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The vegetation history of South Australia

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Abstract: South Australia today is one of the most arid regions on Earth, with a vegetation that is well adapted to either a strongly developed winter rainfall pattern with associated hot, dry summers (mostly near the south coast), or, across the rest of the State, to highly intermittent rainfall and otherwise extremely hot and dry conditions. Despite being a very stable piece of land with a deep geological history, South Australia, as an integral part of Australia, has had a highly variable history in terms of its global positioning and its climate, so that even within the past 65 million years (since the catastrophic event that signalled the end of the Cretaceous), the position of South Australia has changed dramatically, from very close to the South Pole, through to its current position in mid-southern latitudes. During that time the climate has changed to such an extent that the vegetation has reduced by declining from highly diverse, very complex, broad-leafed rainforest, through to today's scleromorphic forests and shrublands and various other forms of desert vegetation. The transition between these extremes has not been a smooth one, and especially in more recent times there has been significant controversy over the impact on the vegetation coincident with the arrival of *Homo sapiens* and the demise of the remarkable megafauna.

Keywords: vegetation history, fire, climate change, rainforest

Introduction

South Australia is an extremely old, flat piece of land that is the result of ancient geological processes. Within the State's boundaries we find evidence of the very earliest forms of life, through to evidence for some of the most recent life-shaping events. From the Precambrian stromatolites and their evidence for the early evolution of life (Hill *et al.* 1999), to the world famous Ediacaran fauna, the exquisitely preserved Emu Bay Early Cambrian fauna on Kangaroo Island, along with the astonishing opals that preserve evidence of a Cretaceous inland sea teaming with life, and finally to the amazing evidence of a highly diverse Pleistocene fauna at the World Heritage Naracoorte Caves, there is significant, if highly interrupted, evidence of unicellular and animal life throughout our State.

The evidence for plant life is sparser. There is little pre-Cenozoic evidence for plant life in South Australia apart from the extensive Triassic plant remains associated with the Leigh Creek coal fields and the occasional pieces of petrified wood associated with the Cretaceous faunas of the opal fields. However, there are some extensive and reasonably well reported Cenozoic plant localities that tell us much about the extraordinary and diverse rainforests that covered a significant part of southern Australia during the early part of the Cenozoic, and most particularly the mid-Eocene (~45 million years ago). These fossil deposits have been used to infer much about the general form of the Australian vegetation at this time as well as the way in which the living flora has developed during the vast amount of time that has passed since then. Despite the general acceptance of this interpretation of the fossil record, evidence has recently begun to accumulate that suggests that the Eocene rainforests may not have been as central to the evolution of the living vegetation as has been previously reported. It now appears that there is a much more complex history that still requires further research to more fully understand, but is at least ready to be presented as a set of hypotheses for future research to test. The remainder of this paper will examine the known data from the Late Cretaceous onwards, how it can be focused on southern Australia to highlight what we know about the evolution of the vegetation, what we can speculate about, as well as what remains unknown and is likely to be so for some time to come.

The genesis of the modern vegetation

The terrestrial vegetation on Earth today is dominated by the angiosperms, or flowering plants. Over the past 20 years there has been a revolution in our understanding of the form and ecology of the earliest angiosperms. Recently, Friis *et al.* (2011) wrote an important book on early angiosperms. The most significant impact reported was the large number of new charcoalified, minute palaeoherb fossils reported

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from the Cretaceous in the Northern Hemisphere. These flowers, fruits and seeds are the products of fire and hence are a record of the history of natural fires in the source vegetation.

Brown *et al.* (2012) noted that "fires were widespread and frequent and … the Cretaceous can be considered a "high-fire" world. This increased fire activity has been linked to elevated atmospheric oxygen concentrations … Some early angiosperms are interpreted as being of weedy form and as having thrived in disturbed environments." The notion that fire was prevalent in the Cretaceous because atmospheric oxygen levels were high is an appealing one, but the evidence for it is controversial, and in at least some cases is based on some circular reasoning (Hill *et al.* 2016). It is no surprise that the vast majority of evidence for early angiosperms is from the Northern Hemisphere, where the majority of people live and known fossil deposits are far more common. However, there has recently been a report of Late Cretaceous plant macrofossils from central Australia that add to the story of the early angiosperms. The Late Campanian-Maastrichtian deposit from central Australia (Carpenter *et al.* 2015) contains plant fossils that indicate nutrient-limited, open, sclerophyllous vegetation, with abundant charcoal as evidence of fire. More than 30 pollen taxa and at least 12 foliage taxa are attributable to the family Proteaceae, including several minute, amphistomatic, and sclerophyllous foliage forms consistent with subfamily Proteoideae. Microfossils, including an abundance of Sphagnales and other wetland taxa, provide strong evidence of a fenland setting. The local vegetation also included diverse Ericaceae and Liliales, as well as a range of ferns and gymnosperms. These fossils provide strong evidence for the great antiquity of fire in the Southern Hemisphere as well as in the Northern Hemisphere, and also of open vegetation in Australia. This record of the early Australian angiosperm-dominated vegetation is extra-ordinarily informative, since prior to this we had little worthwhile evidence of vegetation composition and structure at this time. It is of particular significance when considered in light of the next major vegetation transformation that is well recorded in the fossil record.

