# The Brandy Creek fossil flora

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## Declaration of authenticity

"I, Rachael Louise Keefe declare that the PhD thesis entitled The Brandy Creek fossil flora is no more than 100,000 words in length including quotes and exclusive of tables, figures, appendices, bibliography, references and footnotes. This thesis contains no material that has been submitted previously, in whole or in part, for the award of any other academic degree or diploma. Except where otherwise indicated, this thesis is my own work".

Signature Date

## Abstract

A detailed quantitative study of the fossil flora, palaeoclimate and palaeoecology of the Eocene Brandy Creek fossil site, Bogong High Plains, Victoria, Australia was undertaken. Taxonomic assessment of Leaf macrofossils reveals 18 morphotypes that have affinity with nearest living relatives including Lauraceae genera *Cryptocarya*, *Endiandra* and *Litsea* and the families Cunoniaceae and Elaeocarpaceae. The pollen and spore record at Brandy Creek reveals 36 palynomorphs, with many of them having affinities with fossil and modern Dicksoniaceae, Araurcariaceae and Proteaceae and *Nothofagus*.

The Palaeoclimate of the Brandy Creek flora was reconstructed using Leaf Margin Analysis and Bioclimatic Analysis giving a Mean Annual Temperature (MAT) of 19.7 °C and 18.7 °C respectively. The climate profile of Brandy Creek is indicative of mesothermal rainforests of north eastern Queensland today.

Using both taxonomic information from leaf macrofossil and palynomorphs, combined with palaeoclimate data the Brandy Creek palaeoecology is reconstructed. The result show that the Brandy Creek flora is moderately diverse. The flora at Brandy Creek is representative of the flora that was present in south eastern Australia during the Eocene. The diversity of the Brandy Creek flora is comparable to the modern day forest of north eastern Queensland and is characteristic of simple notophyll – microphyll vine forest with an MAT between MAT of 15.7– 21.7°C and a MAP of 107 – 320cm/yr which is indicative of mesothermal conditions.

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# Chapter 1 Introduction

The late Eocene (37.2 - 33.9mya) marks the end of an interval during which the world's biota evolved into forms recognisable today and the Northern Hemisphere continents adopted their current position, while Australia commenced its northward movement from high southern latitudes (Wing and Greenwood 1993; Quilty 1994; Zachos, Stott and Lohmann 1994; Greenwood and Wing 1995). Analysis of sea surface temperatures shows that the once warm oceans of the early Eocene and for a brief period during the Middle Eocene Climatic optimum (MECO) were between ~ 24 - 28°C and had begun to cool during the late Eocene to ~ 20°C (Huber and Caballero 2011). Carbon dioxide levels that were estimated to be 4400 ppm during the early Eocene and 2000 to 3000ppm again during the MECO had fallen by a further 1000 ppm by the late Eocene (Liu et al. 2009; Bajl et al. 2010; Pearson and Palmer 2000; Huber and Caballero 2011).

The Eocene has been used as a benchmark for understanding climates warmer than those of today, and provides the means to understand better trends in current global warming climate and how these can affect ecosystems (Gajewski 1993; Greenwood and Basinger 1993; Shellito and Sloan 2006; Zachos et al. 2008; Huber and Caballero 2011; Pross et al. 2012; Smith et al. 2012).

The steady increase in the number of documented Eocene floras across Australia and the globe and the development of regional and global calibrations for both palaeoclimate and palaeoecological reconstruction has improved our understanding of how plants adapt to changes in climate as a result of elevated carbon dioxide levels and temperature (Peppe 2010; Greenwood et al. 2003 and 2004; Carpenter et al. 2007 and 2012; Smith et al.2010; Bannister et al. 2012; Lee et al. 2012).

Understanding past palaeoclimate is particularly important given the anthropogenically induced increase in carbon dioxide levels and its effects on the

environment, particularly those resulting in melting of ice at the poles, and increase in sea surface and terrestrial temperatures. Understanding how individual plants and plant communities adapt to shifts in environmental conditions is important to determine conservation and management programs particularly for rare and endangered species. Insight into past environments can assist us to understand how best to manage future climate changes; the plant fossil record allows us to do this.

Paleogene plant fossils have been reported from localities on the Bogong High Plains and other sites from various altitudes in the Eastern Highlands of Victoria (Paterson 1935; Douglas 1978; Christophel 1980; Keefe 2000; Greenwood, Vadala and Douglas 2000; Greenwood et al. 2003; Carpenter et al. 2004). Of these, only three localities are at high altitudes; the late Middle Eocene to Late Eocene localities at Hotham Heights and Brandy Creek and the Oligocene Bundara River locality (Keefe 2000; Greenwood, Vadala and Banks 2000; Greenwood et al. 2003; Carpenter et al. 2004).

Previous research at Brandy Creek provided preliminary data on taxonomic diversity and abundance (Keefe 2000; Greenwood et al. 2003), whereas Carpenter et al. (2004) provided a preliminary taxonomic analysis of the Hotham Heights macro- and microfloras, but provided no quantitative assessment of either the flora (palaeoecology) or estimates of the palaeoclimate.

The research presented in this thesis builds on the preliminary work by Keefe (2000); and reported in Greenwood et al. (2003) by undertaking a quantitative analysis using partial and entire leaf macrofossil. Leaf samples and concomitantly collected palynological samples are used to reconstruct the palaeoecology and palaeoclimate of the Brandy Creek Eocene fossil locality. There were four objectives to the research:

1. Undertake a taxonomic analysis of the Brandy Creek leaf macrofossils;
2. Document the Brandy Creek pollen and spore microflora;
3. Reconstruct the palaeoclimate of Brandy Creek using palaeobotanical climate

proxies;

4. Identify trends in plant community dynamics over the time represented by the sediments exposed at Brandy Creek mine.

The following chapters were prepared as papers intended for publication; therefore, each chapter can be treated separately with each having its own introduction and literature review, methods, results, discussion and conclusions.

**Chapter 2** "Leaf macrofossils of the Brandy Creek Eocene locality, Bogong High Plains, Victoria", builds on the preliminary taxonomic assessment of the Brandy Creek flora by Keefe (2000). For the first time the flora is quantitatively sampled providing the foundations for palaeoclimatic (Chapter 4) and palaeoecological (Chapter 5) reconstructions. Cuticular and gross morphological characters are recorded and hierarchical clustering is used to determine the level of dissimilarity among morphotypes and where possible morphotypes are assigned to nearest living relatives.

**Chapter 3** "The Brandy Creek Microflora (Spores and Pollen)", provides additional information on the floristic character of the vegetation that is absent from the Brandy Creek macrofossil record; microfloral and macrofloral data are complimentary owing to differences in transport and preservation potential between spores-pollen and leaves, and between taxa for the same organ (Greenwood 1991). Using previous identification of pollen and spores across southern Australia, the pollen and spores at Brandy Creek are identified to stratigraphic spore-pollen taxa, and where possible assigned to a nearest living relatives. The data from this chapter contributes to a bioclimatic analysis of the Brandy Creek flora (Chapter 4) and an assessment of plant community structure in Chapter 5.

**Chapter 4** "Palaeoclimate reconstruction of the Brandy Creek Eocene locality, Bogong High Plains, Victoria, Australia", uses two methods to reconstruct palaeoclimate. The first uses a foliar physiognomy method known as Leaf Margin Analysis (LMA). Using

both regional and global calibrations, mean annual temperature for the Brandy Creek flora is calculated based on the proportion of toothed versus non-toothed dicot angiosperm species. A second method, Bioclimatic Analysis, uses nearest living relatives of the leaf, pollen and spores documented in Chapters 2 and 3, and applies the climate tolerances of modern floras to the fossil flora at Brandy Creek. Nearest living relative analogy assumes that the climate tolerances of fossil flora taxa are the same as those of their modern counterparts. The Mean Annual Temperature (MAT) for regional floras is updated with new climate profiles added to the original data set developed by Greenwood et al. (2003). These additional data improve the accuracy of the MAT for Brandy Creek and the other Eocene localities.

Additional indicators of Eocene climate at Brandy Creek are applied, including the presence and grade of epiphyllous fungi in a fossil flora (i.e., fungi found attached to leaf surfaces), as well as additional leaf morphological characters such as the presence of drip tips which can be indicators of wet climates.

**Chapter 5** " Palaeoecological reconstruction of the Brandy Creek Eocene locality, Bogong High Plains, Victoria, Australia", the penultimate chapter, brings together the taxonomic analysis of the macrofossil record determined in Chapter 2 and the pollen and spores fossil record determined in Chapter 3, with the climate analysis in Chapter 4. Collectively, the data and taxonomic determinations from these chapters are used to reconstruct the palaeoecology of the Brandy Creek Eocene locality. Key elements of the chapter include: 1) a review of the floristic composition of the flora, using both the leaf macrofossil and pollen and spore record; and 2) analysis of trends in community dynamics and diversity by comparing the 17 units that have been sampled vertically at the Brandy Creek locality.

Additional data afforded by the Brandy Creek leaf macrofossil and microfossil records contribute to the understanding of the regional (i.e. south eastern Australia) community dynamics during the Eocene. Comparison is made between Brandy Creek and the other Eocene fossil localities from south eastern Australia as well as New Zealand that represent the same or slightly older time frames to determine regional

trends in both floristic composition and diversity. This chapter therefore discusses Brandy Creek in the global context, looking at the common elements of floristic composition, diversity and climate as well as how the Brandy Creek flora compares to regional and global landscapes during this time.

**Chapter 6** provides an overview of the key findings of the research and presents suggestions for further work leading on from this study.

Included in Appendix 1 are 2 papers that in part were generated from the research presented in this thesis, and for which I am co-author. The paper by Greenwood et al. (2003) includes initial data from the Brandy Creek Eocene flora. The second work is an 'in preparation' manuscript prepared by Greenwood, Webb and Keefe for the peer-reviewed science journal 'Geology'. In each case I contributed to the writing and interpretations presented.

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# Chapter 2 Leaf macrofossils of the Brandy Creek Eocene locality, Bogong High Plains, Victoria.

## 2.1 Introduction.

The use of leaf macrofossils has become a commonplace method for the quantitative reconstruction of past floras and by extension past climates (e.g., Mosbrugger and Utescher 1997; Greenwood et al. 2003 and 2010; Uhl et al. 2007; Herman and Spicer 2010). Leaves of terrestrial species, unlike pollen of these very same species, are particularly useful for the construction of local floras due to leaves having a limited dispersal range. Leaves have a tendency to fall in close proximity to the parent plant while pollen, for the most part, is highly mobile and may travel many kilometers from the source of origin (Greenwood 1991; Cronin 1999). Because of the limited dispersal range of leaves, very specific and locality sensitive data can be compiled from the examination of these leaf macrofossils and their use in comparison to extant species (Wilf et al. 1998).

The Brandy Creek fossil site, which contains large numbers of plant macrofossils, is located in the Victorian High Plains Australia. Whilst the Brandy Creek Fossil site is the largest and best known of the plant macrofossil sites, Paleogene plant fossils have also been reported from other localities with various altitudes on the Bogong High Plains and indeed other sites in the Eastern Highlands of Victoria (Paterson 1935; Douglas 1978; Christophel 1980; Keefe 2000; Greenwood 2001; Greenwood et al. 2003; Carpenter et al. 2004). Due to tectonic activity and erosion of the Victorian High Plains there is a generally sparse record of Paleogene deposits in the eastern highlands of Victoria (Holgate et al. 2008). Only three of the known Paleogene localities are at high altitudes: the Eocene localities at Hotham Heights 1km ESE from the Mt Hotham resort on the Great Alpine Road (36°59.65'S, 147°09.32'E, 1733 a.s.l) and Brandy Creek approximately 5 km west of Hotham Heights near Dinner Plain (37°01' S, 147° 13' E 1500 a.s.l) and the Oligocene Bundara River is approximately 0.9 km and 116° SE of Mt Jim on the banks of the Bundara River (36°56.08'S, 147°14.08'E, 1647 a.s.l) (Keefe 2000; Greenwood et al. 2000;

Greenwood et al. 2003; Carpenter et al. 2004).

Records of plant macrofossils at Brandy Creek date back to the 1930's when plant fossils were discovered during gold mining operations. Paterson (1935) recorded the presence of the gymnosperm *Ginkgo L.*, and dicot taxa originally described by the authors as *Laurus L.*, *Eucalyptus L'Her.* , and *Ficus L.*, and the fern *Lastraea*. However, most of these initial identifications now have been shown to be incorrect after re-examination and comparison to additional, more recently collected and identified specimens (Greenwood et al. 2000). Subsequent investigations at Brandy Creek have indicated an infructescence of *Gymnostoma* Casuarinaceae R.Br). Initially described by Douglas (1978), the identification of the infructescence was verified by Christophel (1980) as *Casuarina* subgenus *Gymnostomae*, and confirmed most recently as a species of *Gymnostoma* L.A.S Johnson by Scriven and Hill (1995).

Palynofloras from Brandy Creek sediments were previously determined to belong to the upper *Malvacipollis diversus* zone of the Gippsland Basin palynostratigraphic scheme (Stover and Partridge 1973; Macphail et al. 1994), thus placing these sediments as Early Eocene (55.8 – 48.6 million years before present) (Scriven and Hill 1995; Partridge 1998; Greenwood et al. 2000; Carpenter et al. 2004). However, recent analysis by Holgate et al. (2008) correlated the Brandy Creek palynoflora to the Middle *Nothofagidites asperus* Zone, indicating a Late Eocene age (37.2 – 33.9my before present).

Several preliminary examinations of the Eocene flora at Hotham Heights and Brandy Creek by the author and others suggest that conditions were significantly warmer than at present (Keefe 2000; Vadala and Greenwood 2001; Greenwood et al. 2003; Carpenter et al. 2004). These warmer climates supported plant taxa typical of mesothermal to megathermal rainforest, including a high diversity of Lauraceae Jussieu, Proteaceae Jussieu, Elaeocarpaceae Juss ex D.C. and Cunoniaceae R.Br. Interestingly, the nearest living relatives of the plant macrofossils at Hotham Heights and Brandy Creek are

now restricted to and considered endemic to the Humid Wet Tropical zone of north eastern Queensland (Keefe 2000; Vadala and Greenwood 2001; Greenwood et al. 2003; Carpenter et al. 2004).

This study builds on the preliminary taxonomic assessment of the Brandy Creek flora by Keefe (2000). Taxonomic assignment is based largely on cuticular character, with gross morphological characters recorded when possible. Hierarchical clustering is used to determine the level of dissimilarity among morphotypes and where possible morphotypes are assigned to nearest living relatives.

## 2.2 The use of leaf and cuticular morphology in the identification of leaf macrofossils.

### 2.2.1 Leaf architecture.

The use of leaf architecture and morphology as a means of identifying plants was first attempted by von Ettingshausen in 1861 (Hickey 1973). More recent authors have developed sophisticated leaf architecture classification systems and attempted to standardize leaf architecture terminology and classification (Dilcher 1974; Ellis et al. 2009). The use of leaf architecture has become refined to such a degree as to allow for the delineation of some taxa into taxonomic orders. A prime example of this is a complex taxonomy of the Laurales based on particular characters including features such as; leaves simple, margin entire, venation pinnate, secondary veins brochidodromous and some cases of Lauraceae acrodromous, inter secondary veins common or tertiary veins reticulate to transverse (Hickey and Wolfe 1975). The limitations with these methods is that in many cases individual or a combination of characters, like the ones described above, are not restricted to one family or order, and cannot be used in isolation to identify fossil morphotypes.

### 2.2.2 Leaf cuticle

As the use of leaf architecture has become more sophisticated, the shortcomings of the method have been highlighted. Of particular interest is the question: what morphological features can be used for identification in the absence of clear leaf architectural features? Leaf cuticle characteristics have been identified to be of considerable benefit in the diagnosis of macrofossil families even in the absence of leaf architecture, which can often be the case with fossil macroflora and as is the case at Brandy Creek which has only a small number of complete leaves resulting in cuticle characters being the main form of identification of the Brandy Creek leaf macroflora (Hyland 1989; Pole 2007). The cuticular membrane is highly resistant to oxidation, therefore making it an ideal candidate for preservation in depositional environments and in providing key taxonomic information of past floras (Barclay et al. 2007). Identification of cuticular morphological characteristics to assign fossil morphotypes to an extant family and in some cases a genus or genera, is increasingly being utilised. Taxonomically useful characters include details of the stomatal complex, trichomes bases, and the form and arrangement of epidermal cells. Cuticular morphological identification has been applied to several families typically used to determine fossil floras in Australia, including: Araucariaceae Jussieu (Stockey and Ko, 1986); Myrtaceae Jussieu (Christophel and Lys, 1986); Lauraceae (Hill 1986; Christophel 1986; Bannister et al. 2012); Cunoniaceae, and Elaeocarpaceae (Carpenter et al 2004). Although determination and assignment of particular cuticular morphological types to a given genus or family is possible, there are limitations. These limitations are primarily due to the differing levels of cuticle preservation which can obscure some characteristics. Additionally, the long time period, coupled with evolutionary processes, between taxa of fossil flora and their nearest living relatives can obscure critical details. For the above reasons, it is prudent to assign macrofossils as having only an affinity with a particular genus or family rather than taking the absolutist position.

Lack of clarity in the definitions of morphological and architectural characters used to score morphotypes can be problematic. Certain morphological and architectural characters having many variations and terminology is not consistently used. A typical

example of such a problem relates to epidermal anticlinal walls, which can be straight and easily identifiable; however, the difference between sinuous and curved anticlinal walls is often determined by individual assessment rather than a particular formula. Using a combination of characters to score morphotypes provides a much better and more robust method of identification. It is becoming increasingly common to include multiple characteristics such as epidermal cells' anticlinal and periclinal walls, guard cells, stomata and trichome bases. Using multiple characteristics has made identification and close affinity assignment to extant genera possible (Barclay et al. 2007). Additionally, these multiple character set identifications have allowed authors such as Christophel et al. (1987); Hill (1986); Barrett and Christophel (1990) and Carpenter et al. (2004) and (2007) to assign with some confidence, fossil morphotypes to family and genera based on cuticular morphology. Interestingly, for some families such as Lauraceae these multiple character set identifications are congruous with traditional morphological taxonomic identification tools such as fruits and flowers (Christophel and Rowett 1996).

### 2.2.3 Lauraceae Jussieu

The use of a combined analysis of leaf architecture and cuticular morphological characters as a method of identification of Lauraceae morphotypes and subsequent comparison of these types with extant genera has been almost universally adopted by authors in Australia and globally, Bandulska (1926), Hill (1986); Carpenter et al. (2004) Bannister et al. (2012) (New Zealand); Kovach and Dilcher, (1984) (North America), Lott et al. (2011) Costa Rica; Worobiec (2007) (Poland); Iglesias et al. (2008) (Patagonia). When considering the characters of particular families, not all cuticular features are diagnostically useful. For example, there are a number of features that apply to all genera in the Lauraceae; all are hypostomatic and the stomatal arrangement is paracyctic. Unfortunately, these characters also overlap with other families in the Laurales, having been documented in Myristicaceae R.Br. Because of this high degree of overlap these particular features offer no diagnostic value within the order Laurales unless used in

combination with other more diagnosic features (Upchurch and Dilcher 1990; Christophel and Rowett 1996).

When assigning a fossil morphotype in the Lauraceae family, stomatal characters can be a significant diagnostic tool, with the stomata of particular genera having different configurations and characteristics; e.g., butterfly-shaped cuticular scales (*Cryptocarya R.Br.* and *Beilschmeidia Nees*) and double cuticular scales (*Endiandra R.Br.)*. Individually, these distinctive stomatal characteristics do not assist in the delineation of genera. However, stomatal characteristics used in combination with other cuticular features, including epidermal cells and trichome bases, allow determination of affinities between modern and fossil genera of Lauraceae (Hill 1986; Christophel and Rowett 1996; Carpenter et al. 2007; Nishida and van der Werff 2007). Early identifications of Lauraceae using much less robust multiple character data sets ascribed many 'Lauraceae' to *Laurophyllum* (a form genus - a genus based on non-sexual morphological characters), indicating only general affinity with Lauraceae (Hill 1986; Carpenter and Pole 1995). More recently, work completed by Christophel, Hyland and Whiffin (1993), and Christophel and Rowett (1996), combining leaf venation, leaf shape and cuticle characters of extant Australian Lauraceae taxa, has been used to assign fossil taxa to extant Lauraceae genera. Phylogenetic analysis shows that this combined non-sexual morphological character method has limitations. For example cuticle characters of *Litsea* Lam and *Lindera* Thunb indicate that the two genera can be distinguished; *Lindera* having large stomata and angular subsidiary cells, whilst some *Litsea* are strongly papillate and have a prominent ring around the stomatal complex (Christophel and Rowett 1996). This comparison is based on a single species of *Lindera* in Australia and is therefore not representative of the genus as a whole. Phylogenetic analysis shows that the relationship between *Litsea* and *Lindera* is polyphyletic with at least gross commonality between a number of species in each genera (Li et al. 2008; Fijridiyanto and Nurakami 2009).

***Lauraceae fossil record***

Fossil evidence of Lauraceae is found across the globe and includes flowers, fruits, inflorescences, leaves and wood dating from the mid Cretaceous to the late Paleogene (Drinnan et al. 1990; Herendeen 1991; Eklund and Kvaček 1998; Eklund 1999; Qiu, et al. 1999; Frumin et al. 2004; Renner 2004; Bannister et al. 2012). Lauraceae fossils have been found in the Maastrichtian in the Northern Hemisphere, and the upper Cretaceous in New Zealand (Pole 1992). Paleocene floras containing Lauraceae have been recorded in North America, Princeton chert, British Columbia, Canada (Little, Stockey and Penner, 2009) and central and eastern Europe (Crane 1987; Eklund and Kvaček 1998). The London clay floras include Lauraceae taxa such as *Beilschmeidia*, *Endiandra* and *Litsea* (Chandler 1964; Collinson 1983).

The use of cuticle structures to identify fossil Lauraceae has shown that there is an abundance of Lauraceae fossils in Paleogene floras across Australia. The earliest Australian record of Lauraceae is from the Late Paleocene at Cambalong Creek in New South Wales. The Cambalong Creek fossils contain specimens that have been identified as having an affinity with the Lauraceae genera *Beischmiedia, Cyrptocarya, Endiandra and Litsea* (Vadala and Greenwood 2001). Lauraceae, or species with an affinity to Lauraceae have been described from other Paleogene localities in Australia including Anglesea, Hotham Heights and Brandy Creek in Victoria, Golden Grove in South Australia, Nerriga in New South Wales and the Lefroy Paleodrainange (Pidinga formation) in Western Australia (Christophel, Harris & Syber 1987; Hill 1982, 1986; Carpenter and Pole 1995; Carpenter et al. 2004; Keefe 2000; Greenwood 2001).

The macrofossil record is particularly important in understanding Lauraceae due to lack of microfossils. Absence of Lauraceae pollen in the fossil record due to the poor preservation of the pollen exine (Macphail 1980) means that current understanding of the history of the family depends on its macrofossil record containing predominantly leaves but also fruits, flowers, and wood (Leisman 1986; Macphail 1980; Macphail et al. 1994;

Eklund 1999; Vadala and Greenwood 2001; Hably 2007; Pole 2007; Lee et al. 2012; Bannister et al. 2012).

### 2.2.4 Cunoniaceae R.Br and Elaeocarpaceae Juss

The assignment of fossil morphotypes to either the Cunoniaceae or Elaeocarpaceae cannot be definitively carried out based on leaf and cuticle morphology alone due to the similarities of the two families (Pole 1996). Barnes and Hill (1999) completed a detailed study of Cunoniaceae leaf morphology including cuticles, however a comparative study has not been done for Elaeocarpaceae. Cuticle characters typical of Cunoniaceae/Elaeocarpaceae include a dark staining ring on the inner stomatal ledge, thickened rim of the outer stomatal ledge and T pieces of thickened cuticle at poles of guard cells, although these characters do not occur together in all genera (Pole 1996; 2008).

Fruits and flowers resembling Cunoniaceae have been recorded from Australian localities including Fruits from Middle Eocene Maslin Bay (Barnes and Hill 1999), flowers from Early Oligocene Cethana (Barnes et al. 2001). The earliest record of a Cunoniaceae macrofossil is *Eucryphia falcata* R.S. Hill from the Late Paleocene (Barnes et al. 2001). Leaf macrofossils with an affinity to Cunoniaceae have been found at sites including Cethana and Regatta Point in Tasmania, Anglesea, Hotham Heights and the La Trobe Valley in Victoria, Maslin Bay and Golden Grove in South Australia, and West Dale in Western Australia (Barnes et al. 2001; Carpenter et al. 2004).

Fossil fruit, leaves, pollen and flowers of Elaeocarpaceae have been documented from Paleogene sediments in southeastern Australia, including Lake Eyre Basin (Early Eocene), Anglesea (Middle Eocene), and Golden Grove (Middle Eocene) (Rozefelds and Christophel 1996). The earliest record of Elaeocarpaceae in Australia was recorded by Duigan (1951) who documented 8 leaf macrofossils from various localities in southeastern Australia. Subsequent work by Hill (1988) dismissed Duigan's (1951) taxonomic assignment of the 8 leaf macrofossils to Elaeocarpaceae. Carpenter et al. (2004) described some unidentified angiosperms from Hotham Heights with a possible affinity to

Elaeocarpacae. Vadala (2001) described Elaeocarpaceae aff. *Elaeocarpus* L.from Cambalong Creek in Victoria.

Globally, Cunoniaceae/Elaeocarpaceae fossils have been found from the Miocene of New Zealand (Pole 2008; Lee et al. 2012), Eocene and Oligocene fossil wood aff. Cunoniaceae from Europe (Friis et al. 2011), Elaeocapraceae leaf cuticle from the Oligocene of Italy (Hably 2007), fruits from the Paleogene of North America (Manchester 1999 and Manchester and Kvaček, 2009), and wood aff. Elaeocarpaceae from Antarctica (Francis et al. 2009).

## 2.3 Materials and Methods

### 2.3.1 Locality Description

Fossil leaves that form the basis of this research were collected from Paleogene age sediments that crop out in the abandoned Brandy Creek gold mine. The mine site is located 7.8 km east-southeast of Hotham Heights, Bogong High Plains, northeast of Melbourne, Victoria, Australia, (37° 01’ S, 147° 13’ E; Map reference 8323 Dargo 55HEV 030188), at an altitude of 1500 m asl (above sea level) (Figure. 2.1). Middle Eocene to Late Oligocene basalts that cover parts of the Bogong High Plains crop out at Brandy Creek. Sediments from the locality previously have been dated as Early to Middle Eocene (Scriven and Hill 1995; Partridge 1998). However recent analysis by Holdgate et al. (2008) dated the locality as Late Eocene biostratigraphically through correlation of the microflora with the *Nothofagdities asperus* zone of the Gippsland Basin palynostratigraphic scheme (Stover and Partridge 1973; Macphail et al. 1994; Partridge 1999).

Gold mining operations at Brandy Creek during the 1930's and subsequent erosion have exposed sediments on a cutaway of the hillside with several outcrops showing dark carbonaceous fragments eroding from the sediment. The outcrop sampled for this study is an exposure of fluvial sediments including dark mudstone, siltstone and sandstone in

which sediments are differentiated into discrete layers, with obvious leaves preserved as compression fossils (Figure 2.2 and 2.3)(Greenwood et al. 2000; Keefe 2000).

### 2.3.2 Site Sampling

Sampling from Brandy Creek outcrop provided more than 500 partial or entire leaves across the site for taxonomic analysis. Leaf samples from each unit (Figure 2.2) were selected if an entire leaf,margin, base or apex was evident. Leaf macrofossils were sampled quantitatively to obtain ecological information, such as species dominance and diversity. Field census data from laterally continuous fossiliferous sediments, and studies based on present day leaf litter, have shown that large numbers of specimens (greater than 350) can be used to closely approximate patterns of dominance and overall floristic richness of the original floral community (Burnham et al. 1989, 1993; Burnham et al. 1992; Wing et al. 1995; Wilf et al. 1998). Collections were made vertically to determine temporal variability in taxonomic composition and diversity through time.

### 2.3.3 Fossil preparation.

***Extraction of leaf macrofossils.***

Leaf macrofossils were preserved mostly as compressions with a small number of poorly preserved impressions towards the top of the outcrop, the latter of which were not included in the analysis. Mummified leaves were freed from the mudstone matrix by maceration using dilute (20%) $H_2O_2$ (hydrogen peroxide) using the method of Christophel (1980*)* as modified by Rowett (1991). A small section (up to one centimetre) of leaf was cut from each leaf sample to clear any remaining mesophyll and sediment. Individual sections were placed in test tubes containing 35% $H_2O_2$ combined with several grains of tetra sodium pyrophosphate and covered with parafilm. Tubes were submersed in boiling water for ten minutes in a water bath. If further cleaning was required, cuticles were left in the water bath at a temperature of 80°C for 1- 4 hours, and $H_2O_2$ replenished if necessary. Cleared leaf cuticles were stained using safranin O and mounted on glass microscope slides using Mowiol mounting medium for light microscopy.

Preparation of leaf sections for scanning electron microscopy (SEM) was done with hydrofluoric acid (HF) 49% following the method of Kiger (1971). HF treatment was conducted by Laola Pty Ltd, Perth. Cuticles were soaked in HF for 24 hours to dissolve silicate particles and then rinsed a minimum of ten times with distilled water. Cuticles were returned to Victoria University for further processing, in which the mesophyll was cleared using Jeffrey's Solution (equal parts of 70% $HNO_3$ and 10% aqueous chromic acid; after Stace (1965), modified from Johnson (1940). Stace (1965) noted this process could take between one to four hours depending on the thickness of the cuticle however Brandy Creek cuticles reacted quickly to the solution and most cleared within thirty minutes. Cuticles were cleared when the cuticular envelope became dark brown as the oxidation process proceeded. Subsequent to clearing, cuticles were neutralised by soaking in 5% aqueous $NH_3$ for 15 minutes, then rinsed with distilled water several times.

***Scanning Electron microscopy (SEM)***

Cuticles were mounted on aluminium stubs using double side tape, then air-dried using silica gel in a desiccator for at least 36 hours prior to being sputter coated with gold dust using an Edwards S150B sputter coater. SEM examination and photography was conducted at The University of Melbourne School of Botany using a Phillips XL 30 FEG.

***Photography***

Partial and entire leaves extracted from the mudstone were photographed using Kodak Technical Pan film. Black and white negatives were scanned using a Polaroid Sprint Scan 4000 at 3000dpi. Digital images were taken of the venation patterns of each morphotype using a Zeiss Stemi 2000c dissecting microscope with a DAGE -MTI CCD100 camera attachment. Digital images of leaf cuticle were captured using a Carl Zeiss Axiocam HR, attached to a Zeiss Axioplan 2 light microscope. Images were processed using Adobe photoshop.

### 2.3.4 Taxonomic analysis

Macrofossils were sorted into taxonomic units using established leaf morphological and cuticle characters (Dilcher 1974; Hickey 1973, 1979; Ellis et al. 2009). A large database exists in the botanical literature of diagnostic characters for major Australian families such as Proteaceae Jussieu, Lauraceae, Myrtaceae and Araucariaceae and genera in these families (e.g., Christophel and Rowett 1996; Carpenter 1994; Hill 1986; Bannister et al. 2012).

