

## THE AUSTRALIAN CRETACEOUS AND TERTIARY MONOCOT FOSSIL RECORD

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### Abstract

The pollen record shows palms to be significant elements since the Early Paleocene; and Poaceae and Cyperaceae are present in Eocene and younger sediments from central and southern Australia. Cretaceous and Tertiary Australian monocot macrofossils are poorly known, with most detailed accounts published comparatively recently. Early macrofossil records list *Bambusites*, *Phragmites*, *Poacites* and un-named palms, but many of these records are dubious, and only 6 of the 28 reported localities with 'palms' or 'monocots' have well-studied monocots. The oldest definite record is *Nypa* from the Early Eocene of Regatta Point (Tasmania). Others include *Petermanniopsis* (aff. *Petermanniaceae*) and *Paracordyline* (*Lomandraceae*) from the Middle Eocene of Anglesea (Victoria) and Golden Grove (South Australia) respectively. Undescribed palms are known from Anglesea (cf. *Linospadix*), the Middle Eocene Maslin Bay flora (South Australia), the Western Australian Eocene/Oligocene Plantagenet Beds (cf. *Archontophoenix*), the Tertiary Island Lagoon and Stuart Creek sites in northern South Australia, and localities in central and eastern Australia. Leaves resembling *Smilax* are reported from Maslin Bay, as are rhizomes of rushes (cf. *Phragmites* or *Typha*) from the Early Miocene LaTrobe Valley brown coals (Victoria). Despite a poorly documented monocot fossil record, endemics, such as *Petermanniaceae*, *Archontophoenix* and *Linospadix*, and regional taxa such as *Nypa* and *Cordyline* were clearly present in Australia prior to the Miocene collision with Malesia. Cosmopolitan taxa, such as *Smilax* were apparently represented, but characteristic endemics such as *Xanthorrhoeaceae* are unknown as fossils. Australian fossil monocots currently provide limited phylogenetic information, but some recent studies are informative for phytogeography.

**Key words:** monocots, fossil, leaves, Australia, Tertiary

### INTRODUCTION

The modern Australian flora is rich in monocots, including at least 60 families, of which five are endemic (*Blandfordiaceae*, *Boryaceae*, *Dasyopogonaceae*, *Doryanthaceae*, *Petermanniaceae*, *Xanthorrhoeaceae*), and several others predominantly so, such as the *Lomandraceae* (e.g. *Lomandra* Labill., 50 species native to Australia and two species in New Guinea, one extending to New Caledonia; *Arthropodium* R. Br. about 18 spp. with 13 endemic; *Thysanotus* R.Br., 47 spp., all native and 44 endemic) and *Hemerocallidaceae* (= *Phormiaceae* and *Johnsoniaceae*) with 11 native and 10 endemic genera of the 16 world-

wide. In particular for the *Lilianae*, this represents one of the highest levels of generic and family level endemism in the world (Conran 1995). Some monocot groups seem under-represented in Australia, such as the palms with only about 60 species. For example, the very large *Lepidocaryoid* palm group are centred mainly in the Malay Archipelago and yet are only represented by approximately eight species of *Calamus* L. in Australia (Dowe 1995). Nevertheless, despite this diversity of extant taxa, the present Australian fossil record of the monocots is poorly known.

Probable monocot leaf and pollen remains from Early Cretaceous (Aptian) floras from eastern North America were reported by Herendeen and Crane (1995) as the oldest reliable record of the monocots and an Aptian fossil from Victoria may also represent a monocot (Taylor and Hickey 1990). More recently, Gandolfo *et al.* (1998) suggested that leaves and pollen are too dubious to be considered the oldest record for monocots. The earliest and most reliable record is from the Late Cretaceous (Turonian) of New Jersey, represented by fossil flowers assigned to the saprophytic family Triuridaceae (Gandolfo *et al.* 1998). The Late Cretaceous macrofossil records of North America, south-east Asia and Europe are sparse in comparison to the dicot record, but include Araceae, Arecaceae, Pandanaceae, Potamogetonaceae, and possibly several other monocot families, with the remaining monocots (e.g. Strelitziaceae or Musaceae) first found in the Tertiary (Daghlian 1981; Herendeen and Crane 1995). Herendeen and Crane (1995) suggested that the sparseness of the monocot fossil record was due to low total diversity of monocots compared to dicots, but this rarity also reflects the herbaceous habit of most monocots and the predominance of zoophilous pollination. The leaves of many monocots often decay still attached to the parent plant, and zoophilous plants often are under-represented in palynofloras. Analyses of modern leaf accumulations and pollen rain in Australian rainforests have demonstrated that leaf assemblages formed from these communities are dominated by the leaves of canopy trees and to a lesser extent vines, and the pollen by anemophilous species (Kershaw 1979; Greenwood 1991). The leaves and pollen of monocots are often dramatically under-represented in these assemblages. Additional problems stem from difficulties in identifying poorly preserved parallel-veined leaf fragments and recognising net-veined Liliaceae as monocots and not dicots (Conran *et al.* 1995; Herendeen and Crane 1995).

