface of NMV P198470 is preserved (figs 2a–b), consisting of an elongate, relatively narrow, posterior half of a lower jaw. It measures 18 cm long from the preserved anterior to the posterior tip of the articular, and 5 cm deep from the level of the infradentaries to the dorsal margin of the dentary. Parts of the dorsal and ventral margins are incomplete, most notably the dorsal area anterior to the articular. Most of the surface of the jaw is covered by the prearticular (fig. 2b), which anteriorly carries small patches of denticles (fig. 2b) near the dorsal margin. These patches are replaced posteriorly by a roughened surface of bone, which is marked with a conspicuous crescent-shaped contour (fig. 2b) towards the posterior margin of the prearticular.

Posterior to the prearticular is the articular (fig. 2b), which displays a posterodorsally directed, concave glenoid surface. It is bordered anterodorsally and posteroventrally by two rounded prongs, with the former being preceded by a prominent concave dip in the preserved dorsal margin of the jaw. This could possibly represent the inner margin of the adductor fossa (fig. 2b).

Anterior to this region, the dorsal margin of the jaw is represented by two strips of bone: the dentary (fig. 2b), which is preserved anteriorly, and a presumed coronoid (fig. 2b), represented by a posteriorly positioned ledge that sits lingual to the dentary. Both the dentary and the coronoid are incompletely preserved.

Although the ventral margin of the lower jaw is incomplete anteriorly, a small slither of bone positioned labially to the prearticular may represent the third infradentary (fig. 2b). It is followed by a small break, and then by a similar bone, possibly the fourth infradentary (fig. 2b). This bone is bordered dorsally by a narrow groove, which rises transversely to delineate the margin of the prearticular from a region of exposed meckelian bone (fig. 2b). A small depression is present in this area, ventral to the glenoid surface of the articular. This may represent the opening for the ramus mandibularis of n. facialis (fig. 2b). The posteroventral outline of the jaw shows a distinct concave, step-like margin towards the articular (fig. 2b).

Comparisons to other taxa. Affinities of NMV P198470 to various osteichthyan clades can be eliminated quickly through comparisons of lower jaw gross morphology. NMV P198470 differs from Devonian ‘palaeoniscid’ fishes such as ‘*Mimia*’ and *Moythomasia* (Gardiner, 1984) (fig. 2c) in lacking a dorsally directed glenoid fossa on the articular (and also the latter by the absence of a double prearticular); Devonian actinistians, such as *Miguashaia* (Forey *et al*., 2000) (fig. 2d) and *Styloichthys* (Friedman, 2007) by lacking a ventral mandibular flange protruding below the level of the infradentaries and the ‘sympletic’ articulation at the posterior of the jaw; Devonian dipnoans, such as *Chirodipterus* and *Rhinodipterus* (Jarvik, 1967) by having a prearticular, coronoid series and lacking a principle tooth plate; and porolepiforms, such as *Holoptychius* (Jarvik, 1972) (fig. 2e) by lacking a rounded posteroventral margin and large dorsoventral depth. Among tetrapodomorphs, NMV P198470 differs from rhizodontids by lacking an unossified articular and other meckelian elements (Jeffery, 2003) (fig. 2f); Devonian tetrapods, such as *Ventastega* (Ahlberg and Clack, 1998) (fig. 2g) by lacking an articular situated posterodorsally to the dentary tooth row; and most ‘osteolepidids’, such as *Ectosteorhachis* (Thomson, 1964) (fig. 2h) in having a gentle, transverse posteroventral outline towards the articular.

NMV P198470 is comparable to *Platycephalichthys bischoffi* (Vorobyeva, 1962: plates XVI-XVII) and some specimens of *Eusthenopteron foordi* (fig. 2i; Jarvik, 1980: fig. 125), in which the posteroventral margin of the lower jaw displays a concave profile. This embayment is also present in the unnamed tristichopterid specimen MNHN n° MCD 42 from Tafilalt, Morocco (Lelièvre and Janvier, 1986) (fig. 2k), which also shares the acute crescent shaped contour on the posterior region of the prearticular (fig. 2k). Among the lower jaw morphology of other tristichopterids, a posteroventral concave profile is absent from *Eusthenopteron säve-söderberghi* (Vorobyeva, 1962: plate I), *E. kurshi* (Zupiņš, 2008), *Jarvikina wenjukowi* (Vorobyeva, 1962: plate XXVIII), *Eusthenodon wängsjöi* (Jarvik, 1952) and *Tristichopterus* (Traquair, 1875). A posteroventral embayment is also present in the lower jaw of *Gyroptychius* specimen NRM PZ P1409 (fig. 2j), although this element is preserved in labial view.

tetrapodomorph gen. et sp. indet.

