

Plant communities and climate change in southeastern Australia during the early Paleogene

David R. Greenwood*

*School of Life Sciences and Technology (S008), Victoria University of Technology,
PO Box 14428, Melbourne City MC, VIC 8001, Australia*

Patrick T. Moss

*Department of Geography, University of Wisconsin-Madison,
550 North Park Street, Madison, Wisconsin, 53706, USA*

Andrew I. Rowett

*Mineral Resources Group, Minerals and Energy Resources, SA,
GPO Box 1671, Adelaide SA 5001, Australia*

Anthony J. Vadala

Rachael L. Keefe

*School of Life Sciences and Technology (S008), Victoria University of Technology,
PO Box 14428, Melbourne City MC, VIC 8001, Australia*

ABSTRACT

In this study, data from fossil macrofloras and microfloras in southeastern Australia are used to reconstruct vegetation and climates for the early Paleogene. Our data show that for much of the late Paleocene to middle Eocene, complex, species-rich forests were predominant in southeastern Australia, under mesothermal humid climates (mean annual temperature [MAT] 16–22 °C, coldest quarter mean temperature [CQMT] >10 °C, mean annual precipitation [MAP] >150 cm/yr). A minor cooling episode may have occurred in the mid-early Eocene. Megathermal climates may have been present in lowlands in the latest early Eocene, during the Cenozoic Global Climatic Optimum. These forests were dominated by taxa characteristic of present-day mesothermal-megathermal high-rainfall multistratal forests; e.g., Cunoniaceae, Elaeocarpaceae, *Gymnostoma* (Casuarinaceae), Lauraceae (e.g., *Beilschmiedia*, *Cryptocarya* and *Endiandra*), and Proteaceae. A prominent treefern element (*Cyathea* and *Dicksonia* types) was present in the early Eocene. A number of megathermal taxa, including Cupanieae (Sapindaceae) and *Ilex* (Aquifoliaceae), were present through the early and middle Eocene. Taxa characteristic of modern-day microthermal to mesothermal forests were also present, e.g., *Nothofagus* (Nothofagaceae), *Eucryphia* (Eucryphiaceae), *Libocedrus* (Cupressaceae) and Podocarpaceae (*Acmopyle* and *Dacrycarpus*). The relictual araucarian conifer, *Wollemia*, and other Araucariaceae were present through the late Paleocene to early Eocene. There is limited physiognomic evidence to suggest the late Paleocene to early Eocene forests contained some deciduous canopy trees.

*david.greenwood@vu.edu.au. Present address, Moss: Department of Geography, University of Wisconsin—Madison, 550 N. Park Street, Madison, Wisconsin 53706, USA.

Greenwood, D.R., Moss P.T., Rowett, A.I., Vadala, A.J., and Keefe, R.L., 2003, Plant communities and climate change in southeastern Australia during the early Paleogene, in Wing, S.L., Gingerich, P.D., Schmitz, B., and Thomas, E., eds., Causes and Consequences of Globally Warm Climates in the Early Paleogene: Boulder, Colorado, Geological Society of America Special Paper 369, p. 365–380.

AUSTRALIAN EARLY PALEOGENE ENVIRONMENTS—SETTING AND PRIOR WORK

Worldwide, the warmest interval of the Cenozoic was the early Eocene, the latter part of which has been called the Cenozoic Global Thermal Optimum, or CGTO (Clyde et al., 2001). An additional warm episode in the early Paleogene, the Initial-Eocene Thermal Maximum, or IETM (formerly the late Paleocene Thermal Maximum or LPTM), was marked but of short duration (Zachos et al., 1993, 1994; Röhl et al., 2000). The warm character of the early Paleogene has led to the recognition of the early Paleogene as a test bed for understanding environments and factors controlling climates in a world much warmer than today. Most quantitative paleobotanical investigation of early Paleogene climates and their influence on regional or local vegetation has been based in North America (e.g., Wing and Greenwood, 1993; Wing et al., 1995, 2000; Wing, 1998; Wing and Harrington, 2001). Prior studies of the early Paleogene for southeastern Australia (e.g., Carpenter et al., 1994; Greenwood, 1994; Greenwood and Wing, 1995; Greenwood et al., 2000a) provided only limited analysis of Paleocene and early Eocene floras from the region. Climate was generally warm during this time period, although there may have been a possible cooling episode during the early Eocene (Fig. 1; Greenwood et al., 2000a; Wing et al., 2000; Greenwood and Christophel, 2003). Greater detail than was presented in these earlier studies is required to fully understand environmental change associated with the IETM and the early Eocene warm interval in high-latitude southeastern Australia.

The primary forcing factor for the warm early Paleogene is thought to be high concentrations of atmospheric CO₂. Recent studies however, suggest early Paleogene *p*CO₂ < 500 ppm, concentrations similar to those of the last few decades when *p*CO₂ has been 340–360 ppm, but much lower than those determined using geochemical proxies and modeling (Royer et al., 2001). At these *p*CO₂ values, computer climate models only partially replicate the paleo-proxy climate estimates for continental interiors and high latitudes in the early Eocene (Shellito et al., 2003). However the model-proxy data discrepancies may reflect inaccurate specification of paleovegetation, mountain ranges in some cells and other boundary conditions in the models (Greenwood and Wing, 1995; Sewall et al., 2000; Shellito et al., 2003). A continuing problem however, with model and proxy data comparisons, is the lack of suitable proxy data in key areas of comparison such as Australia.

In this report we reconstruct in detail southeastern Australian latest Paleocene (56–55 Ma) to middle Eocene (49–37 Ma) environments from paleobotanical data. This report attempts to answer two questions: (1) what was the composition and character of vegetation in the late Paleocene to early Eocene, and (2) how did floristic composition change across the interval?

Macrofloras and microfloras from southeastern Australia were selected for four reasons. First, these floras are relatively well known. Second, southeastern Australia is a medium-size

(7° × 10° lat and long) well-defined region at high latitudes in the early Paleogene (Fig. 1). Third, recent research has provided a detailed refinement of the palynostratigraphic schema based on sedimentary sequences from the Gippsland Basin (Partridge, 1999). Finally, paleoclimate can be reconstructed from leaf macrofloras using leaf physiognomy (Greenwood, 2001), and bioclimatic analysis using quantitative “climate envelopes” (Kershaw and Nix, 1988; Kershaw, 1996) can be applied to both macrofloras and spore-pollen assemblages.

CORRELATIONS AND AGE OF EARLY PALEOGENE MACROFLORAS IN SOUTHEASTERN AUSTRALIA

The Cenozoic marine proxy record of sea surface temperatures (SST) for the Southern Ocean and for northeastern Australia show cycles of cooling and warming superimposed on the broad global trend of progressive cooling (Shackleton and Kennett, 1975; Feary et al., 1991). The SST record for northeastern Australia shows that the continent’s northward movement at times negated or at least minimized the effects of the global climatic cooling during the Paleogene (Feary et al., 1991; Truswell, 1993). The greatest late Paleocene and early Eocene climate warming occurred at high latitudes. Southeastern Australia lay at high southern latitudes (~60°S) during the early Paleogene (Fig. 1), and topographic relief was in the order of 400–800 m in the southern sector of the Eastern Highlands (Truswell, 1993; Taylor, 1994). The pattern of Paleogene to early Neogene climate change in southeastern Australia corresponds to floristic changes and shifts in leaf physiognomic signatures over the same time (Truswell, 1993; Greenwood, 1994; Macphail et al., 1994; Greenwood and Christophel, 2003). The Gippsland, Otway and Murray Basins were the depositional areas for much of the sediment removed from the Southern Highlands during the Paleogene (Fig. 1). Stratigraphic assignment of macrofloras presented here is based on terrestrial spore and pollen assemblages, using palynological zones established for the Gippsland Basin (Macphail et al., 1994).

Correlation between the Gippsland Basin palynological zones and the international Cenozoic time-scale has developed over the last 30 yr, and is also based on marine microfossil and nannofossil data and isotopic dating of volcanic rocks (Macphail et al., 1994; Chaproniere et al., 1996; Truswell, 1997). Southeastern Australian Cenozoic palynological zones in Macphail et al. (1994) were correlated with the geochronometric scale of Berggren et al. (1985), and the Australian Tertiary time-scale in Chaproniere et al. (1996) was based on the Berggren et al. (1995) geochronometric scale. The biostratigraphic scheme used here has been updated to the geochronometric scale and European stages given in Hardenbol et al. (1998), and so shows some differences to earlier schemes. This scheme also has revisions and additional subdivisions to the spore-pollen zones based on recent reassessments (Partridge, 1999; 2001, personal commun.). Detailed magnetostratigraphy of terrestrial sediments in western North America by Clyde et al. (2001) indicated

