Australian Paleogene vegetation and environments: evidence for palaeo-Gondwanan elements in the fossil records of Lauraceae and Proteaceae

A.J. Vadala & D.R. Greenwood
School of Life Sciences and Technology, Victoria University of Technology, PO Box 14428, Melbourne City MC, Victoria 8001, Australia

ABSTRACT: Tropical rainforests in the northeast of Australia have been interpreted as being either communities largely comprising taxa that ‘invaded’ newly available environments from Sundaland during and after the Middle Miocene collision of the Australian plate and the Sunda plate, or refugia for humid–mesothermal Gondwanan taxa. Recent biogeographic analyses have suggested four ‘tracks’ (areas of endemism) that potentially account for some previously hypothesised floristic ‘elements’ defined by ‘tropical’ or Malesian origins. Early Cenozoic (Paleogene) macrofossil records of Lauraceae and Proteaceae are informative on these issues. Unequivocal macrofossil evidence for Lauraceae and Proteaceae occurs at least from the Early Paleocene (~ 65 million years, Ma) in Australia. This evidence appears contrary to the suggestion of their past dispersal from Malesia to the Australian plate. Tropical floristic ‘elements’ defined by Malesian origins are not appropriate for elucidating current biogeographic patterns of these families in Australia.

1 INTRODUCTION

This paper reviews and provides macrofossil evidence supporting the ancient nature and Gondwanan origin of extant floristic elements of the Wet Tropics region of northeastern Australia. Traditional descriptive phytogeographic analyses of the extant Australian flora had identified three floristic elements, defined by hypothesised origin (sensu Crisp et al. 1999):
1) a Gondwanan element that comprises a rainforest flora with centres of diversity in the temperate south and humid tropical northeast and shares genera with, or has closely related genera in, other Austral landmasses;
2) an autochthonous element characterised by high endemism and represented by the sclerophyllous and dry-climate adapted vegetation of much of Australia (particularly the southwest of Western Australia);
3) a tropical element composed of taxa shared with southeast Asia, largely centred in the humid tropics and monsoonal tropics (Herbert 1932, 1967; Burbidge 1960; Barlow 1981; Schodde 1989; Crisp et al. 1999).

Rainforests of the Wet Tropics region of northeastern Queensland mainly comprise taxa belonging to the third of these elements. They have been considered as a vegetation type largely comprising taxa that ‘invaded’ newly available environments from Sundaland during and after the Miocene collision of the Australian and Eurasian plates. Alternatively, they have been regarded as refugia for humid mesothermal Gondwanan taxa. These narrative analyses have emphasised the role of either continental drift or long-distance dispersal of plant propagules in shaping the modern flora of Australia. However, more recent biogeographic analyses have stressed the ‘autochthonous’ character of much of the flora of the Wet Tropics (e.g. Webb et al. 1984; Webb et al. 1986; Truswell et al. 1987) that may reflect an ancient Gondwanan heritage that was also proposed by Barlow (1981). Crisp et al. (1999) concluded that the lack of success in identifying generalised biogeographic tracks (sharply differentiated areas of endemism)
within the Australian craton (Australia and New Guinea) may reflect the lack of significant barriers to dispersal and consequently possible range expansion for some taxa across Australia.

Analyses of Australian fossil microfloras have demonstrated that many of the 'tropical' elements of the extant flora of the Wet Tropics region were present in Australia prior to its final separation from the remainder of Gondwana (Truswell et al. 1987; Drinnan & Crane 1990). These floral elements were once presented as descendants of immigrant Malayan or tropical floral elements (see Crisp et al. 1999). Truswell et al. (1987) concluded that some exchange of taxa between the Australian craton and lands to the northwest of Australia had occurred, but had not resulted in any major alteration to the structure or composition of Australian forests. Webb et al. (1984) also suggested that the Middle Miocene was the beginning of arid periods that would not have favoured the spread of rainforest immigrants.

The evidence presented here consists of a review of the Australian macrofossil record of Lauraceae and Proteaceae from the Paleogene (~ 65–23.3 million years (Ma): Fig. 3). New data from a Late Paleocene leaf macroflora from Cambalong Creek in the Southern Highlands of New South Wales are also presented. This macroflora may include the oldest known Australian taxa of tribes Laureae and Cryptocaryaeae of Lauraceae and of tribes Banksiaeae, Oriteae, Stenocarpinae, Helicieae and Knightiaeae (Grevilleoidae) of Proteaceae. These data are used as supporting evidence for the presence of Lauraceae and Proteaceae in eastern Gondwana prior to separation of some Australian landmasses, and clearly precede the Miocene 'contact phase' (Hall 1996, 1997) between Australia and those parts of Malesia from which tropical floral elements may have 'invaded'. Southeastern Australia is important in the evolution of the modern flora due to the interactions between vegetation and the physical environment. The area underwent significant tectonism in the Paleogene during uplift of the Eastern Highlands (Wilford & Brown 1994). Coeval subsidence along a failed rift saw formation of the Gippsland Basin, and the area experienced major sea-level changes associated with initial Antarctic glaciation and the opening of Bass Strait as Australia and Antarctica rifted apart (Crook 1981; Kemp 1981; Powell et al. 1981; Blackburn & Sluiter 1994; Wilford & Brown 1994).  

1.1 The plant macrofossil record

Evidence of the Cenozoic vegetation is abundant throughout southeastern Australia. Microfloras and macrofloras have been recorded from numerous localities spanning the Paleogene and Neogene (Carpenter et al. 1994; Christophel 1994; Macphail et al. 1994; Greenwood et al. in press, and references therein). Paleogene macrofloras in particular constitute a record of the vegetation of Australia prior to its final separation from East Antarctica and preceding the Miocene collision between the Australian craton and the Sunda Arcs.

The most detailed hypotheses regarding palaeovegetation and phytogeography for the Late Cretaceous and Cenozoic of southeastern Australia are currently based on palynology (e.g., Kemp 1981; Martin 1981, 1991, 1994, 1998; Truswell et al. 1987; Drinnan & Crane 1990; Truswell 1990, 1993; Kershaw et al. 1994; Macphail et al. 1994). These have been complemented by systematic taxonomic research on leaf macrofossils (e.g., Christophel 1981, 1989, 1994; Hill 1983, 1992a & b, 1994; Hill & Jordan 1993; Hill & Pole 1992; Hill & Carpenter 1991; Carpenter & Jordan 1997; Jordan et al. 1998; Hill et al. 1999). The Murray and Gippsland Basins provide virtually continuous sequences of Late Cretaceous to Pliocene-Pleistocene palynofloras and the highly detailed dinoflagellate, foraminiferal and sequence stratigraphy for these basins acts as an independent control for spore–pollen zonation (e.g. Holdgate & Sluiter 1991; Macphail et al. 1994). However, reconstructions of palaeovegetation based on palynology have significant limitations. For example, the family Lauraceae is a major component of southeastern Australian (particularly Victorian) Cenozoic macrofloras, yet it is absent from the palynological record because the thin sporopollenin exine of the pollen preserves poorly (Truswell et al. 1987; Drinnan et al. 1990; Martin 1994; Hill et al. 1999; although see Macphail 1980).

Figure 1: Composition of the Late Paleocene macroflora recovered from Cambalang Creek indicated as percentage of 173 total specimens.

Figure 2: Extant distributions of closest living relatives of Late Paleocene Lauraceae and Proteaceae macrofossils recovered from Cambalang Creek. Grey circle for Endiandra indicates that some taxa grow in gallery and temperate forests rather than tropical rainforest. Grey circle for Litsea indicates that one taxon (L. glutinosa) grows throughout coastal northern Queensland, Northern Territory and the Kimberley region of Western Australia. Black circles for Heliciaceae indicate the distribution of Helicia, grey circles for this tribe indicate distribution of Hollandaea, a genus of two species both restricted to small areas in the Wet Tropics region of northeastern Queensland. Distribution shown for Knightiaceae is for Darlingtonia, a genus of two species also restricted to the Wet Tropics region of northeastern Queensland.
Figure 3: Stratigraphic ranges of Lauraceae and Proteaceae macrofossils listed in Tables 2 and 3, using the timescale of Harland et al. (1990) with modifications from Berggren and Aubry (1996). All Proteaceae tribes belong to subfamily Grevilleoideae except Conospermaceae (subfamily Proteoideae). Records for Banksiae are further divided into subtribes. White circles correspond with published records in Tables 2 and 3; grey circles represent unpublished records and possible records (those marked by '?') in Tables 2 and 3. Circles with 'N' indicate New Zealand records; circles with 'C' indicate undescribed taxa from Cambalang Creek; circles with '?' indicate records from localities with an uncertain stratigraphic position.
1.2 **Lauraceae and Proteaceae as targets for research**

Proteaceae and Lauraceae are comparatively well represented temporally and spatially in Australian macrofloras, where oldest fossils are recorded from the early Paleogene (Fig. 3). Proteaceae and Lauraceae leaf macrofossils with cuticular preservation are particularly amenable to identification with high levels of taxonomic resolution due to relatively recent research into extant tribal and generic limits. The tribal taxonomy of extant Proteaceae was established with the detailed and extensive work of Johnson & Briggs (1963, 1975) and revised by Douglas (1995). General cuticular morphological characteristics of the family have been described from macrofloras spanning the Paleogene and Neogene (Blackburn 1985; Hill & Merrifield 1993; Carpenter & Pole 1995; Carpenter & Jordan 1997; Jordan et al. 1998). Cuticular features of fossil extant taxa have been described at subfamilial, generic, tribal and subtribal levels (e.g. Cookson & Duigan 1950; Lange 1978; Hill & Christophel 1988; Hill & Merrifield 1993; Carpenter 1994; Carpenter et al. 1994; Carpenter & Pole 1995; Jordan 1995; Carpenter & Jordan 1997; Jordan et al. 1998; Vadala & Drinnan 1998).