In this report the taxonomically valid macrofloral record of monocots from the Australian Tertiary is reviewed, and anecdotal evidence of fossil monocots and monocot-like taxa discussed and assessed. Our database is drawn from a combination of a reappraisal of the literature, and systematic examination of putative monocot fossil leaf material from sites mainly in southern Australia (Fig. 1). No macrofossil monocots are known from the Cretaceous of Australia, which in part may reflect the rarity of Late Cretaceous macrofloras from this continent (Douglas 1994; McLoughlin and Drinnan 1994). The Australian Tertiary macrofloral record, however, is rich and is yielding significant information on climates and environments of the Early to mid-Tertiary in particular, as well as the phylogeny of some magnoliid lineages, but has hitherto been uninformative on monocot systematics. Rather than provide a 'flora by flora' account, we will summarise the known fossil record of monocot families, and of monocot fossils that are *incertae sedis*.

## THE POLLEN RECORD

The Australian Cretaceous and Tertiary microfossil (fossil pollen and spores) records of vegetation and phytogeography were recently reviewed by Dettmann (1994), and Macphail *et al.* (1994). Tertiary pollen is often referred to form genera rather than attributing individual palynomorphs to extant genera. The

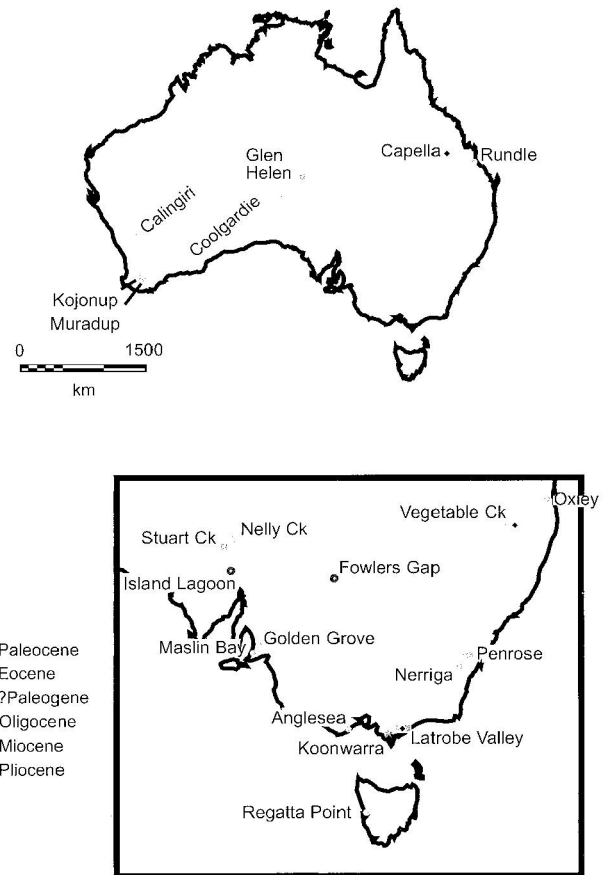


Fig. 1. Location of Tertiary macrofloras discussed in the text.

