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Tetraxylopteris Beck emend. Hammond and Berry (2005), the first aneurophytalean genus recorded in Australia

Brigitte Meyer-Berthaud [a,*], Anne-Laure Decombeix [a], Robert Dunstone [b], Philippe Gerrienne [c], Nicolas Momont [c], Gavin Young [b]

[a] CNRS, Université de Montpellier, Botanique et modélisation de l'architecture des plantes et des végétations (AMAP), F-34098 Montpellier, France
[b] Research School of Physics and Engineering, Australian National University, Canberra ACT 0200, Australia
[c] PPP, Département de Géologie, Université de Liège, Allée du 6 Août, B18, Sart Tilman, B-4000 Liège, Belgium

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ABSTRACT

The Middle to early Late Devonian aneurophytalean progymnosperms represent the basalmost group of lignophytes and may have included the seed plant ancestor. They are widely recorded in Laurussia. Before this work, the only occurrences of Aneurophytales in Gondwana were in Venezuela and Morocco. In this paper we describe one fertile and two vegetative specimens of *Tetraxylopteris* from the Bunga beds at Bunga Pinch Quarry, a locality near Tathra on the south coast of New South Wales. The vegetative specimens consist of two orders of axes, the last order bearing alternately arranged ultimate appendages. Ultimate appendages are three-dimensional, highly dissected, and composed of terete segments of unequal length. The shape and arrangement of the ultimate appendages suggest that the Australian specimens belong to a new species of *Tetraxylopteris*. The association of *Tetraxylopteris* with large lycopsids constrains the age of the Bunga beds to the Givetian–Frasnian interval. The range of dissected ultimate appendage morphologies displayed by the genus *Tetraxylopteris* may have been advantageous in habitats characterized by high light conditions. These morphologies do not show any specialization for lianescence.

1. Introduction

The first papers describing Silurian–Devonian plants from eastern Australia date back to the end of the nineteenth century (McCoy, 1876; Dun, 1897). The earliest vascular plant assemblages of Australia were reported from marine deposits in Victoria (Lang and Cookson, 1931, 1935; Cookson, 1935, 1937). They form the so-called "*Baragwanathia* flora" of Late Silurian–Early Devonian age. In addition to the lycopsid genus *Baragwanathia* Lang and Cookson, 1935, this flora includes zosterophyllopsids (e.g. *Zosterophyllum australianum* Lang and Cookson, 1931) and a number of taxa long considered as affiliated to the rhyniophytes, e.g. *Yarravia* Lang and Cookson, 1935, *Hedeia* Cookson, 1935 and the species *Salopella australis* Tims and Chambers, 1984. The report of sporangial masses referred to as *Dawsonites* by Tims and Chambers (1984) indicates that the "*Baragwanathia* flora" of Devonian age may have also included basal euphyllophytes. Reconsideration of the systematic affinities of *Hedeia* that has since been collected in the Posonchong Formation of Yunnan suggests that this genus, too, may be affiliated to the euphyllophytes (Hueber, 1983; Hao and Gensel, 2001; Hao and Xue, 2013).

The Late Devonian plant assemblages of Victoria and New South Wales are dominated by arborescent lycopsids, of which *Leptophloeum australe* (McCoy) Walton, 1925 is the most prominent (Gould, 1975; Hill et al., 1999; Talent et al., 2000). The Iguana Creek locality in Victoria (McCoy, 1876) and Genoa River in New South Wales (Dun, 1897), however, provide a different perspective, with vegetative leaves of the progymnosperm *Archaeopteris howitti* McCoy, 1876 associated with pteridosperm foliage of *Sphenopteris iguanensis* McCoy, 1876 and *Sphenopteris carnei* Dun, 1897, and petiole bases called "*Cordaites australis*". Remains of *Barinophyton obscurum* (Dun) White, 1905 are also reported from Genoa River. Such communities associating *Archaeopteris* trees with a lower vegetation of seed plants and Barinophytales contrast sharply with the forests of arborescent lycopsids thought to have dominated the northeastern part of Gondwana in the Late Devonian (Talent et al., 2000). Despite the lack of fern remains, the plant assemblages of Iguana Creek and Genoa River are reminiscent of the associations recorded in the Famennian localities of Elkins (West Virginia), Red Hill (Pennsylvania) and the Evieux flora of Belgium (Fairon-Demaret, 1996; Cressler, 2006; Cressler et al., 2010).