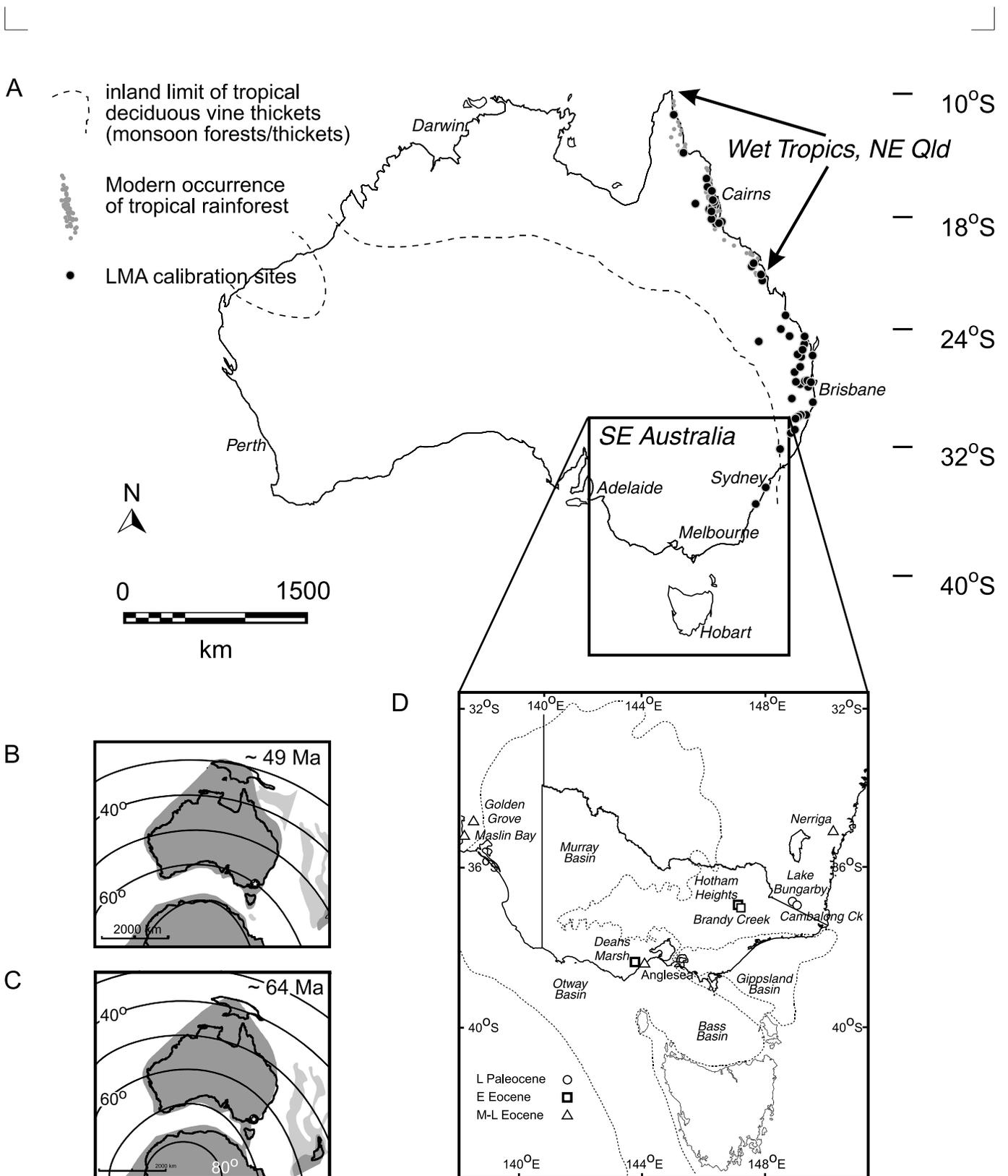


Figure 1. Location and paleogeographic setting for study area. A: Map of Australia showing location of southeastern Australia study area and other locations mentioned in the text, the modern distribution of tropical rainforests, and the location of the LMA calibration sites (Greenwood et al., 2001, personal commun.). B–C: Paleogeographic reconstructions of Australia in the middle Eocene (1B) and Paleocene (1C), adapted from Veevers et al. (1991). D: Detail of southeastern Australia showing the position of the Gippsland Basin and other major Cenozoic basins in the region, and the location of the Paleogene macrofloras discussed in the text (adapted in part from Greenwood et al., 2000b, and Greenwood and Christophel, 2003).

that the terrestrial onset of the CGCO falls within Chron 23r and lasts till Chron C22r. To facilitate comparisons with the North American terrestrial record, the stratigraphic assignment of floras has been related to the magnetostratigraphy in Hardenbol et al. (1998; Figure 2 herein) where possible.

Monaro Plains and region

Paleogene sediments crop out at several sites in southern New South Wales (Fig. 1), including Cambalong Creek and Nerriga (Hill, 1982; Taylor et al., 1990; Vadala and Drinnan, 1998). Outcrop at Cambalong Creek presents abundant well-preserved mummified leaves in well-defined sedimentary layers (Vadala and Drinnan, 1998). The microflora in the Cambalong Creek sediments correlates with the Upper *Lygistepollenites balmei* Zone (Stover and Partridge, 1973), consistent with a late Paleocene (upper Thanetian) age (Taylor et al., 1990). The Cambalong Creek flora probably sits just prior to the IETM (Fig. 2).

The Nerriga macroflora occurs in a lacustrine deposit (Titrango siltstone) that crops out to the north of the Monaro Plains (Hill, 1982). Microfloras in the Titrango siltstone were correlated with the Lower *Nothofagidites asperus* Zone, or the Upper *Malvacipollis diversus* to *Proteacidites asperopolus* Zones of the Gippsland Basin. Basalts associated with the Nerriga site give a corrected K/Ar age of 45.9–42.6 Ma (Hill, 1982), which falls within the lower part of the Lower *N. asperus* Zone (Fig. 2).

Mount Hotham and area (eastern Victorian Highlands)

The area around Mount Hotham in Victoria (Fig. 1) includes several peaks between 1700 and 1900 m. Early Cenozoic basalts are common in the area, capping an Oligocene to Eocene surface that preserves infilled stream systems containing fossiliferous sediments (Orr, 1999; Greenwood et al., 2000b). Outcrop at Hotham Heights and the abandoned Brandy Creek gold mine comprises Paleogene carbonaceous mudstones to silty sandstones that are capped by Eocene basalts (Greenwood et al., 2000b). Microfloras from both sites correlate to the uppermost part ('E') of the *Malvacipollis diversus* Zone or the *Proteacidites asperopolus* Zone, indicating an early Eocene to basal middle Eocene age (Partridge, 1998a; 1998b; 1999, personal commun.). Here we treat Hotham Heights and Brandy Creek as being no younger than that portion of the *P. asperopolus* Zone that falls within the early Eocene (Fig. 2), giving greater weight to the early Eocene indicators (i.e. low counts of *Nothofagidites*; Partridge, 1998b). On available evidence these floras most likely fall within the CGCO (spanning Chrons C23r to C22r).

Western Victoria and South Australia

Two early Paleogene macrofloras from the Otway Basin (Fig. 1) are considered here; the Deans Marsh and Eocene Anglesea floras, from outcrop of the Eastern View Formation

(Christophel et al., 1987; Greenwood et al., 2000b). The Deans Marsh macroflora was considered early Eocene based on palynological correlations (Christophel and Greenwood, 1989). However, Rowett and Sparrow (1994) indicated a lower middle Eocene age based on assignment of the microflora to the Lower *Nothofagidites asperus* Zone, and a biostratigraphic comparison of the dispersed cuticle flora of the Deans Marsh and other Australian Eocene macrofloras. Partridge (1998a), however considered the microflora correlated with his newly defined *Malvacipollis diversus* Zone C. Deans Marsh is thus considered here to be early Eocene (Fig. 2), potentially coinciding with the early Eocene cool interval detected in the western interior of North America (Wing et al., 2000). This age assignment differs from that used in Greenwood et al. (2000a, 2000b) and Greenwood and Christophel (2003).

A rich macroflora has been collected from the Eastern View Formation in a series of fluvio-lacustrine lenses in overburden from the Anglesea open-cut mine (Christophel et al., 1987; Greenwood et al., 2000b). The associated microflora was assigned by Christophel et al. (1987) to the base of the *Triorites magnificus* Zone of the Otway Basin (Harris, 1971), corresponding with the boundary of the Gippsland Basin Lower and Middle *Nothofagidites asperus* zones (equivalent to the P14-P15 boundary). The Anglesea macroflora is thus latest middle Eocene (late Bartonian) in age (Fig. 2), and is the youngest flora considered in this report.

The Golden Grove and Maslin Bay middle Eocene floras were uncovered in clay lenses in massive fluvial sand bodies of the North Maslin Sands in the St Vincent Basin, South Australia (Fig. 1). The Golden Grove clays (North Maslin Sands) are correlated with the Lower *Nothofagidites asperus* Zone of the Gippsland Basin (Alley, 1987; Christophel and Greenwood, 1987; Lindsay and Alley, 1995). Lindsay and Alley (1995) considered the Golden Grove flora to be no older than planktonic foraminifera zone P11. Partridge (1998a), offered evidence for assignment to either the *Proteacidites confragosus* Zone of the Otway Basin (Harris, 1971), which is a time equivalent of the *P. asperopolus* Zone of the Gippsland Basin (Stover and Partridge, 1973), or correlated it with his newly defined *Nothofagidites asperus* Zone A. The Golden Grove flora is here considered to be restricted within Partridge's (1999) *Nothofagidites asperus* Zone A, equivalent to zone P11 and that portion of P12 that correlates with the Lower *N. asperus* Zone A (Fig. 2). Uncertainty in our palynostratigraphic assignment means the flora spans the upper part of Chron C20r and the lower part of Chron C20n (Fig. 2).

FLORISTIC CHARACTER OF SOUTHEASTERN AUSTRALIAN EARLY PALEOGENE VEGETATION

Sampling, preparation and analysis of floristics

Preservation of leaf fossils at most sites was as compressions with the cuticular envelope preserved; this was liberated from the mudstone matrix by maceration with dilute H₂O₂. Ex-