monocot palynomorphs known from the Australian Tertiary and their botanical affinity are given in Table 1. One of the problems with identifying monocots in the pollen record is the lack of taxonomically diagnostic characters for many families, or genera within families (Macphail *et al.* 1994). Nevertheless, the pollen record is informative. No monocot groups are known from Cretaceous floras from Australia (Dettmann 1994), in contrast to North America where several groups, including palms (Arecaceae), are known from Late Cretaceous floras. The earliest records of monocots in Australia do not include Arecaceae (but only by a few million years), but rather Cyperaceae, Restionaceae, Sparganiaceae, and Pandanaceae (?*Freyzinetia* Gaudich.) (Macphail *et al.* 1994). Unassigned palm pollen of the form genus *Arecipites* (= *Monosulcites*) has been reported from a number of Australian localities dated from the Early Paleocene to the Early Miocene (detailed in Dowe 1995). Amongst the earliest Australian palms was *Nypa* Wurmb. (as *Spinizonocolpites prominatus*). Pollen of the Lepidocaryoid climbing palm *Calamus* (as *Dicolpopollis* spp.) is recorded from Middle Eocene (Truswell and Owen 1988), Late Eocene to mid-Miocene (Macphail and Truswell 1989; Martin 1993) and Late Oligocene–Miocene sediments (Truswell *et al.* 1985), indicating either an early introduction of this taxon from south-east Asia, or an older Gondwanan origin (Truswell *et al.* 1987).

The earliest record for grass (Poaceae) pollen in Australia is from the Middle Eocene, only marginally later than in other parts of

**Table 1.** Principal Tertiary monocot fossil pollen taxa, their suggested botanical affinity, and earliest record. Adapted from Dowe (1995) and Macphail *et al.* (1994).

Palynomorph	Botanical Affinity	Earliest Record in Australia
<i>Arecipites</i> (= <i>Monosulcites</i> )	Arecaceae	Early Paleocene
<i>Cyperaceapollis</i>	Cyperaceae	Late Paleocene
<i>Milfordia hypolaenoides</i>	Restionaceae, <i>Hypolaena</i> type	Late Paleocene
<i>Milfordia homeopunctata</i>	Restionaceae, <i>Restio</i> type	Late Paleocene
<i>Sparganiaceapollenites</i>	Sparganiaceae	Late Paleocene
<i>Drytopollenites semilunatus</i>	Pandanaceae, ? <i>Freycinetia</i>	Late Paleocene
<i>Liliacidites</i>	?Liliaceae	Early Eocene
<i>Spinizonocolpites prominatus</i>	<i>Nypa</i>	Early Eocene
<i>Graminidites media</i>	Poaceae	early Middle Eocene
<i>Aglaoreidia qualumis</i>	Sparganiaceae/Typhaceae	Late Eocene
<i>Luminidites phormoides</i>	Hemerocallidaceae, <i>Phormium</i>	Late Eocene
<i>Dicolpopollis</i>	Arecaceae, <i>Calamus</i> type	Late Oligocene
<i>Lateropora glabra</i>	Pandanaceae, <i>Freycinetia</i>	Oligo–Miocene
<i>Ripogonum</i> complex	Smilacaceae, <i>Ripogonum</i>	Middle Miocene

the world. The pollen record is uninformative on the first appearance of endemic monocot families such as the Xanthorrhoeaceae, or key genera such as *Cordyline* Comm. ex R. Br. (Lomandraceae) or *Smilax* L. (Smilacaceae).

### THE MACROFLORAL RECORD

A flowering fossil angiosperm from the Aptian Koonwarra flora of Victoria was considered similar to *Smilax*, but Taylor and Hickey (1990) also noted similarities to the dicots *Asarum* (Aristolochiaceae) and *Piper* L. (Piperaceae). Tertiary Australian monocot macrofossils are poorly known, with most detailed accounts published comparatively recently. Early records list *Bambusites*, *Phragmites*, *Poacites* and un-named palms from Tertiary macrofloras in New South Wales, Victoria, Queensland and Tasmania (Ettingshausen 1888; Johnston 1888; Duigan 1951; Table 2), but many of these records are based on superficial comparisons with extant taxa (Hill 1988). Only six of the 28 localities reported with 'palms' or 'monocots' in Duigan's (1951) catalogue have well-studied monocots (Table 2; Fig. 1). The apparent rarity of macrofossil records of monocots is attributed to the predominant herbaceous character of most taxa, the often indehiscent leaves of some families that decay attached (e.g. Musaceae), and the inherent dominance of the leaf record by the leaves of canopy trees (Greenwood 1991; Herendeen and Crane 1995). Conran *et al.* (1994) also noted that net-veined Liliaceae may be confused with dicots, and thus omitted from accounts of the fossil record of the monocots. Below we review the macrofloral record of Australian Tertiary monocots.