By contrast, intrafamilial relationships within Lauraceae are poorly understood (Eklund 1999). Suprageneric taxonomy of extant Lauraceae is less well established than for Proteaceae and consequently numerous suprageneric classifications for the family exist (see van der Werff & Richter 1996). Bandulksa (1926, 1928) recognized the strong similarities in cuticular morphology between some extant and fossil genera of Lauraceae. However, the lack of good cuticular morphological data for extant and fossil Australian genera of Lauraceae limited the usefulness of this record for many years (see Hill 1986). The published Cenozoic record of the family in Australia is substantial (Hill 1986, 1988a, b) and dates from the Early Eocene (Table I and Fig. 3). Abundant leaf impressions with ascending acrodromous venation led to the gradual development of the concept of a ‘Cinnamomum flora’ (reviewed by Duigan 1951). Most of the early identifications of these Paleogene and Neogene leaves with *Cinnamomum* were based only on gross leaf morphology. However, most of the earliest described leaves could not even be accepted as Lauraceae without cuticular morphological evidence (Hill 1988a). Hill (1986, 1988a) reassigned some of these taxa with adequate cuticular preservation to the genus *Laurophyllum* and the concept of the ‘Cinnamomum flora’ was gradually rejected. Nevertheless, the fossil record of Lauraceae is impressive compared with that of other taxa that are significant in the modern flora of Australia, such as *Acacia*, *Eucalyptus* and *Casuarina*.

Many Paleogene and Neogene Lauraceae from Australia have been described as *Laurophyllum* (e.g. Hill 1996; Carpenter & Pole 1995), a genus indicating only general affinity with Lauraceae and limiting the systematic or phylogenetic use of the record. Subsequent research has demonstrated that leaf venation and shape (Christophel & Hyland 1993) and cuticular morphology (Christophel & Rowett 1996) can be used as reliable characters in the taxonomy of extant Australian Lauraceae. The potential utility of the Australian macrofossil record of Lauraceae has been increased since the first critical work on the Australian taxa (Hill 1986) by refinement of generic and suprageneric concepts in Lauraceae. This has been based on a wide suite of characters (van der Werff & Richter 1996) including cuticular morphology (Christophel et al. 1996) and foliar morphology (Klucking 1987; Christophel & Hyland 1993), and a major revision of the arborescent Australian genera of the family (Hyland 1989).

<table>
<thead>
<tr>
<th>Locality (Age)</th>
<th>Fossil taxon</th>
<th>Extant affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cobungra River</td>
<td><em>Cinnamomum polymorphoides</em></td>
<td>?Lauraceae</td>
</tr>
<tr>
<td>(Early Eocene)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nerriga (Early/Middle Eocene)</td>
<td><em>Laurophyllum acrocryptocaryaoides</em></td>
<td>Cryptocarya (C. bellendenkerana, C. grandis)</td>
</tr>
<tr>
<td>Nerriga (Early/Middle Eocene)</td>
<td><em>Laurophyllum acrodromum</em></td>
<td>?Endiandra: E. pubens group*</td>
</tr>
<tr>
<td></td>
<td><em>L. conspicuum</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>L. acuminatum</em></td>
<td>?Endiandra: E. jonesii group*</td>
</tr>
</tbody>
</table>
L. acutum
L. angulosum
L. squamatum
L. lanceolatum
L. brochidodromum
L. intramarginatum
L. sinatum
L. pubescens
L. arcuatum

Parataxon 5

L. aculum
L. angulosum
L. squamatum
L. lanceolatum
L. brochidodromum
L. intramarginatum
L. sinatum
L. pubescens
L. arcuatum

Parataxon 4

Nelly Creek (Middle Eocene)
Anglesea clay lenses (late Middle Eocene)

Lefroy paleodrainage (Middle/Late Eocene)

Hasties (Late Eocene)

Jungle Creek (Late Eocene)

Kojonup Sandstone (Late Eocene)
Pallinup Siltstone (Late Eocene)
Vegetable Creek (Late Eocene)

Golden Grove (Eocene)

Pascoe Vale (Late Eocene/Early Oligocene)
Sedan Coalfield (Oligocene – Miocene or Late Eocene - Miocene)

Narracan (Early Oligocene)

Dalton (Late Oligocene)
Morwell Open Cut (Late Oligocene)
Darlimurla (Late Oligocene)

Lauraceae

Laurophyllum cf. L. arcuatum
Laurophyllum arcuatum (also L. acuminatum)
Cryptocarya obliquata

Parataxon 4

Endiandra: E. jonesii or E. pubens group
Cryptocarya: C. pleuro sperma group
Cryptocarya: C. pleuro sperma group
Neolitsea dealbata or Litsea: L. fawcettiana group
Endiandra: E. jonesii group
Endiandra: E. jonesii group
Endiandra: E. jonesii group
Endiandra: E. pubens group

Laureaceae

Laureaceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Lauraceae

Cryptocarya praeborovata

Cryptocarya obovata

Cryptocarya australis/C. murrayi/C. mackinnoniana
C. mackinnoniana

Cryptocarya australis/C. murrayi/C. mackinnoniana

Endiandra, ?Cryptocarya

Lyonia

Lauraceae
<table>
<thead>
<tr>
<th>Location</th>
<th>Species/Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tambellup Siltstone (Oligocene)</td>
<td>&quot;Laurophyllum&quot;&lt;sup&gt;5&lt;/sup&gt;&lt;br&gt;L. striatum&lt;sup&gt;4&lt;/sup&gt;&lt;br&gt;L. arcuatum/L. brochiodromum&lt;sup&gt;8&lt;/sup&gt;</td>
</tr>
<tr>
<td>West Dale (?Oligocene)</td>
<td></td>
</tr>
<tr>
<td>Berwick Quarry (Oligocene/Early Miocene)</td>
<td>L. sp. 'sinuous'&lt;sup&gt;14&lt;/sup&gt;&lt;br&gt;L. sp. 'thick'&lt;sup&gt;14&lt;/sup&gt;&lt;br&gt;L. sp. 'butterfly'&lt;sup&gt;14&lt;/sup&gt;&lt;br&gt;L. sp. 'smooth'&lt;sup&gt;14&lt;/sup&gt;</td>
</tr>
<tr>
<td>Newstead (Oligocene/Miocene)</td>
<td>Cinnamomum leichhardtii&lt;sup&gt;9&lt;/sup&gt;&lt;br&gt;Cinnamomum polymorphoides&lt;sup&gt;6&lt;/sup&gt;&lt;br&gt;Crinnamomum polymorphum&lt;sup&gt;13&lt;/sup&gt;</td>
</tr>
<tr>
<td>Maddingley (Miocene)</td>
<td></td>
</tr>
<tr>
<td>Pitfield (Miocene)</td>
<td>Cinnamomum polymorphoides&lt;sup&gt;6&lt;/sup&gt;&lt;br&gt;Cinnamomum polymorphoides&lt;sup&gt;6&lt;/sup&gt;</td>
</tr>
<tr>
<td>Werribee Ck./Lyalls Ck. (Miocene)</td>
<td>Laurus werribeensis&lt;sup&gt;13&lt;/sup&gt;</td>
</tr>
<tr>
<td>Regatta Point (Early/Middle Pleistocene)</td>
<td>L. australum&lt;sup&gt;6&lt;/sup&gt;&lt;br&gt;Cryptocarya nova-anglica/C. sp.nov (Mt. Bellenden Ker, Queensland)&lt;sup&gt;6&lt;/sup&gt;</td>
</tr>
<tr>
<td>Mount Bischoff, Tasmania</td>
<td></td>
</tr>
<tr>
<td>Travertine lake deposits near Hobart</td>
<td></td>
</tr>
<tr>
<td>William Creek, South Australia</td>
<td></td>
</tr>
</tbody>
</table>

*Possible extant affinities of *Laurophyllum* specimens from the Leffroy Palaeodrainage and Nerriga were produced by keying parataxa using the key to extant Australian genera of Christophel & Rowett (1996) where possible from the descriptions and illustrations provided in Carpenter & Pole (1999) and Hill (1986).