Some time after the commencement of the Cenozoic, Australian conditions—and, indeed, those globally—changed significantly. It is probable that atmospheric oxygen levels dropped, reducing the likelihood of fire, and atmospheric carbon dioxide levels rose to relatively high values, probably peaking during the Eocene (Anagnostou *et al.* 2016). At this time, Australia was still connected to Antarctica, which had a direct impact on major ocean currents, some of which circulated water across tens of degrees of latitude in the Southern Hemisphere. Hence, equatorial ocean waters, heated by the intense tropical sun, were transported to high latitudes and took with them vast amounts of stored heat. This provided the capacity for a relatively small equator-to-pole temperature gradient, and facilitated vast amounts of warm water evaporation, leading to very high rainfall. When coupled with the greenhouse effect, brought on by the high atmospheric carbon dioxide levels, the climate was warm and extraordinarily wet, despite southern Australia's connection to Antarctica being at very high southern latitudes. This provided the ideal environment for the establishment of vast, diverse, angiosperm-dominated rainforests.

South Australia has some well-known fossil deposits that demonstrate the extent and diversity of these southern Eocene rainforests (see references in Hill 1994). The two best understood localities are at Maslin Bay, just south of Adelaide, and Golden Grove, located within suburban Adelaide. These sites are both part of the same extensive freshwater sand complex produced by the vast river systems that existed in southern Australia during the mid-Eocene. The plant remains were preserved in fine-grained sediments that accumulated in the cut-off sections of a braided river system. Maslin Bay has been the subject of much more research than Golden Grove, but both sites are disappointingly under-researched. It is clear that these sites represent diverse, angiosperm-dominated rainforests, with a relatively large average leaf size (Fig. 1), indicating that the nearest vegetation of this type today occurs in the tropics and subtropics of Australia and Papua New Guinea. This similarity is reinforced by the limited fossil identification work done on these sites which indicates that, although many tropical families are present (e.g. Lauraceae, Cunoniaceae, Sterculiaceae), there is also strong representation from typically "Australian" or at least Gondwanic plant families, like Proteaceae, Casuarinaceae and Myrtaceae.

However, it is important not to take the comparison with present-day low latitude rainforests too far. For example, a leaf from the Maslin Bay locality has been described as *Nothofagus plicata* by Scriven *et al.* (1995). This leaf is important in that it can be demonstrated with certainty that it belonged to a deciduous species, and most likely winter deciduous. Given the very high latitude of Maslin Bay in the mid-Eocene, this is not particularly surprising, since there would have been very little light at this site in mid-winter, but it cautions against taking the comparison with modern subtropical and tropical forests too far.

These fossil localities, and many others like them in southern Australia, have led to the view that complex rainforests dominated Australia during most or all of the Eocene, and are therefore the likely source of much of the living Australian vegetation. The fact that many of the iconic extant Australian plant families are represented in these fossil floras adds credence to this view. However, in recent years there has been a shift in our understanding and the focus of research is now moving to test a different set of hypotheses.

The Late Cretaceous fossils mentioned earlier open the very real possibility that the current open vegetation of southern Australia has ancient origins, dating back to some of the earliest angiosperm communities, when shrubby, small-leafed vegetation was growing in low nutrient soils with some water restrictions and at least a reasonably high fire frequency. This is in strong contrast to the later warm and wet rainforests with their dominance by large-leaved trees. However, for these Cretaceous plants to have a direct link to the living vegetation, an explanation has to be found for how and where these plants, or their direct descendants with similar ecological preferences, survived through the