Referred specimen. NMV P229479, small parabasally sectioned, polyplocodont tooth.

Locality. Along the Genoa River, approximately 30–50 m upstream from the Yambulla Peak Track (fig. 1).

Description. The specimen, represented by a single tooth (figs 3a–c), measures approximately 1.5 cm from the apex to the preserved parabasal section, and is 8 mm in diameter. Several loose plications (fig. 3a) are present at the base of the external surface. These extend approximately one-third of the total height of the tooth, and are replaced apically by a smooth layer of enamel. The pulp cavity (fig. 3b) is visible in parabasal section, and seems to be free from osteodentine. It is surrounded by loose, simple folds of orthodentine (figs 3b–c), which appear to be interrupted intermediately by bone (fig. 3c).

Comparisons with other taxa. Tooth morphology of NMV P229479 closely matches that of polyplocodont teeth in having a free pulp cavity, simple orthodentine folds and bone of attachment extending between folds (Schultze, 1970: fig. 1a). This morphology is present in rhizodontids, *Megalichthys*, *Eusthenopteron* and *Tristichopterus* (Schultze, 1970). However, the lingual surface of NMV P229479 differs from that of rhizodontids, such as *Barameda* (Holland *et al*., 2007) in lacking fine, raised striae on the enamel.

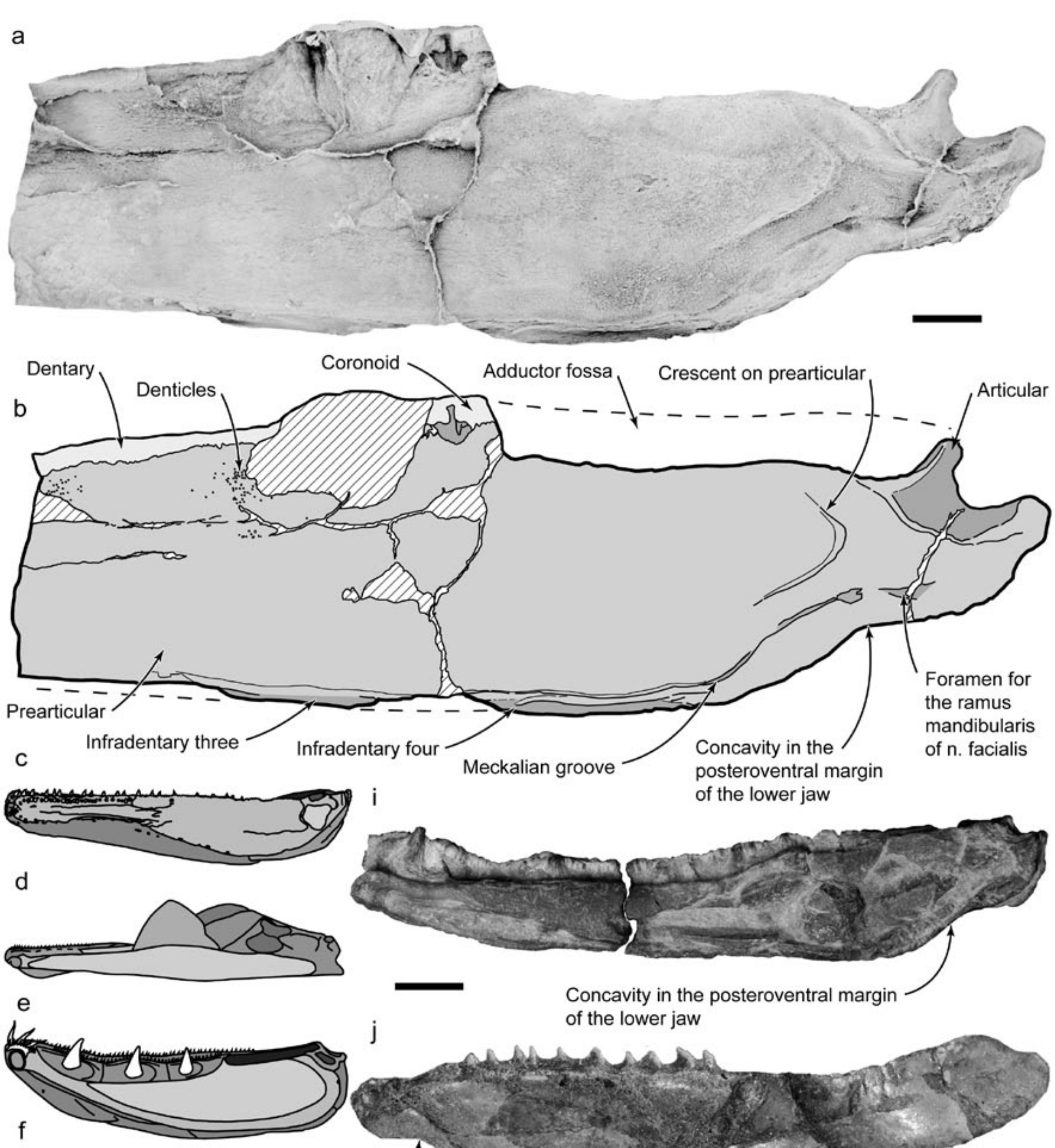

Figure 2. Osteichthyan lower jaws; a, photograph of possible tristichopterid NMV P198470; b, interpretive drawing of NMV P198470; c, *Moythomasia* (modified from Gardiner, 1984); d, *Miguashaia* (modified from Forey et al., 2000); e, *Holoptychius* (modified from Jarvik, 1972); f, *Rhizodus* (modified from Jeffery, 2003); g, *Ventastega* (modified from Ahlberg and Clack, 1998); h, *Ectosteorhachis* (modified from Thomson, 1964); i, *Eusthenopteron* specimen NRM PZ P35; j, *Gyroptychius* specimen NRM PZ P1409; k, tristichopterid specimen MNHN n° MCD 42 (modified from Lelièvre and Janvier, 1986). Scale = 1 cm; scale not included for c–h; all jaws excluding j are in lingual view; j is in labial view.