1 Rowett (1991); 2 Christophel & Greenwood (1987); 3 Christophel, Scriven & Greenwood (1992); 4 Hill & Merrifield (1993); 5 McLoughlin & Hill (1996); 6 Jordan (1997); 7 Pole (1992b); 8 Johnston (1886); 9 Chapman (1926); 10 Chapman (1921); 11 Deane (1925); 12 Paterson (1935); 13 McCoy (1876); 14 Pole et al. (1993); 15 Douglas (1967); 16 Rowett & Christophel (1990); 17 Christophel, Harris & Syber (1987); 18 Leisman (1986); 19 Carpenter & Pole (1995); 20 Conran & Christophel (1998); 21 Hill (1986); 22 Hill (1888a); 23 Ettingshausen (1888).

## 2 MACROFOSSIL EVIDENCE FOR LAURACEAE AND PROTEACEAE

### 2.1 Lauraceae – Laurasian records

Recent phylogenies based on DNA sequence analyses have emphasised the antiquity of Laurales (Qiu et al. 1999). Drinnan & Crane (1990) indicated that Lauraceae had differentiated early in angiosperm evolution, likely by the Albian, ~ 110 Ma. Indeed, fossils of definite lauraceous affinity are known from the early Cenomanian (~ 97 Ma: Drinnan et al. 1990; Eklund & Kvacek 1998). Monosulcate pollen typical of the magnoliid dicotyledon (including Laurales, Winterales and Chloranthaceae) and monocotyledon grade first appear in the fossil record around the Hauterivian (Hughes & McDougall 1987), preceding the appearance of triaperturate pollen typical of the non-magnoliid dicotyledon clade (Crane 1987; McLoughlin et al. 1995).

Supporting this antiquity is a good mid-Cretaceous macrofossil record of Lauracea (Eklund & Kvacek 1998 and references therein). Early Cenomanian (~ 97 Ma) inflorescences and flowers of *Mauldinia mirabilis* were described from the Potomac Group, eastern North America (Drinnan et al. 1990), and Cenomanian *M. bohemica* inflorescences are known from the Peruc-Korycany Formation in the Czech Republic (Eklund & Kvacek 1998). Macrofossils of Lauraceae are common across middle and low palaeolatitudes in the Northern Hemisphere in the Maastrichtian Northern Gondwana and Normapolles Provinces (Crane 1987). Pole (1992a) suggested lauraceous affinity for several leaves with pinnate margins, acrodromous primary venation and percurrent secondary venation from the Upper Cretaceous Taratu Formation, Otago, New Zealand. The Late Cretaceous (Santonian/ Campanian; ~ 83 Ma) coincided with increased...
seafloor spreading between Australia and Antarctica (Veevers et al. 1991), separation of India from Australia (Powell et al. 1981; Wilford & Brown 1994), and initial spreading to form the Tasman Sea (Crook 1981; Veevers et al. 1991). Audley-Charles (1987) suggested that dispersal of land plants between mainland Asia and Australia would have been possible around that time (~90 Ma). However, more recent tectonic reconstructions of the region indicate several thousand kilometres still separated the Eurasian continental margin and the leading edge of the Australian craton at the Early/Middle Eocene, ~50 Ma (Hall 1996, 1997).

Diversity within the Lauraceae persisted in the Paleogene with leaves, wood and reproductive structures being abundant and diverse in macrofloras from most parts of the world (Eklund & Kvacek 1998). Indeed, Paleocene macrofloras spanning northern America, central and eastern Europe (the Southern Laurasian floristic province of the Cenomanian and Normapolles Province of the Santonian–Campanian) are typically dominated by palms, Euphorbiaceae and Laurales (Crane 1987). The London Clay flora contains eight taxa of Beilschmiedia (some possibly attributable to the closely related genus Endiandra), two taxa of Cinnamomum, one taxon of Litsea, one taxon of Crowella, five taxa of Laurocalyx and 30 taxa of Laurocarpus (Chandler 1964). This indicates the existence of two of the three extant tribes of Lauraceae recognised by van der Werff & Richter (1996): Perseeae (as Cinnamomum) and Cryptocaryaeae (as Beilschmiedia, Cryptocarya and Endiandra) in the North Atlantic/European floristic Province during the Paleocene (sensu Crane 1986). Paleocene Lauraceae leaves are also represented in macrofloras preserved in nine other Lower Eocene sedimentary beds from southern England (Chandler 1964), and were a dominant component of the vegetation preserved in both the Bournemouth Beds (Bandulska 1928) and London Clay (Chandler 1964). Exact generic relationships of Lauraceae leaf macrofossils from the Eocene London and Bournemouth Clay floras and from Late Cretaceous and Early Paleogene localities in the Unites States are uncertain beyond the more general ‘Cinnamomum’ and ‘Laurophyllum’ types. The presence of Lauraceae macrofossils in these areas strongly suggest that Lauraceae was a prominent component of early angiosperm plant communities in Laurasia, and substantially predates the earliest known records of the family from Gondwana.

2.2 Lauraceae – Australian records

Published Australian macrofossil records of Lauraceae extend from the Early Eocene (Table 1 and Fig. 3). This extensive record connotes the prominence of Lauraceae in the eastern Australian sector of Gondwana before the formation of a deep marine strait between Tasmania and Antarctica in the early Late Eocene/Early Oligocene and the ensuing development of Circum–Antarctic oceanic circulation (Kemp 1981; Martin 1991; Veevers et al. 1991; Wilford & Brown 1994). These events clearly predate the ‘contact phase’ between the Australian craton and the Eurasian plate in the Miocene (Powell et al. 1981; Truswell et al. 1987; Metcalfe 1990; Hall 1996, 1997: Fig. 3).

Many of the older published records in Table 1 should be considered doubtful. For example Early Eocene and Late Oligocene/Miocene records of Cinnamomum (McCoy 1876; Chapman 1921, 1926; Deane 1925), Cryptocarya (Paterson 1935), and Laurus (McCoy 1876) were made on the basis of leaf morphology, and lack the cuticular morphological information needed for definite placement in Lauraceae (Hill 1988a). Published macrofossils with cuticular preservation enabling secure assignment to Lauraceae date from the Early/Middle Eocene, with Hill (1986) and Conran & Christophel (1998) describing a total of 13 taxa of Laurophyllum from the Nerriga locality in New South Wales (Table 1 and Fig. 3). Conran & Christophel (1998) indicated the fossil taxon L. acrocryptocaryoides from Nerriga had a combination of cuticular morphological characters such as wide, butterfly-shaped cuticular scales and rounded epidermal cells (Conran & Christophel 1988, figs. 2C, 2D) characteristic of extant Cryptocarya (Christophel & Rowett 1996). This reiterates the presence of Lauraceae similar to extant Tribe Cryptocaryaeae in southeastern Australia in the Paleogene (early Middle Eocene; ~50 Ma).

Hill (1986) described 12 taxa of Lauraceae from Nerriga on the basis of micromorphological characters and assigned all to Laurophyllum (Table 1). The taxa described by Hill (1986) may include Endiandra, Cryptocarya and either Neolitsea or Litsea using the key of Christophel & Rowett (1996; Table 1). Laurophyllum acrodromum, L. brochidodromum, L. intramarginatum, L. acuminatum, L. acutum and L. arcuatum described by Hill (1986) all appear to have combina-
tions of micromorphological characters typical of extant *Endiandra* (Christophel & Rowett 1996). These include epidermal cells with irregularly thickened and/or granulate periclinal walls and cuticular scales that appear double (Hill 1986, figs. 7C and 7E, 13C and 13E, 14D, 9C, 10C, 17C). *L. acrodromum*, *L. brochidodromum*, *L. intramarginatum* and *L. arcuatum* also have guard cells with polar extensions or rods (Hill 1996, figs. 7E, 13C, 14D, 17D) while *L. acumina-atum*, *L. acutum* and *L. intramarginatum* have mostly angular adaxial cell wall outlines (Hill 1986, figs. 9B, 10A, 14E). These characters are also typical of extant *Endiandra* in combination with the other characters described above (Christophel & Rowett 1996). The fossil described as *L. lanceolatum* by Hill (1986) has cuticular ledges that appear single, thin and mainly straight (Hill 1986, figs. 9G and 9H), which are typical of extant *Litsea* (Christophel & Rowett 1996). *L. angulosum* and *L. squamatum* from Nerriga appear to have wide, butterfly-like cuticular scales (Hill 1986, figs. 11F, 12E). This implies a close relationship with extant *Cryptocarya* (Christophel & Rowett 1996). These Nerriga fossils suggest the presence in southeastern Australia of Tribes Laureae (as *Litsea*) and Cryptocaryae (as *Cryptocarya* and *Endiandra*; van der Werff & Richter 1996) in the Early/Middle Eocene (~ 50 Ma).

