

***PTILOPHYLLUM MUELLERI* (ETTINGSH.) COMB. NOV. FROM THE OLIGOCENE OF AUSTRALIA: LAST OF THE BENNETTITALES?**

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Several small pinnate leaves of early Oligocene age from Cethana, Tasmania, are newly described and found to be conspecific with *Anomozamites muelleri* Ettingsh. recorded from coeval strata at Emmaville, northern New South Wales. These fossils are most probably referable to the Bennettitales on the basis of leaf size, leaflet shape, and venation patterns, in the absence of diagnostic cuticular details. They are transferred to *Ptilophyllum* on the basis of leaflet morphology and represent the youngest putative bennettitalean remains yet documented. Their occurrence reinforces previous arguments that the highest-paleolatitude fragments of southeastern Gondwana provided moist temperate refugia for the survival of Mesozoic gymnosperm taxa well into the Cenozoic.

Keywords: gymnosperms, Paleogene, extinction, high latitude, ghost lineage, Lazarus taxa.

Introduction

Bennettitales are an extinct clade of seed plants traditionally considered to range from the Middle Triassic to Late Cretaceous. They are characterized by cycadlike foliage and flowerlike reproductive organs and were dominant or codominant elements of many Mesozoic plant communities. The earliest convincing bennettitaleans are those reported from the Carnian Molteno Formation in South Africa (Anderson and Anderson 1989) and from the coeval Lunz Formation in Central Europe (Pott et al. 2007), although unpublished *Weltrichia*-like reproductive structures are known from the slightly older (Middle Triassic) Esk Formation in eastern Australia (S. McLoughlin, unpublished data). Putative Paleozoic records have yet to be verified by cuticular details or reproductive structures (Pott et al. 2010).

Historically, Bennettitales were widely regarded as close relatives of Cycadales (Morris 1841; Miquel 1851). However, recent cladistic analyses indicate that Cycadales and Bennettitales are not closely related, although controversy continues regarding the interpretation of certain reproductive characters and the phylogenetic position of the Bennettitales within the spermatophytes (Friis et al. 2007; Rothwell et al. 2009). Several analyses resolve Bennettitales as a sister group to the Gnetales and angiosperms within an “anthophyte” clade (Crane 1985; Nixon et al. 1994; Donoghue and Doyle 2000; Hilton and Bateman 2006; Friis et al. 2007). On this basis, their stratigraphic range and anatomical character states have become important in evaluating the cladogenesis of the flowering plants.

Bennettitalean foliage varies considerably in size and shape but is generally once pinnate (segmented). Leaves vary from <10 cm to ~70 cm in length, their size seemingly reflecting

adaptation to specific climates, habitats, and statures of the parent plants within the vegetation (Pott and McLoughlin 2009). Bennettitalean leaf segments are typically rhombic, falcate, or linear and incorporate subparallel dichotomous or, in a few cases, anastomosing venation (Watson and Sincok 1992). Where cuticle is preserved, Bennettitales are readily distinguishable from Cycadales by their syndetocheilic as opposed to haplocheilic stomata (Florin 1933). In the absence of cuticular details, bennettitalean and cycadalean foliage can be difficult to discriminate, although the Cycadales typically have larger (30–600 cm) leaves with more diverse venation styles, commonly contracted and thickened leaflet bases, and, in some cases, lobed or spinose margins (Jones 1993; Passalia et al. 2010).

In Australia, bennettitalean fossils (leaves and reproductive structures) are diverse and abundant components of the flora from the Middle Triassic to the Early Cretaceous (Douglas 1969; Gould 1975; Anderson et al. 1999; McLoughlin et al. 2002; Holmes and Anderson 2008). Their diversity and abundance in Australia fell dramatically after the Hauterivian (mid-Early Cretaceous), concomitant with the diversification of angiosperms and the appearance of modern conifer genera (McLoughlin et al. 2010). However, bennettitaleans persisted as minor components of Australian Aptian to Cenomanian floras (de Vis 1911; Walkom 1919; Douglas 1969; Pole and Douglas 1999; McLoughlin et al. 2000, 2010). No post-Cenomanian records are known from this continent apart from the *Anomozamites* (= *Ptilophyllum*) *muelleri* specimens studied herein, and a similar pattern of decline is evident in the New Zealand Cretaceous (McQueen 1956; Daniel et al. 1990; Pole and Philippe 2010).

In the Antarctic Peninsula, bennettitalean leaves represent ~14% of Aptian species diversity (Cantrill 2000). This group persisted (constituting ~3.5% of species) into the Albian but apparently became extinct in that region by the Campanian (Cantrill and Poole 2002). Bennettitales show a similar pattern of declining diversity, distribution, and abundance through the

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Cretaceous in the Northern Hemisphere (Vakhrameev 1981, 1991; Nishida 1991; Watson and Sincock 1992; Kvaček 1995; Coiffard et al. 2007; Butler et al. 2009), with apparent survival in relictual populations at high latitudes toward the end of their temporal range. This is emphasized by records of two species from the Santonian-Campanian Pautût flora of West Greenland (Boyd 1992). These specimens, or the poorly preserved examples of *Zamites* in the Coniacian-Campanian of western Canada (Bell 1957), appear to be the youngest records of Bennettitales in the Northern Hemisphere, given that Maastrichtian examples of *Nilssonina* from northwestern Russia (Vakhrameev 1991) and western Canada (Bell 1949) likely represent cycadales (Peppe et al. 2007; Pott et al. 2007). Unfortunately, pollen records are of little assistance in tracking the stratigraphic range and geographic distribution of the Bennettitales. Their monosulcate pollen is indistinguishable from ginkgoalean, cycadales, and pentoxylean grains on the basis of features visible with light microscopy.

Ettingshausen's (1883, 1886, 1888) studies of the Vegetable Creek and Dalton floras were the first to document whole paleofloral assemblages from the Australian Cenozoic. He assigned many of the taxa in the Vegetable Creek area of New South Wales to genera characteristic of the Northern Hemisphere. In so doing, he lent support to his cosmopolitan theory of a relatively uniform global flora in the Paleogene. Although many of his original identifications have been subsequently revised (Hill 1988a, 1988b), Ettingshausen's descriptive thoroughness was superior to many of his Australian contemporaries; hence, his identification of atypical gymnospermous components in the Australian Paleogene deserves special attention.

Here we reinvestigate enigmatic leaves that Ettingshausen (1886, 1888) attributed to *A. muelleri* from the Vegetable Creek area and document conspecific forms from the Oligocene of Tasmania that represent the youngest putative bennettitalean fossils.