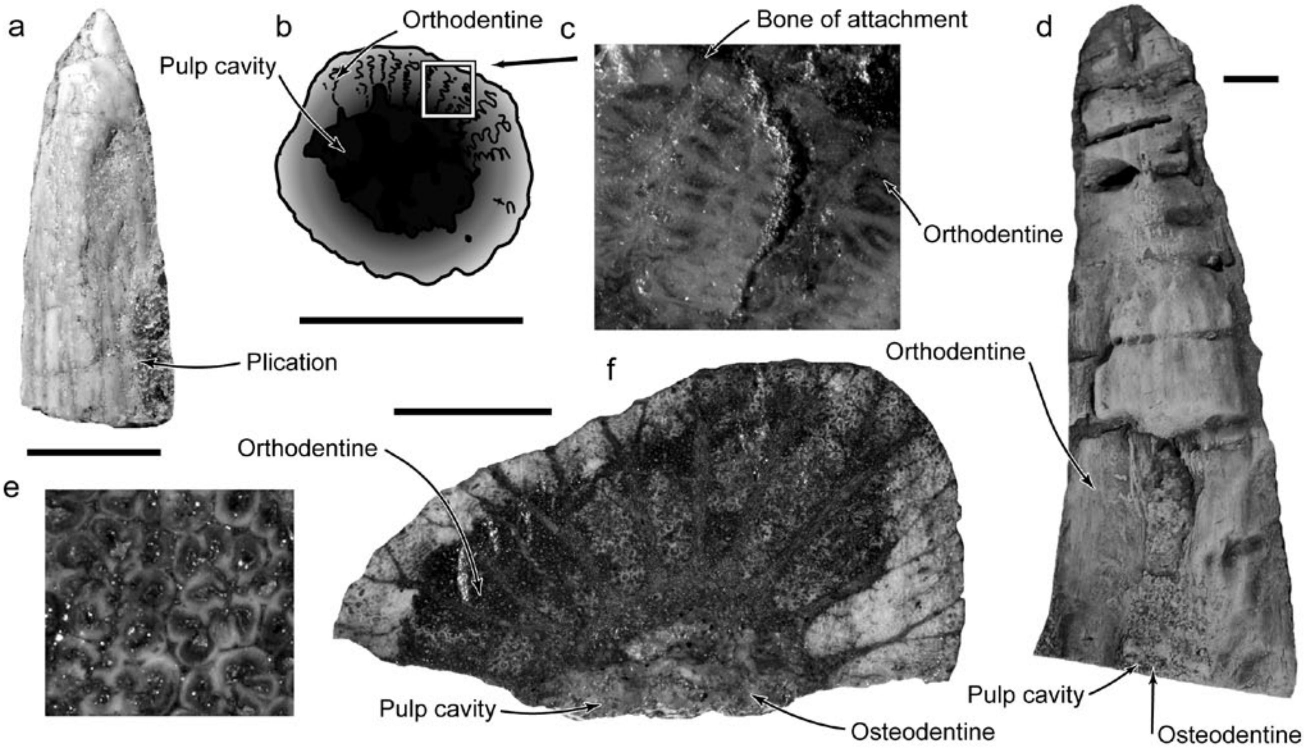

Figure 3. Tooth morphologies of tetrapodomorph fishes; a, labial view of polyplocodont tooth, NMV P229479; b, stylised drawing showing complete parabasal section of NMV P229479; c, orthodentine folding of NMV P229479 in parabasal section; d, vertical section of dendrodont tooth, NMV P229477; e, orthodentine folding of NMV P229477; f, parabasal section of NMV P229477. Scale = 5 mm; scale not included for c, e.

Order Porolepiformes Jarvik, 1942

? porolepiform gen. et sp. indet.

Referred specimen. NMV P229477, a large, vertically and parabasally sectioned dendrodont tooth element.

Locality. Along the Genoa River, approximately 30–50 m upstream from the Yambulla Peak Track (fig. 1).

Description. Specimen NMV P229477 is represented by a large fang (figs 3d–f), being approximately 6 cm in height, although parts of the base may not have been collected. The external surface is badly damaged, preserving no plications, with the proximal end sectioned vertically, exposing the pulp cavity (figs 3d–f). The width of the pulp cavity varies, being approximately half the total width of the specimen (total width = 2.2 cm) towards the proximal end, to be only one-fifth of the total diameter approaching the apex. Inside the pulp cavity is a granular column of bone, probably representing osteodentine (figs 3d, f). Lateral to the pulp cavity are wide expanses of orthodentine (figs 3d–f), which are marked with fine, densely packed lines, representing folding. This intense folding is more apparent in parabasal section, and appears darker and tighter towards the pulp cavity (fig. 3e). Several regions of orthodentine are interrupted by channels of osteodentine emanating from the pulp cavity (fig. 3f). In some instances, these channels appear to bifurcate and narrow as they approach the outer surface of the tooth.

Comparisons with other taxa. The combination of complicated folded orthodentine and a pulp cavity filled with osteodentine in NMV P229477 closely matches the description of dendrodont tooth morphology from porolepiform fishes, such as *Porolepis* (Schultze, 1970) and *Laccognathus* (Schultze, 1969). There is no intrusion of outside bone of attachment between the folds of orthodentine, in contrast to eusthenodont teeth (Schultze, 1970).