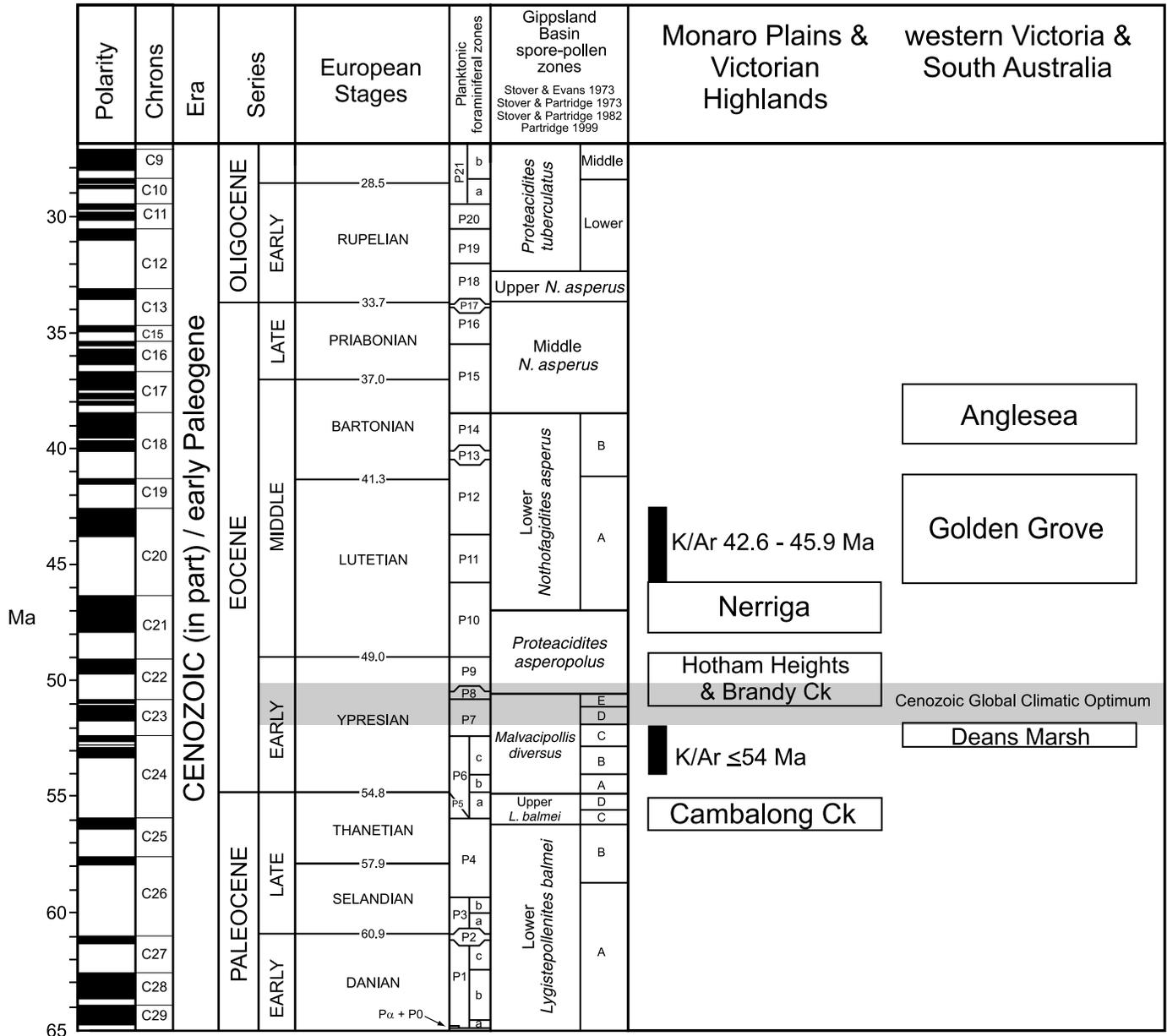


Figure 2. Early Paleogene palynostratigraphic schema for southeastern Australia showing the stratigraphic arrangement of the macrofloras discussed in the text (adapted from Greenwood et al., 2000b). Stratigraphy adapted from Macphail et al. (1994) and Chaproniere et al. (1996), to the geochronometric scale and European stages in Hardenbol et al. (1998), by Partridge (1998a; 1998b; 1999; 2001, personal commun.).

tracted leaves were cleaned with dilute aqueous chromic acid and/or hydrofluoric acid. Leaf floras preserve ecological information, such as dominance and diversity. Field census data from large laterally continuous fossiliferous sediments (e.g., Greenwood and Basinger, 1994; Wing, 1998), and modern leaf litter studies (Greenwood, 1991, 1992; Burnham et al., 1992), have shown that large collections (>600 specimens) will reflect the original floristic richness of the local forest. Anglesea and Golden Grove have been sampled for over two decades in a

quantitative manner along bedding planes. Sampling at the Anglesea mine followed lateral transects within fluvial infill clay lenses as well as between several discrete lenses. Data presented here is from the site 2 transect (Christophel et al., 1987; Rowett and Christophel, 1990). Collections were examined from a single fluvio-lacustrine mudstone deposit at each of Hotham Heights, Brandy Creek, Nerriga, and Golden Grove (Hill, 1982; Christophel and Greenwood, 1987; Greenwood, 1991; Banks, 1999; Keefe, 2000). Sediment samples were collected from a

spoil heap from the abandoned Deans Marsh mine (Christophel and Greenwood, 1989; Rowett and Sparrow, 1994).

Macrofloras were sorted into taxonomic units using leaf architecture and cuticle characters (Hickey, 1973). Identification of the fossil taxa was based on published diagnostic leaf and cuticle characters for key Australian plant families (e.g., Araucariaceae, Proteaceae, and Lauraceae) and member genera (Vadala and Greenwood, 2001, and references cited therein). Many of these taxa are climatically indicative (Kershaw and Nix, 1988). Unless otherwise stated, a 'specimen' refers to a single leaf fragment, or whole leaf or leafy twig.

Spore-pollen counts used in this study were mainly derived from previous studies (e.g., Hill, 1982; Christophel et al., 1987; Taylor et al., 1990), but some data were collected specifically for the study (Partridge, 1998a, 1998b). Identification of nearest living modern analogs for the Tertiary palynomorphs follows the caveats and nomenclature provided in Macphail et al. (1994; Table 1 herein). Standard counts of >100 grains (typically 200 grains) were made in most instances. All data presented here for floras with multiple samples uses the average for each taxon for these samples.

Regional southeastern Australian early Paleogene spore-pollen record

Analysis of spore-pollen floras from terrestrial and marginal marine sediments in drill cores from the Gippsland and Otway Basins in southeastern Australia (Fig. 1), provide a general impression of changes in regional vegetation over the early Paleogene (Truswell, 1993; Macphail et al., 1994). According to Macphail et al. (1994) Araucariaceae (including the highly relictual conifer *Wollemia* as *Dilwynites granulatus*; Chambers et al., 1998), *Nothofagus* and some ferns (e.g., Cyatheaceae, Gleicheniaceae) fluctuated in importance during the Paleocene. Proteaceae were also prominent and diverse in microfloras throughout the Paleocene in southeastern Australia. Proteaceae today includes important canopy trees and understory shrubs in mesothermal-megathermal Australian rainforests (e.g., *Darlingia* and *Helicia*), as well as sclerophyllous forests and woodlands (e.g., *Banksia*). According to Macphail et al. (1994) Paleocene southeastern Australian forests were rich in araucarians and other conifers as emergents above an angiosperm (mostly *Nothofagus*) canopy. These forests included a diverse set of other

TABLE 1. LIST OF FOSSIL PALYNOFORMS AND MACROFLORA AND THEIR NEAREST LIVING RELATIVES FOR FLORAS

Fossil palynomorph	Family	Suggested modern taxon/NLR (palynomorph or macrofossil)	1*	2	3	4	5	6	7
Cyathidites paleospora	Cyatheaceae	<i>Cyathea</i>		p [†]	p	p	p	p	p
Matonisporites ornamentalis	Dicksoniaceae	<i>Dicksonia</i>			p	p			
	Stangeriaceae	<i>Bowenia</i>					m [†]		m
Phyllocladidites mawsonii	"	<i>Lagarostrobos</i>	p	p			p	p	p
<i>Podocarpidites</i> spp.	"	<i>Podocarpus</i>	p	m	p		p	m	m
<i>Araucariacites australis</i>	Araucariaceae	<i>Agathis</i>	p		m	m	p	m	m
"	"	<i>Araucaria</i>	p	m			p		
<i>Banksieaeidites arcuatus</i>	Proteaceae	Musgraveinae						m	m
<i>Proteacidites</i> spp.	Proteaceae	<i>Orites</i>	m		m	m			
"	Proteaceae	<i>Helicia</i>	m		m	m		m	
"	Elaeocarpaceae	<i>Aceratium</i>			m	m			
"	"	<i>Elaeocarpus</i>	m		m	m			
"	"	<i>Sloanea</i>						m	m
Not preserved	Lauraceae	<i>Beilschmiedia</i>	m		m	m		m	m
"	"	<i>Cryptocarya</i>	m	m	m	m	m	m	m
"	"	<i>Endiandra</i>	m	m	m	m	m	m	m
"	"	<i>Litsea</i>	m		m	m	m		m
<i>Haloragacidites harrisii</i>	Casuarinaceae	<i>Gymnostoma</i>	p	m	p	m	m	m	m
	Ebenaceae	<i>Diospyros</i>					m	m	m
	Grossulariaceae	<i>Quintinia</i>							m
<i>Nothofagidites heterus-emarcidus</i>	Nothofagaceae	<i>Nothofagus</i> sg <i>Brassospora</i>	p	p	p		p	p	p
<i>N. asperus</i>	"	<i>Nothofagus</i> sg <i>Lophozonia</i>						p	p
	Eucryphiaceae	<i>Eucryphia</i>	m						
<i>Cupanieidites orthoteichus</i>	Sapindaceae	Cupanieae (aff. <i>Cupaniopsis</i>)		p		p	p	p	p
<i>Illexpollenites</i> sp.	Aquifoliaceae	<i>Illex</i>	p	p	p	p			
	Sterculiaceae	<i>Brachychiton</i>					m	m	m

Note: Some taxa present in floras are omitted as they were not used in the bioclimatic analysis (i.e., not extant in the modern Australian flora so climate envelopes could not be calculated). Palynomorph nearest living relatives (NLR) from Macphail et al. (1994).

*1—Cambalong Creek; 2—Deans Marsh; 3—Brandy Creek; 4—Hotham Heights; 5—Nerriga; 6—Golden Grove; 7—Anglesea. Palynomorphs.

†Macrofloral taxa.

dicots, including *Ilex* (Aquifoliaceae, as *Ilexpollenites*). The importance of *Nothofagus* in the Paleocene forests may be overstated, however, as today trees in this genus are wind pollinated and can produce copious quantities of pollen, and the pollen of anemophilous taxa can swamp the output of zoophilous taxa in the same forest (Kershaw and Strickland, 1990).

According to Macphail et al. (1994) angiosperms with modern mesotherm-megathermal affinities make first appearances and/or increase significantly in abundance and diversity during the latest Paleocene. These taxa include palms (Arecaceae, primarily as *Arecipites* spp.), Olacaceae (*Anacolosidites* spp.), Proteaceae, Sapindaceae (e.g., *Cupaneidites* spp.), and Polygalaceae (*Polycolpites* spp.). By the early Eocene, conifer-*Nothofagus* forests of the early Paleocene had been replaced by diverse angiosperm dominated forests with emergent Araucariaceae, including *Wollemia* and *Araucaria* or *Agathis* (Macphail et al., 1994). A number of taxa made first appearances or became prominent in southeastern Australian microfloras by the early Eocene, including the climbing palm *Calamus* (Arecaceae), and *Gymnostoma* (Casuarinaceae, as *Haloragacidites harrisii*). *Nothofagus* and other mesothermal taxa were present, but likely as a minor component, perhaps reflecting compressed altitudinal and latitudinal vegetation zonation (Christophel and Greenwood, 1989; Truswell, 1993; Macphail et al., 1994). This view is reinforced by high counts of *Nothofagus* (*Brassospora*) pollen (34%–37%), the absence of megathermal pollen types, and macrofossil evidence of *Nothofagus* in northern Tasmanian early Eocene sites (Macphail et al., 1994).

The early–middle Eocene boundary in the Gippsland Basin was characterized by the rise to dominance of *Nothofagidites emarcidus-heterus* (av. 50%–60% of the pollen sum), representing *Nothofagus* subgenus *Brassospora*. Concomitantly, *Gymnostoma* pollen (as *Haloragacidites harrisii*) became consistently abundant (up to 30%), and gymnosperms declined in importance (<30%) compared to the early Eocene (Macphail et al., 1994). Overall angiosperm diversity increased in southeastern Australian microfloras in the middle Eocene compared to earlier times. The regional spore-pollen record is interpreted as reflecting middle to late Eocene vegetation in southeastern Australia as a mosaic of *Nothofagus*-dominated mesothermal rainforest associations, with an overstory of Podocarpaceae (Truswell, 1993; Macphail et al., 1994). This interpretation is not completely in accord with the macrofossil record. *Nothofagus* is scarce as a macrofossil and the southeastern Australian leaf record is dominated by Lauraceae and other common mesothermal-megathermal taxa typical of present-day tropical rainforests of northeastern Australia (Christophel and Greenwood, 1989; Vadala and Greenwood, 2001; Greenwood and Christophel, 2003). Podocarpaceae were diverse in some macrofloras (e.g., Anglesea, some sites in Tasmania), but macrofossils of these taxa are usually not abundant (Carpenter et al., 1994; Greenwood and Christophel, 2003).