Geological Setting and Age

Emmaville Locality

Ettingshausen (1886, 1888) originally indicated that the specimens studied herein were derived from Vegetable Creek, the former name for the modern township of Emmaville in northern New South Wales (fig. 1). However, several fossiliferous sites occur at different stratigraphic levels in this region. The Cenozoic rock units in the Emmaville area have not been given formal lithostratigraphic names. R. Etheridge, in an appendix to the English translation of Ettingshausen's (1888) work, attempted to clarify the distribution of the published fossils amongst the various localities. He indicated that all specimens of "*Anomozamites*" studied by Ettingshausen were derived from the Old Rose Lead, between Hill's and Watson's shafts, this being a tributary of the main Vegetable Creek Deep Lead. The sedimentary blocks from this area hosting the fossils studied herein consist predominantly of friable white to gray laminated claystones. Red-orange ferruginous staining is evident along joints and some bedding planes, and this mineral staining coats many of the leaf impressions. An extensive discussion of the distribution and age

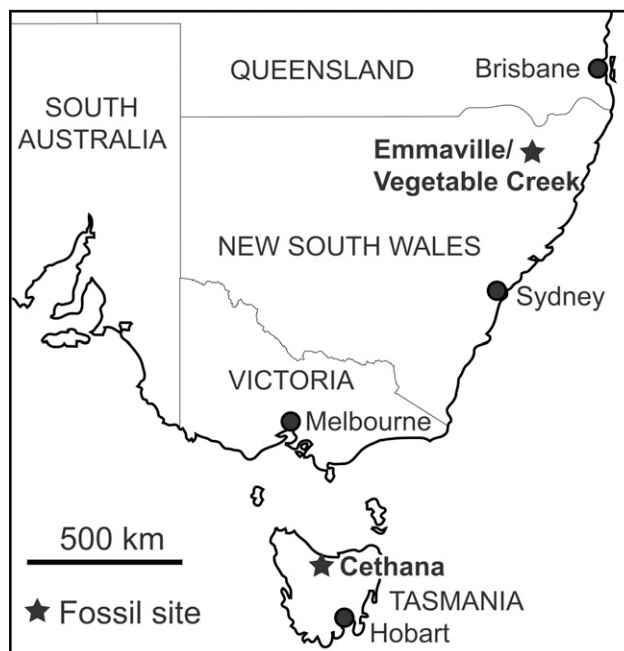


Fig. 1 Map of southeastern Australia showing the Oligocene fossil localities of Emmaville (Vegetable Creek), New South Wales, and Cethana, Tasmania.

of the various fossil localities at Emmaville and surrounding areas was provided by Pickett et al. (1990). Their studies of sections exposed in abandoned tin mines near Emmaville revealed a stratigraphic succession consisting of five Cenozoic units with slightly different lithologies resting on Paleozoic basement (fig. 2). They indicated that Hill's and Watson's shafts lie at Australian Map Grid references 626,408 (approximately 29°27'21"S, 151°35'26"E) and 629,412 (approximately 29°27'31"S, 151°35'05"E), respectively, of the Emmaville 1 : 50,000 sheet, ~1.5 and 2.0 km southwest of Emmaville township. Pickett et al. (1990) were unsuccessful in recovering palynomorphs from sediments at these sites, but on lithological and stratigraphic criteria they proposed that the beds were correlative with units 4 or 5 of pit 1 to the west; these rest immediately above a basalt that Pickett et al. (1990) dated to 30.4 ± 0.3 Ma by K-Ar methods (fig. 2). This suggests an Oligocene (or possibly younger) age for the strata hosting "*Anomozamites*" *muelleri*. On the basis of palynological analyses and radiometric dating of quarry samples, Pickett et al. (1990) noted that other shallow strata in the region around Emmaville ranged in age from middle Eocene to earliest Miocene. In addition to "*A.*" *muelleri*, the Emmaville deposits host a broad range of angiosperm, conifer, and fern remains (Ettingshausen 1886, 1888). Veevers et al. (1991) indicated a paleolatitude of 48°–50°S for the Emmaville area in a paleogeographic reconstruction of the Australian region for the earliest Oligocene.

Cethana Locality

Poorly consolidated creamy yellow to light brown-gray mudstones and siltstones with thin interlaminated sands are

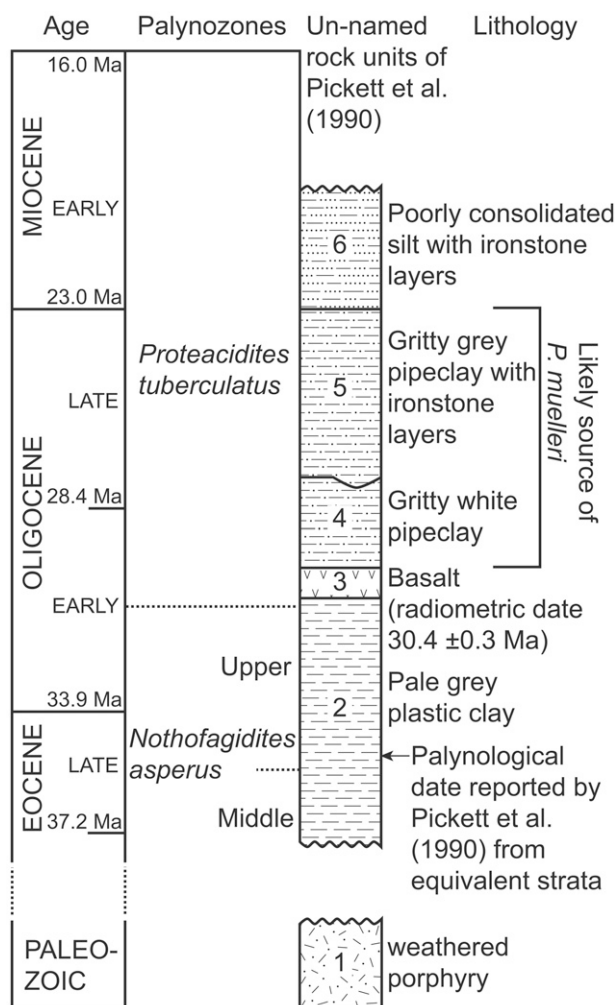


Fig. 2 Stratigraphic column of mid-Cenozoic deposits in the Emmaville district (showing the likely source of the studied fossils), applying the nomenclature of Pickett et al. (1990) correlated to the chronostratigraphic scale of Gradstein et al. (2004).