Discussion

Of the osteichthyan remains from the Genoa River Beds, the lower jaw of NMV P198470 may offer a link to tristichopterid taxa from outside East Gondwana in having a posteroventral embayment in the profile of the lower jaw. This particular feature is present in the *Eusthenopteron*-like tristichopterid material from Famennien of Morocco (Lelièvre and Janvier, 1986), and some specimens of *Eusthenopteron foordi* from the Frasnian of Miguasha, Quebec, Canada (e.g. NRM PZ P35 from the Swedish Museum of Natural History). *Eusthenopteron* is considered among the more primitive members of the Tristichopteridae, along with the Scottish Givetian taxon, *Tristichopterus* (Ahlberg and Johanson, 1997). A possible relationship between these taxa and NMV P198470 is surprising, because the record of tristichopterids in Australia otherwise consists of mandageriids. This includes *Cabonnichthys* Ahlberg and Johanson, 1997 and *Mandageria* Johanson and Ahlberg, 1997 from the Fransian Mandagery Formation of Canowindra, New South Wales; *Eusthenodon* from the Famennian of the Hunter Formation of Grenfell, New South Wales (Johanson, 2004); and the Worange Point Formation, south of Eden, New South Wales (Ahlberg *et al.*, 2001). *Eusthenodon* was initially described from the Famennian of East Greenland (Jarvik, 1952). However, the assignment of the Eden tristichopterid within *Eusthenodon* has been questioned by Young (2008), placing it with the Canowindra tristichopterids in a possibly endemic Gondwanan subfamily — the Madageriidae — based on the presence of accessory vomers on the palate. The only other notable Australian taxon previously linked with the Tristichopteridae is *Marsdenichthys* Long, 1985 from the Givetian of Mt. Howitt, Victoria. This taxon has also been associated with the Rhizodopsidae (Long, 1999), although new material described by Holland *et al.* (2010) shows no affinities to this clade or the Tristichopteridae. In addition, the lower jaw of *Marsdenichthys* (Holland *et al.*, 2010: fig. 2) lacks the posteroventral embayment of NMV P198470 and some tristichopterid taxa. However, evaluating the distribution of the posteroventral lower jaw concavity seen in NMV P198470 throughout the Tristichopteridae requires caution, because the area is either not well preserved or described as the Madageriidae (e.g. Young *et al.*, 1992; Ahlberg and Johanson, 1997; Johanson and Ahlberg, 1997) and *Langlieria* (Clément, 2002); and appears absent from *Eusthenodon wängsjöi* (Jarvik, 1952), *Jarvikina* (Vorobyeva, 1962), the European species of *Eusthenopteron* (e.g. Vorobyeva, 1962; Zupiņš, 2008) and the basal *Tristichopterus* (Traquair, 1875). A poorly developed posteroventral lower jaw concavity also appears in *E. foordi* specimen P.2197 (Jarvik, 1996: fig. 19), although the relevant area in this specimen is possibly crushed. Outside the Tristichopteridae, a posteroventral embayment is also present in the lower jaw of *Platycephalichthys* from the Frasnian of Russia (Vorobyeva, 1962). However, this taxon, which was previously associated with tristichopterids, shares some affinities with 'elpistostegid' fishes, such as *Panderichthys* (Coates and Friedman, in press), and thus may occupy a more crownward phylogenetic position. It is also worth noting that a concave posteroventral profile marks the lower jaw of the cosmine-covered 'osteolepidid' *Gyroptychius* specimen, NRM PZ P1409. Although no cosmine was recorded on the scant labial surface material of NMV P198470 (before preparation), the presence of a posteroventral notch in the jaws of both specimens is potentially significant, as *Gyroptychius* is the sister taxon to the Tristichopteridae in Ahlberg and Johanson (1998) and shares a number of other characters with the group, including vomers with long posterior processes, an elongate ethmosphenoid block, and a trifurcate tail. However, the lower jaws of several specimens of *G. agssizi* (Jarvik, 1948: fig. 74), *G. milleri* (Jarvik, 1948: fig. 80) and *G. groenlandicus* (Jarvik, 1950: fig. 21) have rounded posteroventral profiles. Thus, posteroventral jaw morphology may vary within *Gyroptychius*. Alternatively, this region may be damaged in NRM PZ P1409 and may not represent a shared character between *Gyroptychius* and the Tristichopteridae. Furthermore, *Spodichthys* from the Frasnian of East Greenland has been shown to be the immediate sister taxon to the Tristichopteridae (Snitting, 2008), subsequent to the analysis of Ahlberg and Johanson (1998). This taxon displays a rounded posteroventral lower jaw profile (Snitting, 2008: fig. 7). Thus, it appears unlikely that concave posteroventral mandible morphology was present in *Gyroptychius*, was lost in *Spodichthys* and *Tristichopterus*, and then re-evolved at the node containing *Eusthenopteron*.

The phylogenetic relationships of the polyplocodont tooth NMV P229479 are difficult to discern, based on the widespread prevalence of similar tooth morphology throughout several tetrapodomorph groups, including rhizodontids, megalichthyids, tristichopterids, 'elpistostegids' and early tetrapods (Schultze, 1970). Based on relative size and spatial proximity to each other, it is possible that the lower jaw of NMV P198470 and NMV P229479 are attributable to the same form, although several other Palaeozoic fish sites are known to contain multiple tetrapodomorph fish genera (e.g. Mt. Howitt, Holland *et al.*, 2010). Thus, isolated elements such as these must be interpreted with caution, because they may belong to different taxa.