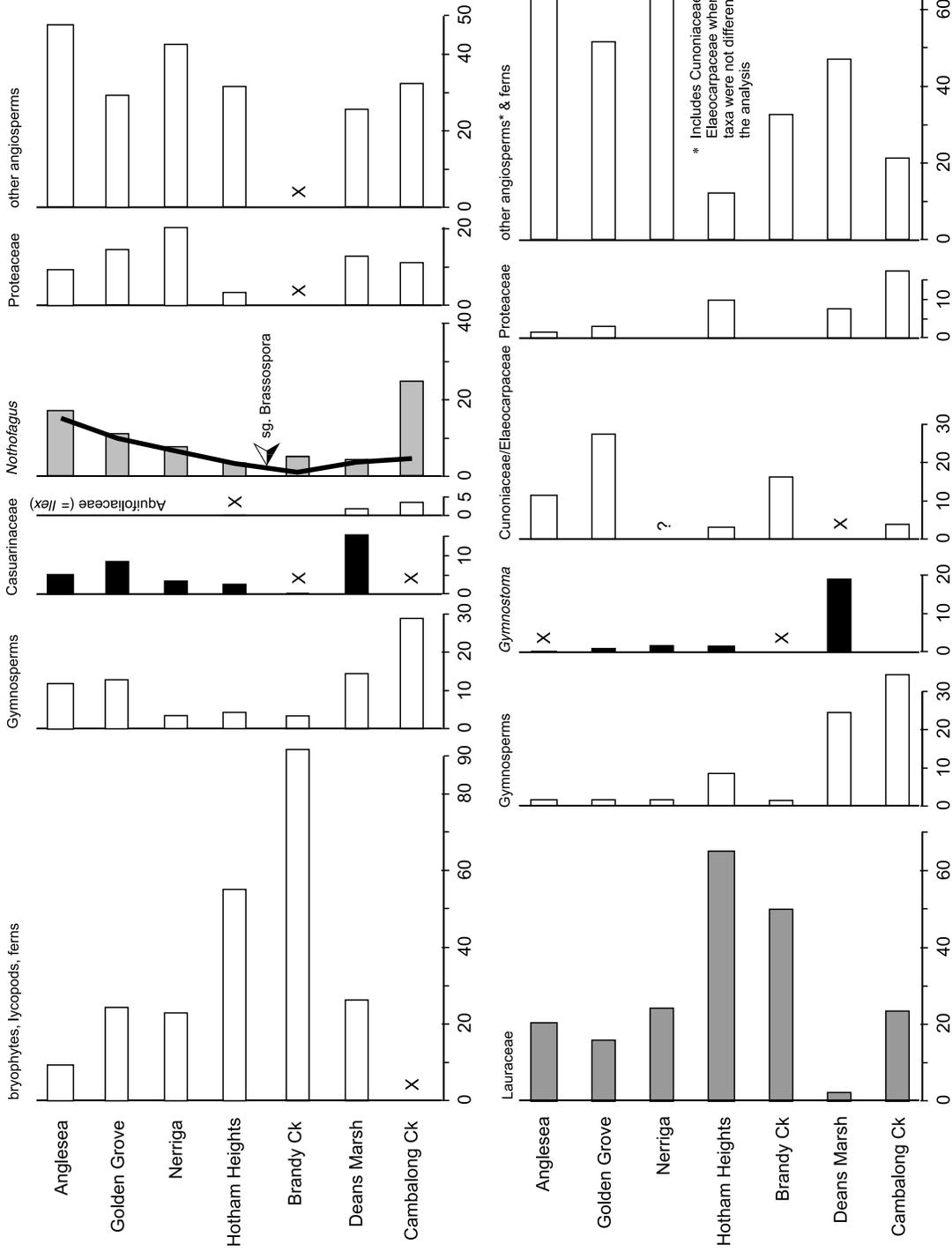
The apparent discrepancy between the spore-pollen and macrofossil records for southeastern Australia reflect vegeta-

tional differences and relative transport potential of pollen and leaves and differential fossilization potential of various taxa (Christophel and Greenwood, 1989; Greenwood, 1991; Truswell, 1993). Wind pollinated taxa (e.g., conifers, and the angiosperms *Gymnostoma* and *Nothofagus*) are often overrepresented relative to zoophilous taxa in multistratal mesotherm-megatherm forests (Kershaw and Strickland, 1990). Lauraceae leaves fossilize well, whereas their pollen does not, and the reverse situation may apply for *Nothofagus* (Macphail, 1980; Kershaw and Bulman, 1994; Vadala and Greenwood, 2001; Greenwood and Christophel, 2003). A satisfactory solution to this apparent discrepancy between the spore-pollen and macrofossil records is analyses of both types of plant organ assemblages (e.g., Blackburn and Sluiter, 1994), an approach that is applied here.

Local Paleogene environments from the spore-pollen record

Abundance data for the principal taxa from the spore-pollen sums and macrofloral records are summarized in Figure 3 for the principal taxa. A more comprehensive (but incomplete) floristic listing for each flora is given in Table 1. The microfloras show a consistent occurrence of a number of taxa at most sites through the early Paleogene (Fig. 3), namely *Nothofagus* (principally subgenus *Brassospora* as the palynomorphs *Nothofagidites emarcidus-N. heterus*), Casuarinaceae (*Haloragacidites harrisii*), diverse assemblages of Proteaceae (*Proteacidites* spp.), and the gymnosperm families Araucariaceae (principally *Araucariacites* spp., but also *Dilwynites granulatus*) and Podocarpaceae (principally *Lygistepollenites/Dacrydium* B, and *Podocarpidites* spp.). Fern and other free-sporing plants fluctuated in abundance and diversity through the early Paleogene, with treeferns such as *Cyathidites paleospora* (*Cyathea*) and *Matonisporites ornamentalis* (cf. *Dicksonia*), prominent in the latest early Eocene Brandy Creek and Hotham Heights floras. Gymnosperms and *Nothofagus* had the highest counts in the late Paleocene and middle Eocene (i.e. Cambalong Creek, Golden Grove and Anglesea). Casuarinaceae had low counts in the late Paleocene, and megathermal taxa such as *Ilexpollenites* (Aquifoliaceae) are largely characteristic of late Paleocene to early Eocene floras. Mesothermal-megathermal taxa such as *Cupaneidites* (Sapindaceae) and *Nothofagus* sg. *Brassospora* are characteristic of the middle Eocene.

The overall pattern demonstrated for the local sites (Fig. 3 and Table 1) is therefore generally consistent with the regional sequence described from cores sampled from within the Gippsland Basin of southeastern Australia (Macphail et al., 1994). The principal difference between the regional record and that reported here from local sites, is the lower counts of *Nothofagus* in the middle Eocene floras (i.e. <20%) than is typically reported for middle Eocene microfloras for the Gippsland Basin and other adjacent basins in southeastern Australia (i.e. av. 50%–60% of the pollen sum).



Specimens: % of total

Figure 3. Changes in the relative abundance (spore-pollen grains, and macrofossil specimen counts) of the principal taxa for southeastern Australia over the late Paleocene to middle Eocene, based on microfloras (A) and macrofloras (B) from the fossil floras. *Nothofagus* sg. *Brassospora* differentiated within total *Nothofagus* for pollen (A) as a solid line. Data from Hill (1982), Christophel and Greenwood (1987), Christophel et al. (1987), Rowett and Christophel (1990), Taylor et al. (1990), Rowett and Sparrow (1994), Banks (1999), Partridge (1998a, 1998b), Keeffe (2000), Vadala and Greenwood (2001). Where multiple samples were counted (spore-pollen and macrofossil), the average of these samples was used.

Local Paleogene environments from the macrofloral record

With the exception of the early Eocene Deans Marsh flora, leaves of Lauraceae are either abundant (>15%) or dominate (i.e. >40%) all of the early Paleogene macrofloras (Fig. 3). The same three genera of Lauraceae repeated in all floras (*Beilschmeidia*, *Cryptocarya* and *Endiandra*), with *Litsea* recorded only from Cambalong Creek and Brandy Creek (Table 1; see also Vadala and Greenwood, 2001). Gymnosperms were most abundant in the Cambalong Creek and Deans Marsh floras, but were present in low counts (<5%) in the middle Eocene macrofloras, although Anglesea had moderate diversity (i.e. 8 species of conifers and cycads). Cycads were recorded in the Nerriga and Anglesea floras (Table 1). Principal conifers in most floras were Podocarpaceae, typically one or more species of *Acropyle*, *Dacrycarpus*, *Dacrydium*, *Phyllocladus*, and *Podocarpus* (e.g., Deans Marsh and Anglesea). Araucariaceae (e.g., *Agathis*, Hotham Heights, possible *Wollemia* at Cambalong Creek) and Cupressaceae (e.g., *Libocedrus*, Cambalong Creek) were rarely encountered. *Gymnostoma* was recorded as both foliage units (i.e. leafy twigs) and as infructescences (i.e. woody seed cones) in all of the Eocene floras (Fig. 4), but was not detected in the late Paleocene Cambalong Creek macroflora, although it occurs in the late Paleocene Lake Bungarby macroflora. The *Gymnostoma* seed cone records were recorded in the counts as a trace, and only where there were no other records for the flora (e.g., Brandy Creek). Cunoniaceae and Elaeocarpaceae can be difficult to discriminate between, and were grouped in the analysis, but included taxa such as *Aceratium* and *Elaeocarpus* (e.g., Hotham Heights and Cambalong Creek respectively), and *Sloanea* (e.g., Golden Grove and Anglesea). These two families were important elements in the Golden Grove and Anglesea middle Eocene floras, but significant counts of these taxa were also recorded for early Eocene floras. Macrofloral remains of *Nothofagus* were not found in any of the floras in this study (Table 1), but have been reported from Eocene floras from Tasmania, and from the Maslin Bay macroflora, which is coeval with the Golden Grove flora (Greenwood and Christophel, 2003).

The Proteaceae were moderately common (i.e. >10%) in only the Cambalong Creek and Hotham Heights floras (Fig. 4). This pattern masks the high diversity of Proteaceae in a number of the floras, with taxa such as the tribes Knightieae (e.g., *Darlingia*), Helicieae (e.g., *Helicia*), Banksieae (e.g., both *Musgravea*-type and *Banksia*-type), detected in a number of the floras (Table 1), and partly also reflects incomplete taxonomic knowledge of some floras (Vadala and Greenwood, 2001). The majority of angiosperm leaf taxa in these macrofloras remain unidentified, although a number of taxa not mentioned here are listed in Table 1 and by Greenwood et al. (2000b) and Greenwood and Christophel (2003).