***Cuticle characters and leaf architecture.***

To determine the number and type of morphotypes present in the samples from Brandy Creek, character lists were constructed, based on characteristics of the Lauraceae family, with the addition of more general characters suitable for other families such as Proteaceae, Elaeocarpaceae and Cunoniaceae. Selection of the character list was based on preliminary work done at Brandy Creek (Keefe 2000). Character lists are broadly based on those of Dilcher (1974) and Christophel and Rowett (1996).

Sorting took place at a number of levels of discrimination. Abaxial and adaxial surface of each cuticle were examined under light microscopy and sorted into broad types based on characters such as vein course cell patterns and areolation pattern. Each cuticle type sorted was further examined using additional character differences, such as presence/absence of trichome bases, frequency and location of stomata. All mounted specimens were assigned to one of these informal groups. A representative specimen was

selected for each morphotype and scored using the character list (Table 2.1). Character scores for each morphotype are presented in Appendix 2. A SEM was used to distinguish characters that could not be seen easily under the light microscope, for example guard cell striations and cuticular scales.

Leaf morphological characters were described using the Manual of Leaf Architecture (Ellis et al. 2009). Descriptions of morphotypes are based on the style used by Paull and Hill (2003) and are presented in the Results below.

***Cluster analysis.***

Cluster analysis was conducted to determine the relationships -among morphotype, based on a defined character set devised by Dilcher (1974) and Christophel and Rowett (1996). The analysis was conducted using PAST (Paleontological Statistics Software Package for Education and Data Analysis Version 2.16; Hammer, Harpe and Ryan 2001). For this analysis Bray Curtis association metric was used with group average link fusion, weighting all character scores equally. Bray Curtis metric was used to determine the level of dissimilarity between each of the morphotypes (Krebs 1989). Dissimilarity is measured based on the number of shared presences, by counting the number of times both morphotypes have the same number of characters present.

The Brandy Creek leaf macrofossils are housed at the Melbourne Museum, Victoria, Australia.

## 2.4 Results

### 2.4.1 Cluster analysis of Brandy Creek morphotypes

The Brandy Creek fossil flora was analysed using Bray Curtis matrix using group average linked fusion based on cuticular characters. The cluster analysis yielded seven clusters, identified on the dendogram as shown in figure 2.4. The point at which the

clusters are separated is at 0.7. At this point most groups can be classified as Cunoniaceae/Elaeocarpaceae; *Cryptocarya* and *Endiandra*. The one group that falls outside of this is *Litsea*, which clusters between 0.6 and 0.7. The clusters are outlined below:

**Cluster 1**

**BC 016, BC 017, and BC 018 aff. Cunoniaceae/Elaeocarpaceae**. BC016 has undulate abaxial and adaxial anticlinal walls, with smooth perclinal walls. BC017 has angular to rounded anticlinal walls and striations on guard cells.BC018 has undulate anticlinal walls on abaxial surface only and perclinal walls are granular.

**Cluster 2**

**BC011, Lauraceae *Litsea bennetti* group.** BC 011 is highly papillate with angular to rounded epidermal cell walls.

**Cluster 3**

**BC012. *Litsea bennettii* group**, BC 012 has undulate anticlinal walls on the adaxial surface and areoles on the abaxial surface.

**Cluster 4**

**BC 009, BC 015, aff. Lauraceae *Cryptocarya***

The dendogram (Figure 2.4) shows that BC 009 and BC 015 are closely aligned based on the level of dissimilarity at less than 0.95. The features that distinguish the two morphotypes from the other clusters, which include *Cryptocarya*, are the presence of areoles. BC 015 is further distinguished from BC009 by the presence of undulate anticlinal walls.

**BC 008 and BC 014 aff. Lauraceae *Endiandra.***

The feature that separates BC008 from other *Endiandra* morphotypes is the presence of T-pieces of thickened cuticle at poles of guard cells. BC 014 is characterised by undulate

anticlinal walls with a high degree of beading particularly on adaxial anticlinal walls of epidermal cells and vein course cells of abaxial surface.

All other *Endiandra* are either grouped together (cluster 6) or individually (cluster 7). At 0.7 dissimilarity, *Endiandra* is clustered with two *Cryptocarya,* but it is clear from the dendogram that as these groups are clustered between 0.8 and 0.9, the *Endiandra* is clearly different from the *Cryptocarya* in this cluster.

**Cluster 5**

**BC 001, BC 002, BC 003 aff. Lauraceae *Cryptocarya***. The character that separates the three morphotypes of *Cryptocarya* (BC 001, BC 002 and BC003) from all others identified is the presence of the mesh- like appearance on the epidermal cell walls.

**Cluster 6**

**BC 004, BC 005, BC 007, Lauraceae *Endiandra*** is characterised by thickening and striations on guard cells.

**BC 006**, **aff. Lauraceae *Endiandra*** is grouped by the presence of mesh-like appearance on epidermal cells of adaxial surface. BC 006 is the only morphotype with an affinity to *Endiandra* to have this characteristic on the adaxial surface.

**BC 010, Aff. Lauraceae *Endiandra*.** BC 010 is distinguished by the absence of characters including thickened guard cells which is evident in BC 004, BC005 and BC007, presence of T pieces of thickened cuticle at poles of guards (BC008) and mesh like appearance on epidermal cells (BC 006).

**Cluster 7**

**BC 013,** Lauraceae aff. *Endiandra* has beaded and ridged anticlinal walls. A fine mesh of epidermal cells surrounds the stomata.

The cluster analysis is based on 76 different characters, however 13 characters have been identified as key characters distinguishing the different morphotypes. These characters are show in Table 2.2. Key feature show that all Lauraceae aff.*Cryptocarya* have

butterfly shaped cuticular scales, while Lauraceae affinity *Endiandra* have double cuticular scales and *Litsea* has single cuticular scales. On a number of the *Cryptocarya* and *Endiandra* specimens there is unusual mesh structure on the epidermal cells. This feature has also been recorded from the Hotham Heights and Nerriga localities (Carpenter 2004; Hill 1986).

### 2.4.2 Taxonomic Descriptions of the Brandy Creek macroflora

**Family: Lauraceae Jussieu**

**Genus: *Laurophyllum* Göppert**

**Morphotypes with affinity to *Cryptocarya* R. Brown**

***Morphotype* BC – 001 Fig. 2.6 - 2.10.**

***Affinity/Identification Cryptocarya pleurosperma* group**

***Count/Specimens* 11 BC 1390**

Leaf symmetrical. Leaf base acute, cuneate. Leaf margin entire. Venation eucamptodromous, spacing uniform, angle uniform. Tertiary venation random reticulate. Higher order veins regular polygonal reticulate. Areoles well developed, with 5 or more sides.

Adaxial surface epidermal cell walls isodiametric, angular to rounded, with mesh appearance of epidermal cells. Epidermal cells elongate over veins. Anticlinal walls smooth, thickened. Periclinal walls smooth to granular. Trichome bases present, with cuticular thickening around pore extending along radial walls of surrounding cells. Abaxial epidermal cell walls isodiametric, angular, with mesh-like appearance of epidermal cells. Epidermal cells elongate over veins. Anticlinal walls smooth, thickened. Periclinal walls smooth to granular. Trichome bases present, porous along vein course cells. Stomata paracytic, randomly orientated with butterfly-like cuticular scales.

**Morphotype BC – 002 Fig. 2.11 – 2.15**

**Affinity/Identification aff*. Cryptocarya pleurosperma* group**

***Count/Specimens* 45** **BC 1608**

Leaf symmetrical, elliptic. Leaf apex acute, acuminate. Base acute, cuneate. Leaf margin entire. Venation eucamptodromous, spacing uniform, angle uniform. Tertiary veins random reticulate. Higher order veins regular polygonal reticulate. Marginal venation looped. Areoles well developed, with five or more sides.

Adaxial epidermal cell walls isodiametric, angular to round with mesh-like appearance of epidermal cells. Epidermal cells elongate over veins. Anticlinal walls smooth, thickened. Periclinal walls smooth to granular. Trichomes bases rare. Abaxial cell walls isodiametric, angular to round with a mesh-like appearance of epidermal cells. Epidermal cells elongate over veins. Anticlinal walls beaded. Periclinal walls smooth to granular. Trichomes bases present. Hydathodes present, epidermal cells surrounding hydathodes cyclocytic. Stomata paracytic with butterfly-like cuticular scales.

Difference between BC001 and BC002

Hydathodes are absent from BC001

***Morphotype BC – 003*** **Fig. 2.16 – 2.19**

***Affinity/Identification Cryptocarya* Not assigned to a group.**

***Count/Specimens* 4** **BC 1205**

Leaf symmetrical. Leaf apex acute, straight. Base acute, cuneate. Leaf margin entire. Venation pinnate.

Abaxial epidermal cell walls isodiametric, angular, rounded to undulate, Epidermal cells elongate over veins. Anticlinal walls smooth, ridged. Periclinal walls smooth to granular. Trichome bases rare. Adaxial cell walls isodiametric, angular, rounded, undulate to sinuous,. Epidermal cells elongate over veins. Anticlinal walls beaded, ridged. Periclinal walls smooth to granular. Trichome bases present. Stomata paracytic with butterfly-like cuticular scales.

***Morphotype* BC – 009** **Fig. 2.20 -2.24**

***Affinity/Identification* aff. *Cryptocarya***

***Count/Specimens* 33 BC1613**

Leaf symmetrical, elliptic. Leaf apex acute, acuminate. Base acute, cuneate. Leaf margin entire. Venation eucamptodromous, brochidodromous, spacing uniform, angle acute. Tertiary veins opposite percurrent, sinuous, uniform, with obtuse angle to primary vein. Higher order veins regular polygonal reticulate. Marginal ultimate looped. Areoles well developed, with five or more sides.

Adaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls smooth, ridged. Periclinal walls smooth to granular. Trichomes bases rare. Abaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls beaded, ridged. Periclinal walls smooth to granular. Trichome bases common. Areoles present. Stomata paracytic with butterfly-like cuticular scales.

***Morphotype* BC – 015 Fig. 2.25 - 2.29**

***Affinity/Identification* aff. *Cryptocarya***

***Count/Specimens* 6 BC 1580**

Leaf microphyll, symmetrical, elliptic. Leaf apex acute, straight, rounded. Leaf margin entire. Venation weak brochidodromous, spacing irregular, angle uniform. Tertiary veins mixed opposite/percurrent, vein course straight, sinuous, angle to primary obtuse. Higher order veins regular polygonal reticulate, marginal ultimate looped. Areoles moderately developed.

Adaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls ridged. Periclinal walls smooth to granular. Trichomes bases rare, mainly over vein course cells. Abaxial epidermal cell walls isodiametric angular, round to undulate. Epidermal cells elongate over veins. Anticlinal walls beaded, ridged. Periclinal walls smooth to granular. Trichome bases common, porous. Hydathodes present. Stomata didactic, paracytic, butterfly-like cuticular scales.

**Morphotypes with affinity to *Endiandra* R. Brown**

***Morphotype* BC – 004 Fig. 2.30 – 2.34**

***Affinity/Identification* aff. *Endiandra jonesii group***

***Count/Specimens* 11 BC 1335**

Leaf symmetrical. Leaf apex acute. Base acute, cuneate. Leaf margin entire. Venation brochidodromous. Vein spacing uniform. Vein angle acute.

Adaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls smooth. Periclinal walls smooth to granular. Trichome bases present. Callimothalloid shields present. Abaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls smooth. Periclinal walls smooth to granular. Trichome bases present, mainly over vein course cells. Callimothalloid shields present. Stomata paracytic with double cuticular scales. Guard cells striated.

***Morphotype* BC – 005 Fig.2.35 – 2.38**

***Affinity/Identification* aff. *Endiandra pubens group***

**Count/Specimens 8 BC 1401**

Leaf architecture absent. Adaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls ridged. Periclinal walls smooth to granular. Trichome bases present. Abaxial epidermal cell walls isodiametric,angular to round. Epidermal cells elongate over veins. Anticlinal walls smooth to beaded. Periclinal walls smooth to granular. Trichome bases very common, porous. Areoles present. Stomata paracytic, anomocytic with double cuticular scales. Guard cells striated, thickened.

***Morphotype* BC –006 Fig.2.39 – 2.42**

***Affinity/Identification* aff. *Endiandra pubens group***

***Count/Specimens* 13 BC1516**

Leaf symmetrical. Leaf apex acute, acuminate. Base acute, cuneate. Leaf margin entire.

Adaxial epidermal cell walls isodiametric, angular to round with mesh-like appearance of epidermal cells. Epidermal cells elongate over veins. Anticlinal walls smooth, thickened. Periclinal walls smooth to granular. Trichome bases present. Abaxial epidermal cell walls isodiametric, angular to rounded. Epidermal cells elongate over veins. Anticlinal walls smooth, ridged, beaded. Periclinal walls smooth. Trichome bases common. Mesh-like appearance of epidermal cells surrounding stomata. Stomata paracytic, anomocytic with double cuticular scales. Guard cells thickened.

***Morphotype* BC – 007 Fig. 2.43 – 2.45**

**Affinity/Identification Not assigned to a group.**

**Count/Specimens 2 BC1526**

Leaf architecture absent. Adaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal cell walls smooth. Periclinal walls smooth to granular. Trichome bases very common. Abaxial epidermal cell walls isodiametric,angular to rounded. Epidermal cells elongate over veins. Anticlinal walls smooth to ridged. Periclinal walls smooth to granular. Trichome bases very common. Stomata diacytic, paracytic with double cuticular scales. Guard cells striated, thickened.

***Morphotype* BC – 008 Fig. 2.46 -2.48**

***Affinity/Identification* Not assigned to a group.**

***Count/Specimens* 2 BC1260**

Leaf architecture absent.

Adaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls buttressed. Periclinal walls smooth to granular. Trichome bases very common. Abaxial epidermal cell walls isodiametric angular, round to undulate. Epidermal cells elongate over veins. Anticlinal walls beaded and ridged. Periclinal walls smooth to granular. Trichome bases common. Stomata paracytic. Stomatal ledge broad with T-pieces of thickened cuticle at poles of guards. Guard cells thickened.

***Morphotype* BC – 010 Fig. 2.49 – 2.53**

***Affinity/Identification* Not assigned to a group.**

***Count/ Specimens* 206 BC1305**

Leaf microphyll, symmetrical, elliptic. Leaf apex acute, straight, acuminate. Base acute, cuneate. Leaf margin entire. Venation eucamptodromous, spacing uniform, angle acute. Tertiary veins random reticulate. Higher order venation regular polygonal reticulate. Marginal ultimate veins looped. Areoles well developed, with five or more sides. Adaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls smooth, buttressed. Periclinal walls smooth to granular. Trichome bases present, glandular. Abaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls granular. Periclinal walls smooth to granular. Trichomes bases common. Stomata paracytic with double cuticular scales.

***Morphotype* BC – 013 Fig 2.54 – 2.57**

***Affinity/Identification* Not assigned to a group.**

***Count/Specimens* 1 BC1051**

Leaf architecture absent.

Adaxial absent. Abaxial epidermal cell walls isodiametric, angular to rounded with mesh-like appearance of the epidermal cell walls. Epidermal cells elongate over veins. Anticlinal walls beaded to ridged. Periclinal walls smooth to granular. Trichome bases common, porous. Stomata paracytic. Guard cells thickened on periclinal wall. Cuticular scales double, inner scale narrow, outer scale broad.

***Morphotype* BC – 014 Fig. 2.58 – 2.62**

***Affinity/Identification* Not assigned to a group.**

***Count/Specimens* 8 BC 1245**

Leaf microphyll, symmetrical, elliptic. Leaf apex acute, straight, acuminate. Base concave-convex, decurrent. Leaf margin entire. Venation eucamptodromous, spacing irregular, angle uniform.

Adaxial epidermal cell walls isodiametric, angular, round to undulate. Epidermal cells elongate over veins. Anticlinal walls beaded. Periclinal walls smooth to granular. Trichome bases rare. Abaxial epidermal cell walls isodiametric, angular, round to undulate. Epidermal cells elongate over veins. Anticlinal walls beaded. Periclinal walls smooth to granular. Trichome bases rare, mainly over vein course cells. Hydathodes present. Stomata paracytic, anomocytic. Guard cells thickened. Cuticular scales double.

**Morphotypes with affinity to *Litsea* Lamarck**

***Morphotype* BC – 011 Fig. 2.63 – 2.67**

***Affinity/Identification* aff. *Litsea bennetti group***

***Count/Specimens* 8 BC 1240**

Leaf architecture absent

Adaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls smooth, beaded and ridged. Periclinal walls smooth to granular. Trichome bases present, porous thickenings. Abaxial epidermal cell walls isodiametric,angular to round. Epidermal cells elongate over veins. Anticlinal walls smooth. Periclinal walls papillate. Trichome bases rare. Subsidiary cells obscured by papillae surrounding stomata. Stomatal ledge straight, narrow, with cuticular collar.

***Morphotype* BC – 012 Fig. 2.68 - 2.70**

***Affinity/Identification* aff. *Litsea bennetti group***

***Count/Specimens* 4 BC 1336**

Leaf architecture absent.

Adaxial epidermal cell walls isodiametric, undulate to sinuous. Epidermal cells elongate over veins. Anticlinal walls smooth to beaded. Periclinal walls smooth to granular. Trichome bases rare. Abaxial epidermal cell walls isodiametric, angular to round. Epidermal cells elongate over veins. Anticlinal walls smooth to granular. Periclinal walls papillate. Trichome bases common, porous with cyclocytic epidermal cell surrounding

trichome base. Hydathodes present. Subsidiary cells obscured by papillae surrounding stomata. Stomatal ledge straight, narrow.

**Family: *aff.* Cunoniaceae/Elaeocarpaceae**

***Morphotype* BC – 016** **Fig. 2.71 -2.75**

***Affinity/Identification***

***Count/Specimens* 37** **BC 1064**

Leaf microphyll, symmetrical elliptic. Leaf apex acute, acuminate, straight. Base acute, cuneate. Leaf margin crenate. Venation brochidodromous, spacing increasing towards base, angle uniform. Tertiary veins mixed opposite, alternate, straight, angle variability inconsistent; angle to primary vein perpendicular. Higher order veins regular polygonal reticulate. Marginal ultimate looped-teeth. Areoles well developed, with five or more sides. Free ending veinlets 1- branched; 2 or more branches. Teeth spacing regular, sinus rounded, apex simple.

Adaxial epidermal cell walls isodiametric, angular. Epidermal cells elongate over veins. Anticlinal walls straight, rounded, undulate, sinuous, knobs. Abaxial epidermal cell walls isodiametric, angular. Epidermal cells elongate over veins. Anticlinal walls straight, rounded, undulate, sinuous, knobs. Stomata randomly orientated anomocytic. Anticlinal walls knobs. T- Pieces of thickened cutin at poles of guards.

***Morphotype* BC – 017** **Fig. 2.76 -2.80**

***Affinity/Identification***

***Count/specimens* 103** **BC 1068**

Leaf elliptic. Leaf apex acute, acuminate. Base acute, cuneate. Leaf margin crenate. Venation weak brochidodromous, agrophic veins simple, spacing irregular. One pair acute basal secondaries. Tertiary veins random reticulate, straight, angle variability inconsistent, angle to primary vein acute. Higher order veins regular polygonal reticulate. Marginal ultimate looped-teeth. Areoles well developed, with five or more sides. Free ending veinlets 1- branched. Teeth spacing regular, sinus rounded, apex simple.

Adaxial epidermal cell walls isodiametric, angular. Epidermal cells elongate over veins. Anticlinal walls straight, rounded, sinuous, knobs, ridges. Periclinal walls striations. Trichome bases present. Abaxial epidermal cell walls isodiametric, angular. Epidermal cells elongate over veins, anticlinal walls straight, rounded, undulate, sinuous, knobs, ridges. Periclinal walls striations, thickened. Trichomes bases present. Glandular/ secretory structure present. Stomata randomly orientated anomocytic. Anticlinal walls knobs, ridges. Periclinal walls of guard cells striate, thickened. T-pieces of thickened cuticle at poles of guards.

***Morphotype* BC – 018** **Fig 2.81 -2.83**

***Affinity/Identification***

***Count/Specimens* 13** **BC 1183**

Leaf microphyll, symmetrical elliptic. Leaf base acute, cuneate. Leaf margin crenate. Venation weak brochidodromous, spacing decreasing towards base, angle uniform. Tertiary veins random reticulate, straight, angle variability inconsistent, angle to primary vein obtuse. Higher order veins regular polygonal reticulate. Marginal ultimate loop-teeth present. Areoles well developed, with five sides. Teeth spacing regular, sinus angular, apex simple.

Adaxial epidermal cell walls isodiametric, angular. Epidermal cells elongate over veins. Anticlinal walls straight, rounded, knobs. Periclinal walls thickened. Abaxial epidermal cell walls isodiametric, angular. Epidermal cells elongate over veins. Anticlinal walls straight, rounded, undulate, sinuous, knobs. Glandular secretory structures present. Stomata anomocytic, cyclocytic. Anticlinal walls knobs. T-Pieces of thickened cutin a poles of guards.

## 2.5 Discussion

### 2.5.1 Lauraceae

Fifteen of the 18 morphotypes 83% were assigned to Lauraceae based on cuticular characters. Figure 2.5. These findings strongly contrast with percentage representation as determined by palynomorh counts described in other parts of this study. Lauraceae, although present in high numbers in the macrofossil record at Brandy Creek, is not documented in the palynomorph count; this reflects the lack of preservation potential of Lauraceae pollen due to exine deterioration (Macphail 1980). The absence of Lauraceae in the Brandy Creek pollen record supports the notion that a holistic approach is required when looking at a fossil flora requiring both leaf and pollen/spores to provide a complete profile. The Brandy Creek palynomorphs are discussed in the following chapter.

For a leaf macrofossil to be assigned to Lauraceae the specimen generally needs to have the following characters; entire margin, hypostomatic, paracyctic stomata, with guard cells and over arching subsidiary cells (Hill 1986; Christophel and Rowett 1996). Individually, these characters are represented in a number of angiosperm families, however collectively they are diagnostics for Lauraceae (Doyle and Endress 2000). Using the key features of Lauraceae in cluster analyses, Lauraceae at Brandy Creek show affinity with three genera; *Cryptocarya* (5 morphotypes), featuring butterfly cuticular scales, *Endiandra* (8 morphotypes) with double cuticular scales, and *Litsea* (2 morphotypes) which have papilliae.

Variation of morphological characters is one of the challenges faced when using leaf cuticle for taxonomic assessment of a flora. For example, Stace (1965) and Wilkinson (1979) noted that there can be a high level of variation in epidermal anticlinal walls. Some highly variable morphotypes, having a combination of both angular and rounded epidermal cell walls, were found in Lauraceae identified at Brandy Creek. There are cases where fossil characters cannot be found in specimens of the modern flora. This is the case for the mesh appearance of the epidermal cells, which is present on 3 of the Lauraceae morphotypes at Brandy Creek, two having affinity with *Cryptocarya* (BC- 001 Figure 8, BC-

002, Figures 13 and 15) and one having affinity with *Endiandra* (BC 006 Figure 40). The meshed epidermal cell feature is documented from other Eocene localities including Hotham Heights and Nerriga, these two floras record the mesh appearance in association with *Endiandra*.. Cuticle characters can also overlap between species of different genera as noted by Li and Christophel (2000), who found that the cuticle characters of *Litsea glutinosa* and *Lindera queenslandica* are similar.

The presence of high numbers of Lauraceae with affinities to *Cryptocarya*, *Endiandra* and *Litsea,* suggests that Lauraceae had a significant presence in the local landscape. The significance of Lauraceae at Brandy Creek is supported by the presence of abundant Lauraceae at nearby Hotham Heights (Figure 2.5). Carpenter et al. (2004) recorded nine species having affinity with *Cryptocarya*, *Endiandra* and *Litsea* at Hotham Heights. Elsewhere in Australia, fossil Lauraceae, identified by cuticular morphological characters, have been recorded. Most notable of these fossil Lauraceae sites is one containing 16 species of *Laurophyllum* from Nerriga, New South Wales, representing 44% of the morphotpyes found at this Eocene site. This high percentage of species at one site represents a major component of the landscape (Figure 2.5) (Hill 1986; Conran and Christophel 1998). Christophel et al. (1987) described Lauraceae from the middle – late Eocene Anglesea flora, with many leaf morphotypes with affinities with modern *Endiandra*, *Litsea* and *Cyrptocarya.* At the site investigated by Christophel et al. (1987) Lauraceae represented 30% of the flora. Lauraceae has been recorded at Golden Grove and Deans Marsh, although they are not as abundant as the above sites comprising approximately 10% of the flora (Figure 2.5) (Barrett and Christophel 1990; Christophel and Greenwood 1987). The thick leaves of Lauraceae aid in their preservation and may account for their high presence in fossil floras in contrast to species with thinner or less persistent leaves. This high preservation level of Lauraceae could overstate the level of importance of Lauraceae in the landscape during this time.

New Zealand Lauraceae has not proved useful in helping to clarify the fossil floras in Australia. Pole (2007) describes 25 morphotypes, which were identified as Lauraceae,

from Miocene sediments of the Manuherikia group New Zealand. Additionally, Bannister et al. (2012), documented 10 morphotypes identified as Lauraceae from the Early Miocene Folder Maar locality in New Zealand. The Lauracae in the New Zealand deposits have no Australian equivalents in either the fossil record or with extant taxa (Bannister et al. 2012).

Lauraceae occur in North America with Kovach and Dilcher (1984) identifying 29 morphotypes as fossil Lauracae from the Middle Eocene Claiborne group in Tennessee, North America. Little, Stockey and Penner, 2009 documented Lauraceae fruits and flowers from Princeton Chert, Princeton Group, British Columbia and Manchester, 1994 recording Lauraceae fruits and seeds from the Clarno formation, Oregon. Wilf et al. (2005), report Lauraceae macrofossils from the Eocene Laguna del Hunco and Rio Pichileufu deposit in Patagonia, Argentina. The London clay flora in England is considered the most diverse Paleogene fossil record in Europe, with more than 150 genera at the locality and more than 30 genera of fruit and seed fossils assigned to Lauraceae (Collinson 1983; Vadala and Greenwood 2001; Kvaček 2010).

### 2.5.2 Cunoniacae/Elaeocarpaceae

Cunoniaceae/Elaeocarpaceae (3 morphotypes) although considered a minor element of the Brandy Creek flora, account for 17% of the macrofossils documented. Cunoniacae is recorded in the pollen sum of Brandy Creek as *Concolpites* affinity *Gillbeea*, however in most cases Cunoniaceae pollen has little diagnostic value as they are present in the pollen sum as syncolpate, dicolp(or)ate or tricolporate grains. (Barnes, Hill and Bradford 2001).

The assignment of fossil morphotypes to either the families Cunoniaceae or Elaeocarpaceae cannot definitively be carried out based on leaf and cuticle morphology alone due to the similarities of the two families (Pole 1996). To distinguish between the two families it would be necessary to have fossil fruits and flowers available, neither of which was found at the Brandy Creek Eocene site.

Cunoniceae and Elaeocarpaceae are not as easily identifiable as the Lauraceae, where there are definitive characters for the family that allow for easy identification of macrofossils. In both Cunoniceae and Elaeocarpaceae there is high variation of characters both between the two families and within genera and species for each family. For example, *Weinmannia* subsidiary cells can be anomocytic, brachyparacytic or encyclocytic (Hopkins and Hoogland 2002). Some genera have T – pieces of thickened cuticle at poles of guard cells as seen in *Schizomeria*, *Ceratopetalum,* and *Platyophus*. These characters relating to subsidiary and guard cells are also evident on Elaeocapaceae leaf cuticle. Vadala and Greenwood (2001) noted the above variation in a number of Elaeocarpaceae morphotypes from Cambalong Creek with affinity to *Elaeocarpus*. Dickison (1975) surveyed the leaf anatomy of species across 24 genera of the Cunoniaceae but only considered a limited number of cuticle characters, and did not discuss characters that are diagnostic for the two families. Individual genera within the Cunoniaceae have been reviewed with cuticle information included in the analysis (e.g., Barnes and Rozefelds 2000; Schimanski and Rozefelds 2002), but to date there has been no comprehensive assessment of cuticular characters for extant taxa of both Cunoniaceae and Elaeocarpaceae.

Cunonicace/Elaeocarpacae morphotypes at Brandy Creek have not been assigned to a genus, however Carpenter et al. (2004) makes reference to a number of unidentified angiosperms which are possibly Cunonicace/Elaeocarpaceae from the Hotham Heights locality. These specimens are similar to those found in this study of the Brandy Creek flora.

The Australian macrofossil record of Cunoniaceae is represented by leaves, leaf fragments, cuticle and reproductive structures. Numerous fossil records suggest that Cunoniaceae was wide-spread during the Paleogene. Barnes et al. (2001) points out that 11 of the 26 genera identified as occurring in Australia today are recorded in the macrofossil record from localities across Australia including Cethana, Maslin Bay, Anglesea, Golden Grove (Barnes et al. 2001). This suggests that the Cunoniaceae was a major component of the landscape during the Paleocene. Nearby Hotham Heights has a

record of only 3 Cunonicaceae morphotypes, 2 with affinity *Wieninnema* (extinct from Australia today) (Carpenter et al. 2004). Today *Weinmannia* has its greatest diversity in South America, Madagascar and South Pacific Islands. The absence of *Weinmannia* from Australian floras is likely to be linked to the northward retreat of rainforests during the Eocene and the use by *Weinamania* of gaps in forest for regeneration (Barnes et al. 2001).

Leaf fossils with affinity to Elaeocarpacae have also been documented from Paleogene sediments including nearby Hotham Heights, Cambalong Creek, Anglesea and Golden Grove (Figure 2.5) (Carpenter et al 2004; Christophel, Harris and Syber 1987; Vadala 2001; Greenwood and Christophel 2005) Globally, Cunonicaceae and Elaeocarpaceae have been recorded from the Laguna de Hunco locality in Argentina (Wilf et al. 2003 and 2005) and nearby in New Zealand Foulder Maar locality (Lee et al. 2012).

### 2.5.3 Modern Counterparts of the Brandy Creek flora

Evidence from Australian and global fossil localities show that Lauraceae, Cunoniaceae and Elaeocarpaceae were abundant in the landscape across southern Australia during the Paleogene. Equally, these families had a greater global distribution than their modern counterparts, reflecting much warmer and more equitable environments during the Eocene. By the Miocene, the Australian continent had cooled and the rainforests that were once widespread across the continent, retreated to north-eastern Australia where conditions remained warm and wet (Greenwood and Christophel 2005).

The modern distribution of Lauraceae, Cunoniaceae and Elaeocarpaceae differs markedly from the distribution of the families during the Eocene. With the exception of a few species, the distribution in Australia of the Lauraceae genera, *Cryptocarya*, *Endiandra* and *Litsea* is confined to tropical rainforests, most commonly in northeast Queensland (Hyland 1989; Tracey 1982; Laidlaw et al. 2007). This is also the case for many of the Cunoniaceae genera including *Acsmithia*, *Caldcluvia*, *Ceratopetalum*, *Gilbeea* and *Schizomeria.* Elaeocarpaceae genera include *Elaeocarpus* (most members), *Sloanea*, and

*Aceratium*. All these genera have been recorded in the fossil record (Rossetto et al. 2007). Laidlaw et al. (2007) recorded nine fossil Lauraceae species, two Elaeocarpaceae and 1 Cunoniaceae species from Cape Tribulation.