exposed in a road cutting ~0.5 km above Cethana Dam, northern Tasmania (41°32'S, 146°07'E; fig. 1). This deposit has been dated via palynostratigraphy as early Oligocene (Macphail et al. 1994), probably within the Lower *Proteacidites tuberculatus* Zone of Stover and Partridge (1973). The maximum age was confidently provided by the presence of *Cyatheacidites annulatus* Cookson and the likely but less certain upper limit by the presence of *Granodiporites nebulosus* Partridge. The relatively high abundance of *Nothofagidites flemingii* (Couper) Potonié grains is also consistent with an Oligocene age (Hill 1984). Cethana appears to belong to a group of contemporaneous assemblages in northern Tasmania that preserve evidence of microthermal-mesothermal wet forest vegetation (Macphail et al. 1994). Identified macrofossils from Cethana include a broad range of austral conifers, numerous *Nothofagus*, Proteaceae and Cunoniaceae species, together with the cycads *Macrozamia* and *Pterostoma*, and several ferns (Hill 1983, 1984; Carpenter and Hill 1988; Hill and Christophel 1988; Hill and Carpenter 1989; Carpenter

1991a, 1991b; Carpenter and Buchanan 1993; Hill and Scriven 1997). Veevers et al. (1991) placed Cethana at a paleolatitude of ~60°S in the earliest Oligocene.

Material and Methods

The studied material from Emmaville was originally collected by T. W. E. David and C. S. Wilkinson, who were then New South Wales geological surveyors, some time in the 1870s to early 1880s (Ettingshausen 1888). Eight specimens held by the Australian Museum, Sydney (AMF6660, AMF51336, AMF58839, AMF59766, AMF59767, AMF59769B, AMF66356, AMF134391), are herein confidently attributed to Ettingshausen's concept of *Anomozamites muelleri*. Most rock samples bearing "A." *muelleri* are white claystones with red-orange ferruginous staining on some leaf impressions. In one case (AMF66356), the cavity left by the decayed leaf appears to have been largely filled by iron oxides and clays to form a thin cast. Two samples (AMF59766, AMF59767) consist of pale grey claystone bearing leaf impressions retaining a small amount of coalified organic matter. The lithology appears to whiten with exposure and weathering; it was described as "white pipeclay" by Etheridge (in Ettingshausen 1888) and "white kaolinitic material" by Pickett et al. (1990). Six specimens from Cethana held in the collections of the Department of Plant Sciences, University of Tasmania (C-257, 258, 384, 455, 458, 662) represent leaf impressions in yellow to light brown-gray siltstones. These specimens were collected by R. S. Hill and students, R. J. Carpenter, G. J. Jordan, and G. J. Davidson, all from the University of Tasmania, during the 1980s.

Macrophotography of the Australian Museum specimens was performed with a Canon EOS 40D digital camera using low-angle illumination from the upper left. For the Tasmanian specimens, a Canon PowerShot G10 was used. Attempts were made to prepare cuticle from organic material recovered from AMF59766 using Schulze's reagent (35% HNO₃ with a few crystals of KClO₃) and 5%–10% potassium hydroxide (KOH). However, only degraded cuticle fragments lacking informative cellular details were recovered. Fluorescence microscopy of this same specimen was performed with a Leica Diaplan microscope with fluorescence equipment at the University of Münster, Germany. However, this procedure also failed to yield any details of epidermal cell outlines or stomata. Fragments of organic film from AMF59766 and mineral infilling of pinnules from AMF66356 were examined using a Hitachi S-4300 field emission scanning electron microscope at the Swedish Museum of Natural History, but they yielded few micromorphological details.

Systematic Paleobotany

Order—Bennettitales

Genus—*Ptilophyllum* Morris in Grant 1840

Type Species—*Ptilophyllum acutifolium* Morris in Grant 1840; Lower Cretaceous; Kachchh, India

Discussion. The separation and typification of bennettitalean leaf morphogenera have been discussed extensively over

the past century (Seward 1917; Harris 1969; Watson and Sincock 1992; Rees and Cleal 2004; Wang et al. 2008; Pott and McLoughlin 2009). Most bennettitalean leaves can be readily assigned to one of several morphogenera on the basis of the shape of the leaflet base, the gross proportions of the leaflets, and the venation pattern (Watson and Sincock 1992). However, there are some cases of ambiguity, in which pinules within a single leaf may bear the characters of different morphogenera. For example, Pott and McLoughlin (2009) outlined the difficulties in consistently differentiating leaves attributed to *Pterophyllum*, *Anomozamites*, and *Nilssoniopteris* on the basis of traditional criteria, and they documented several cases of erroneous identification. Where fragmentary material is available, and where a single population of leaves shows a range of variation, the typical pattern of leaf characters should be used for generic assignment rather than that of individual atypical leaflets. *Ptilophyllum* leaves may be paripinnate and have generally slender falcate (less commonly linear) leaflets with bluntly to sharply pointed apices. The acroscopic margin of the leaflet base is straight or contracted to form a rounded angle, whereas the basiscopic margin is decurrent (Watson and Sincock 1992), although Harris (1969) outlined the difficulty in applying these characters in every case, especially where leaflets are crowded. Leaflets are usually inserted on the upper side of the rachis but leave a large portion of the rachis centre uncovered. In contrast, *Anomozamites* leaves are slender, almost completely and regularly segmented (pinnate), with more or less parallel-sided leaflets that are as long as or, at most, twice the length of their width (Pott and McLoughlin 2009). The leaves generally lack a terminal leaflet (paripinnate). All leaflets are of similar shape, although their dimensions may vary along the leaf. Leaflets are inserted by their whole base laterally on the rachis; the base is typically expanded (decurrent) or straight on both acroscopic and basiscopic margins. Leaflet apices are obtusely rounded or truncated. There is clearly some variation in the material described below with respect to the shape of the acroscopic and basiscopic margins of the pinules where they attach to the rachis. However, it is equally clear—on the basis of leaf size, leaflet shape, and venation—that these leaves belong to a single species. On the basis of the general criteria for separating bennettitalean morphogenera, *Anomozamites muelleri* Ettingsh. is transferred to *Ptilophyllum*.

Species—*Ptilophyllum muelleri* Ettingshausen
1886 *comb. nov.*

Basionym. *Anomozamites Muelleri* Ettingshausen 1886 (p. 9, pl. VIII, figs. 19–22); Ettingshausen 1888 (p. 94–95, pl. VIII, figs. 19–22).