### Palms

The Arecaceae are not diverse in Australia with approximately 22 genera; however, 45% of these and 85% of the approximately 60 species are endemic (Dowe 1995). Most of the extant species are restricted to the higher rainfall coastal fringe of the continent with only a few species occurring in suitable sites in the interior. At least six major palm groups are represented in Australia, although Arecoid palms are the most diverse, with groups such as the Lepidocaryoid palms highly diverse in adjacent landmasses and only poorly represented in Australia. The Coryphoid *Livis-*

*tona* R. Br., however, is the most speciose and widespread Australian genus (approximately 20 species), occurring from eastern Victoria (37° 42'S) to the tip of Cape York (10° 30'S), with most species occurring in the tropics.

The Koonwarra and Winton mid–Late Cretaceous macrofloras from Victoria and Queensland respectively lack any evidence for palms (Douglas 1994; McLoughlin and Drinnan 1994). The absence of palm pollen or macrofossils from the Australian Late Cretaceous may indicate that Arecaceae were a Paleocene introduction. Outside Australia, fossil palms are probably the most abundant monocots in the fossil record, with stems, leaves, flowers, fruits and pollen known from the Late Cretaceous; however, the major radiation in palms appears to have been during the Early Tertiary (Daghlian 1981; Herendeen and Crane 1995). The Arecaceae might be expected to figure prominently in the Tertiary macrofloral fossil record of Australia, as Tertiary macrofloras from North America and Europe include abundant palms (Daghlian 1981; Greenwood and Wing 1995). The Australian Tertiary fossil record (Table 2), however, is quite poor, but does suggest that palms were formerly more widely spread across the Australian continent (as suggested also by some relict populations, e.g. *Livistona mariae* in central Australia). Arecoid, Lepidocaryoid, Nypoid, and possibly Coryphoid palms are known as fossils from Australia.

Only one macrofossil palm species, *Nypa eocenica* Pole, has been validly published from the Australian Tertiary, based on both fronds and fruits. *Nypa* is monospecific, and Early Eocene fossils of *Nypa* from Regatta Point in Tasmania (Fig. 1) appear to be indistinguishable from the modern species. Additional anecdotal Australian records of fossil palms exist, some of which are reported here. Pollen of palms (Table 1) is diverse and well represented from Early Eocene to present day sediments, indicating that palms, despite their poor macrofloral record, were diverse and abundant members of the regional flora. For example, pollen of the mangrove palm *Nypa* (*Spinizonocolpites prominatus*) is common in Early Eocene sediments across southern Australia (detailed in Dowe 1995), yet this taxon is today restricted to areas of the northern Australian coast (north of 18° 30' S on the east coast).

**Table 2.** Australian Tertiary macroflora sites where monocots have been reported. Many records are anecdotal or likely represent systematic assignment that is not based on detailed anatomical comparisons. Sources cited in the text and Greenwood and Conran (unpublished data).

Macroflora	Location	Stratigraphic Age	Piper/ Smilax	Paracordyline	Palms	Other Monocot	Stratigraphic Unit
Mt Eba/Haggard Hill	SAust	Paleocene – Middle Eocene					Munjena Fm equivalent
Regatta Point	Tas	Early Eocene					un-named unit
Oxley (south Brisbane)	Qld	Paleocene – Early Eocene					Oxley Group
Fowlers Gap	NSW	Paleogene					Eyre Fm equivalent
Coolgardie/Darkin Swamp	WAust	Eocene					Pidinga Fm
Nerriga	NSW	Middle Eocene				?	Titringo Siltstone
Poole Creek	SAust	Middle Eocene					Eyre Fm
Maslin Bay	SAust	Middle Eocene					North Maslin sands
Golden Grove	SAust	Middle Eocene					North Maslin sands
Rundle Shale	Qld	Middle Eocene					Curlew Fm
Island Lagoon	SAust	?Eocene / Miocene					?Eyre Fm
Bottle Hill/Woomera	SAust	?Eocene / Miocene					?Eyre Fm
Anglesea	Vic	late Middle Eocene					Eastern View
Barton Range	SAust	Middle – Late Eocene					Pidinga Formation
Na Laura Farm, Muradup	WAust	Late Eocene					Kojonup Sandstone
Calingiri	WAust	Late Eocene					Kojonup Sandstone
Kojonup type loc. (Half Moon Farm)	WAust	Late Eocene					Kojonup Sandstone
Vegetable Ck/Witherden's Tunnel	NSW	Late Eocene – Early Oligocene	?				
Blanche Point	SAust	Oligocene					
Capella/Glencoe	Qld	Oligocene – Miocene					un-named 'float'
Glen Helen	NT	mid Tertiary	?				un-named
Morwell Coal	Vic	Late Oligocene – Early Miocene					Morwell 1A and 1B Seams
Poole Creek South	SAust	Miocene					Etadunna Fm
Stuart Creek	SAust	late Early to Late Miocene				?	Willalinchina Sandstone
Pitfield	Vic	Neogene			?		
Yallourn Coal	Vic	early to mid Middle Miocene					Yallourn Seam
Sentinel Rock	Vic	Middle Miocene – Pliocene					'Sentinel Rock Clay'