There are few records of Middle Devonian to early Late Devonian plant assemblages in Australia that would help understand the transition between the "*Baragwanathia* flora" and the floras of Late Devonian age. The age of the lycopsid flora described from the Yalwal and Bega districts of New South Wales is poorly constrained and may either be

* Corresponding author.
E-mail address: meyerberthaud@cirad.fr (B. Meyer-Berthaud).

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Middle or Late Devonian (Walkom, 1928; Gould, 1975). The most reliable plant record to date consists of numerous specimens of *Leclercqia complexa* (Banks et al.) Bonamo et al., 1988 collected at Storm Hill, in the Broken River area of north-eastern Queensland (Fairon-Demaret, 1974; Meyer-Berthaud et al., 2003). *L. complexa* is a species of herbaceous lycopsids that has a cosmopolitan distribution in the Middle Devonian. Based on lithology and conodont evidence, the age of the fossils from Storm Hill is between Eifelian and early Givetian; it is probably middle Eifelian (Meyer-Berthaud et al., 2003). To date, no Middle Devonian euphyllophytes have been discovered in Australia.

Within the euphyllophytes, phylogenetic analyses suggest that the aneurophytalean progymnosperms are the basalmost group of lignophytes, i.e. of plants that evolved a bifacial cambium producing both secondary xylem and secondary phloem. These analyses suggest that the Aneurophytales may have included the seed plant ancestor (Hilton and Bateman, 2006). The Aneurophytales are comprised of seven genera (Beck and Wight, 1988), but only four, *Aneurophyton* Kräusel & Weyland emend. Schweitzer and Matten (1982), *Triloboxylon* Matten & Banks emend. Scheckler and Banks (1971a), *Rellimia* Leclercq and Bonamo, 1973 and *Tetraxylopteris* Beck emend. Hammond and Berry (2005), are known from external morphology. These are also the only genera for which the reproductive structures are documented. The Aneurophytales have generally been presented as bushy, but there is evidence that at least one genus (*Tetraxylopteris*) showed nonself-supporting aerial stems borne on stout rhizomes (Speck and Rowe, 2003; Stein et al., 2012). The Aneurophytales extend from the Late Eifelian to the Frasnian (Gerrienne et al., 2010; Prestianni et al., 2012).

The far south coast of New South Wales, Australia, has well known Devonian fossil sites ranging in age from Eifelian in the north to Famennian in the southern end of the range and across the Victorian border. Young (2007) listed 30 vertebrate taxa from the area and reported on several plant sites that have yet to be comprehensively studied. This paper describes three specimens found at one of these sites on the southeast coast of Australia. One is fertile, the other two are vegetative, and all are assignable to the aneurophytalean genus *Tetraxylopteris*. The possession of distinctive ultimate appendages on the vegetative specimens extends the range of appendage morphologies displayed by *Tetraxylopteris*. It suggests that the vegetative specimens may represent a new species. The stratigraphical and ecological significance of this discovery is discussed.

2. Locality, stratigraphy, and age

The plant fossils come from a gravel quarry immediately east of the main road about halfway between the coastal towns of Tathra and Bermagui ('Bunga Pinch Quarry', Fig. 1). This is within the western margin of outcrop of the Bunga beds, a sedimentary unit within the 'Boyd Volcanic Complex' as defined by Fergusson et al. (1979) to include 'Eden Rhyolite' and 'Lochiel Formation' of earlier authors. The rhyolite had been interpreted as the base of the Devonian sequence, which is unconformably overlain by two Upper Devonian sedimentary units ('Lochiel' and 'Merrimbula' Formations). Fergusson et al. (1979) mapped a more complex interfingering relationship between sedimentary and igneous rocks, describing the Boyd Volcanic Complex in terms of eight facies associations. The Bunga beds represent their 'Flyschoid facies' of 'dark colored shales containing abundant *Lepidodendron clarkei*', as first recorded by Hall (1959) in the vicinity of Bunga Head. The plant fossils (mainly lycopsids) established a Devonian age for the Bunga beds, which at some localities are overlain by the volcanics, and rest unconformably on folded lithologically similar black shales of Ordovician age. The exposure of sediments and volcanics in the vicinity of Bunga Head is an outlier separated by some 20 km from the main outcrop of the Boyd Volcanic Complex, which extends south from Tathra, inland from Pambula, and to the south of Eden (Fig. 1).