Synonymy. *Anomozamites muelleri* Ettingshausen; Hollick 1932 (p. 182, pl. 13, fig. 3.19–3.22). ?Cycad Carpenter 1991b (p. 35, fig. 6g, 6h; R. J. Carpenter, unpublished data). *Anomozamites muelleri* Ettingshausen; Carpenter 1991b (fig. 6i; R. J. Carpenter, unpublished data).

Lectotype. Since a type specimen was not designated by Ettingshausen (1886) and because his schematic line drawings cannot be related unambiguously to any of the specimens held in the original collections at the Australian Museum, we select AMF59766 (which retains some organic matter and consti-

tutes one of the most complete specimens) as the lectotype (figs. 3A, 4G; this specimen probably equates to Ettingshausen's [1886] stylized illustration [pl. VIII, fig. 22]).

Type locality, unit, and age. Emmaville district, northern New South Wales; unnamed kaolinitic claystone in the Old Rose Lead (paleochannel fill); most probably Oligocene (figs. 1, 2).

Emended specific diagnosis. Pinnate leaf with segments that are elongate-triangular proximally, falcate in midleaf, elongate rhombic near apex, and with a lacrimiform terminal pinule. Segment apices forming a blunt point, inclined toward leaf apex. Six to 15 veins of uniform robustness per segment at densities >4 per mm across midpinule. Veins rarely bifurcating, terminating from midway along basiscopic margin to tip of segment.

Description of the Emmaville specimens. Incomplete leaves with preserved lengths of 21–48 mm (fig. 3A–3H), estimated complete lengths are 48–77 mm; maximum leaf widths are 7.5–12.4 mm; estimated complete length : width ratio is 6.0 : 1 to 7.5 : 1 (lorate-linear). The rachis is relatively stout, tapering distally, in some cases with longitudinal striae or two prominent grooves; maximum width 0.4–0.9 mm. Segments are typically inserted at ~35°–45° to the rachis near the leaf base (fig. 3F–3H), at 50°–70° in midleaf (fig. 4D, 4G, 4H), and at 30° near the apex (fig. 3C). Maximum segment lengths are in the range of 4.9–8.6 mm; maximum width of the segment base varies from 2.2 to 4 mm; maximum width of the segments midleaf (measured perpendicular to the venation) is 1.7–3.0 mm. Segment length : width ratios midleaf are typically 2 : 1 to 4 : 1. The segments have a broad basal attachment, slightly rounded to decurrent on the basiscopic margin (fig. 4A–4H), rounded or forming a very small auricle on the acroscopic margin. Segments are inserted adaxially on the rachis, overlapping the rachis margin by 0.17–0.22 mm (fig. 4D, 4E) and partly obscuring the rachis in impressions of the adaxial leaf surface. Segments are elongate-triangular basally, becoming falcate in midleaf and elongate rhomboid near the apex; a lacrimiform terminal segment is present. The basiscopic margin of each segment is typically broadly rounded or straight but is decurrent in proximal segments (fig. 5A–5H). The acroscopic margin is straight to gently curved (concave) from the base to the tip. Segment apices form a blunt point and are typically inclined toward the apex of the leaf (fig. 4A–4C). Multiple veins emerge from the rachis and run approximately parallel to the margins (fig. 4A–4D, 4G). Veins are slender; in some cases, they bifurcate once in the proximal half of the pinule but are otherwise free and of equal strength; they typically converge slightly in the distal half (fig. 5A–5E). Veins terminate from midway along the basiscopic margin to the blunt tip. Veins are very closely spaced, with densities ranging from 4 to 9.3 per mm across the center of the segments. Segments contain 10–(12)–15 ultimate veins. Segments are typically separated by <0.5 mm along their length but range from abutting basally to separated by up to 3 mm near the apex (fig. 3E, 3H). Segment arrangement varies from opposite to fully alternate, in some cases showing the complete range of architectures on a single leaf. Impressions of the adaxial surface of some leaves show alternate pinule bases forming a slightly sinuous pattern where they obscure the rachis (fig. 4B). Organic remnants of leaves retained on the fossils reveal a homogenous coalified interior and corroded outer layers when