Leaves attributed to the Arecoïd palm *Linospadix* Wendl. have been reported from the Middle Eocene Anglesea flora (Victoria), which includes other monocots and a diverse rainforest flora with taxa that have affinities to modern relatives in subtropical and tropical rainforests in eastern Australia (Greenwood and Christophel in press). Undescribed palms are also reported (Table 2) from the Middle Eocene Maslin Bay flora (South Australia), the Western Australian Eocene/Oligocene Plantagenet Beds (cf. *Archontophoenix* Wendl. and Drude), and the Tertiary Island Lagoon and Stuart Creek sites in northern South Australia (Fig. 2). Anecdotal reports of palms include Barton Range (Eocene) in South Australia (Alley *et al.* 1995), and localities in eastern Australia such as Oxley (Eocene) in Queensland (Ettingshausen 1888; Allen *et al.* 1960).

### Grasses, Sedges and Rushes

The microfossil record of Poaceae is limited worldwide, and Australia is typical. The earliest substantiated grass fossils are Eocene, although Saville (1987) suggested that many of the modern grass tribes appeared during the Early Eocene, and other

authors suggest grasses may have existed in the Late Cretaceous (Crepet and Feldman 1991). Ettingshausen (1888) described species of *Bambusites* and *Poacites* from the Early to mid-Tertiary Vegetable Creek 'flora', and Johnston (1888) illustrated 'probable *Phragmites*' from several sites in Tasmania. In both instances, the illustrations are poor and the original specimens uninformative or unavailable.

Laterally extensive and thick brown Late Oligocene to Early Miocene coal seams in the LaTrobe Valley of Victoria contain abundant rhizomes and leaves of aff. *Gabnia* J.R. & G. Forst. and other indeterminate Cyperaceae, *Typha* L., Sparganiaceae, and Restionaceae (Blackburn and Sluiter 1994). Detailed systematic analysis of these fossils has not been attempted. Abundant parallel-veined leaf fragments from the Miocene Etadunna Formation from near Lake Eyre were interpreted as monocot (Greenwood *et al.* 1990), and are associated with palynofloras interpreted by Martin (1990) as rush- and sedge-dominated swamps. Other sediments in the region (so called 'reed mould silcrete') contain structures that may in some instances be casts of

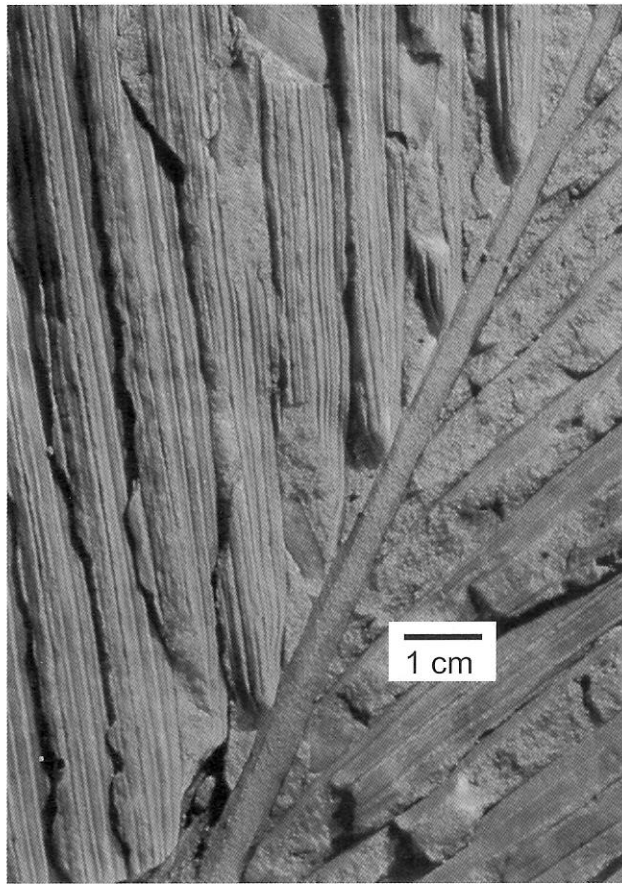


Fig. 2. Palm frond from Island Lagoon, northern South Australia (South Australian Museum). Scale bar = 1 cm.