The macrofloras show similar patterns to the microfloras, with a consistent set of taxa repeating throughout most of the early Paleogene sequence, and with some taxa most abundant in the late Paleocene and early Eocene (e.g., gymnosperms such as

Libocedrus, and Proteaceae), while other taxa are most abundant in the early Eocene (Lauraceae) or middle Eocene (e.g., Cunoniaceae/Elaeocarpaceae). Some taxa were recorded in only a single flora (e.g., *Eucryphia*; Table 1). There are some notable similarities and differences between the two records. The pattern for the gymnosperms, *Gymnostoma* and Proteaceae largely matches the microfloral record. The absence of Lauraceae in the pollen record, as previously noted, is a taphonomic signature, and it seems likely that the apparent near absence of *Nothofagus* in the macrofloral record is also due to taphonomic bias, but also suggests that the role of *Nothofagus* in early Paleogene local vegetation may be less than is implied by pollen-based interpretations (Greenwood, 1991; Truswell, 1993).

SOUTHEASTERN AUSTRALIAN EARLY PALEOGENE CLIMATES

Methods of paleoclimate reconstruction

Bioclimatic analysis. This technique requires the development of "climatic profiles" (i.e. climatic parameters such as MAT and MAP) using bioclimatic analysis of distributions of modern plant genera. The first step of this approach is to identify as many "nearest living relatives" (NLR) as possible in the fossil floras (micro- and macroflora; Table 1). Then a library of "climatic profiles" is produced for several key taxa based on climatic values such as mean annual temperature (MAT), warmest quarter mean temperature (WQMT), coldest quarter mean temperature (CQMT), mean annual precipitation (MAP), warmest quarter mean precipitation (WQMP) and coldest quarter mean temperature (CQMT) (Kershaw and Nix, 1988; Kershaw, 1996; Moss and Kershaw, 2000). The climatic values were generated using a GIS based mathematical surface (incorporated in the BIOCLIM program) for present-day Australia, based on standard meteorological decadal means and a digital elevation model of Australia (Busby, 1991; Houlder et al., 1999). BIOCLIM summaries of climatic variables were generated for each taxa, and the maximum, minimum and percentiles (5, 25, 75 and 95) were calculated. These values constitute the climatic profiles for each taxon (Kershaw and Nix, 1988). Typically profiles were calculated for genera, but in some cases were generated for species groups within a genus, when this degree of taxonomic resolution was possible for fossil material. The zone of overlap for a set of NLR's defines the most likely climate space occupied for an individual early Paleogene flora (Kershaw and Nix, 1988; Kershaw, 1996; Moss and Kershaw, 2000).

For this study, climatic profiles were created for NLR's of 26 taxa found in the fossil spore-pollen and/or leaf floras of southeastern Australia (Table 1). Only a subset of these 26 taxa occurred in each flora. These profiles were based on the modern distribution of genera, which were determined from the electronic database of the Australian National Herbarium (CANB). These were supplemented in some cases using published climate profiles for taxa that are extinct in Australia today (i.e.

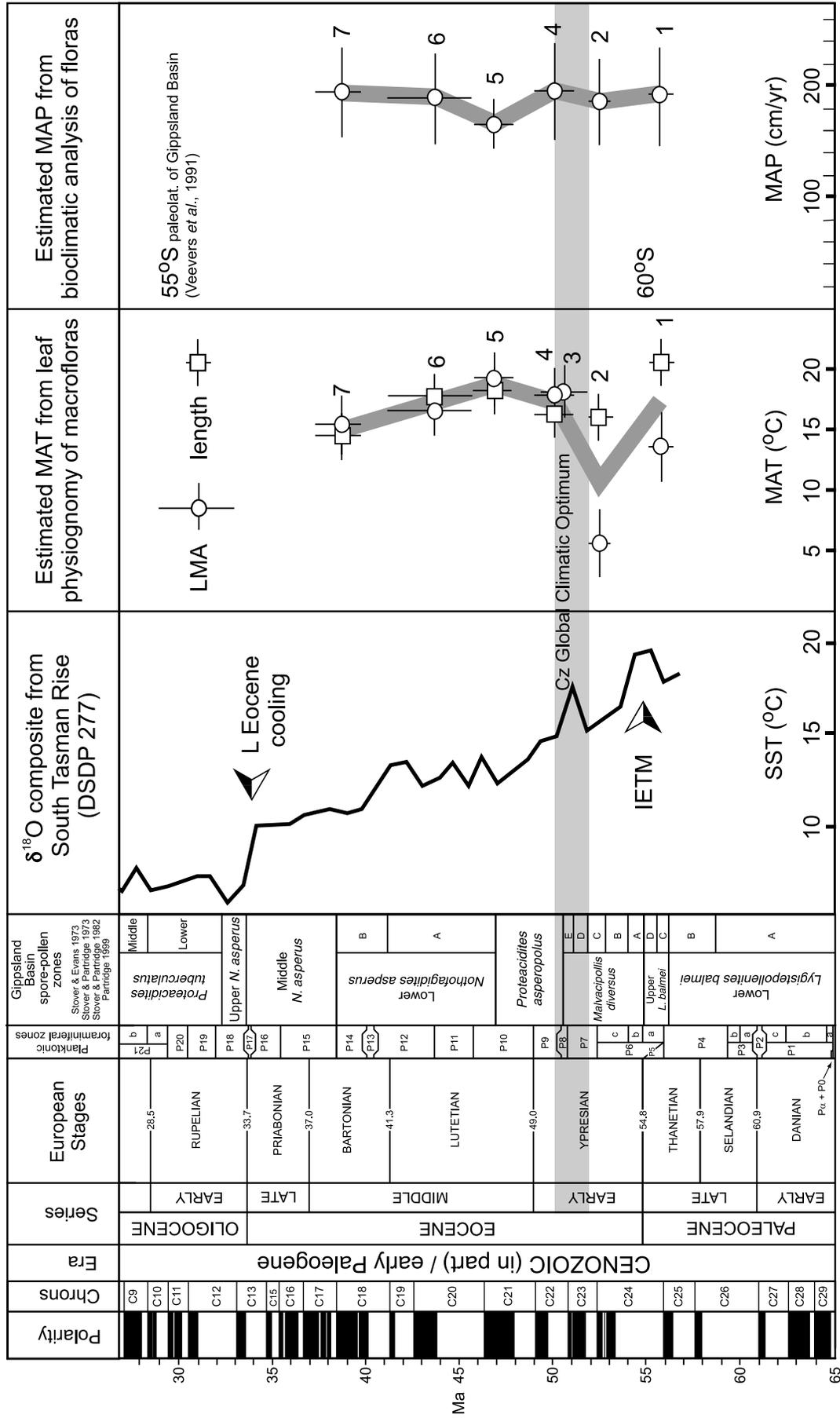


Figure 4. Summary chart of climate change over the early Paleogene for southeastern Australia. Sea surface temperatures for the South Tasman Rise (Shackleton and Kennett, 1975, diagrammatic only, adjusted to Berggren et al., 1995, time scale) are given to show the regional expression of the global Paleogene climate trend. Error bars for leaf margin analysis (LMA) are the binomial sampling error (Wilf, 1997) (equation 3), and for leaf size are the standard error of the estimate (± 2.3 °C) from the regression equation for leaf size (equation 1). Fossil floras: 1 Cambalong Ck, 2 Deans Marsh, 3 Brandy Ck, 4 Hotham Heights, 5 Nerriga, 6 Golden Grove, 7 Anglesea, as per Table 3. IETM—Initial Eocene Thermal Maximum; MAP—mean annual precipitation; MAT—mean annual temperature; SST—sea surface temperature.

regional late Cenozoic extinctions), but still extant on neighboring landmasses (e.g., *Nothofagus* subgenus *Brassospora*, based on published data from Papua New Guinea and New Caledonia; Macphail, 1997). The mean climatic values for each site (Cambalong Creek, Deans Marsh, Hotham Heights, Nerriga, Golden Grove and Anglesea) was calculated by examining the climatic variables (e.g., MAT, WQMT, CQMT, MAP, WQMP and CQMP) for each NLR taxon found at that location. Mean climate values were then calculated for each site based on the range of the individual climatic variable (25–75 percentile values) for each of the NLR taxon and dividing these values by the total number of NLR's found at each site.

Leaf physiognomy. For the leaf physiognomy approach we apply two methods. Firstly, Greenwood's (1992; Greenwood et al., 1999) nontaxonomic method of modern forest floor litter studies, where the mean leaf size for the whole fossil leaf assemblage is the predictor of MAT

$$\text{MAT}_{\text{size}} = 0.1741 \text{ ML} + 4.3197, \text{ standard error} = 2.3 \text{ }^{\circ}\text{C} \quad (\text{equation 1})$$

where *ML* is the mean length of ≥ 100 leaf specimens.

Secondly we apply leaf margin analysis (LMA; Wolfe, 1978; Wilf, 1997), which has been widely applied to North American Paleogene floras. Data from South and North America and east Asia, produce essentially the same statistical relationship between leaf margin proportion and MAT, however preliminary data from Australia had suggested a different relationship between these variables (Greenwood, 1992, 2001). Greenwood et al. (1999; 2001, personal commun.; Greenwood, 2001) completed an analysis of a comprehensive database of wet forest sites (mean annual rainfall >60 cm/yr) spanning a wide range of forest types along the east coast of Australia (Fig. 1). This analysis demonstrated that the regression of the proportion of toothed leaf margins versus MAT has the same slope for Australian floras as for those of other continents, although the intercept is different. The LMA equation is

$$\text{MAT}_{\text{LMA}} = 27.04 P_{\text{margin}} - 2.1213, \text{ standard error} = 2.2 \text{ }^{\circ}\text{C} \quad (\text{equation 2})$$

where P_{margin} is the proportion of dicot species in which the leaf margin lacks teeth ($0 < P_{\text{margin}} < 1$).

This new analysis provides a version of LMA calibrated for Australian conditions, providing more accurate estimates of MAT from Australian Paleogene leaf floras than was previously possible. Applying the method of Wilf (1997), the error of the estimate for LMA is expressed here as the binomial sampling error

$$\sigma[\text{LMA}] = c * (P_{\text{margin}} (1 - P_{\text{margin}}) / r) \quad (\text{equation 3})$$

where *c* is the slope from the LMA regression equation, P_{margin} as defined in (2), and *r* is the number of species scored for leaf margin type for the individual flora.