Tracey (1982) developed a series of vegetation categories of Australian rainforest based on structural attributes including canopy height, degree of canopy closure, complexity of the vegetation mosaic, and the relative abundance of epiphytes and lianes. These structural attributes can be correlated to climate zones on the basis of Mean Annual Temperature and Mean Annual Precipitation and soil type (Webb and Tracey 1981; Tracey 1982; Hilbert, Graham and Hopkins 2007). The rainforest present today in northeastern Queensland include complex mesophyll vine forest (CMVF), complex notophyll vine forest (CNVF) simple notophyll vine forest (SNVF) and simple microphyll vine-fern forest (MVFF). Tracey (1982) also suggests that soil type is a limiting factor for distribution of rainforest species, with the greatest diversity occurring on eutrophic soils (Webb and Tracey 1981).

Comparison of the Brandy Creek fossil flora with the forest categories of Tracey (1982) suggests that the Brandy Creek flora could be considered simple notophyll – microphyll vine forest with a prominent Lauraceae component with Cunonicace, Elaeocarpace and ferns. Ferns, most notably *Cyatheacidities* spp. aff Dicksoniaceae are represented by spores in Brandy Creek palynomorph samples as discussed in chapter 3. It is probable that climatic factors limiting the growth of the Brandy Creek forest would apply during the Eocene as it does today. The Brandy Creek mean annual temperature (MAT) of 15.7 - 21.7 °C and a mean annual precipitation (MAP) of 107 – 320cm/yr. at Brandy Creek is coincident with modern mesothermal rainforest of northeastern Queensland. Climate analysis by Greenwood et al. (2000) of nearby Hotham Heights puts MAT and MAP of 17-22°C and 1900-2200 mm/yr. Updated climate profiles of the flora at Hotham Heights revised MAT and MAP to 14.7 - 24.4°C and 1158 - 3420mm/yr., which is consistent with the Brandy Creek MAT and MAP, although the range of both is large. For full details of the Brandy Creek climate analysis please refer to chapter 5.

## 2.6 Conclusions

The Brandy Creek macrofossil record provides further insight into the character of the vegetation during the Eocene. As with many of the other localities discussed, the presence of Lauraceae in high numbers at Brandy Creek provides further evidence of the importance of this family during the Eocene. Although present as a minor component of the Brandy Creek flora, Cunonicae/Eleaocarpace fossil evidence from other localities shows that Cunoniaceae/Elaeocarpaceae occupied the same forest, as is the case today in modern rainforest such as the mesothermal rainforest of northeastern Queensland.

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**Table 2.1** List of the 79 cuticular characters used to group cuticle specimens in this study. See text for details on source of character list.

| | | | | | |
|---|---|---|---|---|---|
| **Upper Epidermis** | | **36** | Sinuous | | |
| **Stomatal distribution** | | **37** | Irregular rounded | | |
| **1** | Amphistomatic | **Thickening of anticlinal walls** | | | |
| **2** | Hypostomatic | **38** | Smooth | | |
| **Upper epidermal shape** | | **39** | Granular | | |
| **3** | Angular | **40** | Beaded | | |
| **4** | Rounded | **41** | Buttressed | | |
| **5** | Undulate | **42** | Ridged | | |
| **6** | Sinuous | **Thickening on periclinal walls** | | | |
| **7** | Irregular rounded | **43** | Smooth or granular | | |
| **Thickening on anticlinal wall** | | **44** | Striate | | |
| **8** | Smooth | **45** | Domed | | |
| **9** | Granular | **46** | Papillate | | |
| **10** | Beaded | **47** | Ridged | | |
| **11** | Buttressed | **Venation patterns** | | | |
| **12** | Ridged | **48** | A network of higher order veins or veinlets forming areoles | | |
| **Thickening on periclinal wall** | | **49** | No network of higher order veins or veinlets forming areoles | | |
| **13** | Smooth or granulate | **Stomatal arrangement** | | | |
| **14** | Striate | **50** | Diacytic | | |
| **15** | Domed | **51** | Paracytic | | |
| **16** | Papillate | **52** | other | | |
| **17** | Ridged | **Thickening on guard cells** | | | |
| **Venation patterns** | | **53** | Absent | | |
| **18** | A network of higher order veins or veinlets forming areoles | **54** | Present | | |
| **19** | No network of higher order veins or veinlets forming areoles | **Specialised structures surrounding stomata** | | | |
| **Trichome base** | | **55** | Cuticular collar surrounding guard cells | | |
| **20** | Trichome base absent | **56** | Striations on periclinal walls of epidermal cells surrounding guard cells | | |
| **21** | One trichome bases type present | **57** | Papillae surrounding stomata | | |
| **22** | More than one trichome base type present | **58** | Trichomes surrounding stomata | | |
| **Trichome base frequency** | | **Trichome bases** | | | |
| **23** | Rare | **59** | Absent | | |
| **24** | Present | **60** | One trichome base type present | | |
| **25** | Common | **61** | More than one trichome base type present | | |
| **26** | Very common | **Trichome base frequency** | | | |
| **Giant stomata (hydathodes)** | | **62** | Rare | | |
| **27** | Absent | **63** | Present | | |
| **28** | Present | **64** | Common | | |
| **Specialised epidermal structures** | | **65** | Very common | | |
| **29** | Present | **Giant stomata (hydathodes)** | | **Cuticular scales** | |
| **30** | Absent | **66** | Absent | **72** | Double |
| **Miscellaneous** | | **67** | Present | **73** | Single |
| **31** | Information obscured by a covering of trichomes | **Specialised epidermal cells** | | **74** | Narrow |
| **32** | Information obscured by a covering of papillae | **68** | Present | **75** | Broad |
| **Lower Epidermis** | | **69** | Absent | **76** | Butterfly shape |
| **Lower epidermis cells shape** | | **Miscellaneous** | | **77** | Striations |
| **33** | Angular | **70** | Information obscured by a covering of papillae | **78** | T-pieces of thickened cutin at poles of guards |
| **34** | Rounded | **71** | Information obscured by a covering of trichomes | **79** | Small thin area of cutin at poles of guards |
| **35** | Undulate | | | | |

**Table 2.2** Main characters used to distinguish between morphotypes at Brandy Creek. Asterisk (*) represent presence of character.

| | Cuticular scales | | | | Guard cells | | Epidermal cells | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Single | Double | Butterfly like | T-pieces of thickened cuticle | Thickened | Striations | Angular rounded | Undulate sinuous | Thickened | Mesh structure | Knobs ridges | Areoles | Papillae |
| BC 001 Lauraceae aff. *Cryptocarya* | | | * | | | | * | | * | * | | | |
| BC 002 Lauraceae aff. *Cryptocarya* | | | * | | | | | | | * | * | | |
| BC 003 Lauraceae aff. *Cryptocarya* | | | * | | | | | * | | | | | |
| BC 004 Lauraceae aff. *Endiandra* | | * | | | * | * | | | | | | | |
| BC 005 Lauraceae aff. *Endiandra* | | * | | | * | * | | | | | * | * | |
| BC 006 Lauraceae aff. *Endiandra* | | * | | | * | | * | | | * (ad) | | | |
| BC 007 Lauraceae aff. *Endiandra* | | * | | | * | * | * | | | | * | | |
| BC 008 Lauraceae aff. *Endiandra* | | * | | * | | | | | | | * | | |
| BC 009 Lauraceae aff. *Cryptocarya* | | | * | | | | | | | | | * | |
| BC 010 Lauraceae aff. *Endiandra* | | * | | | | | * | | | | | | |
| BC 011 Lauraceae aff. *Litsea bennettii* group | * | | | | | | * | | * | | | | * |
| BC 012 Lauraceae aff. *Litsea bennettii* group | * | | | | | | | * | | | | * | * |
| BC 013 Lauraceae aff. *Endiandra* | | * | | | * | | * | | | * | * | | |
| BC 014 Lauraceae aff. *Endiandra* | | * | | | * | | | * | | | * | | |
| BC 015 Lauraceae aff. *Cryptocarya* | | | * | | | | | * | | | | * | |
| BC 016 aff. Cunoniaceae/Elaeocarpaceae | | | | * | | | | * | | | * | | |
| BC 017 aff. Cunoniaceae/ Elaeocarpaceae | | | | * | | * | * | | | | | | |
| BC 018 aff. Cunoniaceae/Elaeocarpaceae | | | | * | | | * | * | | | * | | |

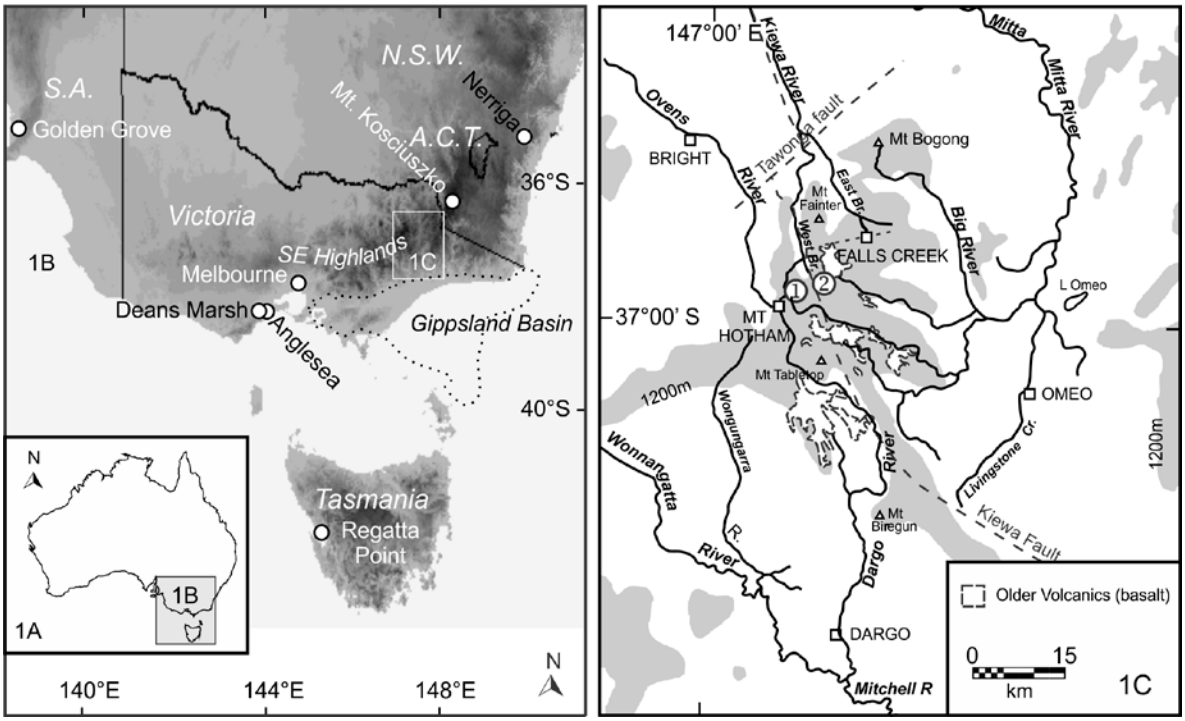



**Figure 2.1** Maps showing the location of macrofloras and microfloras discussed in the text (1B). 1C, detail of the Bogong High Plains showing the land above 1200m a.s.l., outcrop of basalt, and location of the Hotham Heights (1) and Brandy Creek Mine (2) Eocene macroflora sites (Map developed for a manuscript by Greenwood, Webb and Keefe, in prep.).

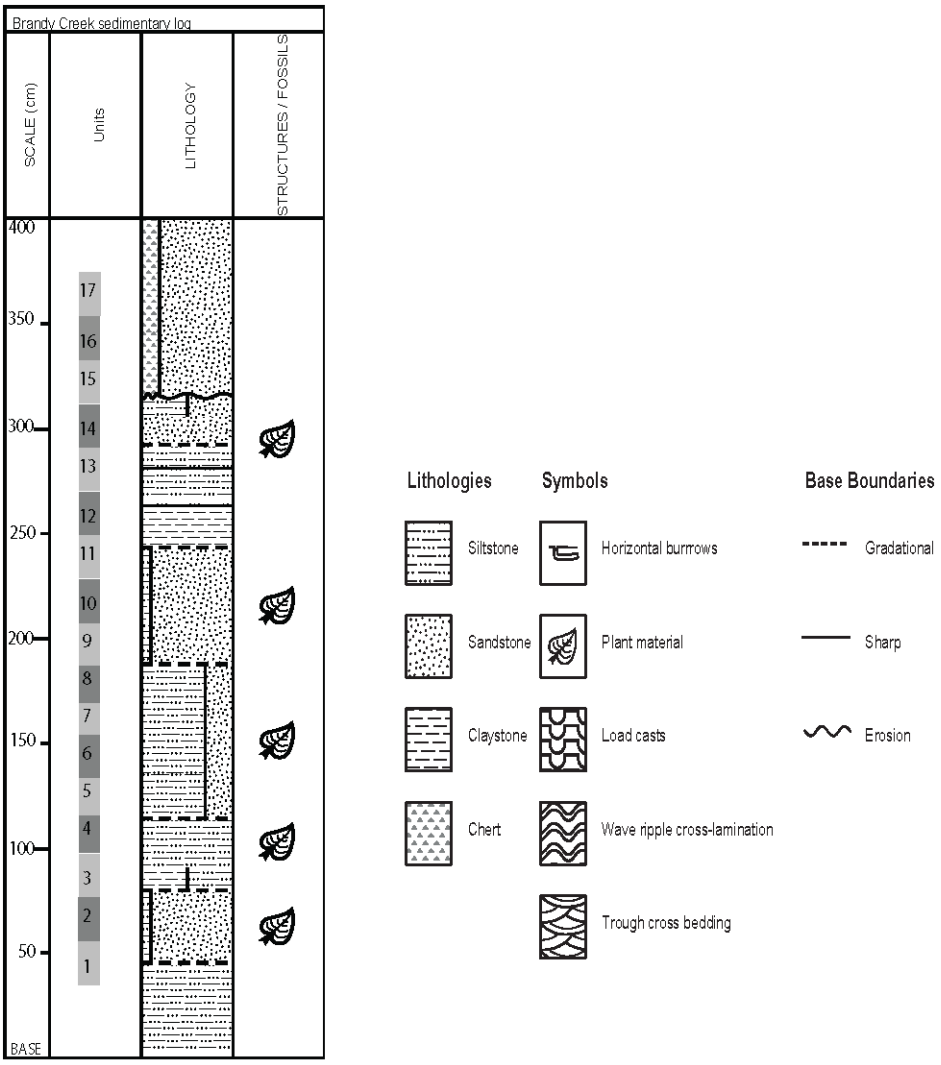



**Figure 2.2** Stratigraphic log of the Brandy Creek outcrop showing units, lithology and fossil structures present.

**Figure 2.3** Brandy Creek outcrop showing laminated siltstone and sandstone containing fossil plant material

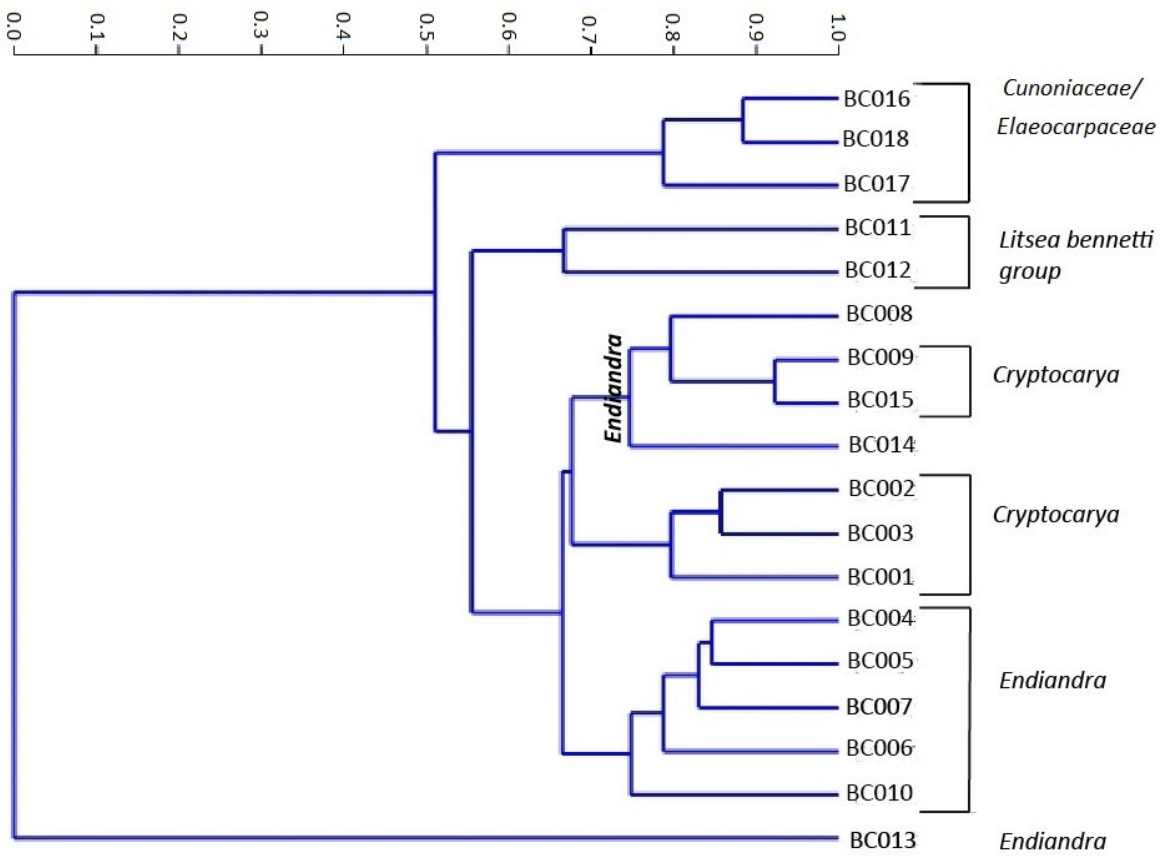



**Figure 2.4.** Dendogram showing the relationships among morphotypes at Brandy Creek. The x axis indicates dissimilarity values. The y-axis shows the Brandy Creek morphotypes.

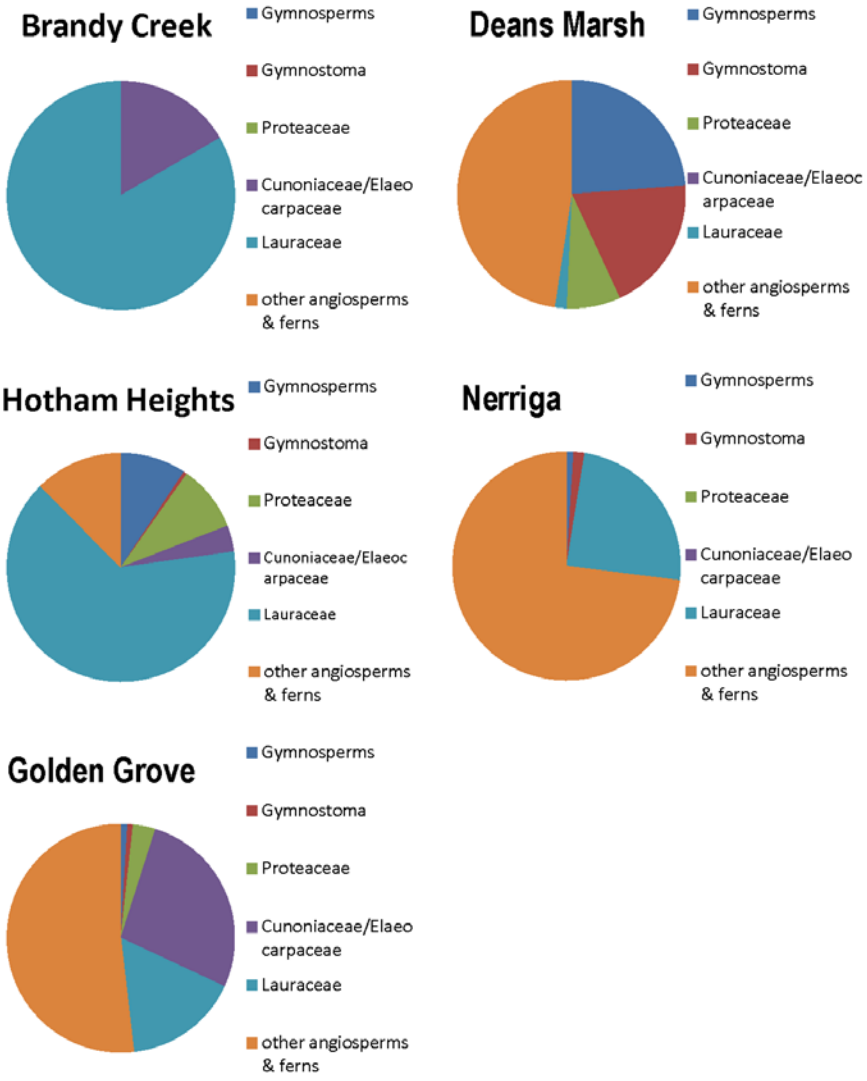
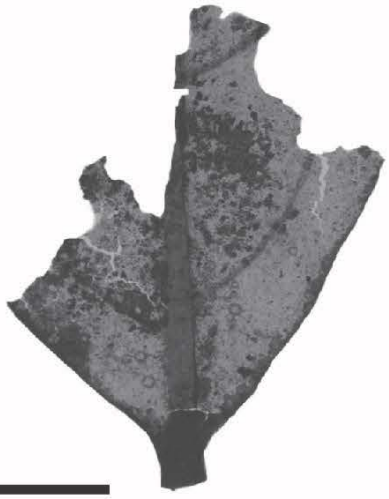


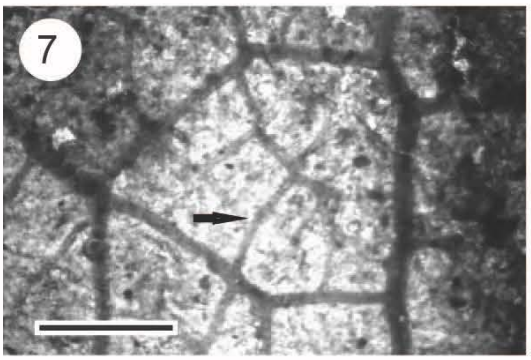

**Figure 2.5**. Floristic composition of Brandy Creek and other Eocene localities in southeastern Australia.

**Figures 2.6 – 2.10.** Brandy Creek 001 Lauraceae aff. *Cryptocarya*. **Fig. 2.6.** Incomplete leaf (BC 1103). Scale bar = 1 cm **Fig. 2.7.** Venation pattern arrow indicates regular polygonal reticulate higher order veins. Scale bar = 2mm. **Fig. 2.8.** LM of adaxial surface; arrow indicates mesh appearance of the epidermal cells. Scale bar = 20µm **Fig. 2.9.** LM of abaxial surface; arrow indicates butterfly-like cuticular scales. Scale bar = 20µm. **Fig. 2.10.** LM of abaxial surface; epidermal walls anticlinal walls thickened, stomate paracytic. Arrow indicates butterfly-like cuticular scales. Scale bar = 10µm. **Figure 2.11.** Brandy Creek 002 Lauraceae aff. *Cryptocarya*. Incomplete leaf (BC 1164) showing eucamptodromous venation. Scale bar = 1 cm.

6



7



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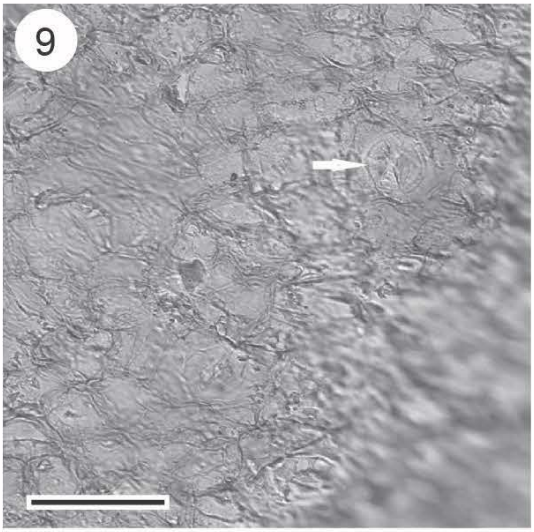

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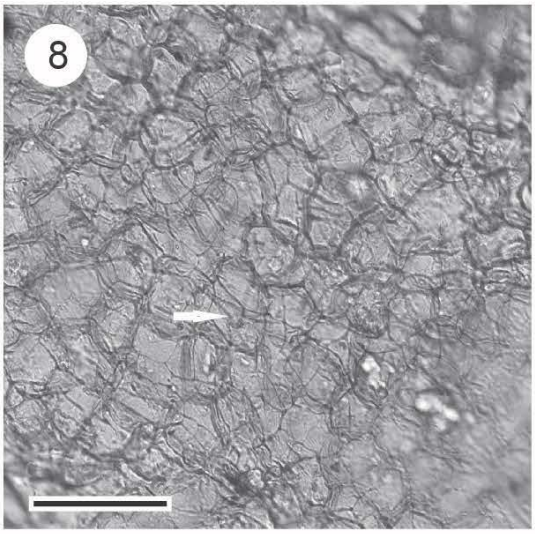

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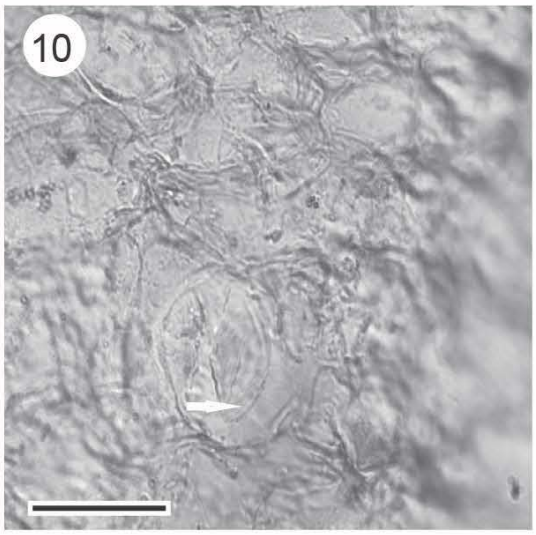

**Figures 2.12 - 2.15.** Brandy Creek 002 Lauraceae aff. *Cryptocarya*. **Fig. 2.12.** Venation pattern arrow indicates regular polygonal reticulate higher order veins. Scale bar = 2mm. **Fig. 2.13.** LM adaxial surface; arrow indicates thickened anticlinal walls and mesh appearance of the epidermal cells. Scale bar = 20µm **Fig. 2.14.** SEM stoma; arrow indicates butterfly-like cuticular scales. Scale bar = 5 µm. **Fig. 2.15.** LM of abaxial surface; arrow indicates beaded anticlinal walls, mesh appearance of the epidermal cells, periclinal walls thickened, arrow indicates stomate paracytic. Scale bar = 20µm. **Figures 2.16 – 2.17.** Brandy Creek 003 Lauraceae aff. *Cryptocarya*. **Fig. 2.16.** Incomplete leaf (BC 1547) showing tip. Scale bar = 1 cm. **Fig. 2.17.** LM of adaxial surface; arrow indicates smooth anticlinal walls. Scale bar = 20µm.