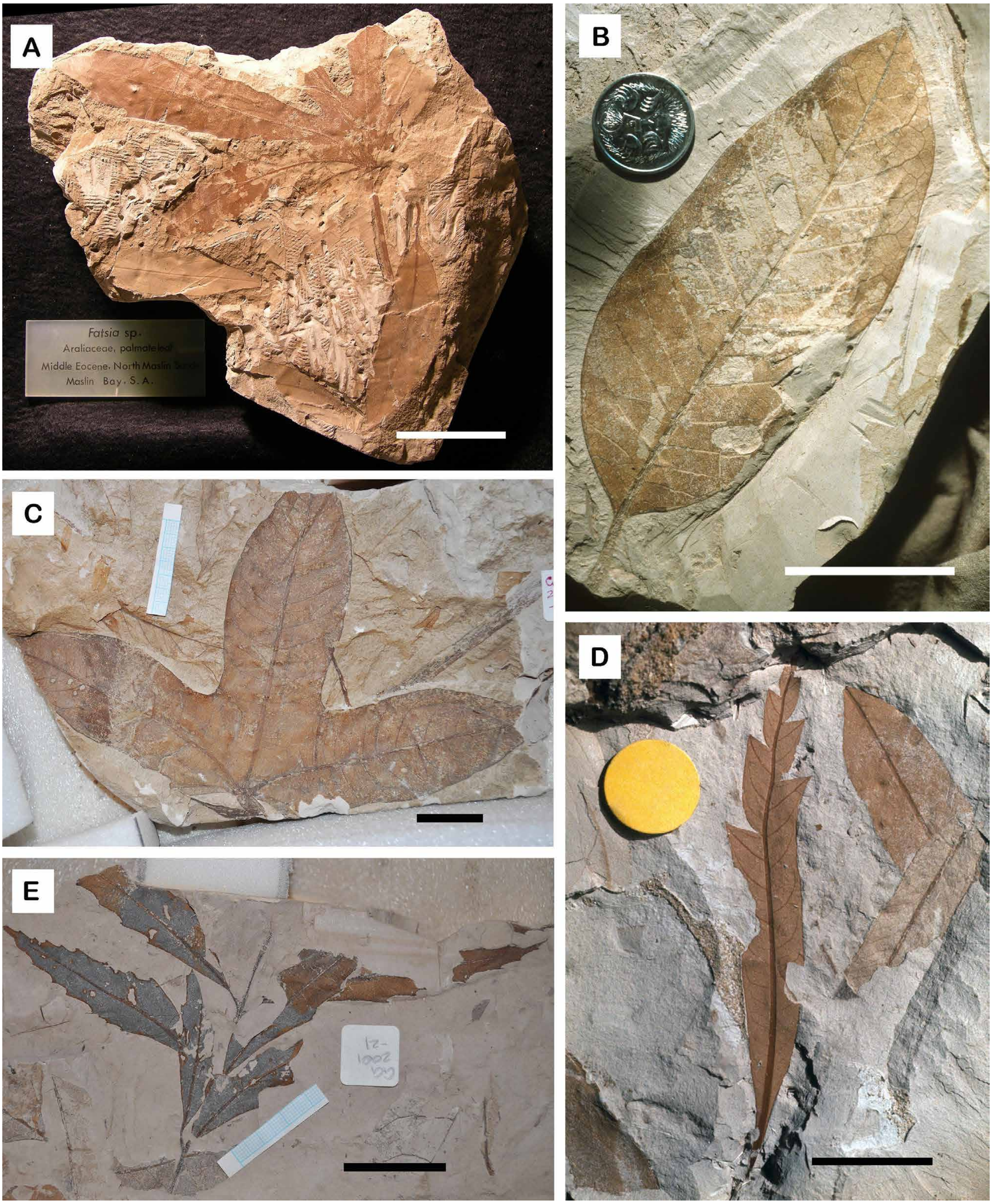

Fig. 1. Angiosperm leaf remains from the mid-Eocene Maslin Bay and Golden Grove deposits. **A** *Parafatsia subpeltata* (Proteaceae, previously assigned to Araliaceae) from Maslin Bay. Modified from Fig. 3A in Carpenter *et al.* (2006). **B** Unidentified entire margined angiosperm leaf from Maslin Bay. **C** Unidentified trilobed angiosperm leaf from Golden Grove. **D** *Banksieaeformis decurrens* (Proteaceae) leaf from Maslin Bay. Modified from Fig. 30 in Hill & Christophel (1988). **E** Probable compound leaf of an unknown angiosperm from Golden Grove. — Scale: A = 5 cm; B–E = 2.5 cm.