Paleoclimate from bioclimatic analysis of fossil spore-pollen and leaf floras

Climatic profiles for each of the seven sites suggest a mesothermal regime, with MAT ranging from 16 to 22 °C (average mean values 18–19 °C) throughout the early Paleogene (Table 2). Warmest quarter mean temperature (WQMT) was <25 °C (average mean values 22–23 °C) and the analysis suggests that coldest quarter mean temperatures (CQMT) were >13 °C (average mean values of 15 °C) for each of the seven sites. This bioclimatic analysis therefore suggests warm winter conditions, with temperatures in the region rarely falling below freezing at each of the sites throughout the early Paleogene (Table 2). Climatic profiles suggest MAP was at least >150 cm/yr (average mean values ~ 170 – 190 cm; Figure 4), consistent with modern rainforest climates of the Australian Wet Tropics (Fig. 1), and that precipitation was strongly seasonal, with the warmest quarter mean precipitation (WQMP) >50 cm (average mean values ~ 60 – 80 cm). This seasonality is further reinforced by precipitation values for the coldest quarter (<30 cm, average mean values ~ 20 cm; Table 2).

The magnitude of variation for all bioclimatic estimates between sites is within the measure of uncertainty for these estimates, however the mean values may reflect climatic change during the early Paleogene. Cambalong Creek (?IETM) and the early Eocene sites, Deans Marsh, Hotham Heights and Brandy Creek, all show warmer temperatures than the middle Eocene sites, Nerriga, Golden Grove and Anglesea. Our estimate for Cambalong Creek is at the upper end of the MAT 14–20 °C range suggested by Taylor et al. (1990). All sites reflect high mean annual rainfall, except Nerriga, which shows significantly lower annual and seasonal rainfall than the other sites. The warmer conditions of the late Paleocene and early Eocene sites is further reinforced by the presence of the megathermal taxa *Ilex* at all of these sites, which is absent at all of the middle Eocene sites (Table 1).

A caveat on the analysis is that three of the taxa, *Gymnostoma*, *Ilex* and *Lagarostrobos*, are represented by a sole species each in the modern Australian flora (and thus our calibration data set). Both *Gymnostoma* and *Ilex* are speciose outside of Australia; non-Australian *Ilex* includes temperate species (e.g., *I. aquifolium* (Europe) and *I. opaca* (southeast USA)), and *Gymnostoma* in Borneo can occur within seasonal swamp forests. It is possible that the modern Australian climatic range of these taxa represents a marked truncation of a broader climatic range for these taxa in the Paleogene. Each of these taxa were minor elements in most floras, and removing these taxa from the analysis had an insignificant effect.

Paleoclimate from leaf physiognomy of macrofloras

Greenwood and Christopel (2003) found that leaf size and the proportion of dicot species with entire leaf margins for southeastern Australia late Paleocene to middle Miocene floras varied in proportion to the northeastern Australian sea surface

TABLE 2. PALEOCLIMATE ESTIMATES BASED ON BIOCLIMATIC ANALYSIS OF SOUTHEASTERN AUSTRALIAN EARLY PALEOGENE FLORAS

Fossil flora (s)*	MAT [†] (°C)	WQMT (°C)	CQMT (°C)	MAP (cm/yr)	CQMP (cm)	WQMP (cm)
Cambalong Creek (16)*	16.3–20.7 (18.5)	20.4–24.3 (22.4)	12.6–17.6 (15.1)	155–240 (198)	14–31 (23)	51–93 (72)
Deans Marsh (11)	16.9–20.6 (18.8)	21.5–24.7 (23.1)	13.3–18.2 (15.7)	146–226 (186)	14–29 (21)	51–88 (70)
Hotham Heights (16)	16.8–21.3 (19.0)	20.9–25.1 (23.0)	13.1–18.3 (15.7)	150–195 (240)	13–28 (21)	54–101 (77)
Brandy Creek (14)	17.2–22.1 (19.6)	20.8–25.2 (23.0)	12.9–18.5 (15.7)	148–234 (191)	14–30 (22)	53–98 (76)
Nerriga (14)	16.8–19.4 (18.1)	21.3–23.4 (22.3)	12.9–15.9 (14.4)	143–190 (166)	13–23 (18)	54–75 (64)
Golden Grove (15)	16.8–21.1 (18.9)	21.0–24.9 (23.0)	12.7–18.1 (15.4)	148–231 (190)	13–30 (22)	54–95 (74)
Anglesea (17)	17.3–21.2 (19.3)	21.1–24.6 (22.8)	12.8–17.8 (15.3)	153–237 (195)	15–32 (23)	59–98 (78)

Note: Values are the mean of the 25th and 75th percentiles for all nearest living relatives in each flora shown as a range (mean in parentheses).

*The number of nearest living relative taxa used for each analysis (analyses).

[†]MAT—mean annual temperature; WQMT—warmest quarter mean temperature; CQMT—coldest quarter mean temperature; MAP—mean annual precipitation; CQMP—coldest quarter mean precipitation; WQMP—warmest quarter mean precipitation.

temperature curve (Feary et al., 1991), and for the early Paleogene, matched the Southern Ocean isotopic sea surface temperature record (Shackleton and Kennett, 1975). Significantly lower values for leaf size and proportion of entire margined leaf species occurred at times of cooling temperatures than for floras from warm intervals. Mean leaf size and proportion of species with entire leaf margins are correlated with mean annual temperature in modern Australian mesic forests, and are indicative of MAT for Paleogene floras (Greenwood, 1992, 2001; Greenwood and Wing, 1995).

A significant effect of the stratigraphy used here is to shift the position of the putative early Eocene cool interval proposed by Greenwood et al. (2000a) and Greenwood and Christophel (2003), from the latest early Eocene (i.e. after the Cenozoic Climatic Optimum) to prior to the CGCO. Mean annual temperatures remained in the mesothermal range for most of the early Paleogene (Fig. 4 and Table 3). Highest temperatures estimated from leaf physiognomy occur in the latest early Eocene to middle Eocene, whilst coolest temperatures were indicated in the mid-early Eocene (MAT <15 °C), although the 2 indices used (leaf size and leaf margin proportion) returned widely divergent estimates of MAT, and significantly, the bioclimatic analysis indicated MAT at Deans Marsh comparable to that at Hotham Heights (Table 2).

The leaf size based estimate for the late Paleocene is based on the published value for the coeval Lake Bungarby macroflora (Hill, 1992; Table 3). The LMA and leaf size estimated of MAT for the 2 floras from the southern Monaro are at the lower and upper ends respectively of the range (14–20 °C) estimated by Taylor et al. (1990). Greenwood and Christophel (2003) speculated that the divergence in the leaf size measures, the common occurrence of quite wide leaves in these floras, and the propor-

tion of toothed leaf margins seen in the early Eocene and late Paleocene likely reflected the presence of a significant number of deciduous dicots in the forest canopy. Extant deciduous forest canopies in eastern North America have generally larger and broader leaves than extant Australian broad-leaved mesic evergreen forests growing under similar MAT (Basinger et al., 1994; Greenwood, 2001). Estimates of MAT based on mean leaf size of predominantly deciduous dicot fossil floras may therefore actually be estimates of mean growing season conditions, and so may potentially overestimate MAT (Basinger et al., 1994; Greenwood, 2001). Fossil wood with well-defined uniform growth rings have been reported from high latitudes sites in Paleocene floras from Arctic Canada and the Southern Highlands of Australia (Basinger et al., 1994; Taylor et al., 1990), a wood character that is consistent with deciduous forests (Greenwood, 2001). Under the mild climates of the early Paleogene, deciduousness at high latitudes would likely be due to the effect of the seasonal light regime at high latitudes (Basinger et al., 1994).

SOUTHEASTERN AUSTRALIAN EARLY PALEOGENE ENVIRONMENTS

Leaf sizes were large throughout the early Paleogene in southeastern Australian macrofloras, but the percentage of dicot species with entire leaf margins was highest in the middle Eocene (Greenwood and Christophel, 2003; Table 3). This apparent discrepancy may reflect the presence of deciduous elements in the late Paleocene and early Eocene floras, and the lack of these elements in middle Eocene forests, as the dominance of species with toothed margins and broad lamina is characteristic of modern deciduous broad-leaved forest (Basinger et al., 1994; Greenwood, 2001). The magnitude of variation for all paleocli-

TABLE 3. FOLIAR PHYSIOGNOMIC DATA AND CLIMATE ESTIMATES FOR SOUTHEASTERN AUSTRALIAN EARLY PALEOGENE FLORAS

Macroflora	Number of dicot spp (<i>r</i>)	% spp. no teeth (<i>P</i>)	Mean length (<i>ML</i> , mm)	MAT (°C)	
				LMA (σ)	Length
1. Cambalong Ck (L Bungarby)*	21	58	No data	13.5 (2.9)	No data
	No data	No data	(93)	No data	(20.8)
2. Deans Marsh	34 [†]	28	67	5.5 (2.9)	15.6
3. Brandy Ck	54 [§]	75	No data	18.2 (2.2)	No data
4. Hotham Hts	26	74	78	17.9 (2.3)	17.8
5. Nerriga	24	79	80	19.2 (2.3)	18.2
6. Golden Grove	21	71	77	17.1 (2.7)	17.6
7. Anglesea	28	65	58	15.5 (2.4)	13.9

Note: MAT-LMA (mean annual temperature—leaf margin analysis), and MAT-length univariate regression are derived from modern Australian mesic vegetation (Greenwood, 1992; Greenwood et al. in prep.; equations 1 and 2). Measurements have been rounded here (but not in calculations) to the nearest whole number. Numbers in the first column refer to Figure 4.

Data for both Lake Bungarby (leaf size, from Hill, 1992) and Cambalong Creek (LMA) were combined, as insufficient leaves were available to calculate mean length for Cambalong Creek.

[†] Only 18 of the 34 dicot taxa had a known margin type.

[§] Only 28 of the 54 dicot taxa had a known margin type.

mate estimates between sites is within the measure of uncertainty for these estimates for a majority of sites, however climatic change during the early Paleogene is indicated. Estimates of terrestrial mean annual temperature (MAT) from foliar physiognomy and bioclimatic analysis over this interval generally track the northeastern Australian marine SST record (Feary et al., 1991; Macphail et al., 1994), with highest MAT values estimated for the middle and early Eocene, but not the regional high-latitude SST record (Fig. 4). The paleobotanical analyses indicate moist (i.e. MAP >150 cm/yr), mesothermal climates (i.e. MAT 16–22 °C, CQMT >10 °C) over the interval, but one line of physiognomic evidence points to a potential cooling episode in the mid-early Eocene. The cooling episode is not detected in our bioclimatic analysis. Uncertainty over the physiognomic MAT estimate for Deans Marsh prevent definitive statements on this putative cooling episode. The general low level of temperature change estimated for southeastern Australia during the early Paleogene appears to contradict the progressive cooling shown in the regional marine isotopic record (Fig. 4). The apparent mild cooling (2–3 °C) from the CGCO to the late middle Eocene in the terrestrial paleobotanical record versus the 6–8 °C drop in SST (Fig. 4), likely is a consequence of continental movement maintaining southeastern Australia in a mesothermal latitudinal zone (e.g., Feary et al., 1991; Truswell, 1993).