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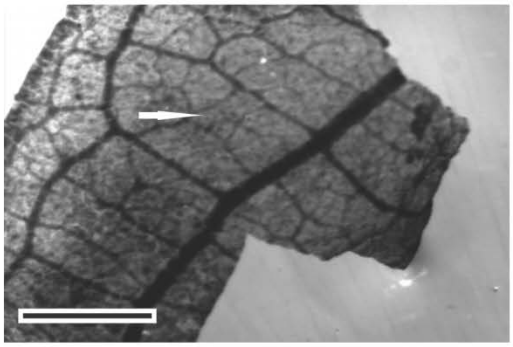

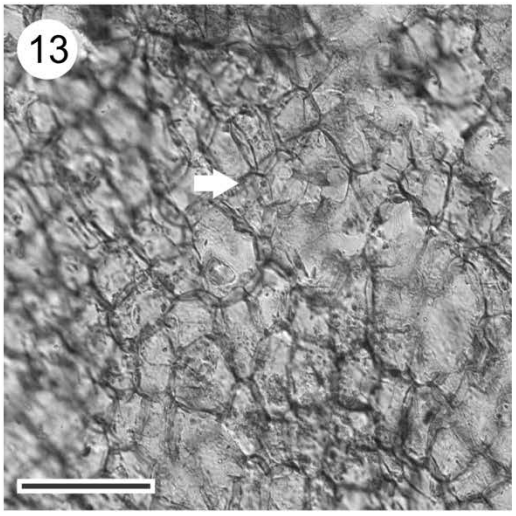


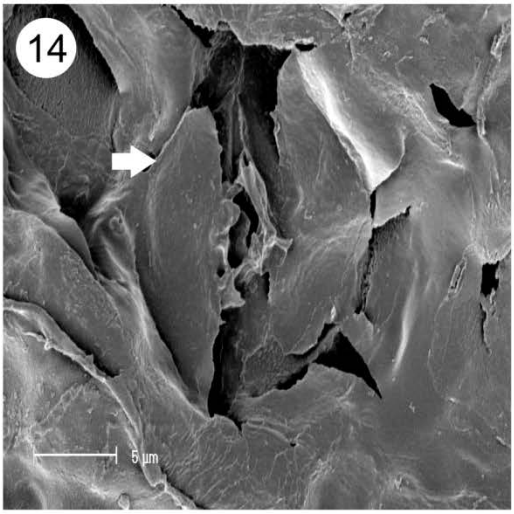


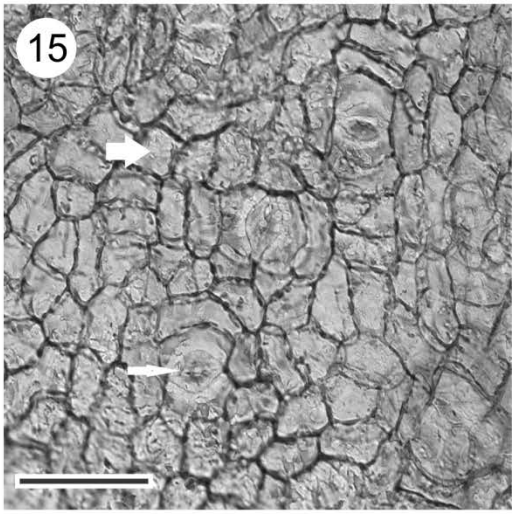


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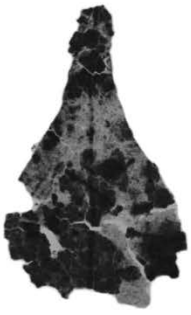
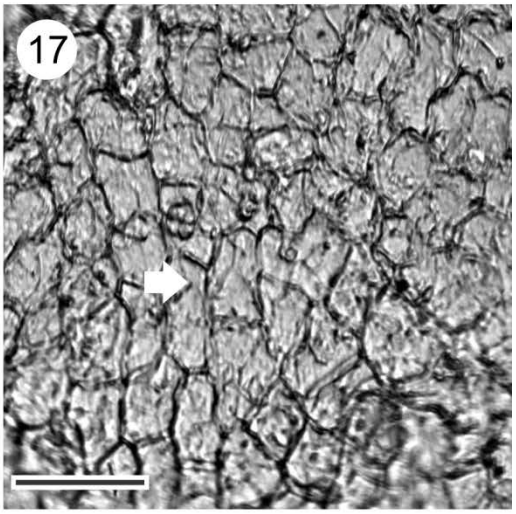
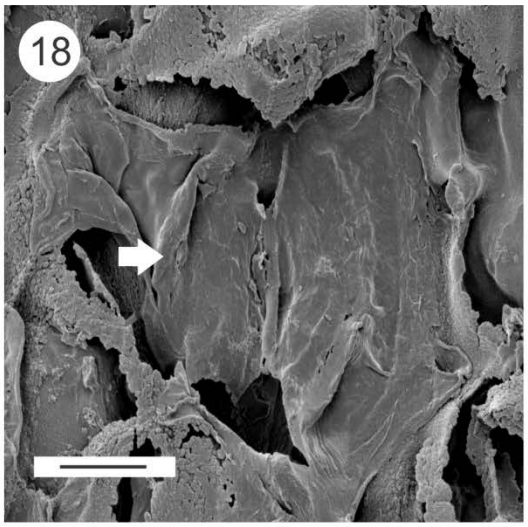




**Figures 2.18 to 2.19.** Brandy Creek 003 Lauraceae aff. *Cryptocarya*. **Fig. 2.18.** SEM of abaxial surface; arrow indicates butterfly-like cuticular scales. Scale bar = 5µm. **Fig. 2.19.** LM of abaxial surface; arrows indicate undulate anticlinal walls, paracytic stomatal complex. Scale bar = 20µm. **Figures 2.20 - 2.23.** Brandy Creek 009 Lauraceae aff. *Cryptocarya*. **Fig. 2.20.** Incomplete leaf (BC 1398) showing entire margin. Scale bar = 1cm. **Fig. 2.21.** Leaf venation pattern arrow indicates high order veins. Scale bar = 2mm. **Fig. 2.22.** LM of adaxial surface showing granular periclinal walls. Scale bar = 50µm. **Fig. 2.23.** LM of abaxial surface showing areoles, arrow indicates porous trichome bases. Scale bar = 50µm.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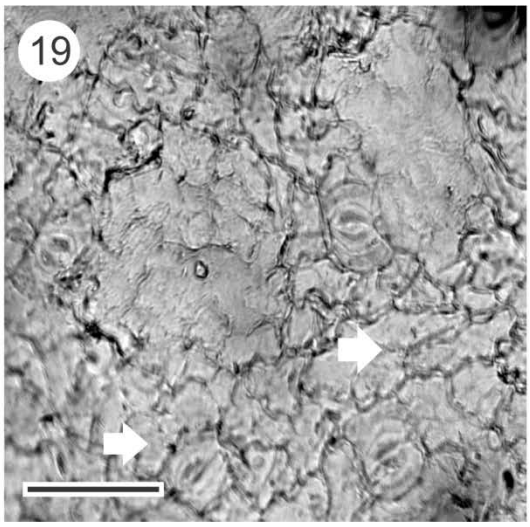
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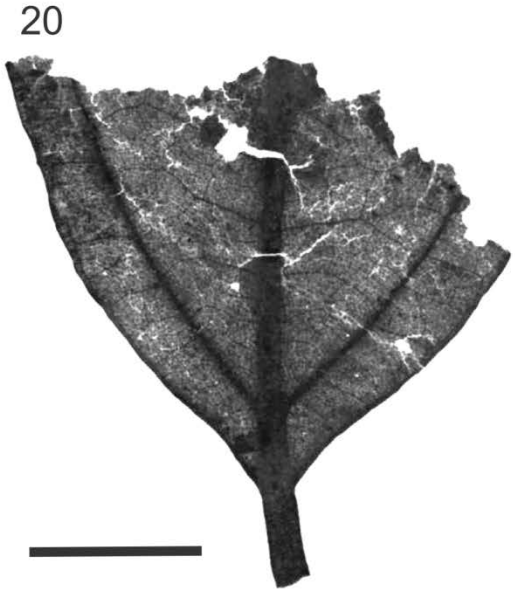
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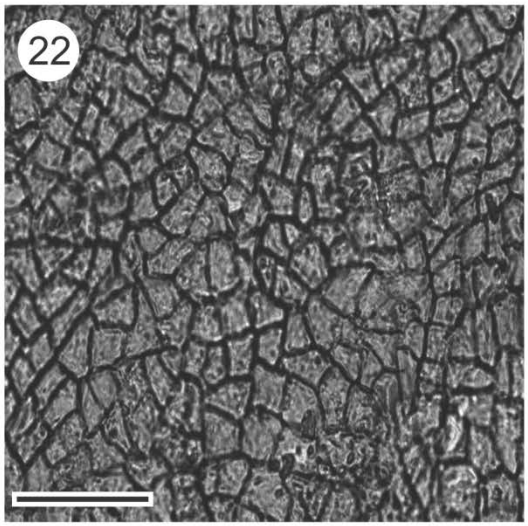
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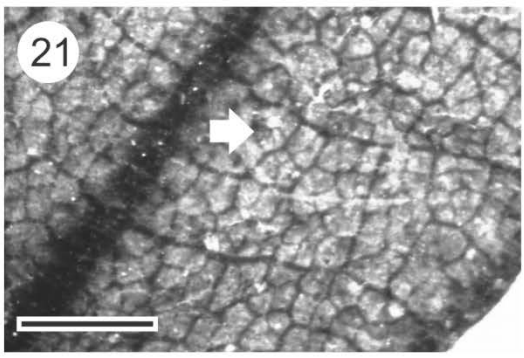
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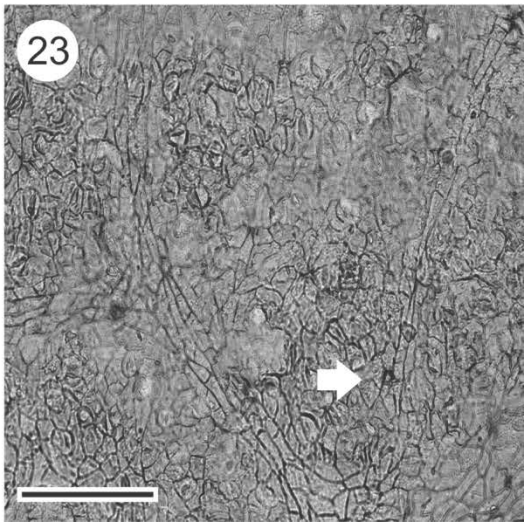
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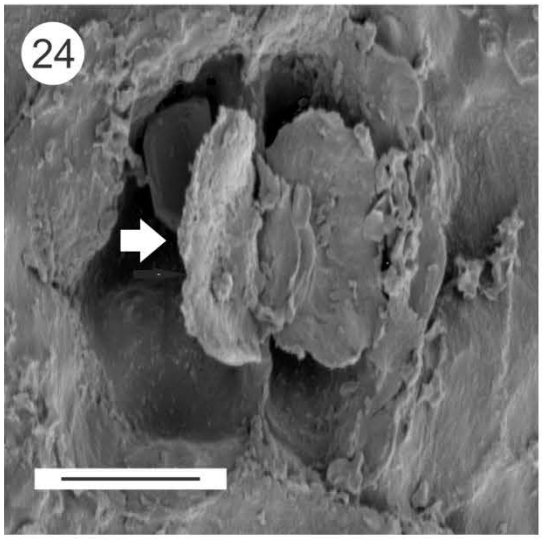
**Figure 2.24.** Brandy Creek 009 Lauraceae aff. *Cryptocarya*. SEM of stomate arrow indicates butterfly-like cuticular scales. Scale bar = 5µm. **Figures 2.25 - 2.29.** Brandy Creek 015 Lauraceae aff. *Cryptocarya*. **Fig. 2.25.** Incomplete leaf (BC114). Scale bar = 2 cm. **Fig. 2.26**. Venation pattern arrow indicates higher order veins. Scale bar = 2mm. **Fig. 2.27.** LM of adaxial surface; arrow indicates straight anticlinal walls. Scale bar = 50µm. **Fig. 2.28.** SEM of stomata; arrow indicates butterfly-like cuticular scales. Scale bar = 5µm. **Fig. 2.29.** LM of abaxial surface; arrow indicates undulate anticlinal walls. Scale bar = 20µm.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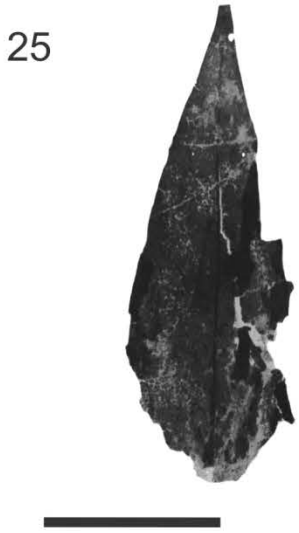
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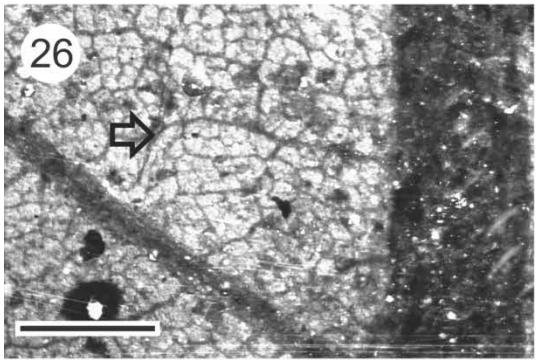
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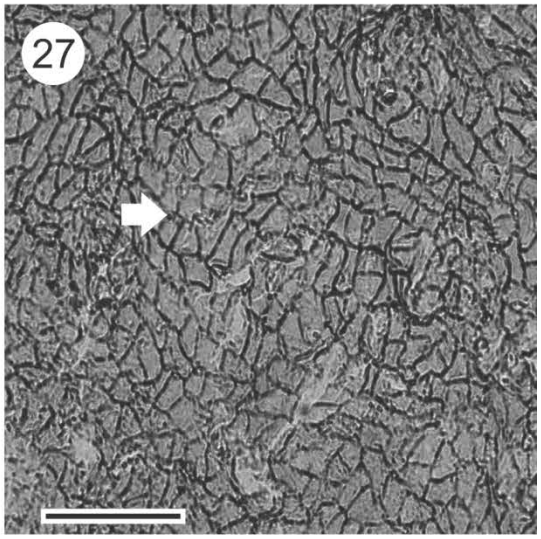
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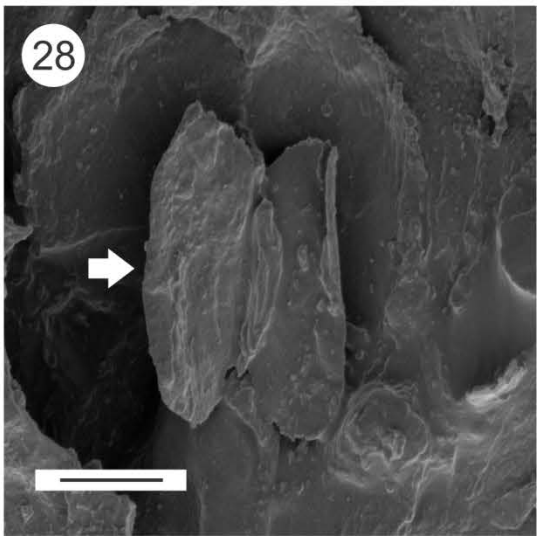
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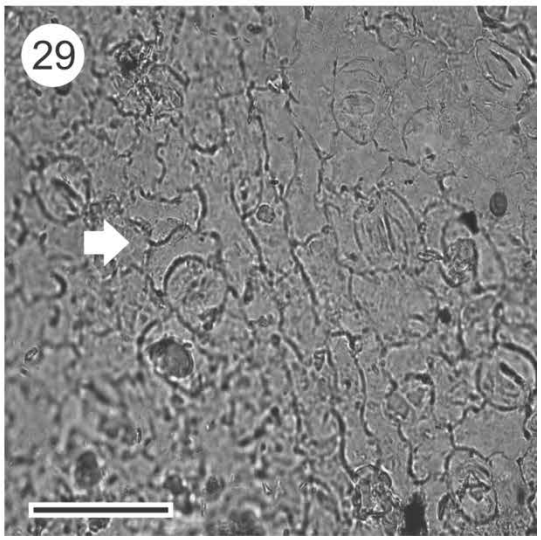
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**Figures 2.30 - 2.34.** Brandy Creek 004 Lauraceae aff. *Endiandra*. **Fig. 2.30.** Incomplete leaf (BC 1335, BC 1258). Scale bar = 1 cm. **Fig. 2.31.** LM of adaxial surface showing epidermal anticlinal walls; arrow indicates callimothalloid shields. Callimothaalloid shields are a type of epiphyllous fungal structure that will be discussed in detail in Chapter 4. Scale bar = 20µm. **Fig. 2.32.** Incomplete leaf showing tip. Scale bar = 1 cm. **Fig. 2.33.** LM of abaxial surface; arrow indicates stomate, periclinal walls of guard cells thickened. Scale bar = 20µm.**Fig. 2.34**. SEM stomata; arrow indicates striations on guard cells, and double cuticular scales (scales numbered 1 and 2). Scale bar = 10µm. **Figure. 2.35.** Brandy Creek 005 Lauraceae aff. *Endiandra*. LM of adaxial surface showing granular periclinal walls. Scale bar = 50 µm.

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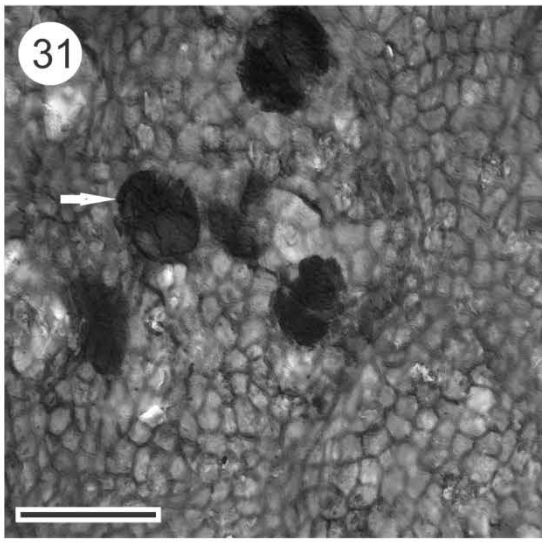


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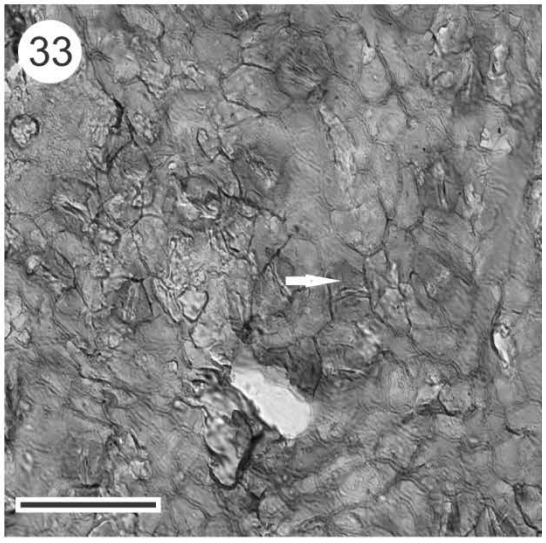
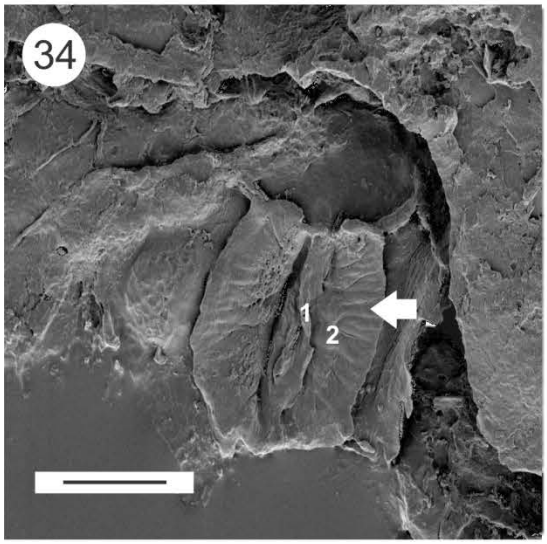
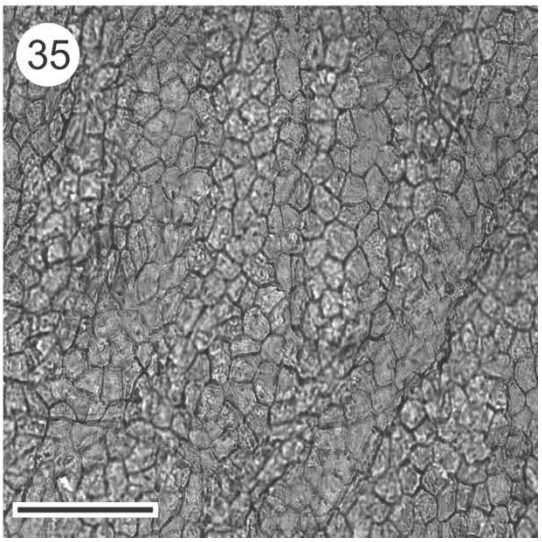
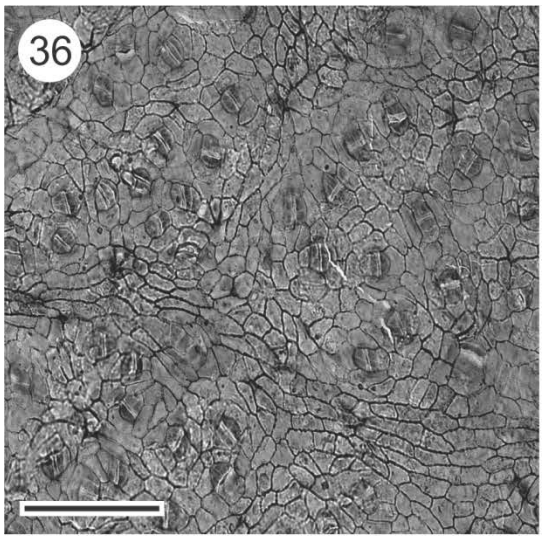
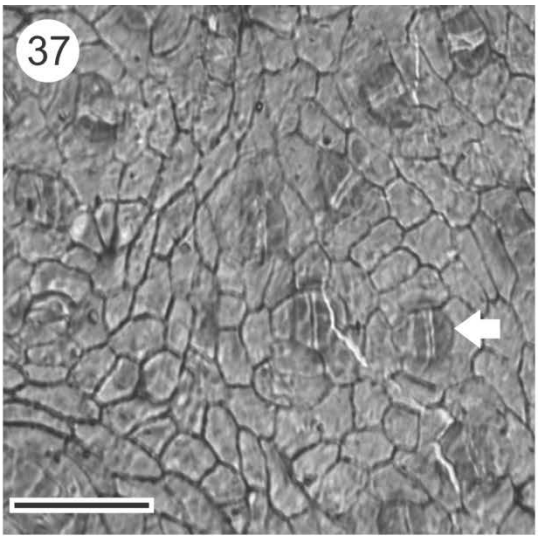


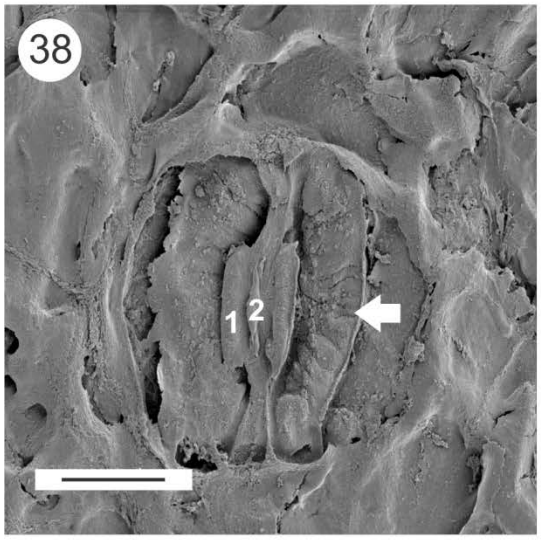



**Figures 2.36 - 2.38.** Brandy Creek 005 Lauraceae aff. *Endiandra*. **Fig. 2.36.** LM abaxial surface showing areoles. Scale bar = 50µm. **Fig. 2.37.** LM abaxial surface showing stomata randomly orientated, periclinal walls of guard cells thickened. Scale bar = 20µm. **Fig. 2.38.** SEM of stomata; arrow indicates striations on guard cells, double cuticular scales (scales numbered 1 and 2). Scale bar = 10µm. **Figures 2.39- 2.41.** Brandy Creek 006 Lauraceae aff. *Endiandra*. **Fig. 2.39.** Incomplete leaf (BC 1108). Scale bar = 1 cm. **Fig. 2.40.** LM of adaxial surface; arrows indicate mesh appearance of epidermal cells. Scale bar = 20µm. **Fig. 2.41**. LM of abaxial surface; arrow indicates mesh like appearance of epidermal cells surrounding guard cells. Scale bar = 20µm.

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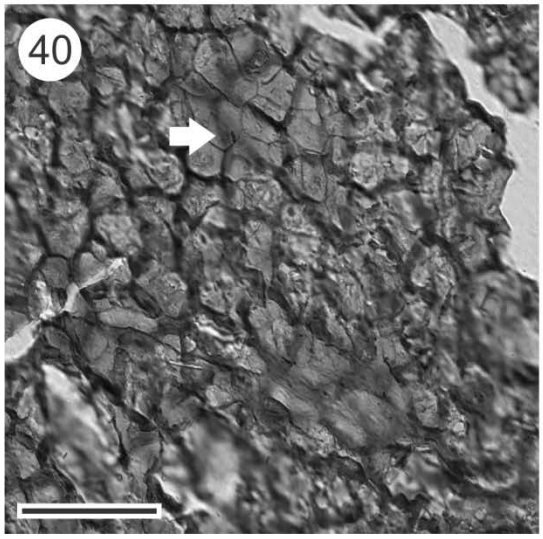


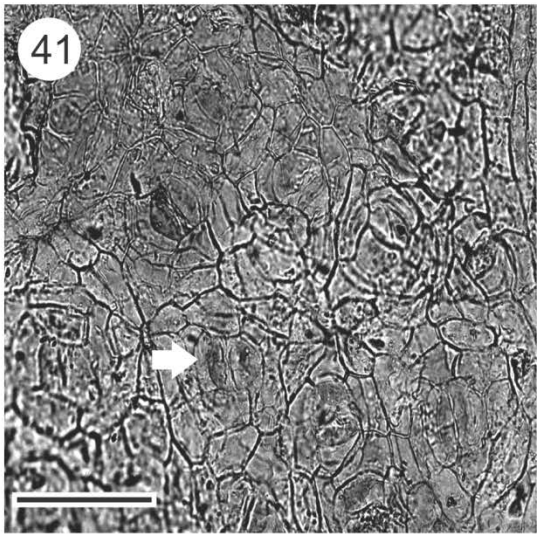
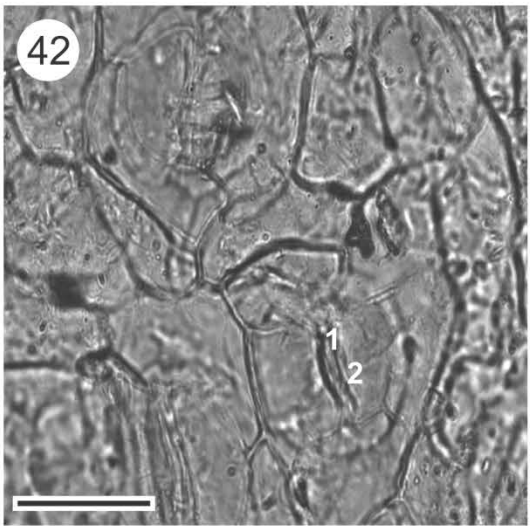