reed shoots and root masses (D. Greenwood, unpublished data), but in general these structures have been interpreted as degassing artifacts (Alley *et al.* 1995).

#### Other Monocot Groups

*Cordyline* (Lomandraceae) is moderately diverse with eight species well represented in eastern Australian rainforests, and so might be expected to be found in the Tertiary 'rainforest' floras of southern Australia. Conran and Christophel (1998) reported the fossil taxon *Paracordyline* from organically preserved leaves from the Middle Eocene Golden Grove (South Australia) macroflora (Figs 1 and 3). This macroflora is interpreted as representing forests equivalent to the modern Notophyll Vine Forests of eastern Australia, with a humid mesothermal climate.

Leaves resembling *Smilax* (Smilacaceae) were reported from Maslin Bay by Scriven (1994), although these require further study to obtain cuticular material. A record of *Piper* (which although a dicotyledon is often difficult to distinguish from fossil Smilacaceae and Dioscoreaceae) from Penrose in New South Wales (Ettinghausen 1888) has been re-examined by us and is now considered to represent more likely a member of the Menispermaceae similar to the genus *Hypserpa*, although cuticular data are needed to confirm this.

The extant monotypic genus *Petermannia* F. Muell. is considered by some authors to represent a separate family, the Petermanniaceae (e.g. Conran and Clifford 1998). *Petermannia cirrosa* F.