Lauraceae also feature prominently in the Middle/Late Eocene (~ 50–35 Ma) of southern Australia (Table 1), at which time there was a substantial seaway in the Indian Ocean, Southern Ocean and Tasman Sea (Fig. 3; Veevers et al. 1991), and the Australian craton was still distant from Sundaland and the Eurasian plate (Hall 1996, 1997). Christophel et al. (1987) described four late Middle Eocene taxa of Lauraceae from the Anglesea clay lenses in southern Australia (Victoria). These macrofossils have strong affinities with extant *Endiandra/Litsea*, *Neolitsea* and *Cinnamomum/Cryptocarya* (Christophel et al. 1987), reflecting a similar range of diversity in Lauraceae as may have been present earlier at Nerriga.

Carpenter & Pole (1995) described ten taxa of *Laurophyllum* from the Middle/Late Eocene Lefroy Palaeodrainage (Pidinga Formation) in Western Australia, some of which may represent *Litsea*, *Lindera* and *Endiandra* (Table 1). Four of the fossil cuticle types described by Carpenter & Pole (1995) have combinations of characters including 'double' cuticular scales (Carpenter & Pole 1995, figs. 25, 37-38, 40, 42-44, 54, 56) typical of extant *Endiandra* (Christophel & Rowett 1996). Fossil type 1 has a combination of characters including granular periclinal walls; single, thin and straight cuticular ledges and prominent abaxial papillae (Carpenter & Pole 1995, figs. 24, 28, 25) that are typical of extant *Litsea* (Christophel & Rowett 1996). Fossil cuticle type 7 has highly sinuous abaxial cell outlines and heavily 'beaded' abaxial anticlinal walls (Carpenter & Pole, 1995 figs. 47, 45) that are typical of the extant genus *Lindera* (Christophel & Rowett 1996).

Lauraceae macrofossils from the Late Paleocene (~ 58–60 Ma) at Cambalong Creek (Taylor et al. 1990) grew at a time when Australia had already been separated from India and New Zealand by a long period of development of the southeast Indian Ocean and Tasman Sea (Powell et al. 1981; Wilford & Brown 1994), although Australia and Antarctica were still partially joined (Veevers et al. 1991). Australia was also still distant from Sundaland, the continental block forming southeast Asia, at approximately 60 Ma (Powell et al. 1981; Hall 1996, 1997).

Lauraceous taxa from the Cambalong Creek macroflora will be formally described in a future publication (Vadala & Drinnan, in prep.). Lauraceae comprise approximately 20% of total taxa in the macroflora, as eight species in four genera (Fig. 1: A.J. Vadala, unpubl.). These fossils predate all published records of Lauraceae from Australia (Table 1 and Fig. 3) and have been identified as extant genera using morphological characters preserved by the mummified leaf cuticles. Primary classification and sorting of fossil specimens was achieved by running the fossil specimens through the key to Australian genera of Lauraceae developed by Christophel & Rowett (1996). This identified fossils belonging to *Beilschmiedia*, *Cryptocarya*, *Endiandra* and *Litsea*. Steps in the key were used to derive a binary (qualitative) character set (28-33 characters) and a continuous (numerical) character set (7 characters) for the fossils specimens and for 25 extant Australian species of *Beilschmiedia*, *Endiandra* and *Cryptocarya*. The two character sets were used in conjunction and separately in pattern analyses for the three genera to determine further taxonomic divisions between specimens. These analyses applied sequential-agglomerative-hierarchical-combinatorial strategies using dissimilarity metrics (Belbin 1987) to the data sets.

The Cambalong Creek Lauraceae indicate the presence in southeastern Australia of taxa similar to the extant tribes Laureae (*sensu* van der Werff & Richter 1996; as *Litsea*) and Crypto-
caryaeae (as Beilschmiedia, Cryptocarya and Endiandra) before the breakup of the last fragments of Gondwana (Powell et al. 1981; Veevers et al. 1991). This precedes the Miocene contact between the Australian continent and Sundaland by ~ 40 Ma (Fig. 3; Powell et al. 1981; Truswell et al. 1987; Metcalfe 1990). The extant distributions of the nearest living relatives of these taxa are shown in Fig. 2 and Table 3.

Extant *Endiandra* consists of approximately 100 species (Table 3; Hyland 1989) occurring from Australia through New Guinea to Malesia and across broader southeast Asia (Fig. 2). Most of the Australian species grow in rainforest (Table 3). *Beilschmiedia* consists of 200-250 extant species (Table 3; Hyland 1989) found in Africa, Australia, South America, New Zealand and New Guinea, through Malesia and broader southeast Asia to India (Fig. 2). The 11 extant Australian taxa of *Beilschmiedia* are all restricted to rainforest habitats (Hyland 1989: Table 3). *Cryptocarya* consists of 200-250 extant species (Hyland 1989) found in Australia, South America, Africa, New Guinea, Malesia and broader southeast Asia (Fig. 2). All 46 Australian species are restricted to rainforest (Fig. 2 and Table 3; Hyland 1989), with habitats varying from north Queensland seasonal rainforests with *Agathis* to drier rainforests of northern NSW and southern and central Queensland, to monsoon forests in northern Queensland, Northern Territory and the Kimberley region of Western Australia (Hyland 1989). *Litsea* consists of 100 species (Hyland 1989) found in Australia, New Zealand, South America, New Guinea, through Malesia and southeast Asia to Japan (Fig. 2). All but one of the 11 Australian species are rainforest trees (Fig. 2 and Table 3; Hyland 1989).

Five species of *Endiandra* have been identified from sediments at Cambalong Creek. The fossil taxa have rounded abaxial epidermal cell outlines, granular inner periclinal walls (Figs. 4 and 5, p) and 'double' cuticular scales consisting of a narrow inner and outer ridge (Figs. 4 and 5; o, i). These characters are typical of most of the 38 extant species of Australian *Endiandra* (Christophel & Rowett 1996). The Late Paleocene species of *Endiandra* are most closely related to the 'E. pubens group' of Christophel & Rowett (1996) and some compare very favourably with extant *E. globosa*, *E. wolfii* and *E. cowleyana* (cf. Fig. 4 and Fig. 5).

One of the fossil taxa from Cambalong Creek has been identified as *Beilschmiedia*. The fossil taxon has thick (> 2.5 µm) epidermal anticlinal walls with buttressed thickenings (Fig. 6, b) and prominent inner stomatal ledges. These characters are typical of most of the 11 extant Australian taxa of *Beilschmiedia* (Christophel & Rowett 1996). The fossil is similar in cuticle morphology to extant *B. tooram* and *B. recurva* (cf. Fig. 6 and Fig. 7) from rainforests of northern Queensland (Hyland 1989). Crisp et al. (1999) described *Beilschmiedia* as one of the genera exhibiting an 'Equatorial track', with an Afro–Indo–Malesian distribution (Fig. 2). Members of this track had been described as the 'tropical element' of the Australian flora by Burbidge (1960) and as the 'Irian Element' by Schodde (1989). Crisp et al. (1999) however alluded to the more likely Late Cretaceous, Gondwana origins of taxa exhibiting this track. A more ancient origin is supported by the presence of *Beilschmiedia* fossils in the Late Paleocene of southeastern Australia.

Twenty-two fossil cuticle fragments from Cambalong Creek have been identified as one species of *Cryptocarya*. The fossils have rounded epidermal anticlinal walls and wide, butterfly-shaped cuticular scales (Fig. 8, s) that are characteristic of most of the 46 extant Australian species of *Cryptocarya* (Fig. 9; Christophel & Rowett 1996). The fossils are similar to extant C. *bidwillii*, C. *clarkeoniana* (cf. Fig. 8 and Fig. 9) and C. * cunninghamii*.