**Figure 2.42.** Brandy Creek 006 Lauraceae aff. *Endiandra*. LM of abaxial surface showing double cuticular scales (scales numbered 1 and 2). Scale bar = 10µm. **Figures 2.43 to 2.45.** Brandy Creek 007 Lauraceae aff. *Endiandra.* **Fig. 2.43.** LM of abaxial surface; arrow indicates stomate. Scale bar = 50µm. **Fig. 2.44.** SEM of adaxial surface showing knobs on anticlinal walls. Scale bar = 20µm. **Fig. 2.45.** SEM of stomata; arrow indicates striations on guard cells, double cuticular scales (scales number 1 and 2). Scale bar = 5µm. **Figures 2.46 to 2.47.** Brandy Creek 008 Lauraceae aff. *Endiandra*. **Fig. 2.46.** LM of adaxial surface showing granular periclinal walls. Scale bar = 50µm **Fig. 2.47.** LM of abaxial surface; arrows indicate thickened guard cells. Scale bar = 50µm.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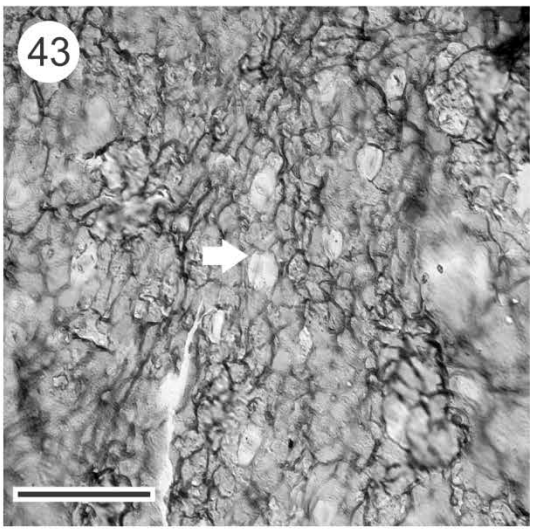
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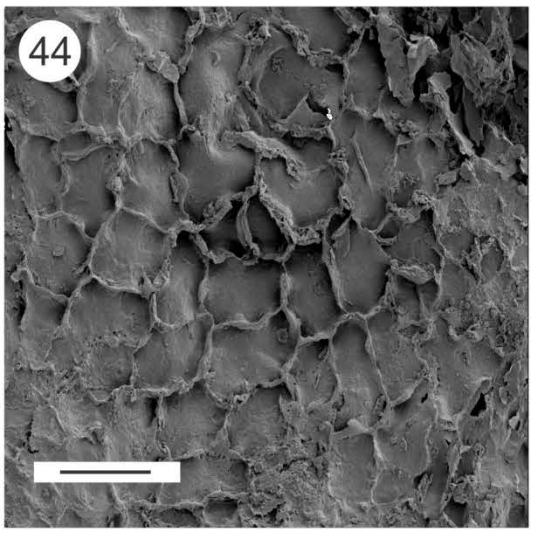
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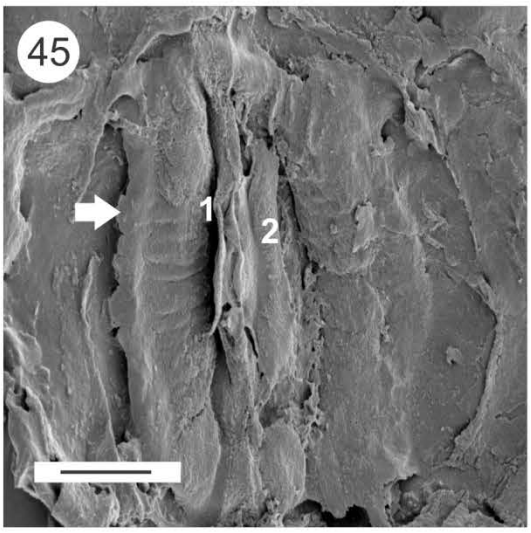
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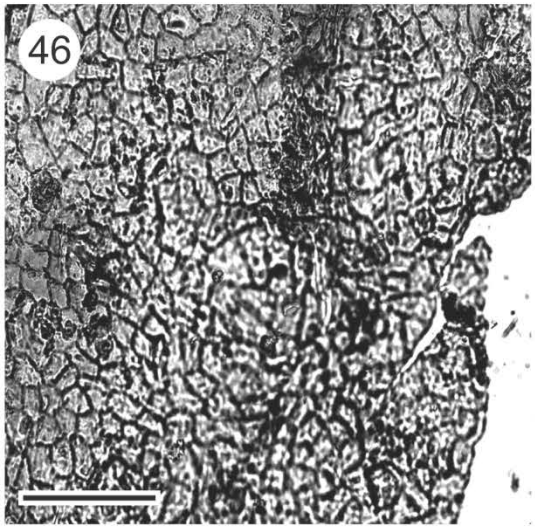
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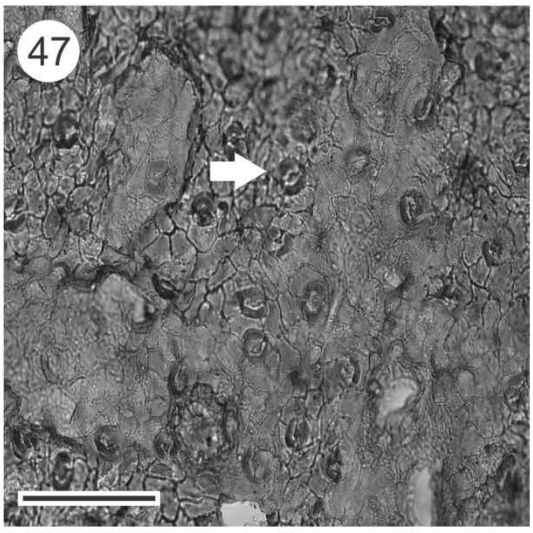
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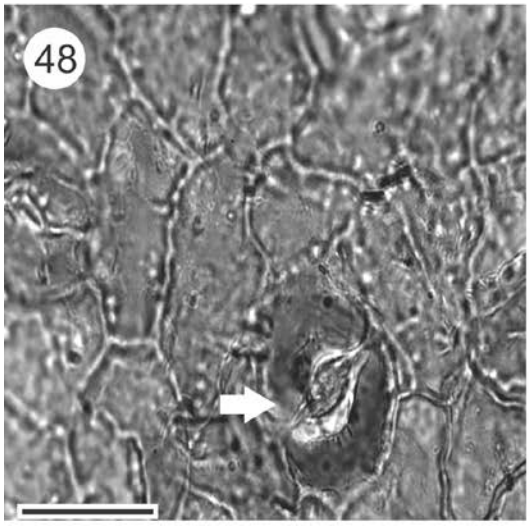
**Figure 2.48.** Brandy Creek 008 Lauraceae aff. *Endiandra*. LM of abaxial surface; arrow indicates stomate with T- pieces of thickened cuticle at poles of guards. Scale bar = 10µm. **Figures 2.49- 2.52.** Brandy Creek 010 Lauraceae aff. *Endiandra*. **Fig. 2.49.** Incomplete leaf (BC010) showing weak eucamptodromous veins. Scale bar = 2 cm. **Fig. 2.50.** Venation; arrows indicates fourth order pattern. Scale bar = 2mm. **Fig. 2.51.** LM of adaxial surface; arrow indicates poral trichome bases. Scale bar = 50µm. **Fig. 2.52.** LM abaxial surface; arrow indicates regular trichome bases. Scale bar = 50µm.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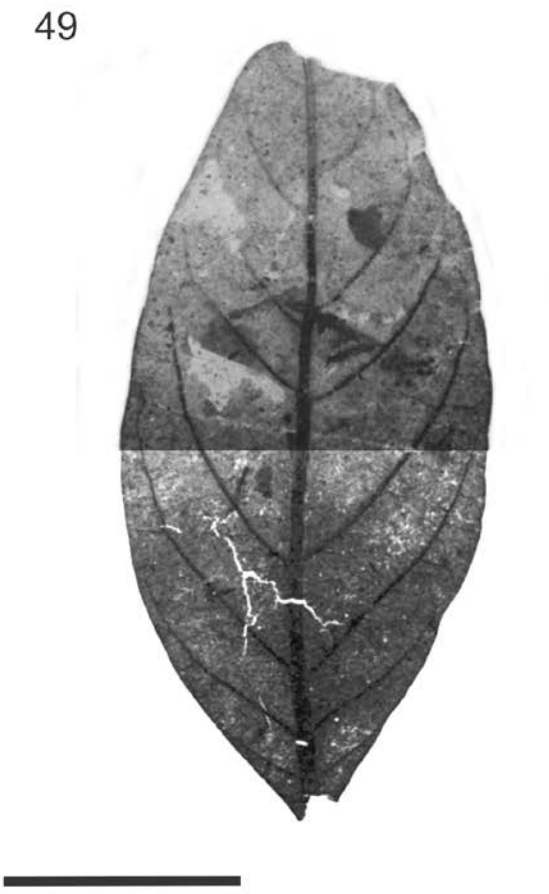
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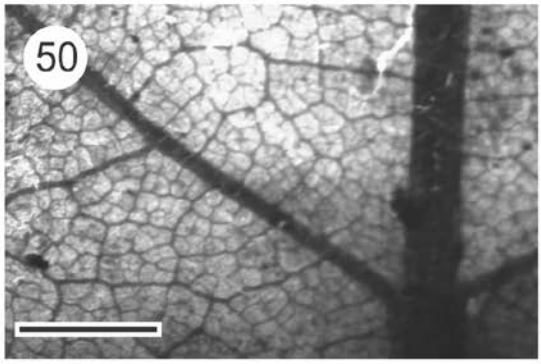
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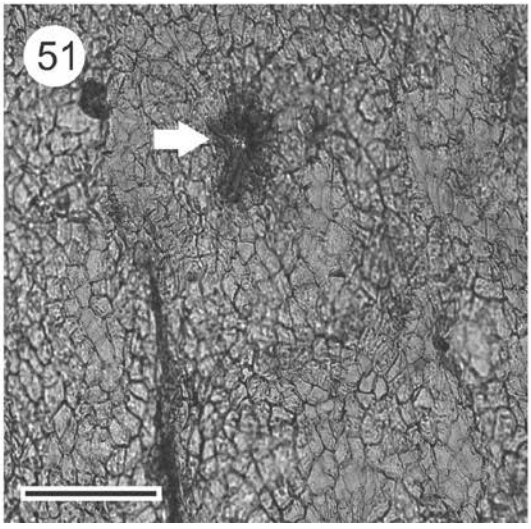
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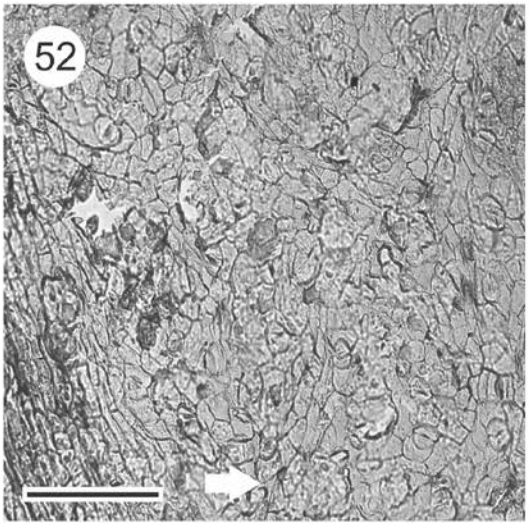
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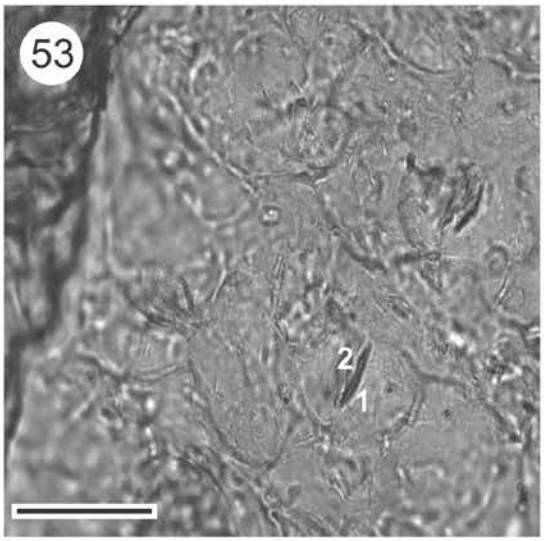
**Figure 2.53.** Brandy Creek 010 Lauraceae aff. *Endiandra*. LM of abaxial surface showing stomata with double cuticular scales (scales numbered 1 and 2). Scale bar = 10µm. **Figures 2.54 to 2.57.** Brandy Creek 013 Lauraceae aff. *Endiandra.* **Fig. 2.54.** LM abaxial surface showing stomatal arrangement. Scale bar = 50µm. **Fig. 2.55.** LM of abaxial surface; arrows indicate beaded anticlinal walls. Scale bar = 20µm. **Fig. 2.56.** LM of abaxial surface arrow; indicates paracytic stomate. Scale bar = 10µm **Fig. 2.57.** SEM of stomashowing double cuticular scales (scales numbered 1 and 2). Scale bar = 5µm. **Figure 2.58.** Brandy Creek 014 Lauraceae aff. *Endiandra*. Incomplete leaf (BC1645) showing entire margin, callimothalloid shields. Scale bar = 1cm.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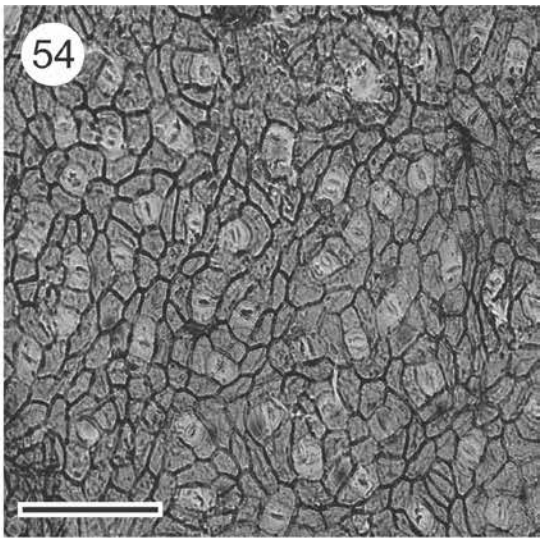
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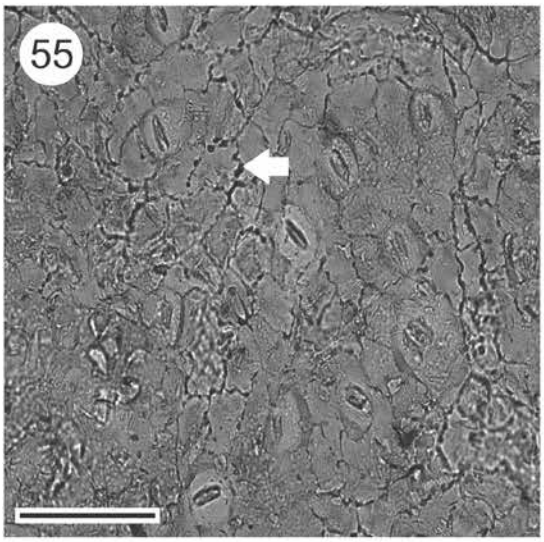
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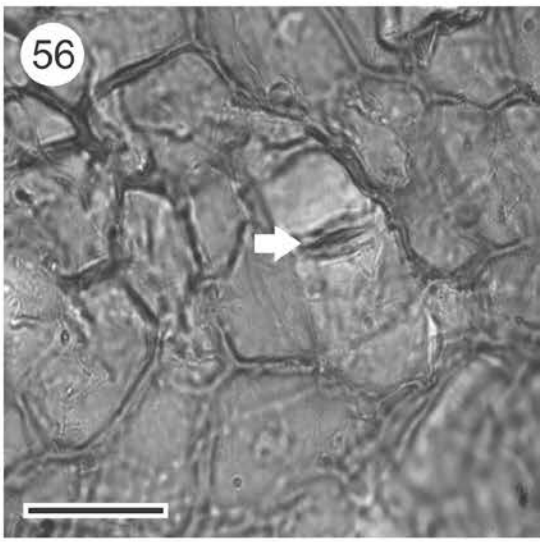
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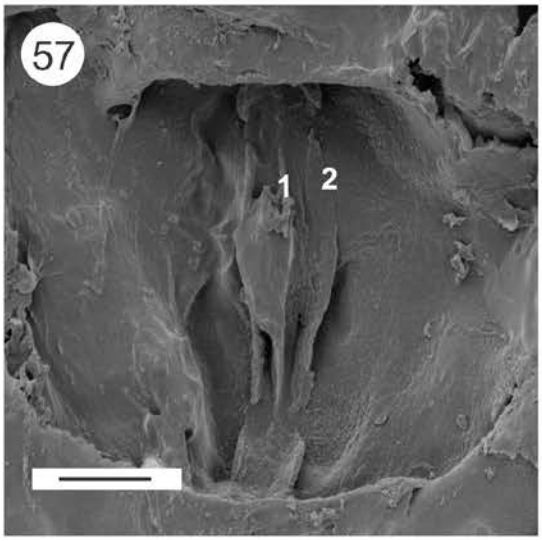
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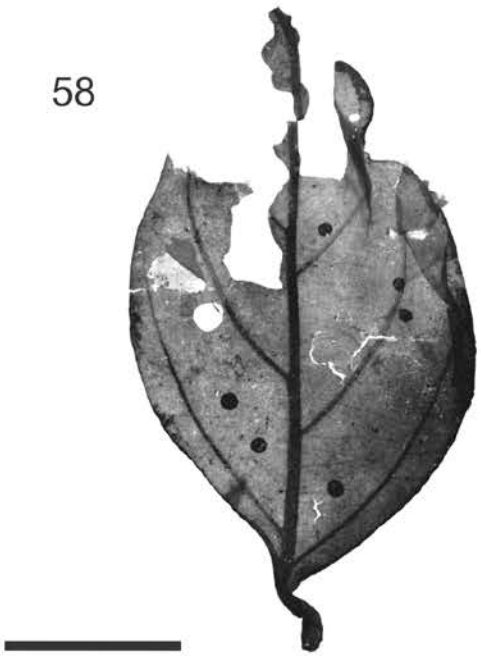
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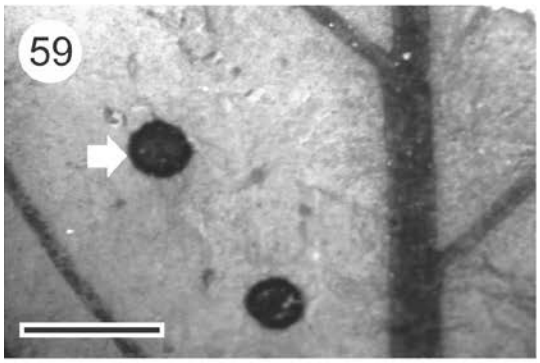
**Figures 2.59-2.62.** Brandy Creek 014 Lauraceae aff. *Endiandra*. **Fig. 2.59.** Arrow indicates callimothalloid shields. Scale bar = 4mm. **Fig. 2.60.** LM of adaxial surface; arrow indicates undulate anticlinal walls with knobs and ridges. Scale bar = 50µm. **Fig. 2.61.** LM of abaxial surface showing areoles and beaded anticlinal walls. Scale bar = 50µm. **Fig. 2.62.** LM of abaxial surface showing double cuticular scales (scales numbered 1 and 2). Scale bar = 10µm. **Figures 2.63 to 2.64.** Brandy Creek 011 Lauraceae aff. *Litsea bennettii* group. **Fig. 2.63.** LM of adaxial surface showing granular periclinal walls. Scale bar = 20µm. **Fig. 2.64.** LM of abaxial surface showing dense covering of papillae. Scale bar = 20µm.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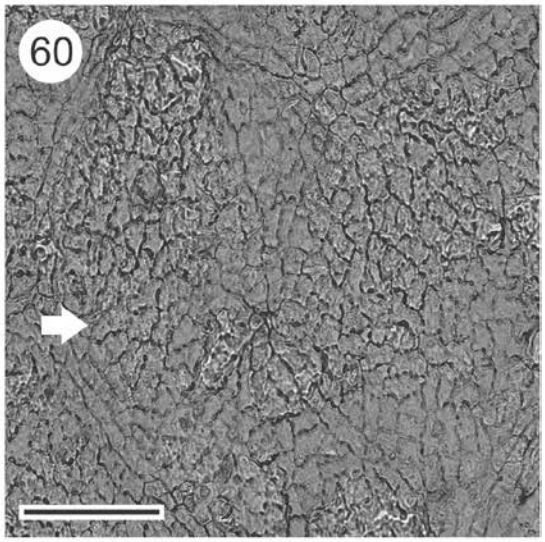
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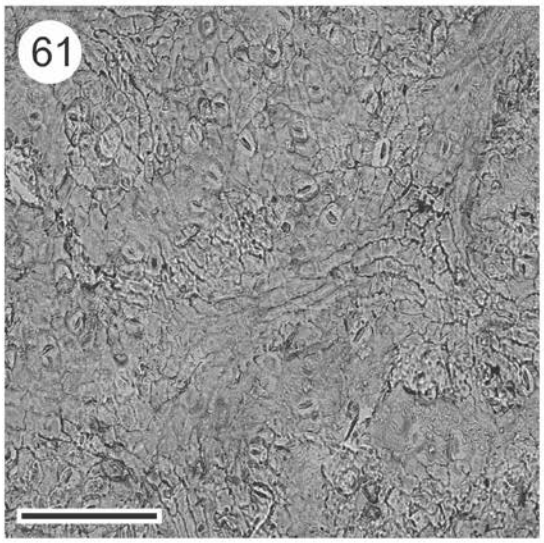
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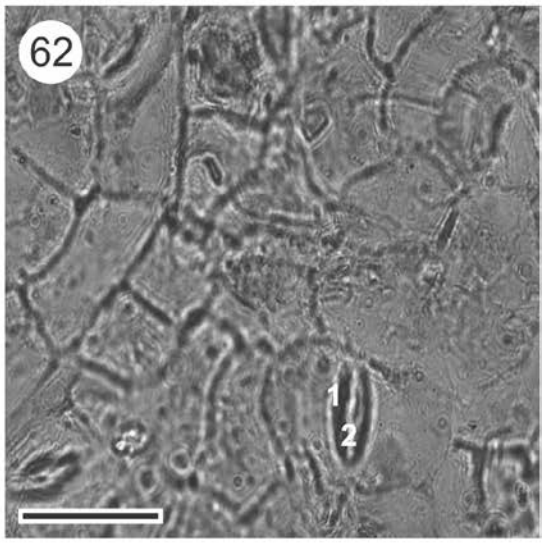
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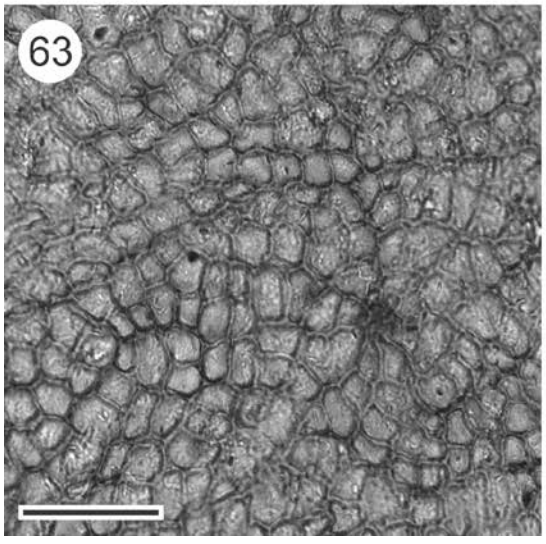
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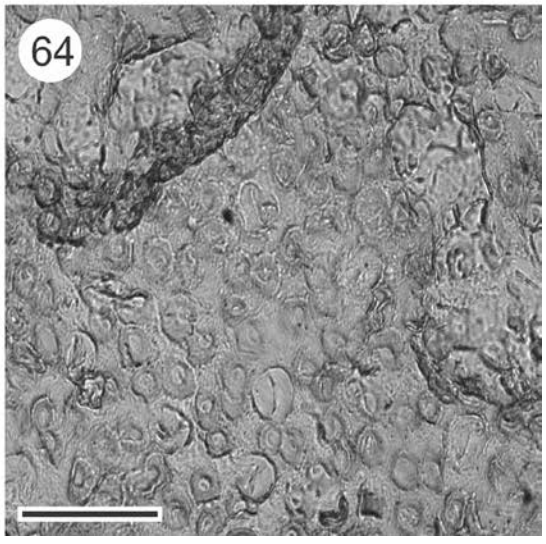
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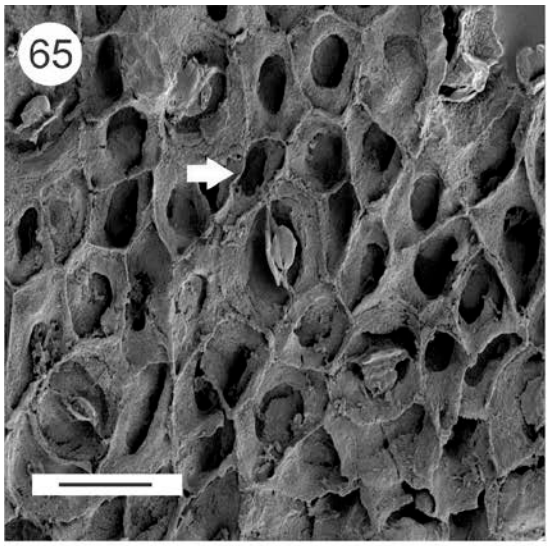
**Figures 2.65 to 2.67.** Brandy Creek 011 Lauraceae aff. *Litsea bennettii* group. **Fig. 2.65.** SEM of abaxial surface; arrow indicates circular depressions of papillae surrounding stomata. Scale bar = 20µm. **Fig. 2.66.** SEM of outer stomatal surface; arrow indicates papillae. Scale bar = 20µm. **Fig. 2.67.** SEM of stomate arrow; indicates cuticular scale. Scale bar = 5µm.

**Figures 2.68 - 2.70.** Brandy Creek 012 Lauraceae aff. *Litsea bennettii* group. **Fig. 2.68.** LM of adaxial surface; arrow indicates undulate anticlinal walls. Scale bar = 50µm. **Fig. 2.69**. LM of abaxial surface showing areoles and papillae, arrow indicates poral trichome bases. Scale bar = 50µm. **Fig. 2.70**. SEM of stomate surrounded by papillae. Scale bar = 5µm.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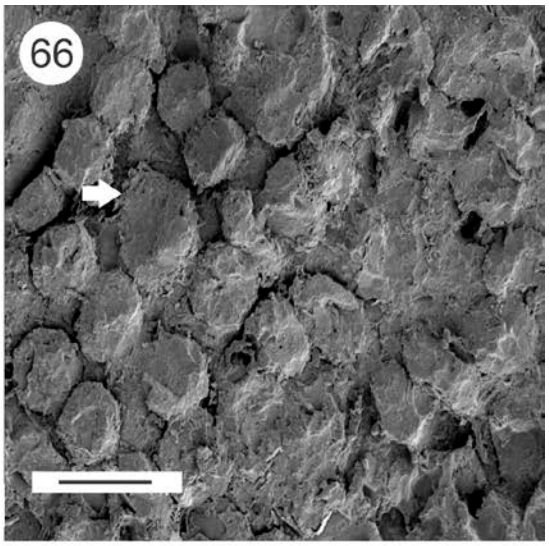
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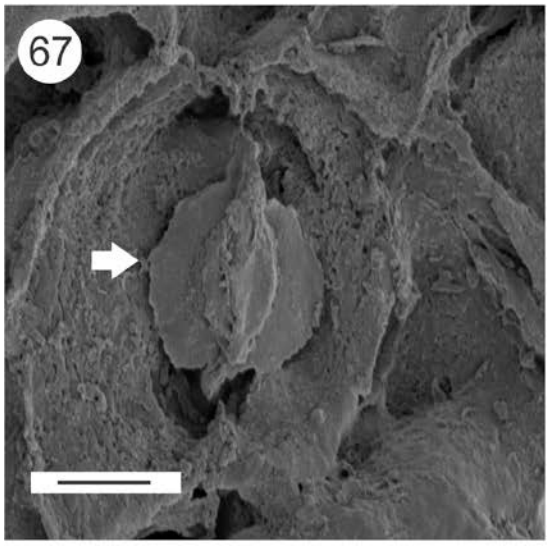
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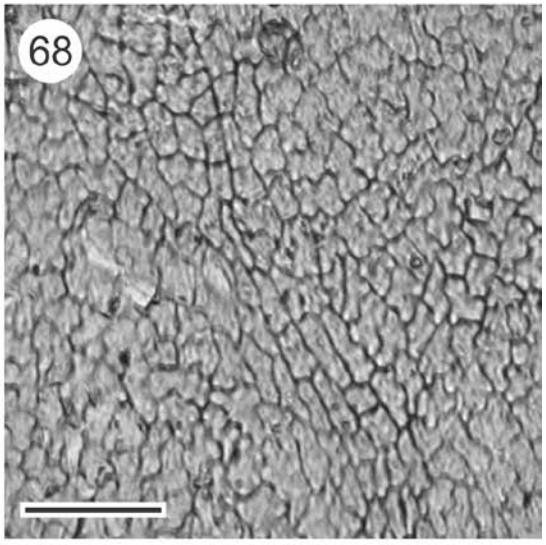
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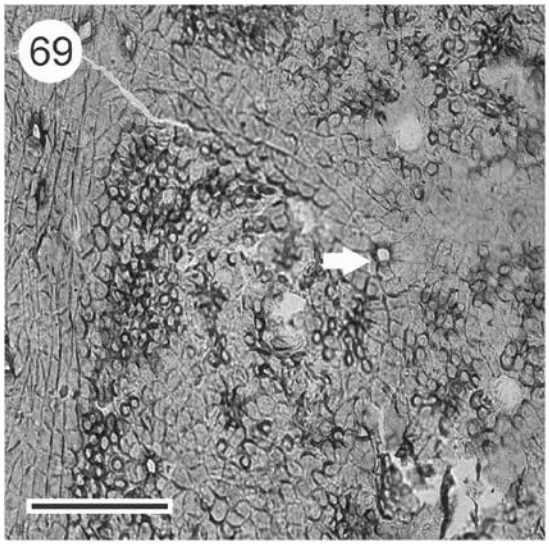
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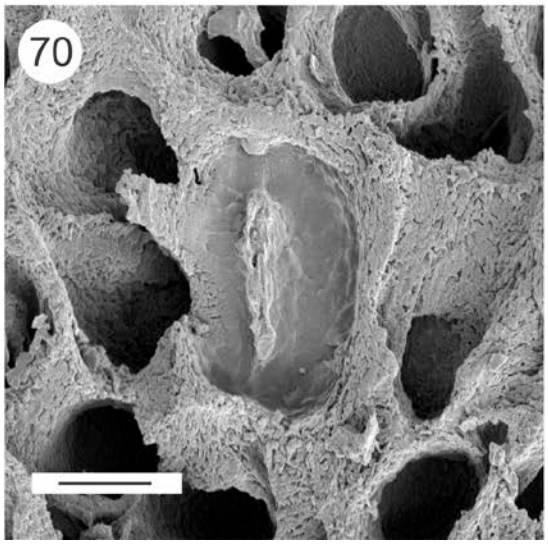
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**Figures 2.71 to 2.75.** Brandy Creek 016 aff. Cunoniaceae/Elaeocarpaceae. **Fig. 2.71.** Complete leaf (BC1009) showing tooth margins and brochidodromous veins. Scale bar = 2cm. **Fig. 2.72.** Tooth and venation pattern; arrow indicates higher order veins. Scale bar = 2mm. **Fig. 2.73.** LM adaxial surface; arrow indicates undulate anticlinal walls. Scale bar = 20µm **Fig. 2.74.** LM abaxial surface showing stomate arrow indicates T-pieces of thickened cuticle at poles of guards. Scale bar = 10µm. **Fig. 2.75.** LM of abaxial surface; arrow indicates undulate anticlinal walls. Scale bar = 20µm.


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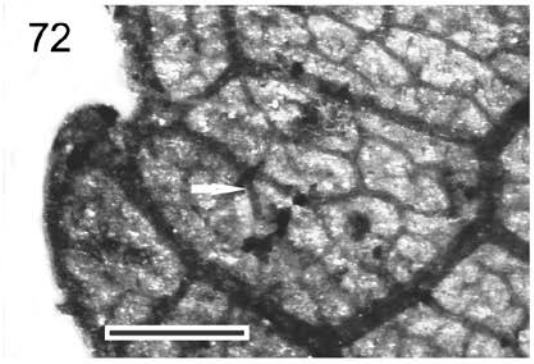
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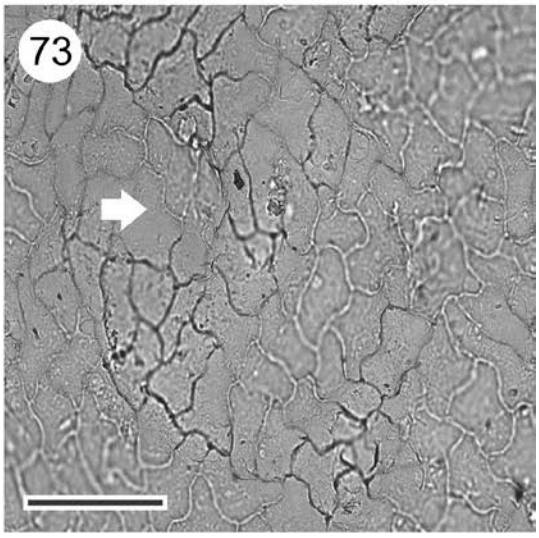
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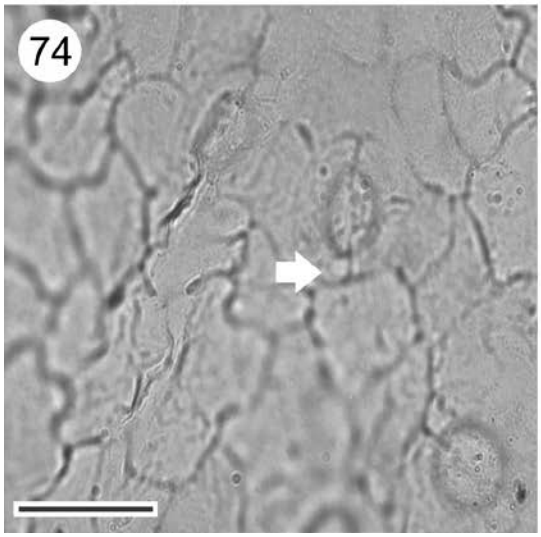
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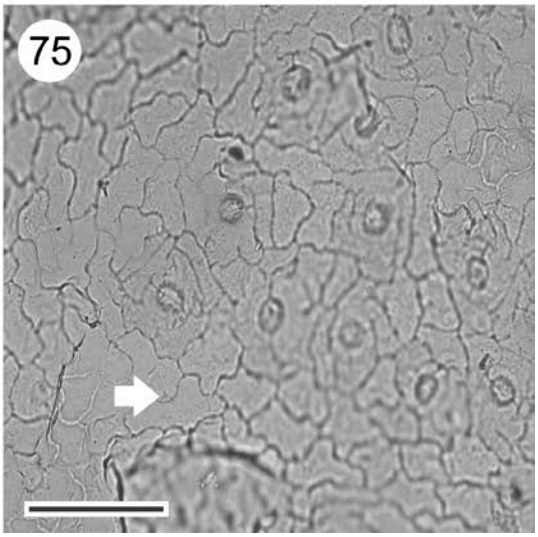
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**Figures 2.76 to 2.80.** Brandy Creek 017 aff. Cunoniaceae/Elaeocarpaceae. **Fig. 2.76.** Complete leaf (BC 1610) showing drip tip, toothed margin. Scale bar = 2cm. **Fig. 2.77.** Venation pattern; arrows indicate higher order veins regular polygonal reticulate. Scale bar = 2mm. **Fig. 2.78** LM of adaxial surface; arrows indicate granular periclinal walls. Scale bar = 50µm. **Fig. 2.79.** LM of abaxial surface showing stomate arrow indicates T-pieces of thickened cuticle at poles of guard cells. Scale bar = 10µm. **Fig. 2.80.** LM of abaxial surface; arrow shows angular anticlinal walls. Scale bar = 20µm.


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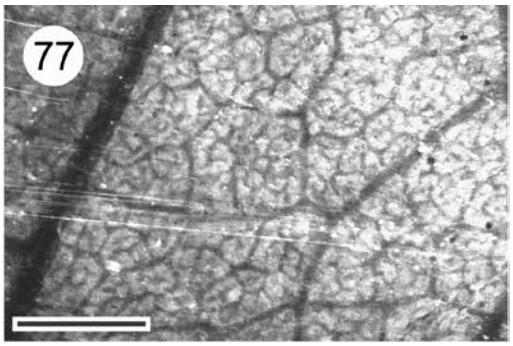
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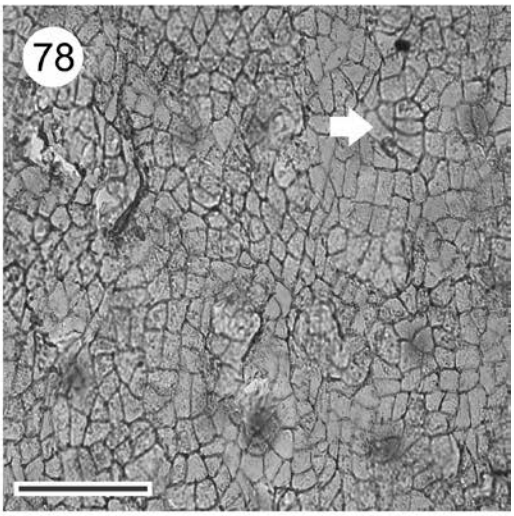
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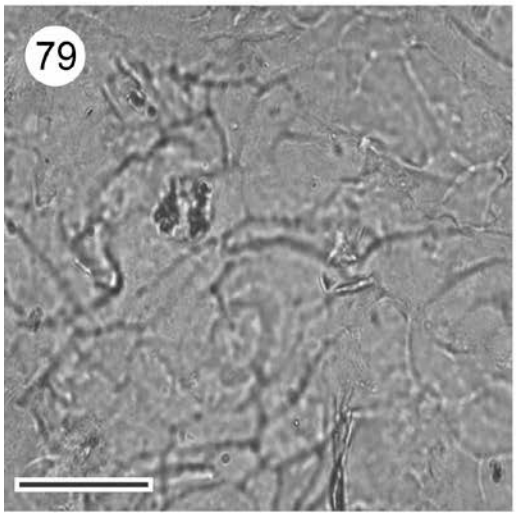
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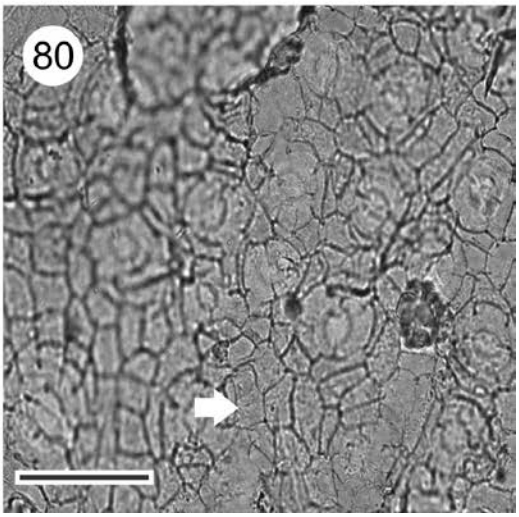
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**Figures 2.81- 2.83.** Brandy Creek 018 aff. Cunoniaceae/Elaeocarpaceae. **Fig. 2.81.** Incomplete leaf (BC 1531) showing toothed margin. Scale bar = 2cm **Fig. 2.82.** Venation pattern; arrow indicates tooth. Scale bar = 2mm. **Fig. 2.83.** LM adaxial surface showing granular periclinal wall. Scale bar = 20µm. **Fig. 2.84**. LM abaxial surface arrow; indicates undulate anticlinal walls. Scale bar = 20µm. **Fig. 2.85.** LM of abaxial surface showing stomate arrow indicates T-pieces of thickened cuticle at poles of guards. Scale bar = 10µm.