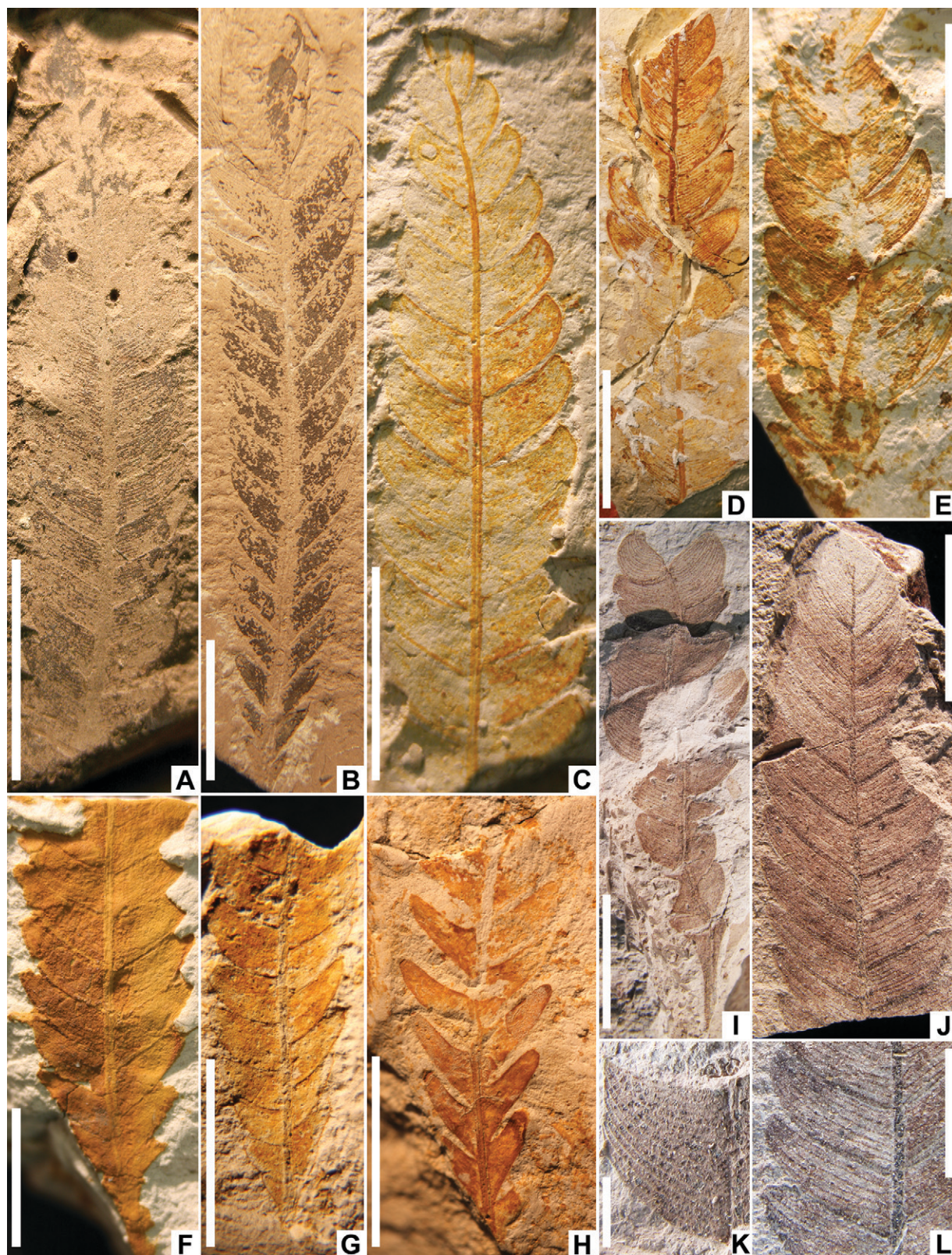


Fig. 3 Leaves of *Ptilophyllum muelleri* Ettingsh. 1886 comb. nov. from Emmaville, New South Wales (A–H), and Cethana, Tasmania (I–L). A, Specimen AMF59766 (lectotype). B, AMF59767. C, AMF6660a. D, AMF51336. E, AMF134391. F, AMF66356. G, AMF59769. H, AMF58839. I, C-258. J, C-455b. K, C-347, enlargement of single leaf segment. L, C-455a, enlargement of leaf segments. Scale bars = 10 mm (A–J), 5 mm (K, L).

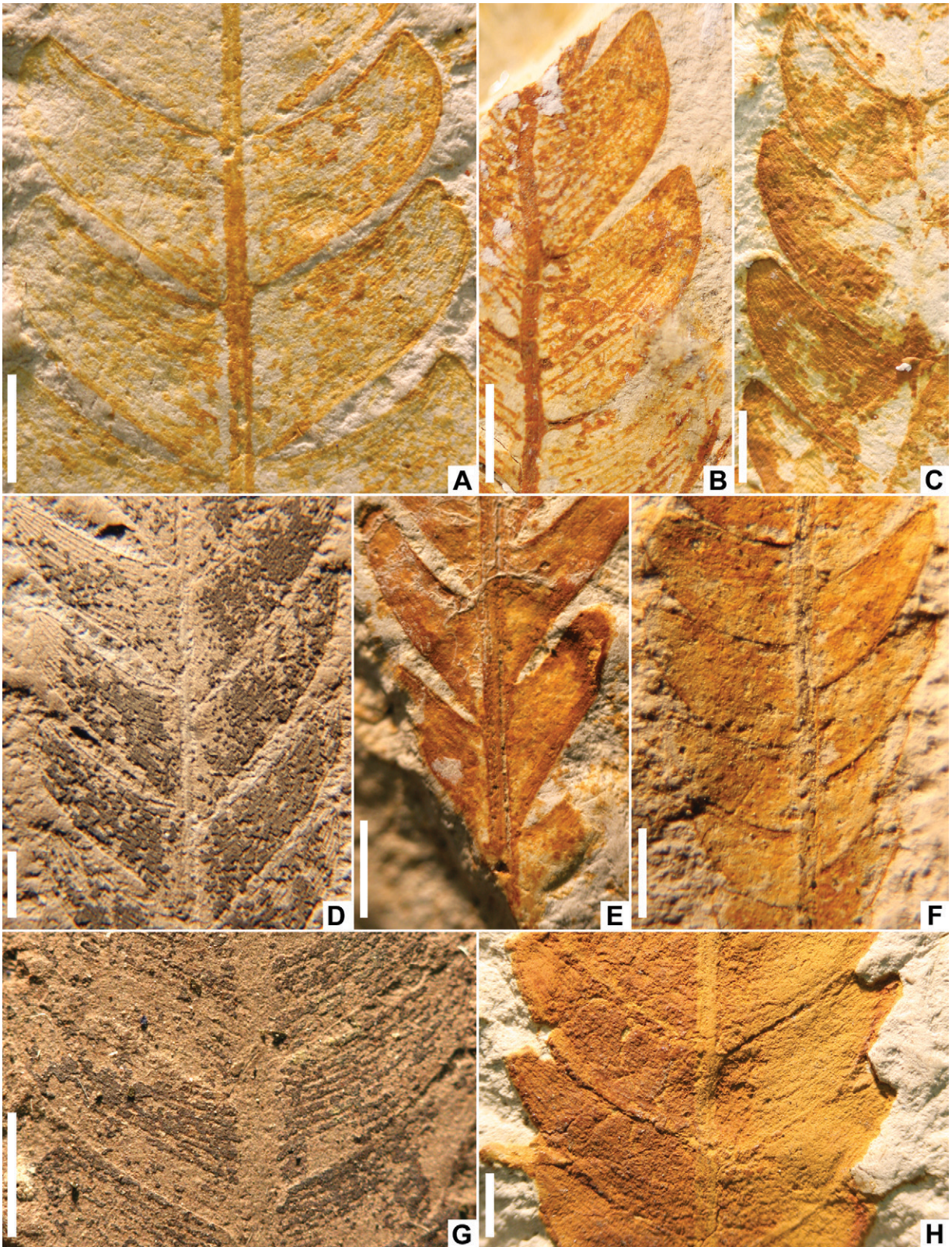


Fig. 4 Enlargements showing the range of leaf segment morphologies of *Ptilophyllum muelleri* Ettingsh. 1886 comb. nov. from Emmaville, New South Wales. A, AMF6660 with arched segment apices. B, AMF51336. C, AMF134391. D, AMF59767. E, AMF58839 with decurrent segment bases. F, AMF59769. G, AMF59766 (lectotype). H, AMF66356. Scale bars = 2 mm.