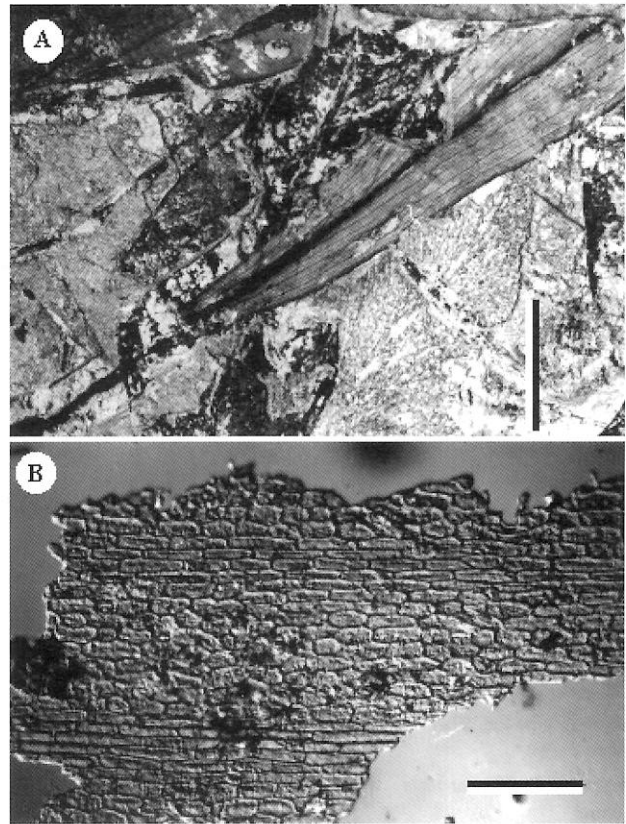


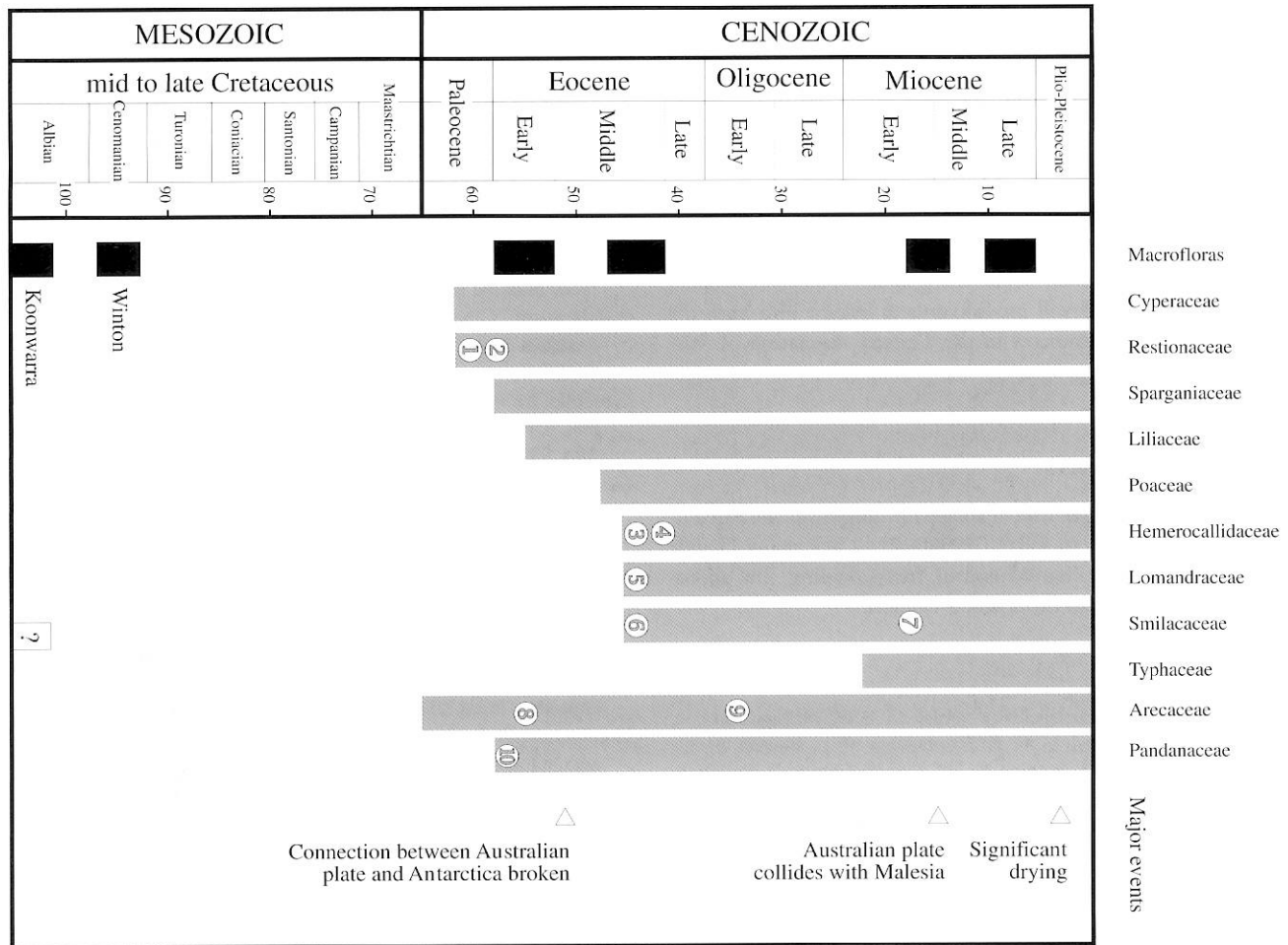
Fig. 3. *Paracordyline aureonemorialis*. A. Holotype GG S18 showing venation detail; scale bar = 10 mm. B. Isotype GG M02 lower cuticle; scale bar = 100  $\mu$ m.

Muell. is an understorey tendrillar woody vine that is restricted to coastal rainforests in southern Queensland and northern New South Wales. Fossil leaves of *Petermanniopsis* Conran *et al.* were reported from the Middle Eocene Anglesea macroflora (Conran *et al.* 1994; Conran and Christophel in press). These leaves are considered on the basis of leaf architectural and cuticular detail to resemble closely the Petermanniaceae, and come from several different macrofossil floristic assemblages, suggesting some degree of habitat adaptability. Conran *et al.* (1994) noted the difficulty in determining a leaf architectural and cuticular character set that unequivocally defines family or generic boundaries for fossil or extant isolated leaves of reticulate-veined Liliaceae.