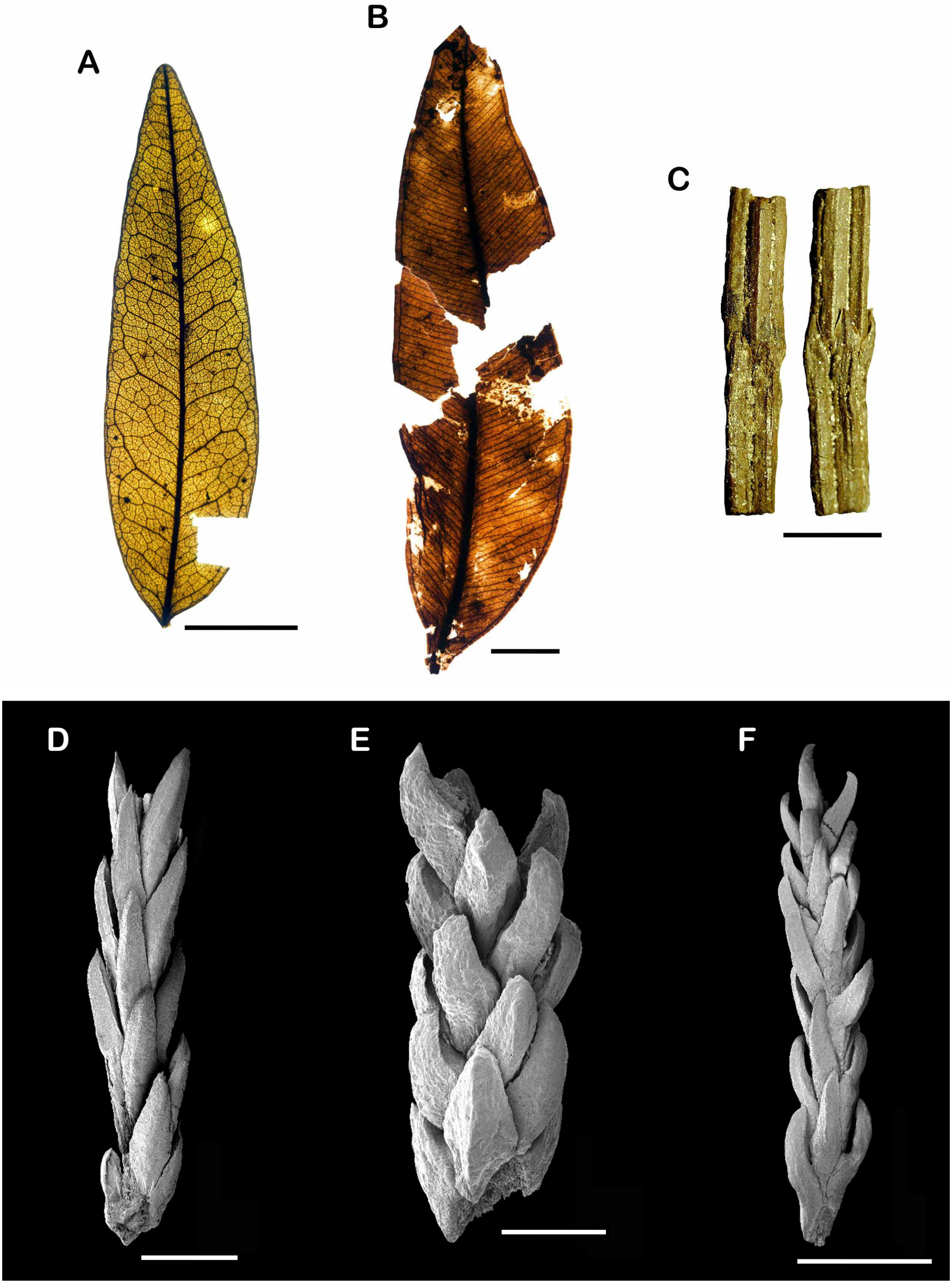

Fig. 2. Plant macrofossils from the mid-Eocene Nelly Creek locality. **A** Unknown angiosperm leaf, possibly a leaflet from a compound leaf. Modified from Fig. 2A in Christophel *et al.* (1992). **B** Leaf of *Myrtaciphyllum eremeaensis* (Christophel *et al.* 1992). **C** Cladodes of *Gymnostoma* (Casuarinaceae). **D–F** Scanning electron micrographs of shoots of *Dacrydium fimbriatus* (Podocarpaceae). Modified from Hill & Christophel (2001), Figs 12, 14 and 17). — Scale: A, B = 1 cm; C = 5 mm; D, F = 2 mm; E = 500 µm.

Eocene rainforest domination. At present the evidence for this comes from two main regions, central South Australia and the west coast of Western Australia.

In central Australia there are two main lines of evidence: mid-Eocene sediments containing very well preserved plant remains from Nelly Creek (Lake Eyre South) and poorly organized evidence from a series of silcretes that bear vast numbers of plant remains as moulds that are often of high quality. The Nelly Creek flora has been the subject of relatively little research, but in comparison with the coastal mid-Eocene sites at Maslin Bay and Golden Grove, the leaves appear to be smaller, the site is less angiosperm-dominated, and the overall diversity is lower. It is important not to over-interpret such a poorly studied locality, but we can say with some certainty that the dominant plant taxon probably bore compound leaves with relatively small and robust, entire-margined leaflets (Fig. 2A); there is a common broad-leafed Myrtaceae taxon present (Fig. 2B); Proteaceae leaves are quite common (Christophel *et al.* 1992); as is *Gymnostoma* (Casuarinaceae) (Fig. 2C; and two species of imbricate-leaved *Dacrydium* (Hill & Christophel 2001, Fig. 2D–F); while a monocotyledon closely related to extant *Dianella* (Conran *et al.* 2003) is important but rare. It appears that Nelly Creek represents a distinctly different vegetation type to that found in the Maslin Bay and Golden Grove sediments, but it is too soon to be sure that Nelly Creek may have more in common with the open, Late Cretaceous vegetation also recovered from central Australia.