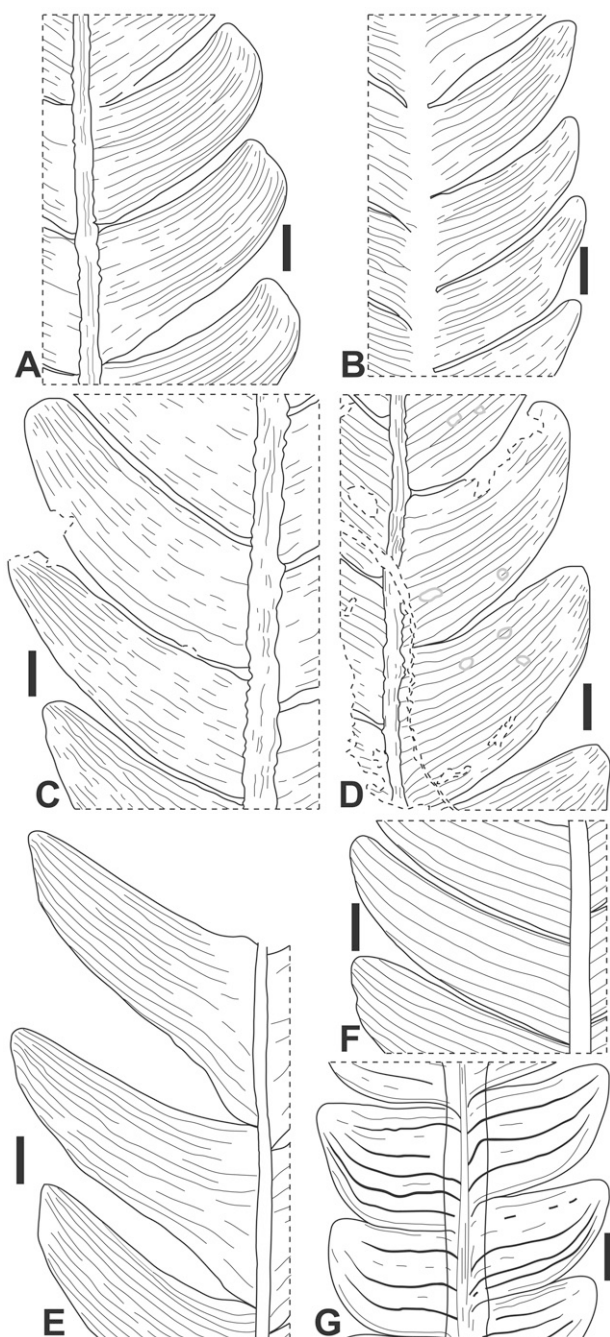


Fig. 5 Line drawings of venation details in *Ptilophyllum muelleri* (A–E) and *Dryandra praeformosa* Ettingsh. (F, G) from Emmaville, New South Wales, and *P. muelleri* from Cethana (F). A, AMF6660. B, AMF59766 (lectotype). C, AMF66356. D, AMF51336. E, AMF59767. F, C-455a. G, AMF66353. Scale bars = 1 mm.

viewed with SEM. The exterior surface of the organic crust locally reveals ill-defined outlines of oblong cells that, in some cases, bear microridges or contraction wrinkles on the periclinal walls, but no stomatal details were obtainable.

Description of the Cethana specimens. The specimens consist of leaves up to 55 mm long and 20 mm wide, with subopposite or alternately arranged segments inserted later-

ally on a prominent rachis (fig. 3I–3L). Two specimens have petioles reaching at least 3 mm long. The segments range from bluntly triangular or rhombic to narrowly falcate (fig. 3I–3L), generally decreasing in area but increasing in relative width toward the base of the leaf. Segments typically reach ~8 mm long, with a 3–10-mm-wide attachment (the maximum segment width) to the rachis. Each segment bears 6–15 equispaced veins that dichotomize sparsely near their base and otherwise pass in nearly parallel courses to the distal margins or slightly converge toward the apex (fig. 3L). No organic remains could be recovered from the leaves.

Discussion

Taxonomic Affinities

The Cethana specimens clearly fall within the range of variation represented by the *Ptilophyllum muelleri* material from Emmaville and, therefore, are assigned to that species. Although Ettingshausen (1888) did not designate repository numbers for his specimens, at least one *P. muelleri* leaf (AMF51336; fig. 3D) has been registered under the name “*Dryandra praeformosa* Ettingshausen, 1886” in the Australian Museum collections. Conversely, one specimen registered as *P. muelleri* (AMF58840) is clearly an example of *D. praeformosa* on the basis of leaf segment shape and venation details. *Dryandra praeformosa* is architecturally very similar to extant *Banksia formosa* (R.Br.) A.R. Mast et K.R. Thiele and is readily distinguished from *P. muelleri* by its proportionally shorter (almost square) leaf segments (fig. 6A, 6B) with fewer (usually only three) and more strongly convergent principal veins (fig. 5G, 6C, 6D).

Some extant species of *Banksia* and fossil species of *Banksiaaeformis* and *Banksiaephyllum* also have short triangular to rhombic leaf segments that superficially resemble those of *P. muelleri* (McLoughlin and Hill 1996; George 1999), but these angiosperms can be distinguished by their more robust major veins, presence of finer subsidiary and interconnecting veins, and strong apical convergence of the principal veins in each leaf segment. *Banksia novae-zealandiae* R.J. Carp., G.J. Jord., D.E. Lee et R.S. Hill from the late Oligocene to early Miocene of New Zealand has leaf segments of similar shape and size to *P. muelleri*, but it is segregated by having only indistinct veins in each segment, whereas the veins of *P. muelleri* are consistently clear and of more or less equal strength. The New Zealand species is also distinguished by its segment margins that slightly recurve onto the abaxial side and the presence of prominent, large-diameter trichome bases over the adaxial surface that give it a distinctly pocked appearance (Carpenter et al. 2010). As for *B. novae-zealandiae*, some *Banksiaephyllum* leaves from the Cethana sediments are known to have quite robust cuticle (Carpenter and Jordan 1997), but none of the specimens of *P. muelleri* from these sediments shows any trace of organic preservation. The superficially similar leaves of the extant angiosperm *Comptonia peregrina* (Linnaeus) J.M. Coulter (Myricaceae) and its putative fossil relatives (e.g., *Comptoniphyllum* Nath.) differ in their possession of lamina glands and interconnected veins of several orders (Berry 1906; Endô and Morita 1932). Any possibility that *P. muelleri* actually represents an angiosperm



Fig. 6 Leaves of *Dryandra praeformosa* Ettingsh. from Emmaville, New South Wales, with leaflet form superficially similar to *Ptilophyllum muelleri*. A, Central portion of leaf, AMF51173. B, Basal portion of leaf, AMF66353. C, Enlargement of leaflet venation (imprint of abaxial surface), AMF51173. D, Enlargement of leaflet venation (imprint of adaxial surface), AMF66353. Scale bars = 10 mm (A, B), 1 mm (C, D).

could be unequivocally discounted only by the future recovery of specimens with cuticular preservation.