The use of polyplocodont and eusthendont tooth morphologies as phylogenetic indicators may help clarify the relationships of advanced tristichopterids. In the cladistical analysis of Clément *et al.* (2009), *Eusthenodon* and *Langlieria* are grouped in an apical clade with *Mandageria* and *Cabonnichthys*. However, the former two taxa are described as having eusthenodont teeth (Schultze, 1970; Clément, 2002), while polyplocodont teeth are recorded from the later (Ahlberg and Johanson, 1997; Johanson and Ahlberg, 1997). It would be of great interest to determine the tooth morphology of the Eden tristichopterid to compare with the Northern Hemisphere specimens of *Eusthenodon* and the tristichopterids from Canowindra, to ascertain phylogenetic information. Curiously, the use of eusthenodont tooth morphology as a character is not included in the phylogenetic analysis of Ahlberg and Johanson (1997) or Johanson and Ahlberg (1997), with *Eusthenodon* coded with *Mandageria* and *Cabonnichthys* as having polyplocodont teeth. It is not stated in the relative literature whether the teeth of *Mandageria* (Johanson and Ahlberg, 1997) and *Cabonnichthys* (Ahlberg and Johanson, 1997) have been sectioned or are only known from natural moulds, as in other tetrapodomorph fishes from Canowindra, such as *Gooloogongia* (Johanson and Ahlberg, 2001). Among other tetrapodomorph fishes, eusthenodont teeth have also been described from *Platycephalichthys* (Vorobyeva, 1959) and *Litoptychus* (Schultze and Chorn, 1998). This latter form, known from the Frasnian of Colorado, United States of America (Schultze and Chorn, 1998), is placed as the sister taxon to the Megalichthyidae in Coates and Friedman (in press).

The identification of NMV P229477 as a dendrodont tooth confirms the record of porolepiform taxa among the Genoa River fauna. In overall proportions, NMV P229477 is slightly larger than the vomerine fang of *Barameda decipiens* from the Carboniferous of Mansfield, Victoria (Holland *et al.*, 2007), a taxon probably 3–4 m in total body length (pers. obs., 2010). As some specimens of the cosmopolitan porolepiform *Holoptychius* exceed 2.5 m in length (Long, 1995), it is not unreasonable to suggest a very large body size for NMV P229477, possibly among the largest recorded for porolepiform fishes.

Of the faunal assemblage recorded from the Genoa River Beds (table 1), the most common taxon represented in the collections of Museum Victoria is the antiarch placoderm, *Remigolepis*, with up to eight registered specimens. Several large incomplete antiarch plates collected from the Genoa River (ANU 3269–3272) are also stored in the Research School of Earth Sciences, Australian National University (Gavin Young, ANU pers. comm., 2010). High occurrences of *Remigolepis* have been noted from the Upper Famennian tetrapod sites of Ningxia, China and East Greenland (Lebedev, 2004). Further similarities between the fossils localities of the Genoa River and East Greenland also occur in the presence of other taxa. As with the Genoa River Beds, the faunal assemblage of the Aina Dal Formation of East Greenland includes *Remigolepis* and *Bothriolepis*, as well as phyllolepid, tristichopterid, porolepiform and tetrapod material (Blom *et al*., 2007). The remains of *Groenlandaspis*, also reported from the Genoa River, are possibly present in the younger Harder Bjerg Formation of East Greenland (Blom *et al*., 2007). Plates attributed to *Groenlandaspis* from the Genoa River (e.g. NMV P186587) show evenly spaced, fine tubercles, similar to the condition in regularly ornamented specimens of *Groenlandaspis* (e.g. Daeschler *et al*., 2003: figs 2, 4). As stated by Young (2006), this material contradicts spurious reports of a smooth, unornamented form of *Groenlandaspis* from the Genoa River by Young (1993), which had been used previously to equate the age of the Genoa River Beds to that of the Famennian Worange Point Formation.

Of the sarcopterygian material collected from the Genoa River, the rounded scales of specimen NMV P230291 are not characteristic of the genus *Holoptychius*, reported from the area by Young (1993). The abovementioned sarcopterygian scales stored in Museum Victoria are marked with fine radiating ridges on the exposed external surface, similar to those preserved in some rhizodontids (e.g. Holland *et al*. 2007: fig. 4) and non-madageriids tristichopterids (e.g. Jarvik, 1952: fig. 30c). This pattern is distinct from the lateral scales of *Holoptychius*, in which the exposed external surface bares much thicker, broadly separated, radiating lines (Cloutier and Schultze, 1996: fig 11a). Aside from the examples described in this paper, several other sarcopterygian teeth have been collected from the Genoa River. Although varying in size and shape, it is difficult to discern the affinities of these specimens without obtaining detailed cross-sections. These specimens include NMV P229478, a partial jaw with several teeth. In contrast to the possible tristichopterid jaw NMV P198470, the incomplete nature of NMV P229478 does not allow detailed comparisons with known sarcopterygian forms.