Most recently an organic macrofossil leaf portion with close affinities to the Hemerocallidaceae genus *Dianella* Lam. has been recovered from the Middle Eocene central Australian Nelly Creek deposit (Figs 1 and 4), and is the subject of ongoing work (L. Cunningham *et al.* pers. comm.). The Nelly Creek flora contains rainforest elements (e.g. *Gymnostoma* and *Agathis*), but has been interpreted as indicating a seasonally dry climate where riparian mesic forests occurred amidst a sclerophyllous hinterland vegetation (Greenwood 1996), an environment consistent with the presence of extant *Dianella*.

#### CONCLUDING REMARKS

The fossil record of monocots is sparse compared to other plant groups, particularly dicots. The paucity of the record in large part can be attributed to taphonomic biases (i.e. lower likelihood



**Fig. 4.** First appearances and known fossil record in Australia of representative monocot groups, based on pollen and macrofossils (1–10). Families without a demonstrable fossil record are not included. The stratigraphic range covered by macrofloras mentioned in the text is indicated. Key: 1, 2 – *Hypolaena* type and *Restio* type pollen (but likely were Australian representatives, not *Hypolaena* s.s. or *Restio* s.s.); 3, 4 – cf. *Dianella* (leaf) and *Phormium* (pollen); 5 – *Paracordyline*; 6, 7 – *Smilax* (leaf) and *Ripogonum* (pollen); 8, 9 – *Linospadix*, *Nypa* and indeterminate palms (leaves and pollen), and *Calamus* type (pollen); 10 – *Freyinetia* (pollen).

of becoming fossilised) that are a function of anatomical and ecological characteristics of many monocots, as summarised below (Greenwood 1991; Herendeen and Crane 1995):

1. Herbaceous habit and indehiscence of leaves in many monocot groups, thus leaves decay attached to plants and so do not enter sedimentary accumulations;
2. Predominantly zoophilous pollen, thus their pollen is under-represented;
3. Swamping of litter-fall by canopy trees, thus diluting input by monocots in understorey;
4. The diversity of dicots is greater than that of monocots;
5. Some monocots occur in habitats with low preservation potential (e.g. grasslands).

Monocots are not recorded in Australia from the Late Cretaceous (Fig. 4), despite good records for Araceae, Arecaceae, Pandanaceae, Potamogetonaceae and possibly several other monocot families at this time outside Australia (Herendeen and Crane 1995). The absence of monocots from Australian Late Creta-

ceous floras, however, partly reflects unsuitable geology, rather than perhaps any real phytogeographic pattern. Despite a poorly documented monocot fossil record (Fig. 4), endemics such as Petermanniaceae, *Archontophoenix* and *Linospadix* (Arecaceae), and regional taxa such as *Dianella* (Hemerocallidaceae), *Calamus*, *Nypa* (Arecaceae), and *Cordyline* (Lomandraceae), were clearly present in Australia prior to the Miocene collision with Malesia. The pollen record shows palms (as *Arecipites*) to be significant elements since the Early Paleocene (including *Nypa* as *Spinizonocolpites prominatus* from the Early Eocene), perhaps revealing a late introduction of the Arecaceae into Australia as the family is well represented in Late Cretaceous floras outside Australia. Poaceae and Cyperaceae are present in Middle Eocene and younger sediments from central and southern Australia, only marginally postdating the earliest macrofloral records elsewhere in the world. Cosmopolitan taxa such as *Smilax* were apparently represented, but characteristic endemics such as Xanthorrhoeaceae are presently unknown as fossils.

Australian fossil monocots currently provide limited phylogenetic information, but some recent studies are informative for analysing historical phytogeography. Monocot fossils from

Middle Eocene macrofloras are currently best known systematically (Table 2; Fig. 4), and indicate a potentially diverse monocot flora (e.g. *Arecaceae*, *Hemerocallidaceae*, *Lomandraceae*, *Petermanniaceae*, and *Smilacaceae*) occurred in the precursors of the present day mesothermal humid forests of eastern Australia. By the Miocene, *Cyperaceae*, *Restionaceae*, *Sparganiaceae*, and *Typhaceae* were prominent in central and south-eastern Australian swamp communities, although the pollen record indicates a longer presence on the continent for these and other monocot groups (e.g. *Pandanaceae*). Continuing analyses of the Australian monocot fossil record will provide greater insight into both the importance of the monocots in the Tertiary vegetation of Australia and their phytogeography, but perhaps also provide useful data on phylogeny.

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