Several authors have recognized the anomalous stratigraphic position of *P. muelleri* and, on this basis, have doubted its

bennettitalean affinities. Seward (1917) noted the presence of *P. muelleri* in the Cenozoic of eastern Australia but offered no firm opinion as to its bennettitalean versus cycadalean affiliation. Kräusel (1928) speculated whether *P. muelleri* might be a dicotyledonous angiosperm or a fern but concluded that he could make no confident identification without personal inspection of the specimens. Hollick (1932, p. 182) doubted the cycadalean or bennettitalean affinities of *P. muelleri* and stated, “The venation, as depicted, is that of a cycad, but the general appearance of the leaf may be regarded as somewhat suggestive of a fern.” Although some ferns (e.g., pinnate *Asplenium* species) may have pinnules of similar shape and size to those of *P. muelleri*, we regard the latter’s affiliation with ferns unlikely on the basis of the combination of its distinctive falcate segments that attach broadly to the rachis and its veins of uniform thickness that are subparallel or converge slightly toward the segment apices.

Many Australian and Antarctic Jurassic–Cretaceous leaves of *Taeniopteris daintreei* McCoy (Pentoxylales) have lobed laminae with dense, high-angle, sparsely dichotomizing veins (Cantrill 2000; McLoughlin et al. 2002). These are differentiated from *P. muelleri* by their less regular lobes (commonly broader than long) that are not arched distally.

Various cycad genera have pinnate leaves containing subparallel veins in each segment. However, such genera typically have linear to elliptical pinnules, in many cases with a contracted, swollen, or twisted base. Further, no extant or fossil cycad has leaf segments of the diminutive size represented in *P. muelleri*. The distinctiveness of *P. muelleri* led Hollick (1932, p. 186) to note, “If this is a cycad it may represent an insular generic type, now extinct, which can not be satisfactorily compared with any now in existence.” Horiuchi and Kimura (1987) apparently also regarded the affiliation with Cycadales doubtful but did not discuss the species in detail.

In contrast, small leaves with distinctive triangular-rhombic-falcate segments are common among several genera of Bennettitales, especially in high-latitude Cretaceous assemblages (Pole and Douglas 1999; Boyd 2000; McLoughlin et al. 2002). The leaflets of *P. muelleri* are very similar in shape and size to those of *Ptilophyllum cutchense* from the Upper Jurassic of Western Australia (McLoughlin and Pott 2009). However, the latter is distinguished by distally divergent veins. Ettingshausen (1888, p. 95) did not compare *P. muelleri* to other species in detail but noted that “one species, however, from the Cretaceous of North Greenland, described by Heer [1874; presumably *Pterophyllum lepidum* Heer, pl. 16, figs. 1–3], shows by its nerves, in some degree oblique to the rachis, a remarkable and specific relation to the fossil from the Eocene beds of Vegetable Creek.” Although cuticular details and reproductive structures are unavailable to determine definitive relationships, we consider that the collective foliar evidence favors a bennettitalean affinity for *P. muelleri*.

Distribution, Paleoenvironment, and Extinction

Bennettitales, together with Equisetales, Pentoxylales, Ginkgoales, and Corystospermales, show a steady decline in diversity in Australia concomitant with the rise of angiosperms (fig. 7; McLoughlin et al. 2010). It is tempting to invoke a causal relationship (competitive exclusion of older plant groups by an-

giosperms) to explain these contrasting diversity trends. However, there may have been additional environmental factors influencing the patterns of floristic diversity and ultimately driving the extinction of several major plant groups.

Ptilophyllum muelleri was apparently an uncommon but relatively widespread element in the vegetation of southeastern Australia during the Oligocene. The two sites known to host this species are ~1350 km apart. Both fossil assemblages are dominated by angiosperm and conifer taxa typical of montane tropical rainforests or cool temperate rainforests (notably *Nothofagus*, *Phyllocladus*, and various other podocarp conifers), but they also contain groups now typical of warmer moist forests (*Agathis*) and genera with sclerophyllous leaves characteristic of low-nutrient heathland communities (*Banksia*- and *Lomatia*-like forms; Carpenter 1991b). This is broadly consistent with there being a terminal Eocene “chill” event that resulted in the early Oligocene paleoclimate of southeastern Australia being moist and cool (microthermal; McGowran et al. 2000). The trigger for this cooling was likely to have been associated with the opening of an oceanic

passage between Antarctica and Australia (Shackleton and Kennett 1975).

The paleoecological signatures of bennettitalean leaves are ambiguous. Although they commonly have thick cuticles, sunken and papillae-protected stomata, and enrolled leaflet margins that are traditionally regarded as xeromorphic features, they are commonly preserved in coal-rich flood basin sediments, suggesting a preference for wetland habitats (Gould 1980; McLoughlin et al. 2002). Pott et al. (2008) proposed that such foliar characters were more likely adaptations to physiological drought (growth on strongly permeable, saline or low-pH soils, or exposure to persistent winds or wind-borne salts) rather than signaling a preference for truly dry conditions. Thus, *P. muelleri* may be a member of the sclerophyllous component of the Cethana and Emmaville assemblages.