The silcrete localities offer a very different form of fossilization. The two major localities, Poole Creek and Stuart Creek (both Lake Eyre South), have recently been summarized by Hill *et al.* (2016). They noted that there is reasonable evidence that Poole Creek is of Middle Eocene age (Greenwood *et al.* 1990), based on macrofossil correlation with Nelly Creek, which in turn has been palynostratigraphically dated (Alley *et al.* 1996). Stuart Creek is regarded as more recent, based on its much more modern looking flora and the general geology. This locality is most reliably dated as Miocene-Pliocene (Rowett 1997), but that remains contentious, with geological evidence supporting an Eocene age. Poole Creek contains a macroflora that has been closely compared with the probably contemporaneous Nelly Creek flora, although there is clear circularity in saying this, since this floral similarity is also the basis for assigning the same ages to the two localities. Few examples could be found of well illustrated specimens from Poole Creek and this flora is in urgent need of further research. The vegetation at Poole Creek has been described as a type of monsoon forest (Greenwood 1996), which is a vegetation type that may well have developed in response to the onset of a regular annual dry season. However, Stuart Creek contains a very well preserved and much more modern looking flora, including indisputable eucalypts, with reasonable species diversity and quite modern looking fruit morphologies (see Lange 1978, 1982; White 1994 for illustrations).

On the west coast of Australia there are abundant examples of plant macrofossils preserved as moulds in the very hard sediment. These include the oldest record of a woody *Banksia* fruit (McNamara & Scott 1983), and much more significantly, examples of leaves of scleromorphic taxa with clear examples of adaptations to low water availability (e.g. Carpenter *et al.* 2010). While the age of these sediments is not well constrained, they do appear to overlap the time when major mid-Eocene rainforests were dominating the southern coast of Australia. Hence we can see at least two broad localities where the taxa that dominated the Late Cretaceous vegetation may have survived during the ultra-wet phase of the mid-Eocene—central Australia and the west coast of Australia.

Therefore it is now possible to identify an alternative to the hypothesis that the modern Australian vegetation largely had its genesis in the mega-diverse rainforests in the mid Eocene of southern Australia. That alternative suggests that at least seasonally dry habitats survived from the Late Cretaceous through to the Oligocene, when Australia began to dry on a far broader scale.

Hill (1998) reviewed the evidence for both scleromorphic and xeromorphic vegetation in the Australian Cenozoic fossil record. He concluded that scleromorphy, the adaptation to low soil nutrients, and especially low phosphorus, was present in the fossil record as far back as he could trace (Late Paleocene), whereas evidence for xeromorphy, the adaptation to low water availability, suggested that this was a much more recent phenomenon and more or less matched the evidence for the mid-Cenozoic commencement of the drying of the Australian continent. However, these conclusions were based on an analysis of the major south-eastern Australian coastal sites, where the Eocene was largely, or perhaps completely, rainforest dominated, and the climate was effectively everwet. It now appears likely that there were other parts of Australia where scleromorphic and possibly xeromorphic adaptations may have been in place for significantly longer—at least Late Cretaceous—and an alternative origin for components of the extant vegetation may have existed.

The Late Cretaceous fossil material reported by Carpenter *et al.* (2015) is also notable for the presence of charcoal particles, which strongly suggests that fire was an important part of the environment. We also know that there is evidence that fire became an important part of the landscape in southern Australia in the Neogene, after Australia finally separated from Antarctica and the climate began the long process of drying to the current levels. It is no surprise that we see fire becoming a more important feature of the Neogene environment, but the interesting question is whether fire remained an important part of some parts of the Australian environment in the long time period between the Late Cretaceous and the broad scale Neogene drying in southern Australia. Hill *et al.* (2016) have addressed this question with regards to the eucalypts, which are the ultimate fire promoters, but this issue has broader ramifications in the vegetation at large. While evidence is sparse, it seems likely that a group of plants like the eucalypts, that have an ecology that is heavily bound to fire promotion and survival, should have always had fire as an integral part of their ecology. The latest evidence, summarized by Hill *et al.* (2016), suggests that eucalypts evolved at around the Cretaceous-Cenozoic boundary and that whereever they survived from that time on, there must have been the capacity for quite regular and large scale fires. In Australia, the most likely place for this to be prior to the Neogene is in central Australia, where there is some evidence of eucalypts at Poole Creek, or on the west coast, where the conditions seem to have been appropriate, but eucalypts have yet to be reported.

There is strong evidence for the drying of the Australian continent in general, sometime after Australia finally separated from Antarctica (Bowler 1982). Today much of Australia is desert, but the fossil record for the vegetation that occurs there is sparse, which is not surprising, given the usual reliance on abundant water for good fossilization. One obvious group of plants that should have shown a clear response to the drying of the continent is the grasses, and their fossil record in Australia was summarized by Macphail & Hill (2002). The macrofossil record of the Poaceae in Australia is almost non-existent and is highly unreliable, but the distinctive pollen can be used to reconstruct at least some of the history of this important taxon. The earliest known records of Poaceae pollen in Australia are from the Early Eocene in the Bonaparte Basin in north-western Australia, but this is followed by rare specimens in the mid-Late Eocene of central Australia, the Lake Eyre Basin in northern South Australia and three locations in south-eastern Australia. There is limited evidence that the Poaceae spread across Australia in the Paleogene in response to an increasingly seasonal climate. The earliest reliable evidence for grasses becoming prominent in the landscape comes from South Australia in probable riparian environments in the western Murray Basin during the Late Oligocene-Early Miocene.