Three cuticle fragments from Cambalong Creek have been identified as a single species of *Litsea*. Fossil cuticles CMB 4-22/35/2c-28 feature prominent thickened rings of cuticle encircling the outer surface of the stomates, and papillae on the outer abaxial surface (Fig. 10, pa). These characters compare favourably with the 'L. bennetti group' of Christophel & Rowett (1996), particularly L. *connorst* (cf. Fig. 10 and Fig. 11), a taxon that grows in rainforests and forest margins in northern Queensland over an altitudinal range of 600-1200 m asl (Hyland 1989).
Figs. 4-13: electron micrographs of fossil cuticles from Cambalong Creek and extant Lauraceae and Proteaceae cuticles; all scale bars indicate 10 μm. Fossils are indicated by the prefix CMB; extant taxa followed by accession numbers in parentheses: MEL = Royal Botanic Gardens Melbourne. Figs. 4-5, inner surfaces of stomates; i = inner stomatal ledge, o = outer stomatal ledge, p = granular inner periclinal wall. Fig. 4: CMB2c-21; Fig. 5: *Endiandra cowleyana* (MEL1604225). Figs. 6-7, inner adaxial surfaces of non-vein-course cells. Fig. 6: CMB4-9, b = buttressed irregular thickening on anticlinal wall; Fig. 7: *Beilschmiedia recurva* (MEL1606701). Figs. 8-9, inner surfaces of stomates; s = cuticular scale. Fig. 8: CMB4-23; Fig. 9: *Cryptocarya clarksoniana* (MEL1605606). Figs. 10-11, inner abaxial surfaces of non-vein-course cells with papillae; pa = outline of base of papilla. Fig. 10: CMB4-35; Fig. 11: *Litsea connorsii* (MEL1604219). Figs. 12-13, outer surfaces of stomates; su = outer surface of subsidiary cell, g = outer surface of guard cell. Fig. 12: CMB2c-24; Fig. 13: *Stenocarpus verticis* (MEL669961).
3 PROTEACEAE

3.1 Proteaceae in Gondwana

Proteaceae have a long macrofossil record from Australia, with earliest published records from the Late Paleocene (Table 2; Carpenter et al. 1994; Vadala & Drinnan 1998). However, the palynological evidence for the family in Australia is diverse and extends to the Turonian (~ 90 Ma; Dettmann & Jarzen 1990; Dettmann 1994; Hill et al. 1999). This precedes the Miocene contact phase between Australia and Eurasia by ~ 75 Ma (Fig. 3).

The rainforest ancestor to the extant subfamilies ('Proto-Proteaceae') was hypothesised by Johnson & Briggs (1963) to have existed somewhere in northern Gondwana (Johnson & Briggs 1975; Dettmann 1989; Hill et al. 1995) prior to the Late Cretaceous and the separation of the gondwanan landmasses (Johnson & Briggs 1975). Dettmann & Jarzen (1991) suggested the phylogeny and ecogeography of extant Proteaceae implied evolution and diversification of the family during the mid-Cretaceous in Gondwana. Johnson & Briggs (1981) proposed that the earliest palynological records of Proteaceae actually post-date the evolution and first appearance of the precursors of extant subfamilies. Despite problems regarding the identification of some fossil proteaceae pollen with extant genera (Martin 1973; Martin 1982; Truswell & Harris 1982; Hill et al. 1995) fossil pollen belonging to Beauprea, Macadamia, Gevuina–Hicksbeachia and Knightia has been reliably identified from Campanian-Maastrichtian (~ 74 Ma) sediments of southeastern Australia, New Zealand and Antarctica (Dettmann & Jarzen 1990, 1991). The oldest palynological record of the family in New Zealand dates from the Campanian or possibly Santonian (Pole 1998). These pollen data reiterate the existence of subfamilies Proteoideae (tribe Conospermeae) and Grevilleoideae (tribes Macadamiae and Knightiae) in the southeast Australian/Antarctic sector of Gondwana from at least the Sononian. Indeed, these genera of Proteaceae along with conifers including Araucaria, Dacrydium, Lagarostrobus and Podocarpus probably constituted overstorey elements of southeastern Australian forests in the Late Cretaceous (Specht et al. 1992). Carnarvonia (subfamily Carnarvonioideae), Telopea (subfamily Grevilleoideae, tribe Embothrieae) and Persoonia (subfamily Persoonioideae, tribe Persooniaceae) probably formed part of the forest understorey, with Stirlingia (subfamily Proteoideae, tribe Conospermeae), Adenanthos (tribe Franklandiaceae) and Beauprea in scleromorphic communities on the fringes of these forests (Dettmann & Jarzen 1991; Dettmann 1994). Forest and scleromorphic communities in southern Gondwana during the Late Cretaceous, therefore, included representatives of four of the extant seven subfamilies, including the two largest subfamilies, Proteoideae and Grevilleoideae.

The palynological record demonstrates the presence of Proteaceae in Australia during the Cretaceous and prior to any contact with southeast Asia (Fig. 3). Indeed, Antarctica and southeastern Australia have been integral to hypotheses regarding the evolution and dispersal of the extant tribes of Proteaceae and their progenitors. Northern Gondwana has been postulated as the origin of some of these ancestors (Johnson & Briggs 1975, 1981; Dettmann 1989, 1994; Dettmann & Jarzen 1990, 1991; Hill et al. 1995; Hill et al. 1999) and the opening of the early Southern Ocean and concomitant habitat changes coincided with diversification of the family (Dettmann 1989, 1994; Hill et al. 1999).

Table 2. Published records of Paleogene and Neogene Proteaceae macrofossils from Australia, excluding Banksiaephyllum and Banksieaeformis (for table of these see Vadala & Drinnan 1998). Records of New Zealand Proteaceae are limited to those described by Pole (1998).

<table>
<thead>
<tr>
<th>Locality (Age)</th>
<th>Fossil taxon</th>
<th>Extant affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mount Somers coal mine, New Zealand (Paleocene)</td>
<td>CUT-P-013&lt;sup&gt;25&lt;/sup&gt;</td>
<td>Proteaceae&lt;sup&gt;27&lt;/sup&gt;</td>
</tr>
<tr>
<td>Regatta Point (Early Eocene)</td>
<td>Unidentified Proteaceae (at least 8 taxa)&lt;sup&gt;28&lt;/sup&gt;</td>
<td>Proteaceae&lt;sup&gt;28&lt;/sup&gt;</td>
</tr>
<tr>
<td>Brooker (Early Eocene)</td>
<td>Euproteaciphyllum brookeren-</td>
<td>?Lomatia&lt;sup&gt;28&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Buckland (Early Eocene) Proteaceae
Livingstone, North Otago, NZ (Early/Middle Eocene) Grevilleoideae cf. Orites
Golden Grove (Middle Eocene) excelsa
Maslin Bay (Middle Eocene) Proteaceae aff. Neorites
Maslin Bay (Middle Eocene) Musgraveanthus
Nelly Creek (Middle Eocene) Maslin Bay cf. Proteaceae III
Cowan and Lefroy Palaeodrainages (Middle/Late Eocene) Maslin Bay cf. Proteaceae IV

Hasties (Middle/Late Eocene) Parataxon 2
Merlinleigh Sandstone, Kennedy Range, WA Banksia archaeocarpa
(Anglesea) fructescence
(late Middle Eocene) Parataxon 12
Kalgoorlie (late Middle Eocene, ~39 my) Bivalved fruit
Anglesea (Late Eocene) Molata fraxinifolia
Kojonup Sandstone Deeplly-dissected leaf
(Late Eocene) Fructification
Lake Lefroy (Late Eocene) Lake Lefroy cf. Proteaceae 1
Nelly Creek (Eocene) L. fraxinifolia 9, 10, 12
Cethana (Early Oligocene) Lomatia xeromorpha 9, 10
Cethana (Early Oligocene) cf. Lomatia 12

Glencoe (mid Early Oligocene) proteaceae 28
Lea River (Early Oligocene) Lomatia 28
Lemonthyme (Early Oligocene) Orites excelsa 29
Leven River Neorites (immature leaves)
(Early Oligocene)
West Dale
(?Oligocene)
Yallourn Open Cut
(Oligocene)
Moonpeelyata
(Late Oligocene/Early Miocene)
Morwell Open Cut
(Oligocene/Miocene)
Sedan Coalfield
(Oligocene/Miocene)
Yallourn and Morwell
(Oligocene/Miocene)
Manuherikia Group, NZ
(Early Miocene)
Benerece
(early/mid Miocene)
Gulgong
(early/mid Miocene)
Gulgong (mid Miocene)
Yallourn Formation
(mid Miocene)
New Zealand (Miocene)
Mangonui Formation,
North Island, NZ
(Late Miocene)
Melville Island (Van Diemen Sandstone)
( ?Late Pliocene)
Regatta Point
(Early Pleistocene)
Marionoak Formation
(Early Pleistocene)
Regatta Point