The Oligocene occurrences of *P. muelleri* are separated from the next youngest Australian bennettitalean records by a ghost lineage of ~65 million years (fig. 7). Even though this seems an exceptionally long stratigraphic gap, similar Lazarus taxon occurrences among Ginkgoales and Corystospermales

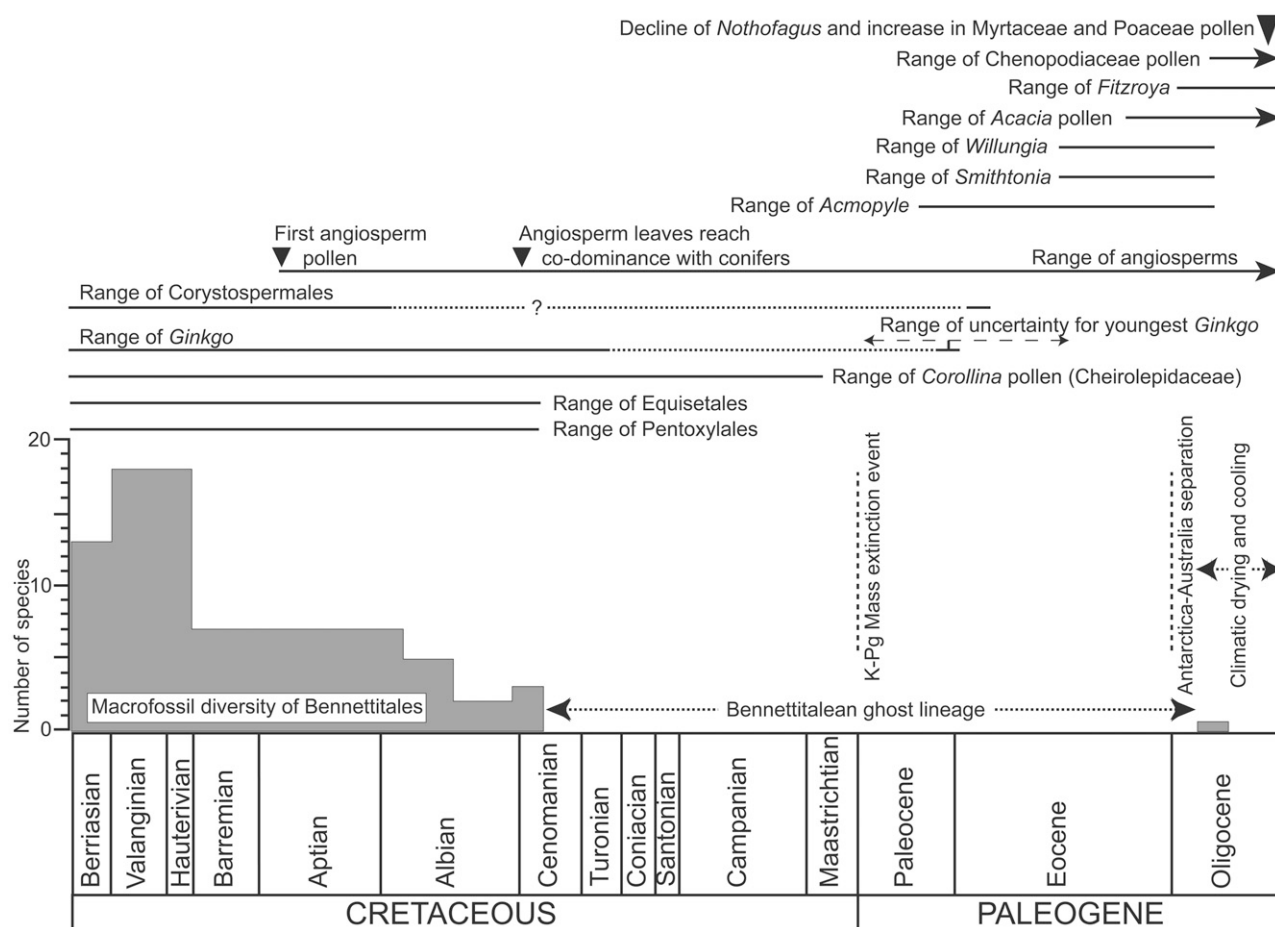


Fig. 7 Diversity of bennettitalean leaf morphospecies through the Cretaceous and Paleogene of Australia plotted against the ranges of other key plant taxa and major regional events (compiled from numerous sources). The single Oligocene species of Bennettitales represents *Ptilophyllum muelleri* described herein. Measures of bennettitalean species diversity are derived from all published records of leaf and cuticle remains from Australia; records are grouped into age categories defined by major palynozones (see McLoughlin et al. 2010). Dotted ranges indicate ghost lineages (presumed ranges currently lacking fossil records).

have been recorded recently from this region (Hill and Carpenter 1999; McLoughlin et al. 2008; fig. 7). These occurrences could attest to there being middle- to high-latitude, cool, moist environments in southeastern Australia and adjacent islands that provided relatively isolated refugia for several plant and animal groups of Mesozoic character in the Paleogene (Worthy et al. 2006; McLoughlin et al. 2008). Indeed, as discussed by McLoughlin et al. (2008), modern Tasmanian ecosystems still support significant numbers of relictual taxa (i.e., those having an origin in the Mesozoic and persisting within a much narrower geographic range than occupied previously). Similar relictualism among ancient Mesozoic gymnosperm groups has been reported from high latitudes in the Northern Hemisphere in floras at least up to the Late Cretaceous (Vakhrameev 1991; Herman and Kvaček 2010) but possibly also extending into the mid-Cenozoic (Reinink-Smith and Leopold 2005). Several palynological studies have proposed that Southern Hemisphere Mesozoic ecosystems were less affected by the end-Cretaceous mass extinction event than their Northern Hemisphere counterparts (Askin and Jacobson 1996; Vajda et al. 2002). To date, comparable high-resolution studies of plant macrofossils across the Cretaceous-Paleogene boundary are not available for the Southern Hemisphere. Broader-scale macrofossil studies have certainly noted some qualitative and quantitative changes in the vegetation across this boundary in New Zealand (Pole and Vajda 2009). However, the growing list of typical Mesozoic groups (now including *Ptilophyllum*) persisting into the Cenozoic of southeastern Gondwana suggests that at higher taxonomic levels, the biota there was less affected by the dramatic extinctions at the close of the Cretaceous than in other regions.

The terminal Eocene “chill” event has also been suggested to correlate with the emergence of more variable, seasonally drier climates across broad parts of Australia and first appearances of a range of typically open, dry habitat taxa—including *Acacia*, *Asteraceae*, *Chenopodiaceae*, *Gyrostemonaceae*, and *Poaceae*—during the Oligocene and Miocene (Macphail et al. 1994; McGowran et al. 2000). The ultimate disappearance of *P. muelleri* in southeastern Australia appears to have occurred around this time of climatic transition. Nevertheless, bennettitaleans seem to have persisted at least as long as many of the conifers that disappeared from the region (Hill and Brodribb 1999) and may well have significantly outlasted Equisetales (McLoughlin et al. 2010), Ginkgoales (Hill and Carpenter 1999), and *Corystospermales* (McLoughlin et al. 2008; fig. 7). The combination of drier and more variable climates in the mid-Cenozoic and competition from diversifying angiosperms (Royer et al. 2003) may have ultimately caused the demise of these archaic gymnosperms.

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