Discussion notes


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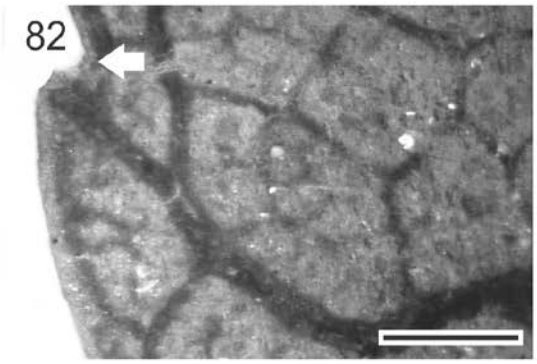
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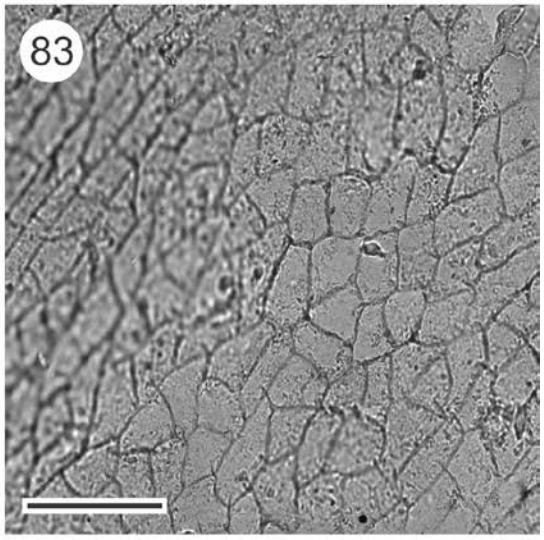
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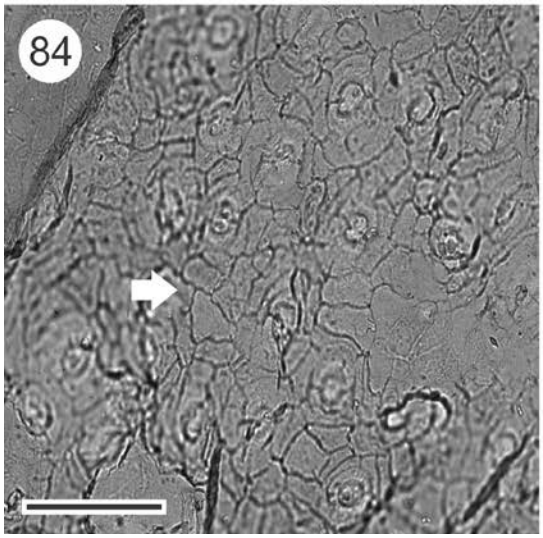
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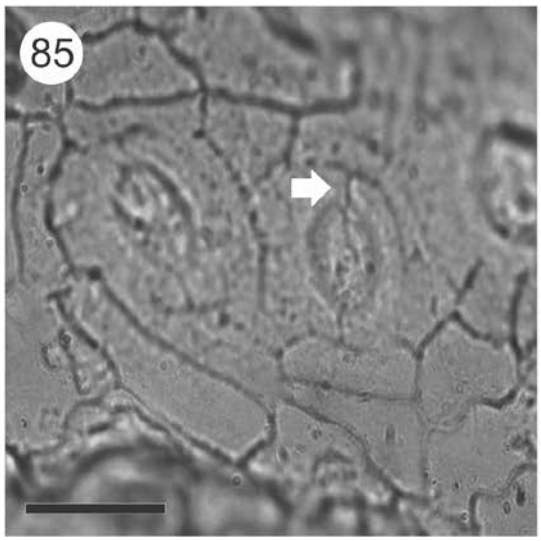
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# Chapter 3 The Brandy Creek Microflora (Spores and Pollen).

## 3.1 Introduction

The Brandy Creek Microflora (Spores and Pollen), provides additional information on the floristic character of the vegetation that is absent from the Brandy Creek macrofossil record; microfloral and macrofloral data are complimentary owing to differences in transport and preservation potential between spores-pollen and leaves, and between taxa for the same organ (Greenwood 1991). Using previous identification of pollen and spores across southern Australia, the pollen and spores at Brandy Creek are identified to stratigraphic spore-pollen taxa, and where possible assigned to a nearest living relatives. The data from this chapter contributes to a bioclimatic analysis of the Brandy Creek flora (Chapter 4) and an assessment of plant community structure in Chapter 5.

### 3.1.1 The value of pollen and spores (palynology).

Palynological studies play an important role in the reconstruction of ancient plant communities by providing floristic characterisation of the vegetation (mostly at a regional level) as well as assisting age determination of fossil localities. The first fossil pollen grains to be documented were identified as *Alnus* by Goeppert in 1844, and came from the Paleogene brown coal sediments of Germany. (Traverse 1988 and 2007). Globally, Paleogene pollen has been documented from China, New Zealand, North America, South America, Europe, India and Africa (e.g., Yao et al. 2009; Lee et al. 2012; Jarzen and Dilcher 2006; Okuda et al. 2006; Willumsen 2004; Tripathi et al. 2009; Scott et al. 2004). As with Paleogene leaf macrofossils, some Paleogene pollen and spores have similarities to modern pollen and spores, allowing for easy comparison between fossil and modern assemblages (Traverse 1988). For example, the diagnostic characters of *Nothofagus* pollen allow for distinctions to be made between ancient and modern temperate and tropical taxa (Hill 1991). Likewise, Podocarpaceae pollen can be typically bisaccate, for example *Dacrydium, Podocarpus, Prumnopitys,* or trisaccate as in *Dacrycarpus, Microstrobus and Microcachrys* for example (Tomlinson 1994; Morley 2011).

Australian Paleogene microfossil reports date back to the 1940's with Cookson's first publication on *Nothofagus* pollen from the Australian Tertiary in 1946. During the end of the 1940's through to the 1960's Cookson and others paved the way for palaeopalynology in Australia (Macphail et al. 1994). Publications included Cookson (1950, 1953, 1954 and 1957); Cookson and Pike (1953 and 1955); Duigan (1951); and Harris (1965, 1971). Since the 1960's, numerous papers have been published on the identification of Paleogene pollen and spores including work by Stover and Partridge (1973); Martin (1978, 1981); Carpenter et al. (2012) and Thornhill and Macphail (2012). Stover and Partridge (1973) also formulated detailed palynological zonation in the Gippsland Basin correlated with Paleogene marine biostratigraphy . These zones allowed for age determination based on the presence or absence of pollen or spore types, (Figure 3.1; Macphail et al. 1994).

Preliminary results of the Brandy Creek pollen and spore record suggested that the locality contained all the elements of an early Eocene flora (Scriven and Hill 1995; Greenwood et al. 2003). Greenwood et al. (2003), more specifically, correlated the microfloras at Brandy Creek to the uppermost part of the *Malvacipollis diversus* zone or the *Proteacidites asperopolus* zone, placing Brandy Creek in the early Eocene. Nevertheless, more recent analysis by Holdgate et al. (2008) correlated the Brandy Creek microflora with the middle *Nothofagidites asperus* zone (late middle to late Eocene) based on the presence of *Cyathidites splendens* Harris 1965, botanically related to the modern *Acrostichum speciosum.* Barbara Wagstaff The University of Melbourne (pers. communication 2012) interprets the earlier counts in Greenwood et al. (2003) as representing a local swamp flora, rather than regional vegetation, leading to incorrect placement of Brandy Creek and Hotham Heights as early Eocene. The Holdgate et al. (2008) age determination of the Brandy Creek flora is used in this thesis (Figure 3.1).

The palynomorph record at Brandy Creek complements the Brandy Creek leaf macrofossil record together providing a more holistic account of the flora during the Eocene. In some cases palynomorphs can be assigned to a nearest living relative, allowing for palaeoclimate and palaeoecological reconstruction of past floras. Palynomorphs also have the added benefit of providing local, extra local and a regional record of past vegetation. The pollen and spore record at Brandy Creek affords additional information

regarding the character of the vegetation at Brandy Creek that is otherwise missing from the macrofossil record.

### 3.1.2 Limitations with the fossil pollen and spore record.

As with the macrofossil record, there are limits to the level of information that the microfossil record can provide. Analysis of pollen and spores only provides a snapshot of past vegetation. In some families, plants occupy a wide range of habitats and represent a number of different vegetation types; however habitat information cannot be discerned if pollen cannot be identified at a generic level. For example, Myrtaceae has a tropical rainforest element (e.g. *Syzygium*) as well as a sclerophyllous element (e.g. *Corymbia* and *Eucalyptus*). Myrtaceae pollen is not particularly distinctive characterised as syncolplate, parasyncolpate, brevicolpate or asyncolpate (Thornhill and Macphail, 2012). To identify Myrtaceae pollen multiple characters are required to distinguish at a genus or species level. This is difficult when dealing with fossil pollen where in some case certain characters are not preserved (Pickett and Newsome 1997). In some cases there is no way of determining if the Myrtaceae pollen represented is from a genus that lived in a dry sclerophyll or a tropical rainforest habitat. In this circumstance the presence of Myrtaceae in the pollen count relies on the assumption that the pollen represents a rainforest genus of Myrtaceae basis on co-occurring rainforest families found in the pollen and spore sum (Martin 1978, 1981).

Like Myrtaceae, other families dominating Australian rainforests have pollen that cannot be identified definitively at a generic level and are therefore grouped as undescribed colpate (*Tricolpites*), colporate (*Tricolporities*) or porate (*Triporopollenities*) (Macphail et al. 1994). For example, Cunoniaceae and Elaeocarpaceae pollen are typically not recognised in Australian Tertiary palynology (Macphail et al. 1994), however some studies recognise dicolpate or tricolpate members of the Cunoniaceae (e.g., Sluiter 1991, 1995; Sniderman & Jordan 2011), and in some cases Cunonicaceae can be assigned to genus for example *Concolpities leptos* has affinity with Cunonicaceae *Gillbeea* type (Stover & Partridge 1973; Macphail 1996). *Nothofagus* has Extant lineages of Nothofagus diversifying between 55 – 35 mya according to molecular and phylogenetic studies, suggesting a cautionary approach is required when assigning fossil *Nothofagus* pollen to a nearest living relative (Cook and Crisp 2005).

Analysis of modern pollen and spore counts have shown that some families such as Proteaceae are common in the landscape, yet are under-represented in the pollen sum (Itzstein-Davey 2003). A number of factors can influence low productivity, dispersal or preservation rates which can influence the under or over representation of species in the pollen record. For example, in rainforests Proteaceae are mostly understory species and their pollen is therefore less likely to reach water bodies and suitable preservation sites. Transport vectors for Proteaceae are predominantly mammal, insect or bird therefore they are less likely than plants that use wind pollination to be transported to water bodies (Dodson 1977). The opposite can be said for Nothofagus which has pollen that is highly productive and readily transported by wind.

The use of extant pollen and spore counts as a base for interpretation of fossil assemblages presents difficulties. For example, microfossil evidence suggests that Proteaceae was a major component of the vegetation during the Paleocene through to the middle Eocene, although macrofossil evidence does not support this idea. One hypothesis for this discrepancy between the macrofossil and microfossil record is the mode of transport for pollen Proteaceae during the Eocene. Extant Proteaceae use mostly animal, bird or insect transport vectors. However extinct forms of Proteaceae with the pollen ranging in size from 20 – 40 um could have used wind pollination (Muller 1979;Hill, 1994). As the vegetation changed over time wind pollinated Proteaceae reduced in numbers and in some cases became extinct, whilst mammal, insect and bird vectors became favoured (Hill, 1994). This being the case, consideration needs to be given to the possible changes in transport vectors for Proteaceae when interpreting the fossil record (Martin 1978; Adam 1992).

The chances of fossilisation has a number of variables including; the amount of pollen produced from a particular family of plant and the distance between the plant source and the sedimentation suitable for fossilisation, which is often close to or in water (Muller 1984). The pollination mechanism of a plant is a major determining factor. Pollen from wind pollinated plants is more likely to be present than pollen from animal, bird or insect pollinated plants. Most wind pollinated plants produce exceedingly large numbers of pollen grains to ensure that at least some of the pollen arrives at its required destination. Mammal, bird and insect pollination is more targeted and selective and subsequently, pollen grains

are produced in much more modest numbers or in some cases is massed in bundles. Due to the high mobility of pollen from wind pollinated plants, it is more likely to reach sediment that is suitable for fossilisation (Muller 1984). Pollen that undergoes fluvial transport behave the same as sediment (silt and mud) when they are wet. Heavy pollen is transported less distance from source, whilst lighter and smaller pollen is transported some distance from source (Moss et.al 2005). Pollen produced by understory or ground cover plants are more likely to over represented in the pollen sum because of localised surf runoff (Moss et.al 2005). The quality of the pollen can also be compromised with fluvial transport (Wagstaff et.al 2013).

In this Chapter, the spore and pollen flora (microflora) of the Brandy Creek late middle Eocene to late Eocene site is presented. The data are interpreted based on the above discussion of the limitations of such an analysis, and contrasted with microfloras from other Australian Eocene fossil floras. In subsequent Chapters, the microflora interpretation is used to complement data from the macroflora (Chapter 2) to reconstruct the climate of the site (Chapter 4) and the palaeoecology of the Eocene Brandy Creek fossil flora (Chapter 5).

## 3.2 Methods and Materials.

### 3.2.1 Fossil sampling on Site.

Seven samples within the Brandy Creek outcrop were selected to be processed for palynological analysis. Samples were spaced vertically within the outcrop so as to provide a survey of the microflora that would complement the macrofloral analysis in understanding the palaeoecology of the site (Chapter 5). Samples were taken from Brandy Creek units 1, 3, 5, 7, 9 and 11 as noted in the lithologic log (Figure 3.2). Of the seven samples processed, three samples were analysed to determine floristic composition of the Brandy Creek spore and pollen sum: sample 1 (unit 1), 3 (unit 3) and 7 (unit 11). This decision was made to allow continued focus on the leaf macroflora, but also recognition that the microflora differed in only minor ways between samples dispersed vertically within the sampled section (chapter 5).

### 3.2.2 Extraction of pollen and spores

Samples were sent to Laola Pty Ltd in Perth for pollen extraction. Their preparation method follows standard mineral sediment processing for palynomorph extraction (Traverse 1988) and is as follows:

1) Samples were treated with Hydrochloric acid (HCL) to remove any carbonates, and then dissolved with hydrofluoric acid (HF) over two days.
2) The material was then washed with water and boiled in hydrochloric acid (HCL).
3) A heavy liquid was used (zinc bromide ($ZnBr_2$) sg 2.1) to float off the organic fraction of the material.
4) The material was then oxidized using nitric acid ($HNO_3$) and potassium chlorate (KCL) for one minute and then washed three times and treated with potassium hydroxide (KOH) (2.5%), and then washed again.
5) Three slides were made of the material filtered over an 11-micron sieve.
6) A single slide per sample of unfiltered material was produced to ensure pollen/spores less than 10 microns were captured for diversity, for example Myrtaceae, Cunoniaceae and Elaeocarpaceae which all have pollen less than 10 microns (Macphail et al. 1994).

### 3.2.3 Taxonomic analysis of the palynological samples

Pollen and spores were sorted into taxonomic units using existing Australian literature on Paleogene spore/pollen record and with assistance from Alan Partridge (BIOSTRATA Pty. Ltd) (Cookson 1950, 1953, 1954, 1957; Cookson and Pike 1955; Stover and Partridge 1973; Macphail 1996). A modified proforma of Eocene spore/pollen provided by Alan Partridge (personal communication 2002) was used to record spore and pollen counts. Counts greater than 500 were done to account for diversity. Filtered and unfiltered slides were examined to account for small pollen grains and to ensure the integrity of the count.

### 3.2.4 Floristic composition

Floristic composition of pollen and spores at Brandy Creek is listed in a contingency table (Table 3.1) showing botanical affinity and the percentage count. These data are displayed as a grouped rank abundance histogram where the 3 major plant groups –

pteridiophytes, gymnosperms, and angiosperms – are presented as separate rank abundance series in order to highlight the importance (dominance vs. rarity) of particular taxa within these plant groups, as well as across the total pollen sum (Figure 3.3).

## 3.3 Results

1702 pollen and spore grains were counted from three samples at Brandy Creek. From these samples 36 different palynomorphs were identified (Table 3.1). The rank abundance histogram (Figure 3.3) shows that the Brandy Creek flora includes pteriophytes that are dominated by *Cyatheacidites* spp. (< 45um) representing 27% of the total count and *Cyatheacidites* spp. (>45um) affinity Dicksoniaceae, representing 13% of the count, whilst most others have moderate representation including *Ischyosporites* spp. (3.7%), *Foveotriletes* sp. (1.5%) and *Baculatisporites* sp. (1.3%), with many rare species including *Rugulatisporites* sp. and *Verrucosisporites kopukuensis* (Couper 1960) Stover in Stover & Partridge (1973), both <1%.

The angiosperms at Brandy Creek make up 41% of the flora, with taxon affinity *Nothofagus* accounting for 19% of the total (Figure 3.3). The grains attributed to *Nothofagus* include *Nothofagidites emaricidus* (Cookson 1959) Harris 1965 (7.7%), aff. *Nothofagus* s.g. *Brassospora*, *Nothofagidities flemingii* (Couper 1953) Potonie 1960 aff. *Nothofagus* s.g. *Brassospora* (5.5%) and *Nothofagidities brachyspinulosus* (Cookson 1959) Harris (1965)(5.9%) aff. *Nothofagus* s.g. *Fuscospora* (Table 3.1). Other angiosperms include *Proteacidites pachypolus (2.9%) and Proteacidites spp. (2.5%)* aff. Proteaceae and *Malvacipollis* sp. (2.7%) aff. Euphorbiaceae. The counts also show a number of rare taxa including *Cupanieidites orthoteichus* (Cookson & Pike 1954) *aff*. Sapindaceae and *Concolpities* sp. aff. Cunoniaceae as well as trace pollen and spores.

The gymnosperms representing only 6.2% of the pollen at Brandy Creek include *Araucariacites australis* affinity Araucariaceae (3.7%) *Podocarpidites sp., Podosporites* sp. and *Parvisaccites* sp. affinity Podocarpaceae, all representing less than 1% of the count.

## 3.4 Discussion

Pollen and spore counts and taxonomic assignment of the Brandy Creek flora shows that the Brandy Creek flora was moderately diverse. Many of the spore and pollen having affinity with modern pteridophyte, gymnosperm and angiosperm families including Araucariaceae, Dicksoniaceace, Nothofagaceae, Podocarpaceae and Proteaceae (Table 3.1).

### 3.4.1 The Brandy Creek Pteridophytes

51% of the spore and pollen count at Brandy Creek is made up of pteridophytes, with *Cyatheacidites* spp. affinity Dicksoniacae a major component of the counts. Spores of *Cyatheacidites* spp. are easily recognisable based on their distinctive shape and size, however their lack of specific diagnostic features can result in low diversity data (Nagalingum et al. 2002). Other taxa such as *Verrucosisporites kopukuensis* affinity Schizeaceae have distinctive characters and are easily identifiable, providing greater taxonomic value (diversity data); Nevertheless they are less abundant than ferns such as *Cyatheacidites* spp. affinity Dicksoniaceae and result in what Nagalingum et al. (2002) referred to as recognition bias.

In modern rainforests Dicksoniaceae includes both treeferns (e.g., *Dicksonia* spp.) and ground ferns (*Calochlaena* spp.) present in the understory vegetation, and this is likely to have been the case for the forest represented by the Brandy Creek flora. Studies of fluvial transport of extant pollen in the Humid Wey Tropics of northeastern Queensland by Moss et. al (2005), found a high representation of *Cyathea* and other monlete psilate spores in the pollen sum. Other Pteridophytes including *Gleichenia* and *Lycopodium* also present in samples, which is consistent with the results from Brandy Creek. Taphonomic bias may also play a role in the high proportion of *Cyatheacidites* spp. in the Brandy Creek counts, with a single tree fern shedding up to 750 million spores. Although most are transported in air currents, in closed forest this distance may be minimal (Page 1979). Thus, the large number of spores deposited by most fern species may over-represent fern numbers in a fossil population.

At nearby Hotham Heights, *Ischyosporites gremius* affinity Dicksoniaceae were recorded in the macro and micro floras (Carpenter et al. 2004). Partridge (1998) and

Greenwood et al. (2003) also noted a high abundance of *Cyathacidites paleospora* (Cyatheaceae) (12.2%) *and Ischyosporites irregularis* (33.7%) affinity Dicksoniaceae. Pteridophytes spores are well represented across a number of localities in south eastern Australia including Deans Marsh, Golden Grove and Nerriga (Table 3.2 and Figure 3.4).

### 3.4.2 Brandy Creek Gymnosperms.

Gymnosperms represent 6.2% of the total pollen count at Brandy Creek(Figure 3.3.). The taxa recorded as pollen have affinity with the extant conifer families Araucariaceae and Podocarpaceae, and also the non-conifer Ephedraceae.

Araucariaceae is the most abundant of the gymnosperms and is represented by the palynomorphs *Araucariacites australis* (Cookson 1957) and *Dilwynites granulatus* (Harris 1965).. Extant Araucariaceae have large pollen grains and the pollen is wingless, making long distance dispersal difficult by aeolian method (Kershaw and McGlone 1995; Kershaw and Wagstaff 2001; Williams and Adam 2010)). However analysis of fluvial transport of modern Araucariaceae pollen suggest that it can travel some distance from source in riverine environments (Moss, Kershaw and Grindrod, 2005). The water body present at Brandy Creek was most likely an oxbow and therefore the Araucuariaceae pollen present is representative of local Araucariaceae and not the result of pollen transported from other parts of the region. It is possible that the extant genera *Agathis* and *Araucaria* were both present, however fossil pollen on its own cannot be used to separate between the two genera (Kershaw and Wagstaff, 2001). Thus, it is not possible to document the genera at a locality in the absence of leaf macrofossils (Macphail et al. 1995). The pollen *Dilwynities granulatus* is considered to represent the living Araucarian *Wollemia,* as it has diagnostic characters which separate it from other genera (Macphail et al. 1995). Carpenter et al. (2004) documented a gymnosperm leaf fossil at nearby Hotham Heights as Araucariacae aff. *Agathis* sp. as well as the pollen taxa *Araucariacities australis* and *Dilwynities granulatus.* Podocarpaceae, a relative of the Araucariaceae is also likely to have been a local component of the landscape. Podocarpaceae was recorded in both macro and micro floras at the nearby Eocene Hotham Heights site (Carpenter et al. 2004).

In the Eocene Brandy Creek, Hotham Heights, Nerriga, Golden Grove and Deans Marsh microfloras, gymnosperms represented a low percentage of the pollen sum (Figure 3.4), suggesting that they lived alongside angiosperms and ferns. With the rise of the angiosperms gymnosperms were likely to be rare in the landscape occupying marginal habitats (Kershaw et al. 2001; Brodribb and Field, 2010; Crips and Cook, 2011

### 3.4.3 The Brandy Creek Angiosperms.

The angiosperms at Brandy Creek account for 41% of the total count, with *Nothofagus* (as *Nothofagidites spp.*) contributing 19% of the spore and pollen sum (Figure 3.3). The percentage of *Nothofagus* in the pollen sum at Brandy Creek is high compared to nearby Hotham Heights, and other Eocene localities such as Nerriga, Deans Marsh and Golden Grove (Figure 3.4) (Martin 1981). Carpenter et al. (2004) recorded low counts of *Nothofagus* pollen (<4%) in the Hotham Heights microflora, however Holdgate et al. (2008) recorded *Nothofagus* counts between 30 and 65% for Hotham Heights and Brandy Creek samples, possibly reflecting the presence of *Nothofagus* in the near local or local vegetation. The high count recorded by Holdgate (2008) is consistent with the data from this research. The variability in results between the Carpenter et.al (2004) and the Holdgate (2008) and results in this thesis highlights the need for multiple samples within a single site and multiple localities to be sampled in order to understand local and regional vegetation.

The late middle to late Eocene Anglesea flora shows a significant increase in *Nothofagus* relative to older floras from SE Australia, with *Nothofagidities* taxa making up 27.5% of the count and *Nothofagidities* s.g. *Brassospora* making up 24.5% of that count (Christophel, Harris and Syber 1987). The trend of increasing presence of *Nothofagus* with ever younger age continues during the Oligocene at which time there is a peak in the abundance of *Nothofagus* (Martin 1978). Examples of this include the Berwick Quarry flora in Victoria with 81% of the pollen flora attributed to *Nothofagus* (Hill 2001; Steart, Greenwood and Boon, 2005).

The timing of the diversification of extant lineages of *Nothofagus* (55 - 35mya) corresponds well with the macrofossil record (Cook and Crisp 2005). The *Nothofagus* macrofossil record is restricted to the middle Eocene and Oligocene of Tasmania with

macrofossils recorded from Little Rapid River, Pioneer and Cethana localities. (Hill 1991, 1994; Hill et al. 1999; Jordan and Hill 1999). Fossil evidence from the Oligocene Little Rapid River in Tasmania, suggest that tropical and temperate genera of *Nothofagus* co-occurred during this period, which is not the case for extant *Nothofagus* (Hill 2001). *Nothofagus* leaf macrofossils on mainland Australia, are not recorded until the early Miocene in Kiandra sediments (Paull and Hill 2003) and the Miocene in Bacchus Marsh Victoria (Christophel 1989). The absence of *Nothofagus* in the leaf macrofossil record from Hotham Heights and Brandy Creek could be the result of the fragility of the leaf cuticle rather or their proximity in relation to depositional environment rather than its absence from the landscape (e.g., Paull and Hill 2003; Carpenter et al. 2004).

Proteaceae pollen at Brandy Creek account for an aggregate of 2.7% of the total count. The percentage of Proteaceae pollen at Brandy Creek and nearby Hotham Heights is low. Although no macrofossil Proteaceae are recorded at Brandy Creek, Carpenter et al. (2004) documents nine leaf morphotypes with affinity to Proteaceae as well as pollen having affinity to Proteaceae from the Hotham Heights locality. The family is recorded in both the pollen and leaf macrofossil record at Golden Grove, Deans Marsh and the late middle to late Eocene Anglesea flora, where there is an unusually high number of Proteaceae pollen taxa (20), given that during this time Proteaceae diversity begins to decrease in relation to an increase in the presence of *Nothofagus* in the landscape (Christophel 1989). One theory for the decline of Proteaceae in the landscape is a shift in pollination mechanism from predominately wind to mammal, insect, or bird over time (Christophel 1989: Hill 1994).

Analysis of Proteaceae modern pollen 'rain' has also shown that Proteaceae can be under represented in the pollen counts. Martin (1978) records 4% Proteaceae pollen from a study site of 13 Proteaceae species, and Hassell (2000) had similar results with less than 3% Proteaceae making up the pollen count. These low counts are not reflective of the dominance that Proteaceae has in the landscape. Under representation in the pollen count can be attributed to the plant profile of Proteaceae which is typically understory plant leading to low dispersal of pollen. Additionally, Proteaceae pollen is large and heavy making it difficult to transport. The pollination mechanisms of Proteaceae are mammal, insect or

bird and because of this have low pollen production volume, further contributing to under representation in the palynological count (Hassell 2000).

The presence of a few dominant taxa such as *Cyatheacidites spp.* and *Nothofagidites emarcidus* (Cookson 1959) Harris 1965 and *Nothofagidites brachyspinulosus* with many common taxa such as *Tricolporites sphaerica* Cookson 1957 (*Rhoipites sphaerica* (Cookson 1957) Pocknall & Crosbie 198) and *Araucariacities australis* and many rare taxa such as *Podocarpidities sp*., *Gleicheniidites sp.* and *Ericipites sp*. is consistent with the sampling of modern pollen and spores. Kershaw and Strickland (1990), in a 10 year pollen trapping study of Mt Lewis in the tropical rainforest of northeast Queensland, grouped the pollen/spores trapped into three categories; the local component (plants within 10 meters of traps), extra local (plants outside the local area but within the sample area), and a regional component (all other pollen found outside the local and extra local area). Kershaw and Strickland (1990) found that pollen representing the local component had the greatest dominance and suggests that the difficulty for pollen transport in closed forest could be one reason. Kershaw and Strickland'sidea does not explain the high proportion of *Nothofagus* in the pollen sum at Brandy Creek and the absence of *Nothofagus* in the leaf macrofossil record. *Nothofagus* pollen has been found on Chatham Island, 700-800km east of the nearest *Nothofagus* forest in New Zealand (Dodson 1976), but typically in low numbers. Rowe (2012), in an analysis of pollen and spore counts of the Torres Straits Islands, found that non-rainforest tree pollen can be represented in the pollen sum of a rainforest site, however this is expected to be limited in a closed canopy rainforest. Interestingly, Rowe (2012) found that some regional pollen dominated the pollen counts, but did not contribute greatly to the diversity of the pollen sum, as is the case for *Nothofagus* at Brandy Creek. Similar findings were documented by Walker and Sun (2000) who conducted pollen trapping at the Atherton Tableland of north eastern Queensland.

### 3.4.4 The Eocene Southern Hemisphere Flora

The pollen and spore record at Brandy Creek share some similarities with other Southern Hemisphere floras (i.e., New Zealand, Antarctica, southern South America) that likely retained some land connections during the Eocene or at earlier times, allowing floristic exchange (Cantrill et al. 2011).

The Pikopiko fossil forest in New Zealand is considered late Eocene in age (Lee et al. 2012). The microflora from Pikopiko shares some floristic elements with Brandy Creek including a diverse range of Pteridophyte spores, gymnosperms including Araucariaceae (*Araucaria* and *Wollemia*) and Podocarpaceae (*Podocarpus*) and angiosperms such as Proteaceae, *Nothofagus* (*Fuscospora and Brassospora* type), and *Cupanieidites* aff Sapindaceae. Many elements of the New Zealand fossil record are not present in the modern flora of New Zealand, however they are present in the rainforest flora of Australia and include Proteaceae, Casuarinaceae, and Lauraceae (Lee et al. 2012).

Macro and micro fossil floras to the south of Australia tell a different story with the middle Eocene Cucullea flora, Antarctica, representing cooler climate adapted vegetation compared with Australia. Nethertheless the flora has similar angiosperm diversity to the Brandy Creek flora, and includes morphotypes with affinity to Nothofagaceae, Lauraceae, Proteaceae, Elaeocarpaceae, Cunoniaceae and Myrtaceae (Francis et al. 2008). The flora has been described as subtropical to cool temperate mixed forests and is evidence of the Eocene warmer world transitioning to cooler climate vegetation during the middle Eocene (Francis et al. 2008). Pross et al. (2012) analysed sediments offshore from Wilkes Land in west Antarctica and found a shift in floristic composition from the early to middle Eocene. The highly diverse early Eocene flora includes many taxa i.e. *Lygodium* (Cyatheaceae), *Beauprea* (Proteaceae) and *Anacolosa* (Olacaeae) that have modern counterparts in subtropical and tropical rainforest in Australia and to the north of Australia in New Guinea and New Caledonia today. These forests are characteristic of mesothermal and meagathermal rainforest. By the middle Eocene the Wilkes Land flora includes high percentages of *Nothofagus* as well as Araucariaceae and Proteaceae, and is temperate in nature.