Proteaceae cf. *Alloxylon*17
Proteaceae cf. *Stenocarpus*17
Proteaceae spp. 1-6
Proteaceae aff. *Conospermum*6
Proteaceae sp. 128
Proteaceae aff. *Darlingia*6
Proteaceae aff. *Orites*6
Proteaceae aff. *Stenocarpus* or *Oreocallis*6
Parataxon S1 001 ‘Banksieaephyllyum aff. *B. laeve*’13
Parataxon LC 004: ‘B. aff. *B. fastigatum*’15
Parataxon LC 012: ‘B. aff. *B. obovatum*’15
Proteaceae taxa 58, 59, 60, 616
Proteaceae cf. *Alloxylon* (e.g., *A. wickhamii*, *A. pinnata*17)
Proteaceae cf. *Stenocarpus*17
Proteaceae spp. 1-6
Proteaceae aff. *Conospermum*6
Proteaceae aff. *Darlingia*6
Proteaceae aff. *Orites*6
Proteaceae aff. *Stenocarpus salignum*6
*Parataxon S1 001 ‘Banksieaephyllyum aff. *B. laeve*’13
Parataxon LC 004: ‘B. aff. *B. fastigatum*’15
Parataxon LC 012: ‘B. aff. *B. obovatum*’15
Proteaceae taxa 58, 59, 60, 616

?*Euplassa*19,21
?*Gevuinae-Hicksbeachia*19,21
*Macadamia*19,21
*Athertonia*24

*Wilkinsonia bilaminata*1
*Wilkinsonia bilaminata*1
*Wilkinsonia bilaminata*6
*Wilkinsonia bilaminata*6

?*T. papuana*19,21
?*Turrililia bleasdalei*19,21
*Macadamia ternifolia*
*M. tetraphylla*19,21
*Embothriaceae*29
*Heliciaceae: Helicia*29

Grevillea sp. A (‘deeply lobed’)26
Grevillea sp. B (‘serrate’)26
Grevillea sp. C (‘deeply serrate’)26

Proteaceae cf. *Dilobia*24
*Agastachys odorata*22
*Banksia kingii*22
*B. strahanensis*12
*Cenarrhenes nitida*22
*Hakea sp.*22
*cf. Lomatia*22
*Orites revoluta*22
*O. truncata*22
*Proteaceae cf. Lomatia*22
*Telopea truncata*22
*Telopea cf. mongaensis*22
*Telopea strangulans*22

Grevillea sp. A (‘deeply lobed’)26
Grevillea sp. B (‘serrate’)26
Grevillea sp. C (‘deeply serrate’)26

*Agastachys odorata*22
*Banksia saxicola - B. canei*22
*B. spinulosa*12
*Confarrhenes nitida*22
*Hakea*22
*?Lomatia*22
*Orites revoluta*22
*O. diversifolia/O. milliganii*22
*Lomatia/Knightia/Orites*22
*Telopea truncata*22
*Telopea mongaensis*22
*Telopea*22

*Orites revoluta*22
*O. acicularis*22
*O. revoluta*22

*O. revoluta*22
*O. acicularis*22
*O. revoluta*22
3.2 Proteaceae after the isolation of Australia

The palynological record also indicates a high abundance and diversity of Proteaceae during the Paleogene, particularly during the Late Paleocene/Eocene (~56 Ma: Martin 1978; Martin 1982; Hill et al. 1985). The macrofossil record corroborates these pollen data (Table 2), and fossils with cuticular preservation provide the most reliable and unambiguous evidence for proteaceous affinity (Carpenter & Jordan 1997; Jordan et al. 1998). Records of tribes Grevilleae and Banksiae, which now dominate the sclerophyllous flora of Australia, are abundant in the Paleogene and Neogene macrofossil records of cuticle (Table 2). The oldest macrofossils able to be attributed with confidence to Proteaceae have been described from the Late Paleocene of the Southern Highlands of New South Wales (Fig. 3). Carpenter et al. (1994) described cuticles of Banksiaephyllum taylorii from Lake Bungarby and Vadala & Drinnan (1998) described B. praefastigatum from nearby Cambalong Creek. These taxa have simple leaves with serrate margins, superficial stomates, epidermal cells with irregularly thickened anticlinal walls and trichome bases with some degree of thickening (Carpenter et al. 1994; Vadala & Drinnan 1997). These characters are typical of extant Banksia and Dryandra, which are indistinguishable on these criteria alone, and the fossils are consequently attributed to the proteaceous fossil genus Banksiaephyllum (tribe Banksieae; Cookson & Duigan 1950).

The published fossil record of Proteaceae is extensive throughout the Cenozoic of southeastern Australia, and comprises mainly subfamily Grevilleoideae (Table 2 and Fig. 3: Hill et al. 1995; Carpenter & Jordan 1997; Jordan et al. 1998; Vadala & Drinnan 1998). The Paleocene and Early Eocene (~65–35 Ma) macrofossil record corresponds to an apparent increase in diversity and abundance of Proteaceae pollen during the Late Paleocene/Eocene (Martin 1978; Martin 1982; Hill et al. 1995), prior to the complete separation of the Australian continent from Antarctica in the Late Eocene/Early Oligocene (Crook 1981; Veevers et al. 1991; Wilford & Brown 1994). This preceded the Australian craton/Sunda Arc collision in the Late/Middle Miocene (Crook 1981; Powell et al. 1981; Hall 1996, 1997) by ~20–15 Ma (Fig. 3).

The Paleogene macrofossil record of tribe Banksiaeae (consisting of subtribes Banksiinae and Musgraveinae) is in concord with the size and diversity of the tribe in the modern flora of Australia (Table 3). The record for Banksiinae (consisting of Banksia and Dryandra) is extensive: 27 taxa of Banksiaephyllum and Banksieaformis have been described from Western Australia, South Australia, Victoria and Tasmania, although the identification of several may be doubtful (Carpenter & Jordan 1997; Jordan et al. 1998). These range in age from Late Paleocene (~60 Ma) to Early Mioene (~23 Ma; Fig. 3; also reviewed in Vadala & Drinnan 1998). Dettmann & Jarzen (1991) hypothesized that both rainforest and sclerophyll members of Proteaceae had evolved by the Campanian/Maastrichtian (~74 Ma). Indeed, the oldest described taxa of Banksiaephyllum exhibit either sclerophyllous or more mesic characters by the Paleogene (Carpenter et al. 1994; Hill et al. 1995; Vadala & Drinnan 1998). The record of Musgraveinae is also impressive (Fig. 3 and Table 2). Christophel & Greenwood (1987) recorded Middle Eocene Musgravea flowers from Golden Grove, and at least three taxa of Banksiaeae have been recov-
erased from the Middle/Late Eocene Lefroy and Cowan Palaeodrainages in Western Australia (Carpenter & Pole 1995). Two of these taxa have been described as Musgravea (Pole 1998). Mid- to late Middle Eocene inflorescences of Musgravea have also been recovered from Anglesea in Victoria and Golden Grove in South Australia (Fig. 3 and Table 2; Christophel 1984).

Table 3: Australian and worldwide abundance of extant genera and tribes to which Lauraceous and proteaceous fossils from Cambalang Creek are most similar.

<table>
<thead>
<tr>
<th>Tribe</th>
<th>Total species</th>
<th>Species in Australia</th>
<th>Endemic species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tribe Laureae: Litsea</td>
<td>~ 100</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Tribe Cryptocaryae: Beilschmiedia</td>
<td>200-250</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Cryptocarya</td>
<td>200-250</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td>Endiandra</td>
<td>~ 100</td>
<td>38</td>
<td></td>
</tr>
<tr>
<td>Tribe Proteaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tribe Oriteae: Orites</td>
<td>9</td>
<td>7</td>
<td>4*</td>
</tr>
<tr>
<td>Tribe Stenocarpinae: Stenocarpus</td>
<td>~ 25</td>
<td>9</td>
<td>7**</td>
</tr>
<tr>
<td>Tribe Heliciineae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tribe Knightieae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tribe Banksieae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Banksia</td>
<td>76</td>
<td>76</td>
<td>75</td>
</tr>
<tr>
<td>Dryandra</td>
<td>93</td>
<td>93</td>
<td>93</td>
</tr>
</tbody>
</table>

* 4 taxa endemic to Tasmania
**2 taxa extend to New Guinea and Aru Is.
***1 taxon extends to New Guinea
1 Hyland (1989); 2 George & Hyland (1995); 3 Foreman (1995a); 4 Foreman (1995b); 5 Hyland (1995a); 6 Hyland (1995b); 7 George (1999a); 8 George (1999b).

The Cenozoic macrofossil record of tribe Knightieae is less extensive than that of Banksieae (Fig. 3 and Table 2). Lange (1978) identified Darlingia/Knightia (tribe Knightieae) from Middle Eocene Maslin Bay and Carpenter & Pole (1995) described Darlingia from the Middle/Late Eocene Cowan and Lefroy Palaeodrainages in Western Australia. Late Eocene leaves with a combination of characters similar to either Darlingia or Orites were also described from Anglesea (Christophel 1984).

The oldest Australian macrofossil record of tribe Oriteae is Middle Eocene Neorites from Golden Grove in South Australia (Christophel & Greenwood 1987), although Pole (1998) described leaves with similarities to extant Orites excelsa from Early/Middle Eocene sediments in New Zealand (Table 2 and Fig. 3). Late Middle Eocene specimens of Orites (Rowett & Christophel 1990) and leaves of either Orites or Darlingia (Christophel 1984) have been described from Anglesea in Victoria.