The Late Neogene in Australia was characterized by rapid climatic fluctuations, leading to drying and/or increasingly seasonal climates (Hill *et al.* 1999). Kershaw *et al.* (1994) and Macphail (1997) demonstrated that in the Late Neogene there was a broad negative relationship between the relative abundance of Poaceae and annual rainfall. In the Quaternary, seasonally dry climates characterized by seasonal summer drought, were widespread over much of inland Australia, and these conditions were conducive for the spread of a Poaceae-Asteraceae-Chenopodiaceae association (Hope 1994).

Perhaps one of the most interesting unresolved issues in Australian vegetation history, as in other parts of the world, is the interaction between the megafauna and the vegetation and, by inference, the impact of the extinction of the megafauna on the vegetation (e.g. Barnosky *et al.* 2016). Miller *et al.* (2005) provided extensive data from South Australian fossil egg shells of emus and the extinct giant flightless bird *Genyornis newtoni* and concluded that their data were consistent with a permanent reduction in the food sources available to the emus around 45–50,000 years ago at the same time that *G. newtoni* became extinct. They speculated that human ignition of the landscape rapidly converted a drought-adapted mosaic of trees, shrubs, and nutritious grasslands to the modern fire-adapted desert scrub. However, Murphy *et al.* (2012) re-analysed these data and concluded that there was no evidence to support the hypothesis that landscape burning by humans caused the megafaunal extinctions, and they proposed the alternative hypothesis that increasing aridity in the Late Pleistocene may have led to a change in the vegetation and, consequently, the diet of *Genyornis* at this time. This is one of the few studies that links evidence for vegetation change with megafaunal extinction, but it also demonstrates how confused this area of research is at present. It is now not even clear that the egg shell analysed belonged to *Genyornis* (Grellet-Tinner *et al.* 2016). Research in other parts of Australia have also linked vegetation change to the demise of the megafauna (e.g. Rule *et al.* 2012), but this was in a very distinctly different vegetation setting.

Another example of vertebrate fossils that impact on our thinking about the vegetation is the remarkable report of a diverse and very well preserved middle Pleistocene (200–400,000 years old) fauna from caves within the Nullarbor Plain by Prideaux *et al.* (2007), who noted that the diverse herbivore assemblage, which includes two species of tree kangaroo, “implies substantially greater floristic diversity than that of the modern scrub-steppe”. In the detailed report of the tree kangaroo fossil that followed, Prideaux & Warburton (2008) concluded that the morphology of the limbs “bears the hallmarks of a primarily arboreal lifestyle”. Prideaux *et al.* (2007) note that the climate when these fossils were alive was likely to have been very similar to the climate today, and hence we have a vegetation problem to solve: how is it that tree kangaroos, with adaptations for an arboreal lifestyle, were living in what is now a treeless plain, around 200–400,000 years ago in a climate similar to that which prevails today? This is a grand question that impacts not just on the Nullarbor Plain, but on much of arid southern Australia.

Conclusion

The living vegetation of South Australia is the end product of tens of millions of years of evolution, mostly in isolation of other continents, and under extremely different climatic conditions. It appears that the vegetation history of South Australia, along with the rest of the continent, may be much more rich and complex than first thought—far from a homogenous coast-to-coast Eocene rainforest being the cradle for the origin of the living vegetation, we are seeing evidence for a much more varied vegetation, with the origins of many of our scleromorphic/xeromorphic taxa perhaps occurring as far back as the Cretaceous. The number of fossil deposits that provide useful information for reconstructing the vegetation history is small, and so we must make the most of all the evidence we have. The reality is that research on most localities has barely commenced and we have much yet to learn from them. It is also likely that new deposits will be found in future that will add significantly to our understanding. Nevertheless, what we do have provides a useful framework of hypotheses that are open to scrutiny, and much will be gained in the future by a systematic approach to improving the quantity and quality of data that can be applied to testing them.