Floras from the late Eocene East Antarctica Prydz Bay Flora share many common pollen and spore taxa with Brandy Creek including *Gleicheniidites* spp. aff. Gleicheniaceae, *Baculatisporities* sp. aff. *Hymenophyllaceae* and *Polypodiisporities* spp. aff. Polypodiaceae. Gymnosperms including Araucariaceae (*Araucariacites australis, Dilwynites granulatus*), Podocarpaceae (*Podocarpidities* spp.) are also present. Angiosperms dominate the Prydz Bay flora and include Sapindaceae, Casuariniaceae, Myrtaceae, *Nothofagus* (*Brassospora*)

and Proteaceae. This flora is described a mosaic of rainforest trees, scleromorphic shrubs and wetland herbs (Truswell and Macphail 2009).

Both Australia and South America lay at high southern latitudes during the Eocene with many of the fossil taxa found in South America having nearest living relatives found in the Humid Wet Tropics of northeastern Queensland (Dettman 1989; Thornhill et.al 2012). The highly diverse middle Eocene Laguna del Hunco and Rio Pichileufu, macro floras of Patagonia, Argentina for example have nearest living relatives that include Sapindaceae, Lauraceae, Myrtaceae, and Araucariaceae (Wilf et al. 2005). The floristic character of Laguna del Hunco and Rio Pichileufu is similar to the Miocene of Chile, both localities showing a connection between Australian and South American flora with the presence of Araucariaceae, Podocarpaceae and Myrtaceae as well as a high percentage of ferns (Le Roux 2012).

### 3.4.5 Modern counterparts of the Brandy Creek pollen and spores

Evidence from the Australia fossil record shows that many of the families represented in the Brandy Creek pollen and spore record were abundant in the landscape across southern Australia (including Tasmania) during the Eocene. Many of these taxa had a much greater distributional range than modern counterparts reflecting warmer, moister and less seasonal climates during the Eocene.

Many of the families represented as pollen and spores at Brandy Creek, as with the families represented in the Brandy Creek macrofossil record, retreated north during the Miocene as the continent cooled. A number of these families have modern counterparts living outside of Australia today including taxa such as, *Nothofagdities emarcidus* aff. *Nothofagus brassospora* type, which is found in New Guinea, New Caledonia and Asia.

Others such as *Podocarpus* and *Prumnopitys,* which have modern analogs with restricted ranges in Australia (as canopy dominants in north eastern Queensland rainforest), have greatest modern representation in tropical regions outside of Australia in areas of New Guinea and New Caledonia (Christophel 1989; Williams and Adams 2010).

Whilst Araucariaceae continued its presence in the north eastern Queensland region up until 45,000 -40,000 years ago there was a decline after a significant increase in burning (Kershaw 1986). The nearest living relatives of *Araucaria* and *Agathis* are almost absent from the complex rainforest of north eastern Australia, with the dense canopy not allowing an opportunity for regeneration below a shaded canopy (Enright and Hill 1995; Williams and Adam 2010). Today Araucariaceae remains an important component of SE Queensland vegetation for example Bunya Mountains and on Frazer island living on the margins of complex rainforests (Huth and Holzworth, 2005). Outside of Australia Araucaria and Agathis have greatest diversity in New Caledonia (Hill 1995).

In the Eocene *Cyatheacidities* affinity Dicksoniaceae, like their modern equivalents, were restricted to areas that have high rainfall. Both the modern and ancient members of this group would have occurred in rainforest vegetation similar to that found from the Tasmanian cool temperate rainforest to the rainforest of the Humid Wet tropics. The presence of *Cyatheacidities spp.* and other ferns at Brandy Creek suggests a moist environment.

The floristic character of Brandy Creek pollen and spores found in this study, support earlier work based on the leaf macrofossil data (Chapter 2). These data suggest that the Brandy Creek flora is representative of a simple notophyll - microphyll vine forest (SNMVF). Collectively, the Lauraceae (represented in the macrofossil record), and other families represented in the pollen sum including Cunonicaeae, Araucariacae, Dicksoniaceae and Proteaceae have genera that are present today in SNMVF in north eastern Queensland (Chapter 5). Nearest living relatives of the Brandy Creek flora can therefore be used to determine mean annual temperature and mean annual precipitation of the flora during the Eocene. The Brandy Creek mean annual temperature (MAT) of 15.7– 21.7°C and a mean annual precipitation (MAP) of 107 – 320cm/yr. is indicative of modern mesothermal rainforest of north eastern Queensland (Nix 1982; Kershaw and Nix 1988) (Chapter 4).

## 3.5 Conclusions

The Brandy Creek palynomorphs indicate a highly diverse flora during the Eocene, representing both a regional (*Nothofagus*) and local (Dicksoniaceae, Araucariaceae and Proteaceae) characterisation of the flora. The local component is supported by macrofossil evidence at nearby Hotham Heights, which includes macrofossils with nearest living relatives of Proteaceae, Cunoniaceae and Araucariaceae. Fossil localities in south eastern Australia show that many of the families were widespread across the region. Many of the families that are represented in the Brandy Creek flora have nearest living relatives in north eastern Queensland, with the flora typical of a mesothermal simple notophyll - microphyll vine forest (rainforest) of north eastern Queensland today.

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**Table 3.1** Fossil pollen and spore species ('palynomorphs') list for Brandy Creek. (x equal < 1%). P = Pteridophytes, G = Gymnosperms and A = Angiosperms.

| *Species list pollen and spores* | *Botanical Affinity* | *count* | *category* |
|---|---|---|---|
| *Cyathidites sp. (<45µm)* | Dicksoniaceae | 27% | P |
| *Cyathidites sp. (>45µm)* | Dicksoniaceae | 13% | P |
| *Ischyosporites sp.* | Dicksoniaceae? | 3.70% | P |
| *Foveotriletes sp.* | Lycopodiaceae | 1.50% | P |
| *Baculatisporites* | Hymenophyllaceae | 1.30% | P |
| *Cyatheacidites annulatus* | Dicksoniaceae | <1% | P |
| *Cyathidites subtilis* | Cyatheaceae | <1% | P |
| *Gleicheniidites sp.* | Gleicheniaceae | <1% | P |
| *Laevigatosporites sp.* | Numerous monolete ferns | <1% | P |
| *Matonisporites sp.* | Dicksoniaceae | <1% | P |
| *Polypodiidites sp.* | Polypodiaceae | <1% | P |
| *Polypodiisporites sp.* | Polypodiaceae | <1% | P |
| *Rugulatisporites sp.* | Thyrospteridaceae | <1% | P |
| *Verrucosisporites kopukuensis* | Schizaeaceae | <1% | P |
| *Araucariacites australis* | Araucariaceae | 3.70% | G |
| *Dilwynites granulates* | Wollemia (Araucariaceae) | <1% | G |
| *Ephedra sp.* | Ephedraceae | <1% | G |
| *Podocarpidites sp.* | Podocarpus | <1% | G |
| *Podosporites sp.* | Podocarpaceae | <1% | G |
| *Nothofagidites emarcidus* | Nothofagaceae: Nothofagus subgenus Brassospora | 7.70% | A |
| *N. brachyspinulosus* | Nothofagaceae: Nothofagus subgenus Fuscospora | 5.90% | A |
| *N. flemingii* | Nothofagaceae: Nothofagus. subgenus Brassospora | 5.50% | A |
| *Tricolporites sphaerica* | | 4.10% | A |
| *Tricolp(or)ites spp.* | unidentified angiosperm | 3.90% | A |
| *Proteacidites pachypolus* | Proteaceae | 2.90% | A |
| *Malvacipollis sp.* | Euphorbiaceae | 2.70% | A |
| *Proteacidites sp.* | Proteaceae | 2.50% | A |
| *Concolplites sp.* | Cunoniaceae | 1.40% | A |
| *Cupanieidites orthoteichus* | Sapindaceae | <1% | A |
| *Ericipites scabratus* | Ericaceae | <1% | A |
| *Milfordia sp.* | Restionaceae | <1% | A |
| *Myrtaceidities spp.* | Myrtaceae | 1.60% | A |
| *Parvisaccites sp.* | Podocarpaceae: Dacrydium bidwillii type | <1% | A |
| *Triporopollenites spp.* | Proteaceae | <1% | A |
| *Haloragacidites harrisii* | Casuarinaceae | <1% | A |
| *Polycolpites sp.* | | <1% | A |
| *Tricolpities reticulates* | Gunneraceae | <1% | A |
| | Total count | 1702 | grains |

**Table 3.2.** Comparison of pollen and spore count for Brandy Creek and other early to late Eocene localities in south eastern Australia (Partridge, 1998). Note total count for Golden Grove was not available.

| Species List | Brandy Creek 2000 | Brandy Creek 2003 | Hotham Heights | Nerriga | Golden Grove | Deans Marsh |
|---|---|---|---|---|---|---|
| *Araucariacites australis* | * | * | * | * | * | |
| *Baculatisporites sp.* | * | * | * | * | * | * |
| *Concolplites sp.* | | * | | | | |
| *Cupanieidites orthoteichus* | * | * | | | * | * |
| *Cyatheacidites annulatus* | | * | | | | |
| *Cyatheacidites spp. (<45µm)* | * | * | * | | | |
| *Cyatheacidites spp. (>45µm)* | * | * | * | * | * | * |
| *Cyathidites subtilis* | | * | | | | |
| *Dilwynites granulatus* | * | * | * | | * | * |
| *Ephedra sp.* | | * | | | | |
| *Ericipites scabratus* | | * | * | | | |
| *Foveotriletes sp.* | | * | | | | |
| *Gleicheniidites sp.* | | * | | * | | * |
| *Haloragacidites harrisii* | * | * | * | * | * | * |
| *Ischyosporites sp.* | * | * | * | | | * |
| *Laevigatosporites spp.* | * | * | * | | * | * |
| *Malvacipollis sp.* | * | * | | * | * | * |
| *Matonisporites sp.* | * | * | * | | | |
| *Milfordia sp.* | | * | | | | |
| *Myrtaceidites sp.* | * | * | * | * | * | |
| *Nothofagidites emarcidus/heterus* | | * | * | * | * | * |
| *N. flemingii* | * | * | | * | | * |
| *N. brachyspinulosus* | * | * | * | * | * | |
| *Parvisaccites sp.* | | * | | | | |
| *Podocarpidites sp.* | * | * | * | * | * | * |
| *Podosporites sp.* | | * | | | | |
| *Polycolpites sp.* | | * | | * | * | |
| *Polypodiidites/Verrucatoporites spp.* | | * | | | * | |
| *Polypodiisporites spp.* | | * | | | | |
| *Proteacidites pachypolus* | | * | | | * | |
| *Proteacidites spp.* | * | * | * | * | * | * |
| *Rugulatisporites sp.* | * | * | | | * | * |
| *Tricolp(or)ites spp.* | * | * | * | * | * | * |
| *Tricolpities reticulatus* | | * | | | | |
| *Tricolporites sphaerica* | * | * | * | | | * |
| *Triporopollenites spp.* | | * | | | * | * |
| *Verrucosisporites kopukuensis* | * | * | * | | * | * |
| **Total count** | **252** | **1702** | **201** | **113** | **N/A** | **116** |

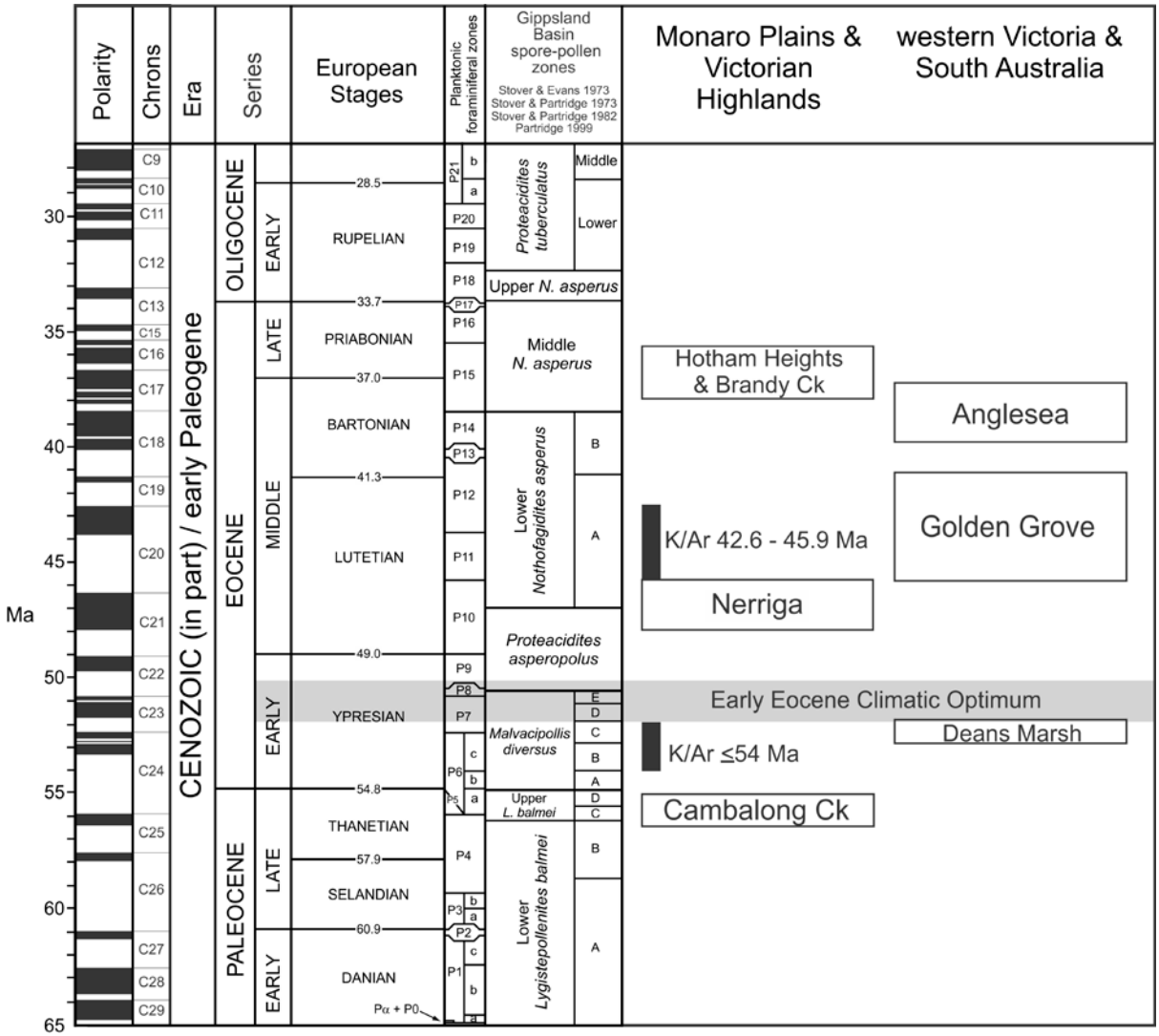


**Figure 3.1** Paleogene palynostratigraphic schema for south eastern Australia, showing the updated placement of Brandy Creek and Hotham Heights as late middle to late Eocene (adapted from Greenwood et al. 2003).

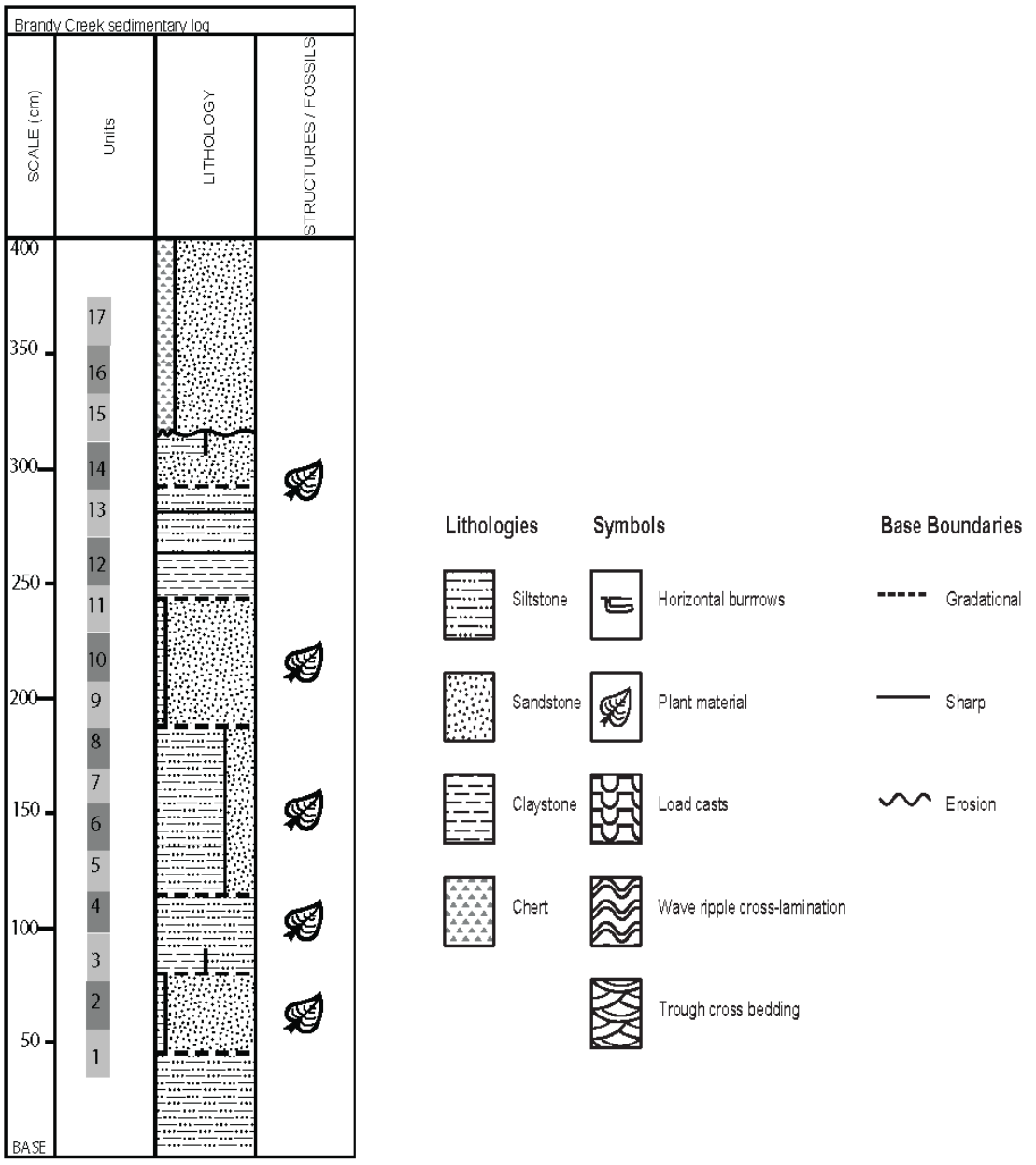


**Figure 3.2** Stratigraphic log of the Brandy Creek outcrop showing scale, units, lithology, and fossil structures present and key.

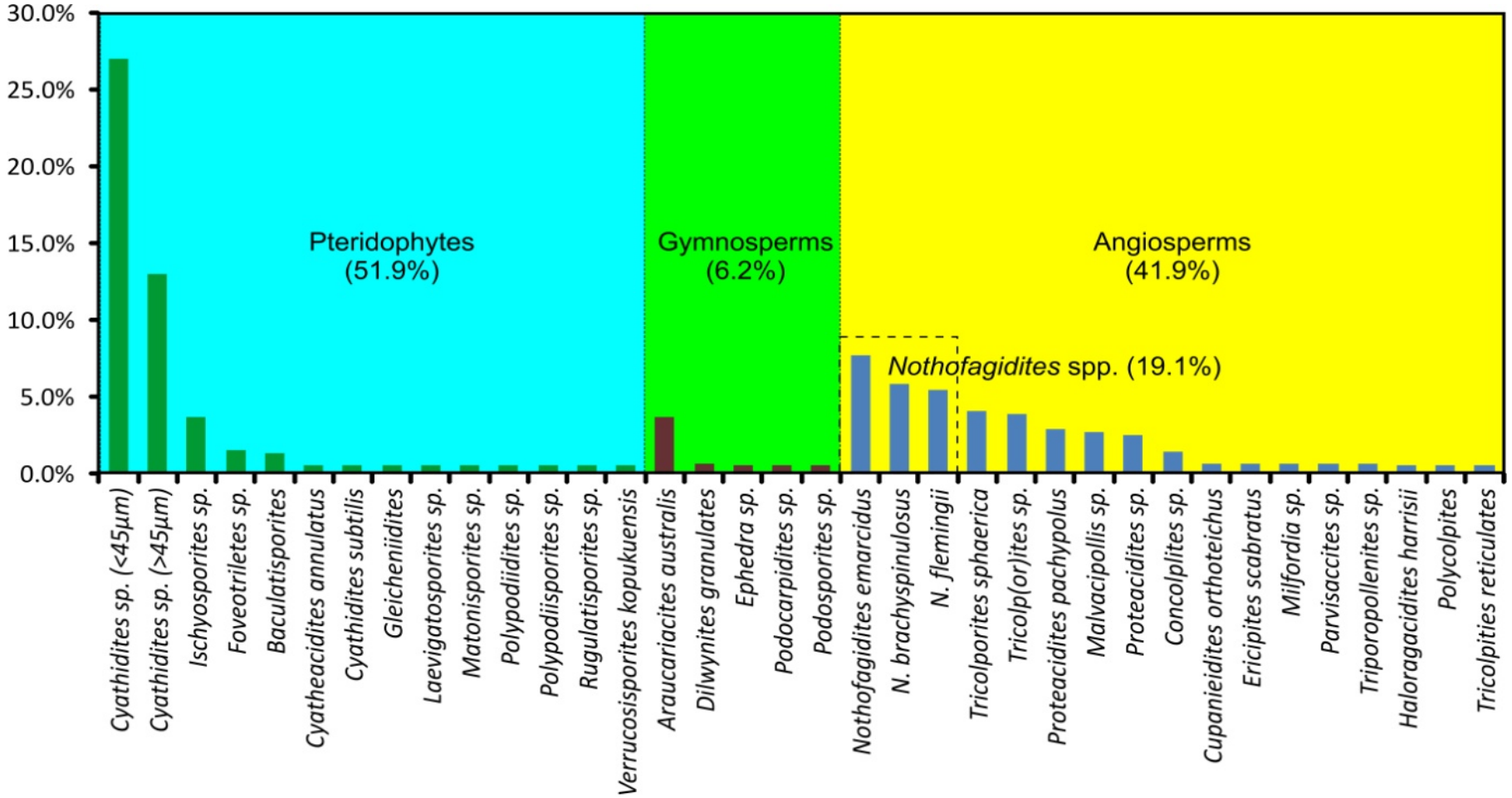


**Figure 3.3.** Abundance Histogram of the Brandy Creek palynomorphs showing the percentage contribution of individual palynomorphs and combined Pteridophytes (51%), Gymnosperms (6.2%) and Angiosperms (41.9%).

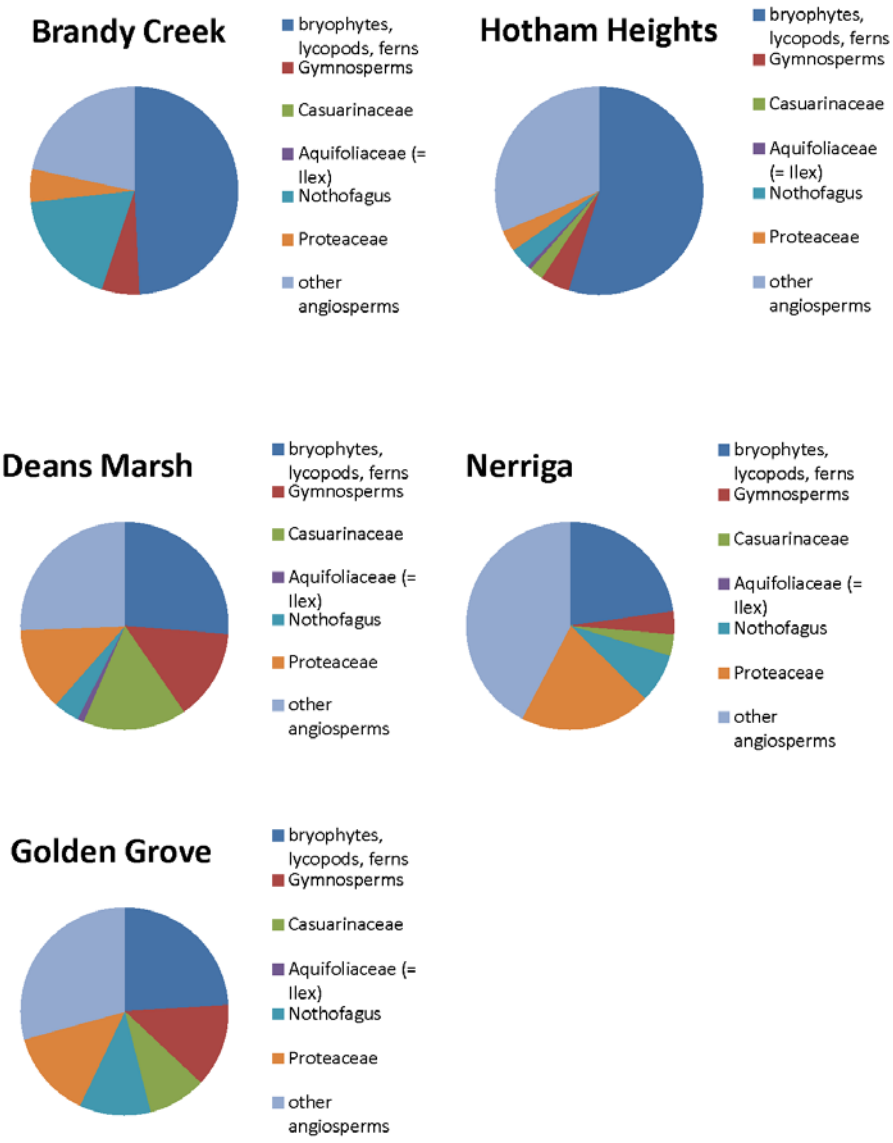


**Figure 3.4.** Floristic composition of Brandy Creek and other Eocene floras based on palynomorph counts.

# Chapter 4. Palaeoclimate Reconstruction of the Brandy Creek Eocene locality, Bogong High Plains, Victoria.

## 4.1 Introduction

The Eocene (55.8 – 33.9 million years before present) was a warm interval during which the world's biota evolved into forms recognisable today and the Northern Hemisphere continents adopted their current positions (Wing and Greenwood 1993; Zachos, Stott and Lohmann 1994; Greenwood and Wing 1995). Australia at this time during the Eocene lay well south of its current position and adjacent to Antarctica, but separated from Antarctica by a water gap as far east as what is now Tasmania, with this connection severing during the Eocene (Quilty 1994; Pross et al. 2012). This warm interval has been used as a benchmark for understanding climates warmer than those of today, and provides the means to understand better understand trends in current global warming climate and how these can affect ecosystems (Gajewski 1993; Zachos et al. 2008; Smith et al. 2012). Fossil and other evidence from Australia and North America indicate that Eocene forests grew close to the poles and that many organisms, typical of modern tropical environments such as palms and crocodiles, occupied areas that are currently too cold to support them (Willis and Molnar 1991; Markwick 1994, 1998; Greenwood and Wing 1995; Francis et al. 2008; Huber and Caballero 2011; Eberle & Greenwood 2012; Pross et al. 2012).

Two methods to reconstruct palaeoclimate at Brandy Creek. The first uses a foliar physiognomy method known as Leaf Margin Analysis (LMA). Using both regional and global calibrations, mean annual temperature for the Brandy Creek flora is calculated based on the proportion of toothed versus non-toothed dicot angiosperm species. A second method, Bioclimatic Analysis, uses nearest living relatives of the leaf, pollen and spores documented in Chapters 2 and 3, and applies the climate tolerances of modern floras to the fossil flora at Brandy Creek. Nearest living relative analogy assumes that the climate tolerances of fossil flora taxa are the same as those of their modern counterparts. The Mean Annual Temperature (MAT) for regional floras is updated with new climate profiles added to the original data set developed by Greenwood et al. (2003). These additional data improve the accuracy of the MAT for Brandy Creek and the other Eocene localities.

Additional indicators of Eocene climate at Brandy Creek are applied, including the presence and grade of epiphyllous fungi in a fossil flora (i.e., fungi found attached to leaf surfaces), as well as additional leaf morphological characters such as the presence of drip tips which can be indicators of wet climates.

### 4.1.1 Paleoclimate during the Eocene

Palaeoclimate indicators or climate proxies, along with climate modelling, have been used to reconstruct past climates. Increases in temperature during the Eocene have been attributed to high concentrations of greenhouse gases including carbon dioxide and methane (Zachos et al. 2008). Today global carbon dioxide ($CO_2$) levels are approximately 390ppm and have been increasing steadily since the Industrial Revolution (Thoning et al. 1989; Tans and Keeling 2012). $CO_2$ levels during the Eocene have been estimated to be a variety of concentrations ranging from 500 - to 4400ppm (Pearson and Palmer 2000; Pagani et al. 2005; Fletcher et al. 2008; Smith et al. 2010; Huber and Caballero 2011; Royer et al. 2012).

Influx of carbon dioxide into the atmosphere has been attributed to an increase in volcanic activity associated with North Atlantic rifting as well as oxidation of methane (Pearson and Palmer 2000). There is growing evidence that methane produced from wetlands (swamps, marshlands, bogs and lakes), which covered three times as much of the earth's surface during the Eocene, in comparison with today was a major contributor to greenhouse gas emissions. Forests and marine sediments were minor contributors (Sloan et al. 1999; Beerling et al. 2009; Deconto et al. 2012).

Some estimates indicate that tropospheric methane concentrations for the Eocene were between 2000 – 4000 ppm (Beerling et al. 2009). Sloan et al. (1999) suggest that there is a link between high methane concentrations and polar stratospheric cloud forcing. When methane is released into the troposphere, it has a short residence time before chemically changing to $CO_2$ and $H_2O$ vapor in the stratasphere. The water vapour creates polar stratospheric clouds. This blanket of clouds warms the troposphere and therefore the earth surface by trapping outgoing

long wave radiation. Warming, coupled with the insulating cloud cover resulted in a low sea surface temperature gradient latitudinally and consequently created a globally more equable climate (low seasonality) during the Eocene (Sloan et al. 1999).