Tribe Embothrieae is preserved in the macrofossil record mainly as Lomatia, although the oldest fossil may be a Late Paleocene taxon from Cambalang Creek, with affinities to Stenocarpus (see above). Jordan et al. (1998) described two Early Eocene taxa of Euproteaciphyllum from Tasmania that have strong micromorphological similarities with extant Lomatia (Table 2). Carpenter & Pole (1995) described a Middle/Late Eocene Lomatia macrofossil from the Cowan and Lefroy Palaeodrainages as indistinguishable from the extant northeast Queensland rainforest taxon L. fraxinifolia; another late Middle Eocene Lomatia fossil from Kalgoorlie probably has the same affinities (Table 2; Carpenter 1994).

Other tribes of Grevilleoideae are less extensively represented in the Paleocene and Eocene macrofossil records (Fig. 3). Blackburn (1981) identified Maslinia grevilleoides from the Middle Eocene Maslin Bay locality as closely related to extant Grevillea (tribe Grevilleae; Fig. 3). Many other tribes are represented in the record by fossils with suggested or implied affinities (Table 2). For example, Lange (1978) identified Middle Eocene leaves with possible affinities to Helicia (tribe Heliciineae) and Grevillea (tribe Grevilleae) from Maslin Bay (Table 2 and Fig. 3). Fossil leaves with possible affinities to Grevillea have also been described from Anglesea.
(Christophel 1984) and the Late Eocene (~ 36 Ma) Kojonup Sandstone in Western Australia (Table 2 and Fig. 3; McLoughlin & Hill 1996). The only published taxon of subfamily Proteoideae from the Paleocene or Eocene is Middle/Late Eocene Cenarrhenes nitida (tribe Conospermeae) from Hasties in Tasmania (Table 2 and Fig. 3; Jordan et al. 1998). The Australian macrofossil record of Proteaceae from the Oligocene (~ 35-23 Ma) and the Neogene (~ 23-1 Ma; Table 2) indicates the family was equally diverse following the separation of the Australian and Antarctic continents in the Late Eocene/Early Oligocene and the collision of the Australian plate with the Sunda Arcs in the Middle Miocene (Fig. 3).

Proteaceae macrofossils from Cambalong Creek other than Banksieaephyllun (see above) will be formally described elsewhere, but likely represent the earliest macrofossils of tribes Embothriæae, Helicieae and Oriteæae described from Australia (subfamily Grevilleioideae; A.J. Vadala, unpubl.). These fossil taxa have cuticular characters described by Carpenter & Jordan (1997) as typical of Grevilleioideae. These include granulation on the inner cuticle surface, hypostomaty, with stomates aligned randomly over the cuticle rather than parallel to the long axis of the leaf, and most have trichome bases associated with at least one epidermal basal cell. Most of the fossil taxa are too fragmentary to allow reliable comparisons of leaf morphology with extant taxa, and most lack enough distinctive cuticular morphological features to be placed with confidence in any extant genus of Proteaceae. However, the fossils all have brachyparacytic stomates and most have trichome bases overlying one or several epidermal cells, characters typical of the fossil proteaceous genus Euproteaciphyllun (Carpenter & Jordan 1997; Jordan et al. 1998).

Each fossil taxon from Cambalong Creek has a suite of cuticular characters enabling it to be compared favourably with taxa in either one of the extant tribes Banksieae, Embothriæae, Helicieae, Knightiæae or Oriteæae in subfamily Grevilleioideae. Distributions of the nearest living relatives of the fossils are shown in Fig. 2 and Table 3. Carpenter (1994) described tribal and generic characteristics of extant taxa growing in the Wet Tropics region of north Queensland; certain of these extant taxa share many similarities with proteaceous macrofossils from Cambalong Creek, and contribute to a solid taxonomic framework for the fossils.

Fossil proteaceous cuticles from Cambalong Creek were compared with those of 19 extant taxa representing two subfamilies, six subtribes and five tribes on the basis of a data set of 32 micromorphological characters. Pattern analyses of the data sets were conducted as for the Lauraceae fossils from the locality (described above). Two fossil taxa compare favourably with extant taxa in tribe Embothriæae (including the genus Stenocarpus; Table 1) on the basis of thickened bands of cuticle over the outer surface of guard cells and subsidiary cells (Fig. 12; g, su), which are characteristic of most extant taxa in the tribe (cf. Fig. 12 and Fig. 13; Carpenter 1994). These fossils share many micromorphological characters with extant Stenocarpus simulatus and S. verticis, including striated or rugulated outer abaxial surfaces, superficial stomates, prominent inner cuticular ledges and epidermal anticlinal walls with irregular thickenings.

One fossil taxon from Cambalong Creek is very similar in cuticular morphology to two extant taxa in tribe Helicieae: Hollandaeæa riparia (subtribe Hollandaeinae) and Helicia glabriflora (subtribe Heliciinae: cf. Figs. 14 and 16 with Figs. 15 and 17). The fossil has highly granular inner periclinal surfaces (Fig. 16, p), typical of extant Helicia and Hollandaeaæa (Fig. 17, p; Carpenter 1994), and all three taxa have vein courses marked by elongate cuticular striations. The fossil taxon has a thickened ring of cuticle over the outer surface of the guard cells and striated thickening over subsidiary cells (Fig. 14; g, su), which are typical of extant subtribe Heliciinae, including Hollandaeæa riparia (Fig. 15; g, su: Carpenter 1994). The inner stomatal structure of the fossil is similar to that of H. riparia in terms of prominent inner cuticular ledges (Fig. 16; i), granular periclinal walls over the guard cells and thickened, heavily granular periclinal walls over the subsidiary cells. The fossil taxon differs from extant Heliciaæaæ by not having trichomes, which are large and characteristic in extant taxa of the tribe, though very rare in H. riparia (Carpenter 1994).

A fourth fossil taxon from Cambalong Creek appears closely related to extant Darlingia (tribe Knightiæae), a genus of two species endemic to rainforests of north-east Queensland (Table 3 and Fig. 2; Hyland 1995b). Epidermal cell outer surfaces of the fossil are covered in intricate striations (Figs 18 and 20, st) that are typical of extant Darlingia (Figs. 19 and 21, st), Eucarpha and Knightia in subtribe Knightiinae (Carpenter 1994; Carpenter & Pole 1995).
Figs. 14-23: electron micrographs of fossil cuticles from Cambalong Creek and extant Lauraceae and Proteaceae cuticles; all scale bars indicate 10 μm. Fossils are indicated by the prefix CMB; extant taxa followed by accession numbers in parentheses: MEL = Royal Botanic Gardens Melbourne; AWD = A.W. Douglas. Figs. 14-15, outer surfaces of stomates, labelled as for Figs. 12-13. Fig. 14: CMB4-62a; Fig. 15: *Hollandaea riparia* (MEL712266). Figs. 16-17, inner surfaces of stomates; i = inner stomatal ledge, p = granular inner periclinal walls. Fig. 16: CMB4-62a; Fig. 17: *Helicia glabriflora* (MEL232949). Figs. 18-19, outer surfaces of stomates; g = outer surface of guard cell, st = cuticular striations. Fig. 18: CMB2c-29; Fig. 19: *Darlingia darlingiana* (AWD629). Figs. 20-21, outer surfaces of trichome bases; c = thickened collar, st - cuticular striations. Fig. 20: CMB2c-39; Fig. 21: *D. darlingiana* (AWD629). Figs. 22-23, outer surfaces of stomates; g = outer surface of guard cells. Fig. 22: CMB4-14; Fig. 23: *Orites diversifolia* (MEL593824).
The thickened ring of cuticle over the outer surface of the guard cells of the fossil (Fig. 18, g) is also characteristic of extant Knightiinae (Fig. 19, g; Carpenter 1994; Carpenter & Pole 1995). The fossil has large trichome bases with a raised ring (collar) of cuticle around the insertion point of the foot cell (Fig. 20, c), and pronounced radiating striations (Fig. 20, st). These characters are also typical of extant Knightiinae (Fig. 21; c, st: Carpenter 1994). However, the fossil has cuticular thickenings at the poles of the guard cells, which are not present in extant Knightiinae (Carpenter 1994). This fossil may indicate the existence of either Darlingia in particular, Knightiinae generally, or a close relative in the Late Paleocene in the Southern Highlands. This correlates with the Cretaceous occurrence in southeastern Australia of pollen similar to that produced by extant Knightia (Dettmann & Jarzen 1991; Specht et al. 1992).