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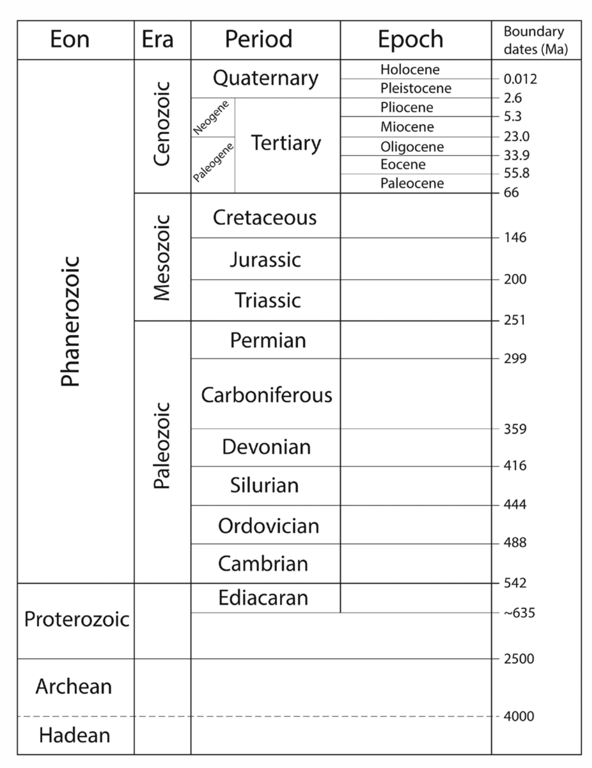

Eon	Era	Period	Epoch	Boundary dates (Ma)
Phanerozoic	Cenozoic	Quaternary	Holocene	0.012
			Pleistocene	2.6
		Neogene Tertiary	Pliocene	5.3
			Miocene	23.0
		Paleogene	Oligocene	33.9
			Eocene	55.8
			Paleocene	66
	Mesozoic	Cretaceous		146
		Jurassic		200
		Triassic		251
	Paleozoic	Permian		299
		Carboniferous		359
		Devonian		416
		Silurian		444
		Ordovician		488
		Cambrian		542
Proterozoic		Ediacaran		~635
				2500
Archean				4000
Hadean				

Fig. 3. Geological timescale.

References

Alley, N.F., Krieg, G.W. & Callen, R.A. (1996). Early Tertiary Eyre Formation, lower Nelly Creek, southern Lake Eyre Basin, Australia: Palynological dating of macrofloras and silcrete, and palaeoclimatic interpretations. *Australian Journal of Earth Sciences* 43: 71–84.

Anagnostou, E., John, E.H., Edgar, K.M., Foster, G.L., Ridgwell, A., Inglis, G.N., Pancost, R.D., Lunt, D.J. & Pearson, P.N. (2016). Changing atmospheric CO_2 concentration was the primary driver of early Cenozoic climate. *Nature* 533: 380–384.

Barnosky, A.D., Lindsey, E.L., Villavicencio, N.A., Bostelmann, E., Hadly, E.A., Wanket, J. & Marshall, C.R. (2016). Variable impact of late-Quaternary megafaunal extinction in causing ecological state shifts in North and South America. *Proceedings of the National Academy of Sciences* 113: 856–861.

Bowler, J.M. (1982). Aridity in the Late Tertiary and Quaternary of Australia. Pp. 35–45. In: Barker, W.R. & Greenslade, P.J.M. (eds), *Evolution of the Flora and Fauna of Arid Australia*, pp. 35–45. (Peacock Publications: Glen Osmond).

Brown, S.A.E, Scott, A.C., Glasspool, I.J. & Collinson, M.E. (2012). Cretaceous wildfires and their impact on the Earth system. *Cretaceous Research* 36: 162–190.

Carpenter, R.J., Hill, R.S. & Scriven, L.J. (2006). Palmately lobed Proteaceae leaf fossils from the middle Eocene of South Australia. *International Journal of Plant Sciences* 167: 1049–1060.

Carpenter, R.J., Jordan, G.J., Lee, D.E. & Hill, R.S. (2010). Leaf fossils of *Banksia* (Proteaceae) from New Zealand: an Australian abroad. *American Journal of Botany* 97: 288–297.

Carpenter, R.J., Macphail, M.K., Jordan, G.J. & Hill, R.S. (2015). Fossil evidence for open, Proteaceae-dominated heathlands and fire in the Late Cretaceous of Australia. *American Journal of Botany* 102: 2092–2107.

Christophel, D.C., Scriven, L.J. & Greenwood, D.R. (1992). An Eocene megafossil flora from Nelly Creek, South Australia. *Transactions of the Royal Society of South Australia* 116: 65–76.

Conran, J.G., Christophel, D.C. & Cunningham, L. (2003). An Eocene monocotyledon from Nelly Creek, central Australia, with affinities to Hemerocallidaceae (Lilianae: Asparagales). *Alcheringa* 27: 107–115.

Friis, E.M., Crane, P.R. & Pedersen, K.R. (2011). *Early Flowers and Angiosperm Evolution*. (Cambridge University Press: Cambridge).

Greenwood, D.R. (1996). Eocene monsoon forests in central Australia? *Australian Systematic Botany* 9: 95–112.

Greenwood, D.R., Callen R.A. & Alley, N.F. (1990). The correlation and depositional environment of Tertiary strata based on macrofloras in the southern Lake Eyre Basin, South Australia, 46 pp. *Department of Mines and Energy, South Australia, Report Book* 90/15.