The magnitude of climate warmth in the late Paleocene and latest early Eocene, however may be ‘masked’ by the paleoelevation of Cambalong Creek, Hotham Heights and Brandy Creek. The middle Eocene sites are at low altitudes (<200 m to ~550 m; Hill, 1982; Greenwood and Wing, 1995). Current elevation for the Paleocene site is ~800 m and the early Eocene sites are above 1400 m. Geomorphic evidence suggests that both areas were ~800 m above sea level during the Paleogene (Taylor, 1994; Orr, 1999). If these floras were deposited from local vegetation grow-

ing at ~800 m paleoelevation, then lowland sites at the same latitude would have experienced higher MAT. Applying the global average lapse rate (~0.59 °C/100 m; Meyer, 1992), 800 m elevation equates to MAT 4–5 °C higher than the estimates, namely 22–23 °C \pm 2 °C, and implies mesothermal to megathermal thermal regimes in southeastern Australia in the late Paleocene and latest early Eocene (e.g., Taylor et al., 1990; Macphail et al., 1994). The paleo-proxy estimates of MAT >20 °C for southeastern Australia is much higher than computer climate model output for southeastern Australia, which indicate early Eocene MAT <10 °C (Sewall et al., 2000; Shellito et al., 2003).

MAT estimates >20 °C are consistent with the observation by Macphail et al. (1994) that the early Eocene was the acme in development of lowland megathermal species-rich rainforest in southeastern Australia. Macphail et al. (1994) also suggested that mesothermal species-rich rainforests reached their maximum development in southeastern Australia during the middle-late Eocene (Figs. 1 and 2). Our paleoclimate analysis quantifies this hypothesis at the local scale, indicating slightly warmer conditions in the late-early Eocene than the middle Eocene. Macphail et al. (1994) stressed the continuity of many taxa throughout the Eocene, but noted a floristic shift in response to the establishment of mesothermal conditions by the middle Eocene expressed in part by a locally variable but very widespread expansion of *Nothofagus* subgenus *Brassospora* in microfloras (Fig. 3). Mesotherm-megatherm forests likely occupied parts of this landscape at periods of peak warmth, such as during the CGCO of the early Eocene.

These Paleogene forests contained many taxa closely related to extant taxa found in mesotherm-megatherm rainforests in northeastern Australia’s ‘wet tropics’ (Fig. 1). Other Paleogene taxa are not present in Australia but extant in the tropical rainforests of nearby landmasses (Vadala and Greenwood, 2001;

Greenwood and Christophel, 2003). Other taxa appear to persist today only in microtherm-mesotherm forests and other vegetation types. Present-day patterns reflect 'sifting' of a regional biota during the vicissitudes of Cenozoic climate change, and particularly the climate oscillations of the Quaternary. What is apparent from the southeastern Australian record, is that the low level of temperature variation was reflected in the continuity of floristic composition in local vegetation, but that a transition from mesotherm-megatherm climates to mesotherm climates at the early-middle Eocene boundary in that region was a driving force for community reorganization (Fig. 3). Many plant taxa originated, or first migrated into the area during the interval (Truswell, 1993; Macphail et al., 1994; Vadala and Greenwood, 2001; Greenwood and Christophel, 2003). However, the greatest shifts in community composition during the early Paleogene are the replacement of mesotherm-megatherm taxa by mesotherm taxa, such as the rise to dominance of *Nothofagus* subgenus *Brassospora* in microfloras (Fig. 3).

ACKNOWLEDGMENTS

This work was funded by grants from the Australian Research Council to DRG and PTM (A39802019 and small grants scheme). RLK is in receipt of an APRA postgraduate scholarship. NSF and the conference organizers kindly provided financial assistance to RLK and DRG to participate in the Wyoming meeting. Analysis and interpretation of spore-pollen based stratigraphy was greatly facilitated at various stages by analyses and discussions with Alan Partridge (Biostrata Pty. Ltd.). We would also like to thank Andrew Drinnan, John Webb, Peter Kershaw and Stephen McLoughlin, for advice and practical assistance, and Mike Pole and Scott Wing for their valuable constructive criticism and advice on an earlier version of the paper. Permits to work in the Alpine National Park were provided by DNRE (Victoria). Larry Doyle and the staff of the Mount Hotham Management Authority kindly gave permission for access and provided material support.

REFERENCES CITED

- Alley, N.F., 1987, Middle Eocene age of the megafossil flora at Golden Grove, South Australia: Preliminary report, and comparison with the Maslin Bay Flora: Transactions of the Royal Society of South Australia, v. 111, no. 3, p. 211–212.
- Banks, M., 1999, The early Eocene macroflora of Hotham Heights [undergraduate thesis]: Melbourne, Victoria University of Technology, 209 p.
- Basinger, J.F., Greenwood, D.R., and Sweda, T., 1994, Early Tertiary vegetation of Arctic Canada and its relevance to palaeoclimatic interpretation, in Boulter, M.C., and Fisher, H.C., eds., Cenozoic plants and climates of the arctic: NATO ASI Series, v. 27 I: Berlin, Springer Verlag, p. 176–198.
- Berggren, W.A., Kent, D.V., Flynn, J.J., and Van Couvering, J.A., 1985, Cenozoic geochronology: Geological Society of America Bulletin, v. 96, p. 1407–1418.
- Berggren, W.A., Kent, D.V., Swisher, C.C., III, and Aubry, M.-P., 1995, A revised Cenozoic geochronology and chronostratigraphy, in Berggren, W.A., et al., eds., Geochronology, time scales, and global stratigraphic correlation: SEPM (Society for Sedimentary Geology) Special Publication 54, p. 129–202.
- Blackburn, D.T., and Sluiter, I.R.K., 1994, The Oligo-Miocene coal floras of southeastern Australia, in Hill, R.S., ed., History of the Australian vegetation: Cretaceous to Holocene: Cambridge, UK, Cambridge University Press, p. 328–367.
- Burnham, R.J., Wing, S.L., and Parker, G.G., 1992, The reflection of deciduous forest communities in leaf litter: Implications for autochthonous litter assemblages from the fossil record: Paleobiology, v. 18, no. 1, p. 30–49.
- Busby, J.R., 1991, BIOCLIM: A bioclimatic analysis and prediction system, in Margules, C.R., and Austin, M.P., eds., Nature conservation: Cost effective biological surveys and data analysis: Melbourne, CSIRO Publications, p. 64–68.
- Carpenter, R.A., Hill, R.S., and Jordan, G., 1994, Cenozoic vegetation in Tasmania: Macrofossil evidence, in Hill, R.S., ed., History of the Australian vegetation: Cretaceous to Holocene: Cambridge, UK, Cambridge University Press, p. 276–298.
- Chambers, T.C., Drinnan, A.N., and McLoughlin, S., 1998, Some morphological features of Wollemi Pine (*Wollemia nobilis*: Araucariaceae) and their comparison to Cretaceous plant fossils: International Journal of Plant Science, v. 159, no. 1, p. 160–171.
- Chaproniere, G., Shafik, S., Truswell, E.M., MacPhail, M.K., and Partridge, A., 1996, Cainozoic (Chart 12), in Young, G.C., and Laurie, J.R., eds., An Australian Phanerozoic timescale: Melbourne, Oxford University Press, p. 175–186.
- Christophel, D.C., and Greenwood, D.R., 1987, A megafossil flora from the Eocene of Golden Grove, South Australia: Transactions of the Royal Society of South Australia, v. 111, no. 3, p. 155–162.
- Christophel, D.C., and Greenwood, D.R., 1989, Changes in climate and vegetation in Australia during the Tertiary: Review of Palaeobotany and Palynology, v. 58, p. 95–109.
- Christophel, D.C., Harris, W.K., and Syber, A.K., 1987, The Eocene flora of the Anglesea locality, Victoria: Alcheringa, v. 11, p. 303–323.
- Clyde, W.C., Sheldon, N.D., Koch, P.L., Gunnell, G.F., and Bartels, W.S., 2001, Linking the Wasatchian–Bridgerian boundary to the Cenozoic Global Climatic Optimum: New magnetostratigraphic and isotopic results from South Pass, Wyoming: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 167, p. 175–199.
- Feary, D.A., Davies, P.J., Pigram, C.J., and Symonds, P.A., 1991, Climatic evolution and control on carbonate deposition in northeast Australia: Palaeogeography, Palaeoclimatology, Palaeoecology (Global and Planetary Change Section), v. 89, p. 341–361.
- Greenwood, D.R., 1991, The taphonomy of plant macrofossils, in Donovan, S.K., ed., The processes of fossilization: London, Belhaven Press, p. 141–169.
- Greenwood, D.R., 1992, Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates: Review of Palaeobotany and Palynology, v. 71, p. 142–96.
- Greenwood, D.R., 1994, Palaeobotanical evidence for Tertiary climates, in Hill, R.S., ed., History of the Australian vegetation: Cretaceous to Holocene: Cambridge, UK, Cambridge University Press, p. 44–59.
- Greenwood, D.R., 2001, Climate: Wood and leaves, in Briggs, D.E., and Crowther, P.R., eds., Palaeobiology II: London, Blackwell Scientific Publishers, p. 484–487.
- Greenwood, D.R., and Basinger, J.F., 1994, The paleoecology of high-latitude Eocene swamp forests from Axel Heiberg Island, Canadian High Arctic: Review of Palaeobotany and Palynology, v. 81, p. 83–97.
- Greenwood, D.R., and Christophel, D.C., Origins and Tertiary history of Australian 'tropical' rainforests, in Moritz, C., et al., eds., Tropical rainforest diversity: Past and future: Chicago, Illinois, University of Chicago Press, in press.
- Greenwood, D.R., and Wing, S.L., 1995, Eocene continental climates and latitudinal gradients: Geology, v. 23, p. 1044–1048.
- Greenwood, D., Puchalski, B., and Baldyga, D., 1999, Leaf physiognomy and climate relationships in Australian mesic forests: International Botanical Congress, 14th, St. Louis, Missouri, Abstracts, p. 538.
- Greenwood, D.R., Vadala, A.J., and Banks, M., 2000a, Climates and changes in