Published geological maps for the vicinity of Bunga and Goalen Heads (Lewis et al., 1994; Rickard and Love, 2000; Giordano and Cas, 2001) show different detail of the sedimentary and volcanic outcrops, but the main area of sedimentary rocks lies to the north of the main area of volcanics. The sediments extend inland some 3 km from the original type area for the Bunga beds, comprised of mainly finely bedded carbonaceous dark shales, with some interbedded silts and sandstones, exposed for about 9 km along the coast. Stratigraphic thickness of coastal exposures varies between 40 and 200 m (Fergusson et al., 1979; Cas et al., 1990). The Bunga Pinch Quarry producing our plant specimens is about 2.5 km inland, and could be 700 + meters stratigraphically above the coastal exposures, if consistent dip and little structural complexity of the intervening strata is assumed (Burrow and Young, 2012). However, where well exposed on the coast, the Bunga beds may exhibit complex folding, faulting, intrusive dykes, etc. (e.g. Giordano and Cas, 2001, fig. 10) so this may not be valid.

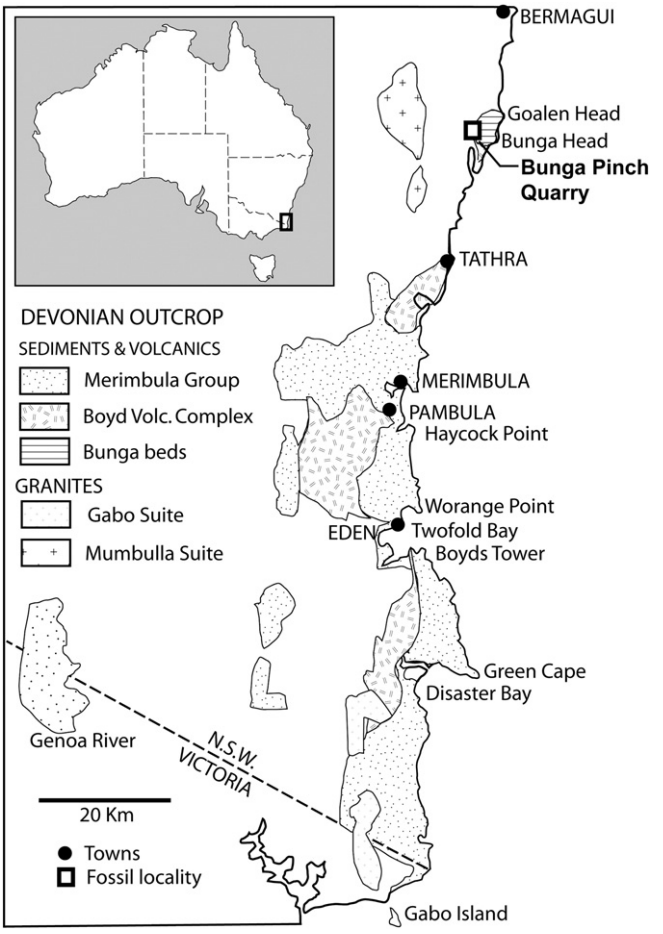

Fig. 1. Devonian outcrops on the far south coast of New South Wales and adjacent Victoria (after Young, 2007).

The two types of lycopsids originally illustrated by White (1986, fig. 90; 1988, p. 39) probably came from the coastal outcrops at Bunga Beach, and similar examples from Bunga Pinch Quarry were figured by Young (2007, fig. 3d–f; see also Plate I, 2 in this paper). The coastal outcrops at Bunga Beach have also produced significant fossil fish remains (sharks, sarcopterygians, actinopterygians; Young, 1982, 2007; Long and Young, 1995; Choo, 2009), and sarcopterygian scales and acanthodian remains have been found in Bunga Pinch Quarry and nearby black shale exposures (Burrow, 1996; Burrow and Young, 2012).

Age constraints on the Bunga beds were discussed by Young (2007). A Middle Devonian age was suggested for the fish, consistent with an Early–Middle Devonian age originally proposed for the plants (Hall, 1959; White, 1986, 1988). This contrasts with geological interpretations of a Late Devonian age for the Boyd Volcanic Complex (e.g. Fergusson et al., 1979; Lewis et al., 1994). An update of the fish biostratigraphy