A fifth fossil taxon of Proteaceae from Cambalong Creek (Fig. 22) bears many similarities to extant Orites and Neorites, and may represent a Late Paleocene relative of Oriteae, providing some support for the hypothesis of Johnson & Briggs (1975) that Orites must have evolved by the Paleocene. This fossil is characterised by heavy thickening over the outer surface of the guard cells (Fig. 22, g), abaxial trichomes associated with 2–3 basal cells and striations over the vein-courses only. These characters are typical of extant Oriteae (e.g. Orites diversifolia: cf. Fig. 22 and Fig. 23; Carpenter 1994). The Late Paleocene fossil is similar to three taxa endemic to north Queensland montane rainforests, *O. megacarpa*, *O. excelsa*, and *O. fragrans* in terms of granular inner cuticular surfaces and abaxial trichome structure (Carpenter 1994). The oldest described example of tribe Oriteae (consisting of extant genera *Orites* and *Neorites*) dates from the Early Oligocene (~ 35 Ma; Carpenter & Jordan 1997), although Christop hel et al. (1987) suggested a late Middle Eocene (~ 38 Ma) fossil from Anglesea in Victoria may have been related to extant *Orites*.

The proteaceous taxa from Cambalong Creek described above are significant macrofossil evidence for taxa related to tribes Banksieae, Embothrieae, Helicieae, Knightieae and Oriteae in south-eastern Australia approximately 60 Ma. This closes the wide temporal gap that has existed between the earliest occurrence of these tribes in the macrofossil record and the palynological record. The oldest published macrofossils are Middle Eocene taxa possibly related to *Darlingia* (tribe Knightieae: Table 2; Lange 1978), while the palynological record dates from the Campanian-Maastrichtian, including forms with affinities to extant *Adenanthos*, *Beauprea*, *Stirlingia* (Proteoideae), *Persoonia* (Persoonioideae), *Carnarvonia* (Carnarvonioideae) and Grevilleoideae including *Gevuina-Hicksbeachia*, *Grevillea*, *Knightia*, *Macadamia*, *Telopea*, and possibly *Embothrium* (Dettmann 1989; Dettmann & Jarzen 1990, 1991; Specht et al. 1992).

4 DISCUSSION

The nature of the palaeobotanical record, particularly the macrofossil record with identifications based on cuticular characters, reiterates the ancient nature of Lauraceae and Proteaceae in Australia. Johnson & Briggs (1981) hypothesised that most of the tribes and subtribes of Proteaceae had evolved by the beginning of the Late Cretaceous, well before any known fossils with the characteristics of extant Proteaceae. The published macrofossil records (Table 2) correspond on a more general level with the hypothesis of Late Cretaceous diversification of Proteaceae in southern high latitudes (Dettmann & Jarzen 1991). Macrofossil and palynological evidence support an ancient presence of Proteaceae in Gondwana (~ 90 Ma; Dettmann 1989, 1992, 1994; Dettmann & Jarzen 1991; Hill et al. 1993), notwithstanding the unpublished Late Paleocene taxa from Cambalong Creek. The palaeobotanical record is consistent with the hypothesis of Dettmann & Jarzen (1990) that evolution and initial diversification of several clades within Proteaceae (e.g. subfamilies Proteoidae and Grevilleoidae) occurred in the region of the embryonic Southern Ocean before the separation of Australia from Antarctica. The palynological and macrofossil records are consistent with the hypothesis of Johnson & Briggs (1975) that Proteaceae originated before the Middle Cretaceous as part of a mesic, moist forest flora and dispersed with the breakup of Gondwana. This is reflected in biogeographic data superimposed onto phylogenies based on Proteaceae chloroplast sequences (atpB gene and the atpB–rbcL intergenic spacer), which evince divergence of the major groups in the family prior to or during the break-up of Gondwana (Hoot & Douglas 1998). By contrast, many published Cenozoic lauraceous fossils from Australia are younger than those at Cambalong Creek, Nerriga and Angle-
sea described above (Table 1). The more reliable of these descriptions, such as Eocene/Oligocene and Miocene Cryptocarya (Leisman 1986; Rowett 1991; Pole et al. 1993) and Endiandra (Rowett 1991), all nevertheless preceded the ‘contact phase’ or collision between Australia and southeast Asia in the Miocene (Fig. 3; Truswell et al. 1987; Metcalfe 1990; Hall 1996, 1997).

The long Australian fossil record of Lauraceae and Proteaceae demonstrates that the pre-Cenozoic distribution of these plant taxa throughout the Australian region was significant to the current biogeography of these groups, as reviewed for the Austral landmasses by Drinnan & Crane (1990). These distributions arose before the Cenozoic, and prior to any floristic exchanges between the Australian Craton and Malesia. The fossil record and extant distribution of Proteaceae and Lauraceae consequently imply neither family was introduced into the Australian Craton via Malesia subsequent to the Miocene contact phase. Australia and South America are centres of diversity of extant Proteaceae. Forty-six of 79 genera and 1100 of approximately 1700 species of Proteaceae are found in virtually all except the most arid habitats in Australia (Douglas 1995). Most taxa of the sclerophyllous subtribe Banksiinae (the fossil record of which extends to the Late Paleocene, ~58–60 Ma; Fig. 3) are endemic to Australia, and most are restricted in distribution to the Southwest botanical province of Western Australia (George 1999a, b). This high degree of diversity and endemism reiterates a long evolutionary history for the Proteaceae on the Australian landmass.

Martin (1981) recognised a disjunction between traditional concepts of ‘floristic elements’ defined on the basis of extant distributions, and the Cenozoic fossil record, which indicates that many extant northern Australian taxa with ‘tropical’ distributions have been in Australia since the Paleogene. Martin (1981) also proposed that the Cenozoic fossil record of such taxa exemplified continual floral evolution closely linked to climatic change since the Cretaceous, rather than indicating recent migrations from the Malesian region. The temporal and spatial extent of the macrofossil record reviewed here indicates this could be the case for genera with a long fossil history in Australia and even longer records in Europe and North America, specifically Beilschmiedia, Cryptocarya and Endiandra, for example. Beilschmiedia, Cryptocarya, Endiandra, Litsea and Neolitsea are all typical tree components of tropical and subtropical forests in Australia, with all but Beilschmiedia also typical of warm temperate forests (Specht 1981). These closed forests and sclerophyll communities of Australia contain a flora that Specht (1981) suggested must be regarded as of ancient origin. The palynological record indicates that these closed forests were present over most of southern and central Australia in the Paleogene; however, there is no extant equivalent vegetation for comparison with most of these fossil assemblages (Martin 1981).

The macrofossil record for Lauraceae and Proteaceae presented is contrary to the thesis of Herbert (1932) that the rainforests of north Queensland are ‘essentially Malaysian’. The ‘palaetropic element’ was defined on the basis of presumed Malaysian or tropical origin (Herbert 1932, 1967). Proteaceae and Lauraceae constitute part of this northeast Queensland rainforest flora, but Proteaceae first appeared in the Australian region soon after the early diversification of the family in Middle or Late Cretaceous. The flora of Australia at that time was probably the result of a gradual shift in floristic composition of plant communities from the Neocomian to the Senonian, with mostly deciduous gymnosperm communities dominated by forms with cosmopolitan Jurassic affinities and with no modern analogues (Hill et al. 1995) disappearing and being replaced by angiosperms (McLoughlin et al. 1995). The Australian palaeobotanical record of Lauraceae is not as ancient, but nevertheless indicates the presence of the family in southeast Australia many millions of years prior to contact between the Australian craton and Malesia (Fig. 3).

The paleobotanical evidence presented in this review reiterates in a specific sense the importance of the Cretaceous flora of Gondwana to the biogeography of some extant Austral angiosperms, discussed in detail by Drinnan & Crane (1990). Barlow (1981) suggested that the temperate and subtropical rainforests of eastern Australia were derived from an ancient Gondwana flora. The Gondwanan origins of at least some extant rainforest taxa in northeastern Australia previously considered to be of Indo–Malayan or Malesian origin suggested by the fossil record presented here was also indicated by the detailed ecological data of Webb et al. (1984). This plant macrofossil record complicates earlier concepts of the extant flora of Australia being com-
posed of discrete ‘elements’, some of which were defined by distinct Malesian, Antarctic or ‘autochthonous’ origins.

ACKNOWLEDGEMENTS

The authors are grateful to Associate Professor Ian Metcalfe for the opportunity to contribute to this volume, to Associate Professor Andrew Drinnan and Dr Stephen McLoughlin for valuable comments and suggestions on the manuscript, to Professor James Ross and the staff of the Herbarium, Royal Botanic Gardens Melbourne for use of the extant Lauraceae and Proteaceae collections, and to Dr Andrew Douglas for access to his collection of extant Proteaceae. Fossil data from Cambalong Creek presented in this report was gathered whilst AJV was a postgraduate student in the School of Botany, The University of Melbourne. Preparation of this report was funded by Australian Research Council Large Grant A39802019 to DRG.

REFERENCES