Table 1. List of Museum Victoria specimens collected from the Genoa River.

Museum number	taxon	material
NMV P229529	*Remigolepis*	Plate
NMV P229545	*Remigolepis*	Plate
NMV P230039	*Remigolepis*	Plates and scales
NMV P230040	*Remigolepis*	Plate
NMV P230041	*Remigolepis*	Plate
NMV P229544	*Remigolepis*	Plates, shoulder joint
NMV P186587	*Groenlandaspis*	Plate
NMV P186582	*Groenlandaspis* and *Remigolepis*	Plate impressions
NMV P230038	*Bothriolepis*, *Remigolepis* and ?phyllolepid	Plate impressions
NMV P230683	Placoderm indet.	Plate
nMV P230682	Placoderm indet.	Plate
NMV P229476	Placoderm indet.	Plate
nMV P230042	Sarcopterygian indet.	Tooth
nMV P230043	Sarcopterygian indet.	Tooth
nMV P229478	Sarcopterygian indet.	Partial jaw and teeth
nMV P230291	Sarcopterygian indet.	Scales
nMV P229477	Porolepiform indet.	Tusk
nMV P229479	Tetrapodomorph indet.	Tooth
nMV P198470	Tetrapodomorph indet.	Jaw
nMV P41321	Tetrapod indet.	Trackways 1 and 2
nMV P41322	Tetrapod indet.	Trackway 3

In regards to the age of the Genoa River Beds, the potential record of phyllolepid material is compelling as a biostratigraphic indicator. This record consists of elements observed in the field by Anne Warren (pers comm., La Trobe University, 2009), as well as the impression of a plate on specimen NMV P230038 (table 1), a large block red sandstone. This material is of great importance, as the record of phyllolepids from Australia extends to Givetian and Frasnian fossil sites (Young, 2005), in contrast to the Famennian range for the group from Euramerican localities (e.g. Blom *et al*., 2007). This record could support an earlier, possibly Frasnian, age for the Genoa River localities, as suggested by Young (2006). It should be noted that although five phyllolepid genera have been described from the pre-Famennian sites in Australia (listed in Young, 2010), indeterminate phyllolepid material has also been reported from other Famennian sites in East Gondwana (Young, 2005: fig. 4). Furthermore, the possible impression of a phyllolepid plate on NMV P230038 consists of a small, incomplete region of parallel ridged ornament. This region could alternatively be interpreted as the parallel, laterally running ridges marking the anterior ventrolateral plate of *Remigolepis* (e.g. Johanson, 1997: fig 12e). Nevertheless, the report of phyllolepid plates in the field (Anne Warren, pers comm., 2009) possibly provides significant new information regarding the age of the Genoa River Beds. Of the other placoderm taxa reported from the Genoa River, *Bothriolepis, Remigolepis*, and *Groenlandaspis* have been recorded from both Frasnian (e.g. Canowindra; Young, 2008) and Famennian (e.g. Grenfell; Johanson, 1997) fossils sites from Australia.

The possibly Frasnian age of the Genoa River Beds does not contradict current ideas regarding the occurrence and dispersal of tristichopterid and porolepiform fishes throughout the early Late Devonian. Such hypotheses include the origin of the Tristichopteridae in Euramerica, based on the presence of the stem taxon *Spodichthys* and the earliest member of the group *Tristichopterus* in the Northern Hemisphere (Snitting, 2008). The discovery of NMV P198470 from the Genoa River may support the dispersal of the group to Gondwana as early or before the Early–Mid Frasnian, rather than at the Frasnian–Famennian boundary. This scenario is possibly contradicted by the presence of tristichopterid material from the Givetian Bunga Beds, on the south coast of New South Wales (Young, 2007; 2008). However, this material, including scales and an isolated cleithrum, does not include any known tristichopterid synapomorphies, and should be regarded with caution.

The age of porolepiform material from other East Gondwana sites far exceeds that of NMV P229477. This includes elements from the Pragian–Eifelian Dulcie Sandstone and Cravens Peak Beds of Central Australia (Young and Goujet, 2003). This East Gondwanan record appears as old as the earliest porolepiform taxa from the Northern Hemisphere, such as *Porolepis* (Jarvik, 1972).

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