- forest floristics during the Paleocene and Eocene in southeastern Australia: *GFF*, v. 122, p. 65–66.
- Greenwood, D.R., Vadala, A.J., and Douglas, J.G., 2000b, Victorian Paleogene and Neogene macrofloras: A conspectus: *Proceedings of the Royal Society of Victoria*, v. 112, p. 65–92.
- Hardenbol, J., Thierry, J., Farley, M.B., Jacquin, T., de Graciansky, P.-C., and Vail, P.R., 1998, Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins, *in* de Graciansky, P.-C., et al., eds., *Mesozoic and Cenozoic sequence stratigraphy of European basins: SEPM (Society for Sedimentary Geology) Special Publication 60*, p. 3–14.
- Harris, W.K., 1971, Tertiary stratigraphic palynology, Otway Basin, *in* Wopfner, H., and Douglas, J.G., eds., *The Otway Basin of southeastern Australia: Melbourne, Special Bulletin of the Geological Surveys of South Australia and Victoria*, p. 67–87.
- Hickey, L.J., 1973, Classification of the architecture of dicotyledonous leaves: *American Journal of Botany*, v. 60, no. 1, p. 17–33.
- Hill, R.S., 1982, The Eocene megafossil flora of Nerriga, New South Wales, Australia: *Palaeontographica Abt. B*, v. 181, p. 44–77.
- Hill, R.S., 1992, Australian vegetation during the Tertiary: Macrofossil evidence: The Beagle, Records of the Northern Territory Museum of Arts and Sciences, v. 9, p. 1–10.
- Houlder, D., Hutchinson, M., Nix, H., and McMahon, J., 1999, ANUCLIM version 5.0 user guide: Canberra, Centre for Resource and Environmental Studies, Australian National University, 73 p (paper copy) and CD-ROM.
- Keefe, R.L., 2000, Windows on an ancient forest: The Palaeoecology of the early Eocene flora of Brandy Creek Mine, Eastern Highlands, Victoria [undergraduate thesis]: Melbourne, Victoria University of Technology, 98 p.
- Kershaw, A.P., 1996, A bioclimatic analysis of Early to middle Miocene brown coal floras, Latrobe Valley, southeastern Australia: *Australian Journal of Botany*, v. 45, no. 3, p. 373–383.
- Kershaw, A.P., and Bulman, D., 1994, The relationship between modern pollen samples and environment in the humid tropics region of northeastern Australia: *Review of Palaeobotany and Palynology*, v. 83, p. 83–96.
- Kershaw, A.P., and Nix, H.A., 1988, Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant taxa: *Journal of Biogeography*, v. 15, p. 589–602.
- Kershaw, A.P., and Strickland, K.M., 1990, A 10 year pollen trapping record from rainforest in northeastern Queensland, Australia: *Review of Palaeobotany and Palynology*, v. 64, p. 281–288.
- Lindsay, J.M., and Alley, N.F., 1995, St Vincent Basin, *in* Drexel, J.H., and Preiss, W.V., eds., *The geology of South Australia*, volume 2: The Phanerozoic: Adelaide, South Australian Geological Survey Bulletin 54, p. 208–217.
- Macphail, M.K., 1980, Fossil and modern pollen of *Beilschmiedia* (Lauraceae) in New Zealand: *New Zealand Journal of Botany*, v. 18, p. 149–152.
- Macphail, M.K., 1997, Late Neogene climates in Australia: Fossil pollen- and spore-based estimates in retrospect and prospect: *Australian Journal of Botany*, v. 45, p. 425–464.
- Macphail, M.K., Alley, N.F., Truswell, E.M., and Sluiter, I.R.K., 1994, Early Tertiary vegetation: Evidence from spores and pollen, *in* Hill, R.S., ed., *History of the Australian vegetation: Cretaceous to Holocene: Cambridge, UK, Cambridge University Press*, p. 189–261.
- Meyer, H.W., 1992, Lapse rates and other variables applied to estimating paleoaltitudes from fossil floras: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 99, p. 71–99.
- Moss, P.T., and Kershaw, A.P., 2000, The last glacial cycle from the humid tropics of northeastern Australia: Comparison of a terrestrial and a marine record: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 155, p. 155–176.
- Orr, M.L., 1999, Tectonic geomorphology of the Bogong and Dargo High Plains region, east Victorian highlands, Australia [Ph.D. thesis]: Melbourne, University of Melbourne, 155 p.
- Partridge, A.D., 1998a, Miscellaneous palynological samples from macroplant fossil localities in Australia: *Biostrata Report 1998/8*, Biostrata Pty. Ltd., Melbourne, 19 p.
- Partridge, A.D., 1998b, Palynological analysis of macroplant fossil locality, Hotham Heights, Victoria: *Biostrata Report 1998/12*, Biostrata Pty. Ltd., Melbourne, 3 p.
- Partridge, A.D., 1999, Late Cretaceous to Tertiary geological evolution of the Gippsland Basin, Victoria [Ph.D. thesis]: Melbourne, LaTrobe University, 439 p.
- Röhl, U., Bralower, T.J., Norris, R.D., and Wefer, G., 2000, New chronology for the late Paleocene thermal maximum and its environmental implications: *Geology*, v. 28, p. 927–930.
- Rowett, A.I., and Christophel, D.C., 1990, The dispersed cuticle profile of the Eocene Anglesea clay lenses, *in* Douglas, J.G., and Christophel, D.C., eds., *Proceedings of the 3rd IOP Conference, Melbourne, July 1988: Melbourne, A-Z Printers and International Organisation of Palaeobotanists*, p. 115–21.
- Rowett, A.I., and Sparrow, A.D., 1994, Multivariate analysis of Australian Eocene dispersed cuticle floras: Influence of age, geography, and taphonomy on biozonation: *Review of Palaeobotany and Palynology*, v. 81, p. 165–183.
- Royer, D.L., Wing, S.L., Beerling, D.J., Jolley, D.W., Koch, P.L., Hickey, L.J., and Berner, R.A., 2001, Paleobotanical evidence for near present-day levels of atmospheric CO₂ during part of the Tertiary: *Science*, v. 292, p. 2310–2313.
- Sewall, J.O., Sloan, L.C., Huber, M., and Wing, S., 2000, Climate sensitivity to changes in land surface characteristics: *Global and Planetary Change*, v. 26, p. 445–465.
- Shackleton, N.J., and Kennett, J.P., 1975, Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: Oxygen and carbon isotope analyses in DSDP sites 277, 279, and 281, *in* Kennett, J.P., et al., eds., *Initial reports of the Deep Sea Drilling Project: Washington, D.C., U.S. Government Printing Office*, v. 29, p. 743–755.
- Shellito, C.J., Sloan, L.C., and Huber, M., Climate model constraints on atmospheric CO₂ levels in the early–middle Paleogene: *Palaeogeography, Palaeoclimatology, Palaeoecology* in press.
- Stover, L.E., and Evans, P.R., 1973, Upper Cretaceous–Eocene spore-pollen zonation, offshore Gippsland Basin, Australia, *in* Glover, J.E., and Playford, G., eds., *Mesozoic and Cainozoic palynology: Essays in honour of Isabel Cookson: Geological Society of Australia Special Publication 4*, p. 55–72.
- Stover, L.E., and Partridge, A.D., 1973, Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin, southeastern Australia: *Proceedings of the Royal Society of Victoria*, v. 85, p. 237–286.
- Taylor, G., 1994, Landscapes of Australia: Their nature and evolution, *in* Hill, R.S., ed., *History of the Australian vegetation: Cretaceous to Holocene: Cambridge, UK, Cambridge University Press*, p. 60–79.
- Taylor, G., Truswell, E.M., McQueen, K.G., and Brown, M.C., 1990, Early Tertiary palaeogeography, landform evolution, and palaeoclimates of the Southern Monaro, N.S.W., Australia: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 78, p. 109–134.
- Truswell, E.M., 1993, Vegetation changes in the Australian Tertiary in response to climatic and phytogeographic forcing factors: *Australian Systematic Botany*, v. 6, no. 5, p. 533–558.
- Truswell, E.M., 1997, Palynomorph assemblages from marine Eocene sediments on the west Tasmanian continental margin and the South Tasman Rise: *Australian Journal of Earth Science*, v. 44, p. 633–654.
- Vadala, A.J., and Drinnan, A.N., 1998, Elaborating the fossil history of Banksiinae: A new species of *Banksiaephyllum* (Proteaceae) from the late Paleocene of New South Wales: *Australian Systematic Botany*, v. 11, p. 439–463.
- Vadala, A.J., and Greenwood, D.R., 2001, Australian Paleogene vegetation and environments: Evidence for palaeo-Gondwanic elements in the fossil records of Lauraceae and Proteaceae, *in* Metcalfe, I., et al., eds., *Faunal and floral migrations and evolution in southeast Asia-Australasia: Lisse, Netherlands, Swets and Zeitlinger*, p. 196–221.
- Veever, J.J., Powell, C.McA., and Roots, S.R., 1991, Review of seafloor spreading around Australia, 1: Synthesis of patterns of spreading: *Australian Journal of Earth Sciences*, v. 38, p. 373–389.

- Wilf, P., 1997, When are leaves good thermometers? A new case for leaf margin analysis: *Paleobiology*, v. 23, p. 373–390.
- Wing, S.L., 1998, Late Paleocene–early Eocene floral and climatic change in the Bighorn Basin, Wyoming, *in* Aubry, M.-P., et al., eds., Late Paleocene–early Eocene climatic and biotic events in the marine and terrestrial records: New York, Columbia University Press, p. 380–400.
- Wing, S.L., and Greenwood, D.R., 1993, Fossils and fossil climates: The case for equable Eocene continental interiors: *Philosophical Transactions of the Royal Society of London, series B*, v. 341, p. 243–252.
- Wing, S.L., and Harrington, G.J., 2001, Floral response to rapid warming in the earliest Eocene and implications for concurrent faunal change: *Paleobiology*, v. 27, p. 539–563.
- Wing, S.L., Alroy, J., and Hickey, L.J., 1995, Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 117–156.
- Wing, S., Bao, H., and Koch, P., 2000, An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic, *in* Huber, B., et al., eds., *Warm climates in Earth history*: Cambridge, UK, Cambridge University Press, p. 197–237.
- Wolfe, J.A., 1978, A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere: *American Science*, v. 66, p. 694–703.
- Zachos, J.C., Lohmann, K.C., Walker, J.C.G., and Wise, S.W., 1993, Abrupt climate change and transient climates during the Paleogene: A marine perspective: *Journal of Geology*, v. 101, p. 191–213.
- Zachos, J., Stott, L., and Lohmann, K., 1994, Evolution of early Cenozoic marine temperatures: *Paleoceanography*, v. 9, p. 353–387.

MANUSCRIPT ACCEPTED BY THE SOCIETY AUGUST 13, 2002