Grellet-Tinner, G., Spooner, N.A. & Worthy, T.H. (2016). Is the "Genyornis" egg of a mihirung or another extinct bird from the Australian dreamtime? *Quaternary Science Reviews* 133: 147–164.

Hill. R.S. (ed.) (1994). *History of the Australian Vegetation: Cretaceous to Recent.* (Cambridge University Press: Cambridge).

Hill, R.S. (1998). Fossil evidence for the onset of xeromorphy and scleromorphy in Australian Proteaceae. *Australian Systematic Botany* 11: 391–400.

Hill, R.S. & Christophel, D.C. (1988). Tertiary leaves of the tribe Banksieae (Proteaceae) from south-eastern Australia. *Botanical Journal of the Linnean Society* 97: 205–227.

Hill, R.S. & Christophel, D.C. (2001). Two new species of *Dacrydium* (Podocarpaceae) based on vegetative fossils from Middle Eocene sediments at Nelly Creek, South Australia. *Australian Systematic Botany* 14: 193–205.

Hill, R.S., Truswell, E.M., McLoughlin, S. & Dettmann, M.E. (1999). Evolution of the Australian flora: fossil evidence.

In: Orchard, A.E. (ed.), *Flora of Australia*, Vol. 1 (2nd edn): 251–320. (ABRS/CSIRO: Australia).

Hill, R.S., Beer, Y.K., Hill, K.E., Maciunas, E.C., Tarran, M.A. & Wainman, C.C. (2016). Evolution of the eucalypts – an interpretation from the macrofossil record. *Australian Journal of Botany* 64: 600–608.

Hope, G.S. (1994). Quaternary vegetation. In: Hill, R.S. (ed.), *History of the Australian Vegetation: Cretaceous to Recent,* pp. 368–389. (Cambridge University Press: Cambridge).

Kershaw, A.P., Martin, H.A. & McEwen Mason, J.R.C. (1994). The Neogene: a period of transition. In: Hill, R.S. (ed.), *History of the Australian Vegetation: Cretaceous to Recent*, pp. 299–327. (Cambridge University Press: Cambridge).

Lange, R.T. (1978). Carpological evidence for fossil *Eucalyptus* and other Leptospermeae (subfamily Leptospermoideae of Myrtaceae) from a Tertiary deposit in the South Australian arid zone. *Australian Journal of Botany* 26: 221–233.

Lange, R.T. (1982). Australian Tertiary vegetation. In: Smith, J.M.B. (ed.), *A History of Australasian Vegetation*, pp. 44–89. (McGraw-Hill: Sydney).

Macphail, M.K. (1997). Late Neogene climates in Australia: fossil pollen- and spore-based estimates in retrospect and prospect. *Australian Journal of Botany* 45: 425–464.

Macphail, M.K. & Hill, R.S. (2002). Palaeobotany of the Poaceae. In: Mallett, K. & Orchard, A.E. (eds), *Flora of Australia*, Vol. 43 (Poaceae 1 Introduction and Atlas): 37–70. (ABRS/CSIRO: Canberra).

McNamara, K.J. & Scott, J.K. (1983). A new species of *Banksia* (Proteaceae) from the Eocene Merlinleigh Sandstone of the Kennedy Range, Western Australia. *Alcheringa* 7: 185–193.

Miller, G.H., Fogel, M.L., Magee, J.W., Gagan, M.K., Clarke, S.J. & Johnson, B.J. (2005). Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* 309: 287–290.

Murphy, B.P., Williamson, G.J. & Bowman, D.M.J.S. (2012). Did central Australian megafaunal extinction coincide with abrupt ecosystem collapse or gradual climate change? *Global Ecology and Biogeography* 21: 142–151.

Prideaux, G.J., Roberts, R.G., Megirian, D., Westaway, K.E., Hellstrom, J.C. & Olley, J.M. (2007). Mammalian responses to Pleistocene climate change in southeastern Australia. *Geology* 35: 33–36.

Prideaux, G.J. & Warburton, N.M. (2008). A new Pleistocene tree-kangaroo (Diprotodontia: Macropodidae) from the Nullabor Plain of south-central Australia. *Journal of Vertebrate Paleontology* 28: 463–478.

Rowett, A. (1997). Earthwatch '96. *MESA Journal* 5: 27–29.

Rule, S., Brook, B.W., Haberle, S.G., Turney, C.S.M., Kershaw, A.P. & Johnson, C.N. (2012). The aftermath of megafaunal extinction: Ecosystem transformation in Pleistocene Australia. *Science* 335: 1483–1486.

Scriven, L.J., McLoughlin, S. & Hill, R.S. (1995). *Nothofagus plicata* (Nothofagaceae), a new deciduous Eocene macrofossil species, from southern continental Australia. *Review of Palaeobotany and Palynology* 86: 199–209.

White, M.E. (1994). *After the Greening: The Browning of Australia*. (Kangaroo Press: Kenthurst).