A predicted warmer world during the Eocene is supported by the marine fossil record with supplemental confirmation based on carbon, oxygen and boron isotope data (Lange 1982; Pearson and Palmer 2000). Shells of pelagic foraminifera contain oxygen and carbon isotopes that were incorporated during the life of the organisms. The ratios of isotopes of carbon ($^{13}C$: $^{12}C$) and oxygen ($^{18}O$:$^{16}O$) relative to a standard ($\delta^{13}C$ and $\delta^{18}O$) are fixed according to environmental conditions and the metabolic processes of each species at the time the organism was alive (Zachos et al. 2001). Such marine carbonate oxygen isotopic data indicate a rapid warming of oceans around Australia during the Eocene with ocean temperatures approximately 10 degrees higher than today (Lange 1982; Wing and Greenwood 1993; Zachos et al. 2001; Greenwood and Wing 1995). These carbon and oxygen isotope data are supported by Boron isotope data ($\delta^{11}B$), again using planktonic foraminifera shells, which provide a ratio of boron isotopes to determine sea water pH levels from which atmospheric $CO_2$ levels can be calculated. Boron isotope data support the notion of $CO_2$ levels greater than 1000 ppm during the Eocene and possibly as high as 3000ppm during the Paleocene/Eocene boundary (Pearson and Palmer 2000).

Stomatal frequency indices (stomatal index and stomatal density) are a method used to determine palaeoatmospheric $CO_2$. Stomatal pores located on the leaf surface are mainly for the plant to exchange $CO_2$ and water vapour. Stomatal frequency can alter in response to environmental variables such as temperature, rainfall, irradiance, and carbon dioxide level (Royer 2001). Various authors have shown that there is an inverse relationship between stomatal frequency and $CO_2$ levels and have used this to reconstruct the partial pressure and atmospheric $CO_2$ in the Eocene [Retallack 2001 (~2000ppm) Kürscherner et al. 2001(~500ppm) Royer et al. 2001 (~400ppm), Greenwood et al. (2003b), and Smith et al. (2010)]. This wide range of values may reflect variability in $CO_2$ levels during the Eocene, or it may be a reflection

of the uncertainty that comes with using this paleo-proxies (Pearson and Palmer 2000; Smith et al. 2010).

The clearest limitation to the use of stomatal indices is the requirement for there to be a closely related living relative of the fossil for calibration of stomatal index with $CO_2$ levels. This limitation curtails the number of inferences that can be made using stomatal indices, with many species identified in fossil floras not having closely related living relatives (Royer et al. 2001). Another limitation is that the stomatal frequency can vary among the tip, base, margin and midrib on the same leaf; it may also vary between surfaces (dorsal, ventral) and between individual leaves on the same plant (Royer et al. 2001; Scarr, Greenwood and Scarpaci 2008). An additional difficulty of using stomatal frequency as a palaeoclimate proxy is the variability in the quality and quantity of the material available from fossil localities, with some offering only fragments, whilst others offer partial or whole leaves (Scarr et al. 2008).

Fossils of organisms other than plants, can provide a supplement to plant derived paleoclimate data. Evidence from North America, Europe, Asia, South America and Australia, shows that there was a global distribution of fossil crocodilians during the Paleogene (Marwick 1994, 1998, 2007), which is consistent with above freezing winter temperatures at high latitudes during the Paleocene – Eocene. For example the crocodilian, *Allognathosuchus* was discovered in the Canadian Arctic on Ellesmere Island in rocks Paleocene –Eocene age. (Martin and Lauprasert 2010; Eberle et al. 2010; Eberle and Greenwood 2012).

Fossil crocodilians have been recorded from Paleogene localities in Australia, mostly in Queensland (Willis 1997), as exemplified by the Eocene genus *Kambara*. Evidence suggests that the genus *Kambara* was present prior to the separation of Australia and Antarctica, and Antarctica and South America, and this animal together with other crocodilians took advantage of the existing land bridge (Willis 1997).

Paleoclimate indicators and climate proxies are useful in understanding current climate changes. The Ecoene is a period which is considered to most closely match the changes in climate the earth is experiencing today (Pross et.al. 2012). There is overwhelming evidence

that anthropogenically induced climate change is occurring at a much faster rate than what would normally occur in nature. Today carbon dioxide levels are sitting at approximately 385 ppm, steadly creeping up to the levels recorded during the Eocene between 400ppm - 2000pmm (depending on the climate proxy data used)(IPCC, 2007). During the Paleocene – Eocene Thermal Maximum atmospheric 1500 - 2000 gigatonnes of $CO_2$ was release into the atmosphere over a period of 1000 years (short in geological time) and global temperatures increased between 5° and 8°C (Birerly and Kingsford, 2009; Pross et al. 2012; ) The IPCC 2007 report is predicting that global temperatures will increase by 2.0°C by the end of the 21$^{st}$ century relative to the 1900's. These changes will likely result in an increase in acidification of oceans; sea level rises; decrease in Artic ice cover; changes in global water cycles and extinctions. Changes of this magnitude was also experienced during the Eocene, however these changes occurred of 1000's or millions of years, not over centuries (IPCC report 2007).

### 4.1.2 Palaeoclimate reconstruction through palaeobotanical proxies.

The distribution of plant species and even higher taxonomic ranks today is closely correlated to climate parameters such as Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) (Axelrod and Bailey 1969; Greenwood et.al 2003a and 2004). This correlation allows for both taxonomic and non taxonomic methods to be used to reconstruct the palaeoclimate of the Brandy Creek flora. Non-taxonomic analysis was based on foliar physiognomy of leaf macrofossils using leaf margin analysis (Wilf 1997; Greenwood et al. 2004; Greenwood 2007). The taxonomic method used was a Bioclimatic analysis using nearest living relatives with analogous leaf macrofossils and palynomorphs. Additional information on palaeoclimate can be gained by looking at other morphological features of leaves, such as drip tips and the use of epiphyllous fungi as climate indicators (Lange 1978; Spicer 1990).

#### *Leaf Margin Analysis*

It is widely accepted that leaf physiognomy (i.e., shape, size and the presence of distinctive traits such as marginal teeth) is correlated with temperature and precipitation. Cool

temperate forest plants generally have leaves which are toothed, whilst tropical rainforests are more likely to have species with entire or non-toothed leaf margins (Wolfe 1971, 1978, 1979; Baker - Brosh and Peet 1997; Peppe et al. 2011).

Numerous hypotheses have been put forward as to why some leaves have teeth and others do not. Givinish (1978) proposed that the entire margin of a leaf is related to the thickness of the leaf; leaves with teeth are often thin and 'flimsy' and therefore have greater resistance to water flow whilst, thicker leaves reduce resistant to flow of water on the exterior of the leaf resulting in infill of the intercostal area resulting in entire margins.

Baker-Brosh and Peet (1997) and Royer and Wilf (2006), proposed that leaves teeth of deciduous leaves mature earlier than the basal and medial portions of the deciduous leaf. This differential in maturation time allows for high photosynthetic activity to occur along the margins whilst the rest of the leaf is growing. Early maturation of the teeth of a leaf ensures that the overall leaf maximizes the short period of abundant light that is available in a deciduous forest. Baker-Brosh and Peet (1997) and Royer and Wilf (2006) also found that non deciduous species have fewer teeth because they flower throughout the growing season and thus the sap flow is more continous. The above authors also noted that toothed leaf margins enhance carbon uptake early in the growing season by increasing sap flow at the point of synchronised flowering. One further advantage of teeth on leaves was identified by Feild (2005) who proposed that teeth may prevent leaf guttation by minimising root pressure thereby reducing the chances of freeze thaw embolism in cooler climates.

Physiognomic signatures are useful in the reconstruction of palaeoclimate, and can be applied in the absence of taxonomic information. Leaf margin analysis (LMA) is a non-taxonomic method used to recreate palaeoclimates. LMA was first developed by Bailey and Sinnott (1915, 1916), after they noticed a correlation between the number of species with untoothed leaves and mean annual temperature for North American flora. Bailey and Sinnott's observations were further developed by Wolfe (1971 and 1978) who created a linear regression calibration for LMA for vegetation in East Asia.

The program known as CLAMP (Climate Leaf Analysis Multivariate Program) developed by Wolfe 1993, uses multiple leaf physiognomic characters such as lamina size and shape, apex and base. Recognising that leaf macrofossils do not always have all the characters required for CLAMP analysis, Wilf (1997) compared the univariate LMA model and the multivariate CLAMP model on the same flora and found no significant differences in reconstructed mean annual temperatures.

Regional history has also been shown to be important, with the leaf-climate correlation being different between Northern and Southern Hemisphere flora with a higher percentage of entire leaf margins in Southern Hemisphere floras than for floras with the same temperature range in the Northern Hemisphere (Bailey and Sinnott 1916; Greenwood 1992; Greenwood et al. 2004; Little, Kembel and Wilf 2010).

The observed differences between the northern and southern hemisphere expression of LMA has resulted in the development of regional LMA calibrations for northern and southern Hemisphere floras including Australia, South America, Southern Africa, North America and SE Asia, (Greenwood et al. 2004; Hinojosa et al. 2011; Steart et al. 2010; Wolfe 1971, 1979; Aizen and Ezcurra 2008). Peppe et al. (2011) developed a global calibration based on 92 sites, however the calibration results were shown to be weaker than the regional calibrations, giving a larger standard error, i.e. reduced precision of the estimates of mean annual temperature.

***Leaf Margin Analysis Australian vs. world. What is the difference?***

Bailey and Sinnott (1916) first noted and proposed that the absence of a large land mass in the southern hemisphere coupled with historically cold climates, as noted in the geological record, prevented the development of deciduous forests. This is in contrast to the deciduous forests of the northern hemisphere that are most commonly associated with toothed species. In the northern hemisphere deciduous forests evolved in mid to low latitudes. As a response to seasonally arid conditions large, highly productive leaves were lost. Today deciduous forest occupy the mid to high latitudes of the northern hemisphere and deciduous species lose leaves as a response to polar light regime (Askin and Spicer, 1995). Whilst in the Southern

Hemisphere evergreeness was considered advantageous to deal with extreme temperatures at polar latitudes (Antarctica) requiring less energy to produce photosynthetic organs during spring (Askin and Spicer, 1995).

Explanation to account for the reduced number of deciduous species in Australia include phylogeny, low phosphorus levels in the soil, low temperature amplitudes, variability in rainfall, and the absence of a connection between Australia and other high latitude landmasses which are home to cold adapted taxa; the absence of a substantive mountain range in the present and during the Paleogene compared to north and south America, with a suitable climate for cool adapted taxa, and the northward drift of Australia during the Paleogene reduced the impact of cooling climates on the Australian flora (Macphail et al. 1994; Greenwood et al. 2004; Peppe et al. 2011).

The notion that there is a greater percentage of species with entire margined leaves in Australian forests was observed by Greenwood (1994). When LMA was applied by Greenwood (Greenwood and Wing 1995) to Australian fossil leaf assemblages using the North American linear regression model, the predicted MAT was much lower than the actual MAT of the nearest living relatives of the fossil flora. To overcome this, Greenwood et al. (2004) developed a linear regression model that was calibrated for Australian vegetation. This linear regression model is based on Leaf Margin Analysis of woody dicot species from 113 sites in Australian rainforest with a MAT of 10.8° C to 24.9°C and a mean annual precipitation of 717-3686 mm/yr. (Greenwood et al. 2004). Greenwood et al. (2004) found that when applying Australian derived linear regression to Australian Paleogene floras the regression slope was in line with the slope of other linear regressions from the Americas and Asia, suggesting there is a global response to temperature by vegetation. These authors also found the intercept in the Australian database was higher compared to the other databases and this correlated well with the low proportion of species with marginal teeth in the Australian LMA.

***Limitations with Leaf margin analysis***

There are a number of assumptions that are made when applying leaf margin analysis to fossil floras. Several authors observed what is termed the freshwater margin effect (Burnham 2001; Greenwood 2005; Kowalski and Dilcher 2003). The freshwater margin effect is where the proportion of toothed species is higher at lake and stream margins, therefore fossil depositional sites may have a cool temperature bias of 2-8°C. Peppe et al. (2011), in a study using additional leaf traits to determine MAT and MAP, found that the fresh water effect is unlikely to impact MAT for palaeoclimate reconstruction as most calibration sites contain vegetation from wet soils.

Regional calibrations assume that evolution and extinction subsequent to the deposition of the fossils have not changed leaf climate relationships and their expression in lineages (Jordan 1997; Hinojosa et al. 2011; Little et al. 2010). Regional calibrations also assume that environmental factors such as soil, temperature, and water availability are the same for fossils as modern counterparts (Peppe et al. 2011). Phylogenetic traits independent of environmental constraints have been shown to exist in some families, for example species in the Lauraceae family which occur in the Northern and Southern Hemisphere under different climate regimes are untoothed (Carpenter et al. 2007; Little, Kembel and Wilf 2010) Carpenter et al. (2007), describes a toothed Lauraceae leaf from the early Eocene Regatta Point, Tasmania *Bandulskaia aestuaria* Carpenter, Jordan and Hill sp. nov. Toothed margins are generally associated with wet environments, with Carpenter et al. (2007) indicating that *Bandulskaia aestuaria* lived in close proximity of tidal channels, and thus wet soils. *Bandulskaia aestuaria* from the early Eocene Regatta Point is the earliest occurance of Lauraceae with toothed leaves.

The relative richness of species with particular traits is affected by factors other than temperature or precipitation, including differential origination or extinction among clades suggesting possible inconsistency of trait-climate relationships through time (Wolfe and Upchurch 1987; Little et al. 2010). Adaptations to climate changes can involve many aspects of plant biology, including anatomy, physiology and biochemistry and therefore leaf traits will not necessary respond strongly to climate (Wright et al. 2007).

***Bioclimatic Analysis***

Bioclimatic analysis (Kershaw and Nix 1988; Greenwood et al. 2003a) is essentially the same as coexistence analysis (Mosbrugger and Utescher 1997) and both methods have been used to reconstruct past climates based on the development of climate profiles including Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) for a fossil flora. The application of bioclimatic analysis to reconstruct palaeoclimate of fossil flora is based on nearest living relative analogy (NLR). This method uses both macro and microfossils that can be identified at the species, genus, or family level.

An assumption is made in bioclimatic analysis that the climate requirements of the nearest living relatives of the fossil taxa are analogous to the past climates in which the fossil taxa lived (Kershaw and Nix 1988; Chaloner and Creber 1990; Wing and Greenwood 1993; Mosbrugger 1995; Hill and Scriven 1997). Wing and Greenwood (1993) proposed that a number of key taxa be used to constrain minimum palaeotemperature estimates including palms, which are today intolerant to frost and live in mild climates with a MAT $> 10°C$. It is unlikely that extinct species of these highly diverse plants possessed greater tolerance of cold than extant taxa (Wing and Greenwood 1993; Greenwood and Wing 1995).

Bioclimatic analysis relies on the correct identification of the fossil taxon and correct identification of its nearest living relative, and is generally not used on floras that pre-date the Paleogene (Chaloner and Creber 1990; Houlder et al. 1999). The method does not account for evolutionary changes in plant distribution such as phylogeny and regional history, that are independent of climate variables (Wing and Greenwood 1993).

Several key papers have been published that identified nearest living relatives of many Australian fossil floras, however in many instances this is only to a familial and generic level, rarely to a species level (e.g., Christophel and Rowett 1996; Carpenter 1994; Hill 1986). To overcome this limitation it is necessary to use regional floras from the same area to reconstruct palaeoclimates (Axelrod and Bailey 1969). A database of climate envelopes for Australian families, species and genera has been developed (Greenwood et al. 2003a; Gallagher et al. 2003

and Pross et al. 2012). Over time, additional climate envelopes have been added to the database to improve bioclimatic results. These climate envelopes have been applied to fossil floras using nearest living relative analogy (Greenwood et al. 2003a and 2004; Pross et al. 2012).

***Epiphyllous fungi as indicators of Eocene climates***

Epiphyllous fungi – that is, fungi found attached to leaf surfaces – have been recorded from the Jurassic through to the modern (Cookson 1947; Dilcher 1965; Lange 1976, 1978; Wells and Hill 1993; Traverse, 2007), including the Eocene of Hampshire Basin, Southern England (Smith, 1980) and the Miocene deposit at Kiandra New South Wales (Selkirk 1974). The Kiandra deposit shows fungi growing on Lauraceae (Selkirk 1974).

The use of epiphyllous fungi as an indicator of climate is not new to palaeobotany. Cookson (1947) recorded fungi from eight Oligocene – Miocene sites in the Southern Hemisphere and commented that the nearest living relatives of the fungi were found in extant moist tropical rainforest environments. Cookson (1947) also noted that humidity rather than temperature was the limiting factor for fungal growth. Dilcher (1965) and Lange (1976; 1978) further developed the use of epiphyllous fungi as climate indicators and proposed that the level of structural complexity of the epiphyllous fungi could be correlated with climate, with structural complexity increasing as climate became more wet and humid. To demonstrate this, Lange (1976) collected leaf litter samples across Australia and graded the epiphyllous fungi from simple (grade I) to complex (grade V). He concluded that epiphyllous fungal characters in wet humid climates such as tropical rainforest were much more complex than those in drier climates. Experiments conducted by Wells and Hill (1993) of extant environments disputed these claims and indicated that much more research was needed before epiphyllous fungi could be used with confidence as climate indicators.

A number of authors have stated that epiphyllous fungi need to be used in conjunction with other climate indicators, such as macrofossil, microfossil and marine fossil evidence (Cookson 1947; Dilcher 1965; Selkirk 1974; Sherwood-Pike et al. 1988).

## 4.2 Materials and Methods

Leaf Margin Analysis and Bioclimatic Analysis were applied to the Eocene Brandy Creek flora. For leaf margin analysis, leaf margins were scored based on presence/absence of teeth (Wilf 1997). A tooth is defined as a vascularised projection of the leaf margin separated by sinuses that are incised less than one quarter the distance to the mid vein (Wilf 1997; Ash et al. 1999; Ellis et al. 2009). A morphotype with an untoothed margin is scored a 1, a score of 0 is assigned to morphotypes with teeth, and a score of 0.5 for morphotypes that presented both toothed and untoothed variants (Wolfe 1993). Scores are shown in Appendix 3.

Leaf margin analysis works by inverting the regression where the independent variable (number of untoothed species) is known and the (MAT) dependant variable is unknown (Wolfe 1971 and 1979). Wolfe (1971) proposed that for statistically viable results, an assemblage of at least 30 taxa is required; other authors such as Burnham et al. (2005) suggest an assemblage with greater than 25 taxa/species is required to produce a result having a margin of error ± 3°C.

A summary of leaf margin equations used for the Brandy Creek flora is shown in Table 4.1. The LMA equation most suited to the Brandy Creek flora is equation 1, developed by Greenwood et al. (2004), derived from 113 modern sites in Australia. Greenwood et al. (2004) provided a second equation based on sites with greater than 20 woody species, however this is not used for Brandy Creek which has 18 morphotypes suitable for LMA. For comparison, Brandy Creek MAT was calculated using the global LMA equation by Peppe et al. (2011) shown in Table 4.1. The global calibration formulated by Peppe et al. (2011) replaces regional calibrations for both the Northern and Southern Hemispheres. The equation incorporates regional differences including biogeographical history, immigration of taxa, in situ evolution of taxa, extinctions and losses of lineages. To account for these variables the global calibration has a large standard error of ± 4.8°C, i.e. has lower precision than using the Australian LMA calibration equation.

For the Bioclimatic analysis, nearest living relatives (NLR's) of the Brandy Creek Flora (macroflora and microflora) were identified to the genus level (Table 4.2). Nearest living relative

distribution data (latitude and longitude) were obtained using the Australian National Herbarium Specimen Information Register (ANHSIR) database (URL http://www.anbg.gov.au/cgi-bin/anhsir). This information forms the basis of the Bioclimatic analysis using ANUCLIM version 6.1, which contains BIOCLIM (Busby 1991; Houlder et al. 1999; Xu and Hutchinson 2012).

Climate profiles are generated using a geographic information system (GIS) mathematical modelling program within BIOCLIM. The climate values generated include mean annual Temperature (MAT), warmest quarter mean temperature (WQMT), coldest quarter mean temperature (CQMT), mean annual precipitation (MAP), warmest quarter mean precipitation (WQMP), coldest quarter mean precipitation (CQMP). These parameters include the maximum and minimum values plus the percentiles (5, 25, 75 and 95). Climate profiles of other localities including Hotham Heights, Nerriga, Deans Marsh, and Golden Grove published by Greenwood et al. (2003a), are updated to reflect availability of additional climate profiles for Australian genera since the 2003 publication (Pross et al. 2012). The climate profiles used in the Bioclimatic Analysis are shown in Appendix 4.

Counts of epiphyllous fungi were done using palynological slides (Chapter 3). Epiphyllous fungi were graded based on Lange (1978) and a modified key developed by Wells and Hill (1993) (Table 4.3). Unfiltered palynological slides were used to ensure small epiphyllous fungi were included in the count.

## 4.3 Results.

### 4.3.1 Leaf margin analysis.

The results for leaf margin analysis of the Brandy Creek flora are presented in Table 4.4. 83.3% of the Brandy Creek leaf morphotypes had non-toothed margins. The MAT of the Brandy Creek site using the Australian LMA equation is estimated at 19.7 ± 1.9°C. The estimate generated from the global LMA equation is a slightly warmer result at 21.8 ± 1.8°C. Comparison

of Brandy Creek and other Eocene floras (Table 4.5) shows a similar MAT across the region, with the exception of Deans Marsh. It was also found that the percentage of non toothed species is low, 28% at Dean's Marsh compared to Brandy Creek 83.3%, and the other Eocene floras that generally have entire margins estimates of above 70%. Wolfe (1979) proposes that a flora that has greater than 75% estimate of entire margins is characteristic of tropical rainforest. Typically, a high proportion of toothed leaves is correlated with cooler climates and in Australia is characteristic of Cool Temperate Rainforest. These characteristic of Cool Temperate Rainforest are shown by the MAT for Deans Marsh with an MAT of 5.5°C.

### 4.3.2 Bioclimatic analysis.

Results of the Bioclimatic analysis are presented in Tables 4.4 and 4.5. The bioclimatic envelope for MAT at Brandy Creek is 15.7 – 21.7°C. The mean of the estimated range of possible MAT values derived using bioclimatic analysis, 18.7°C, is within the standard errors of the MAT estimated using LMA, 19.7 ± 1.9°C ..Table 4.4. and Figure 4.1. Similar MAT estimates are found for the other Eocene sites with MAT ranging from 15.5 to 23.9°C (Table 4.6.).

Brandy Creek Warm Quarter Mean Temperature (WQMT) is calculated at 22.7°C (21.0 - 24.4°C), with similar results found for the Golden Grove flora with a WQMT of 22.3°C (20.0-24.6).The lowest WQMT 21.9°C, is at Nerriga. For the CQMT there is little variation among the Eocene localities which have a CQMT range of 14.3°C (Deans Marsh) to 15.7°C (Hotham Heights). Brandy Creeks CQMT is 15.2 °C. (Table 4.6).

Mean annual precipitation (MAP) for Brandy Creek is estimated at 213 cm/yr (107 – 320 cm/yr). MAP for the Eocene floras ranges from 186 to 259 cm/yr. Deans Marsh has a much lower MAP compared to the other localities, whilst Golden Grove has the highest MAP of all sites in Table 4.6. Coldest Quarter Mean precipitation (CQMP) is similar for all localities with Brandy Creek having a CQMP estimated as 8 – 48 cm, and all localities estimated as between 7 – 52 cm. WQMP for Brandy Creek is 40 – 162 cm with the WQMP for all localities between 39 – 169 cm.

Both the LMA and Bioclimatic analysis places Brandy Creek in the mesothermal zone (Nix 1982), which is defined as having a temperature range falling between 15 and 20°C. Comparing Brandy Creek and the other Eocene localities with observed MAT of modern floras, Figure 4.2. places the Eocene flora in the same range as that for the modern mesothermal rainforest of eastern Australia. The outlier is Deans Marsh, for which the LMA based MAT is 5.5°C, the result of a low percentage of entire margin leaves. Nethertheless, bioclimatic results for Deans Marsh place the locality alongside the other floras in the mesothermal range.

### 4.3.3 Epiphyllous Fungi

Results of Epiphyllous Fungi counts are in Table 4.7. Grade 3 fungi was most abundant at Brandy Creek, at 39%, followed by Grade 2, 28%, Grade 4 21% with a small percentage for Grade 1 6% and Grade 5 4%. According to Lange (1976), Grade 1 germlings are most likely to be found in dry sclerophyllous forest or open woodland. Grade 2 germlings have been recorded from open woodlands, dry sclerophyllous and semi deciduous forests. Grades 3 and 4 germlings, which were the most abundant at the Brandy Creek locality, have representation in dry sclerophyll forests, semi deciduous forests, wet sclerophyll forests and rainforest. The highest Grade of germlings found at Brandy Creek was grade 5, representing 4% of the total count. Although Grade 5 germlings are in lower percentages at Brandy Creek, their presence suggest warm and wet climate characteristic of rainforest. Figure 58 (Chapter 2) shows callimothalloid shields on the leaf surface of *Endiandra* (Lauraceae affinity).

## 4.4 Discussion

The results presented here update previous palaeoclimate estimates for Brandy Creek and other Eocene floras published by Greenwood et al. (2003a & 2004), using Leaf Margin Analysis and Bioclimatic Analysis. Greenwood et al. (2003a) derived a MAT for Brandy Creek using LMA on 54 morphotypes, however taxonomic revision reduced the number of morphotypes to 18 as described in chapter 2. The MAT of 19.7 °C ± 1.9°C based on 18

morphtypes confirms the earlier preliminary estimate from Greenwood et al. (2003a) which 18.2°C ±1.9°C. Although a smaller sample size compared to Greenwood et al. (2003a), the proportion of entire margin leaves is much greater for this study (83.3%), as opposed to 75% used in the previous LMA estimate. A higher proportion of entire leaves is more likely to reflect tropical rainforest (Wolfe 1978) and therefore result in a higher LMA MAT.

Regionally, the Eocene floras represented in this chapter all have similar MAT's using LMA, with the exception of Deans Marsh (5.5°C). Deans Marsh LMA results in a cooler climate reconstruction, due to a lower percentage of untoothed leaves (28%) compared with the other localities, where entire margined species comprise above 65% of their respective floras. The Deans Marsh leaf macrofossil assemblage has a very different taxonomic character than the leaf macrofloras used for LMA from the other localities. Rowett and Sparrow (1994) place Deans Marsh flora as Lower *Nothofagidites asperus* zone with the Deans Marsh MAT's using LMA corresponding to a cooling of sea surface temperatures that occurred during the middle Eocene and the late middle Eocene. This cooling period could have selected for taxa which could adapt to cooler climates (Christophel 1995, p. 179; Greenwood et al. 2003a; Greenwood and Christophel 2005. This differential based on a different taxonomic character has resulted in a MAT using LMA of 5.5°C compared to MAT of 18.8°C using bioclimatic analysis.

With the exception of Deans Marsh, the LMA results are consistent with MAT's derived from Bioclimatic analysis. Bioclimatic profiles (14 taxa) for nearest living relatives of the Brandy Creek Eocene flora produced a slightly lower MAT of 18. 7°C compared with the bioclimatic analysis of Greenwood et al. (2003a), who estimated the MAT 19.6°C, based on 12 taxa.

MAT estimated using Bioclimatic analysis is derived mostly from climate envelopes for family and genera of nearest living relatives at Brandy Creek and the other Eocene floras. The use of higher level taxa can result in a broader range of estimated MAT, with the climate envelopes of families and genera encompassing a greater climate range than at a species level (Nix 1982; Kershaw and Nix 1988).

Bioclimatic analysis of the fossil floras relies on both climate envelopes for leaf and pollen/spores nearest living relatives. Although the climate envelope for the families and genera represented by leaves, i.e. Lauraceae and Cunoniaceae are a closer reflection of local climate conditions, the pollen/spore sums, represent both the local and regional flora, leading to a much broader climate profile for the Eocene floras (Kershaw and Nix 1988).

The climate profile of Brandy Creek sits within the mesothermal range of MAT 14 - 20 °C as described by Nix (1982), with the WQMT and CQMT range of 14 - 24 °C, (the maximum limits of species in the coldest and warmest months). MAP of 213cm/yr also conforms to the mesothermal range definition (mesothermal range>150cm/yr). These mesothermal conditions are represented across all the Eocene floras in Figure 4.1 and are indicative of the palaeoclimate across south eastern Australia during the Eocene, when there was little or no seasonal variation. The Eocene was a period when species richness in mesothermal rainforest was likely to be at maximum levels (McGowran et al. 2000).

Comparison of MAT for the Eocene fossil flora with taphonomic and observed MAT of modern localities across eastern Australia (Figure 4.2) shows that the MAT of Brandy Creek using both LMA and NLR is closest to mesothermal rainforest in present day north eastern Queensland. Locations such as Mt Lewis, Ella Bay and Dorrigo have similar climate profiles to Brandy Creek sharing many of the same rainforest families including Lauraceae, Elaeocarpaceae and Cunoniaceae.

Epiphyllous fungi as climate indicators using the technique developed by Lange (1978) have been met with caution (Wells et al. 1993; Phipps and Rember 2004). Fossil evidence shows that epiphyllous fungi were a component of Australasian rainforest during the Eocene, with fungi recorded at Hotham Heights (Carpenter et al. 2004) and from the late Eocene Pikopiko fossil forest, New Zealand (Lee et al. 2012).

A latitudinal gradient exists for fungi, with greatest abundance and diversity occurring in the world's tropical regions (Arnold and Lutzoni 2007). Epiphyllous fungi are found in tropical forests of the world including Central and South America, Africa, Asia and Australia (Toomey et

al. 2009). In modern tropical rainforests epiphyllous fungi have been shown to play an important role in rainforest ecology. Epiphyllous fungi have a symbiotic relationship with their host plant. They have been shown to also reduce the damaged caused by leafcutter ants, which is likely due to the chemical composition of the fungi being unpalatable to the ant (Mueller and Wolf-Mueller 1991). Epiphyllous nitrogen fixation can contribute to the nitrogen supply in tropical forests by converting gaseous nitrogen to a usable form for plants (Bentley 1987; Wanek and Portl 2005). Found mostly on leaves, plants have adapted over time to compensate for reduced light for photosynthesis by increasing chlorophyll production in the areas of the leaf populated by the fungi (Gilbert et al. 2007).

The distribution of epiphyllous fungi in rain forest habitats is varied. Gilbert et al., (2007) study of epiphyllous fungi in Australian and Panamanian rainforests, showed that epiphyllous fungi are more diverse in the understory than in canopy trees, and common plant species are more to likely have fungi present than rare species. Juveniles of understory plants have a greater number of epiphyllous fungi than the equivalent adult plant, fungi are not restricted to a particular family or species, and canopy openness (light availability) can impact epiphyllous distribution in the understory (Gilbert et al. 1997; Arnold and Lutzoni 2007). Environmental conditions are a controlling factor, with greater numbers of fungi more likely to occur during wet season than dry (Paulus et al. 2006; Gilbert et al. 2007).

## 4.5 Conclusions

Numerous studies have shown that both taxonomic and non taxonomic methods can be used to reconstruct palaeoclimates of a fossil flora (e.g., Kemp, 1978, 1981; Christophel, 1981; Christophel and Greenwood 1988; Kershaw and Nix 1988; Truswell and Harris 1982, Christophel and Greenwood, 1989; Wing and Greenwood 1993; Greenwood et al. 2003b and 2004). These studies have shown that it is necessary to use multiple palaeoclimate prediction methods as a means of reducing the error of individual climate proxies.

The two methods used in this study to reconstruct palaeoclimate at Brandy Creek are in general agreement, with Leaf Margin Analysis and Bioclimatic analysis giving a MAT of 19.7 °C

and 18.7° respectively. Both results place Brandy Creek in the mesothermal rainforest zone as described by Nix (1982). The mesothermal rainforests of Australia share many taxa that are present in the Brandy Creek flora including Lauraceae and Cunoniaceae.

## 4.6 References

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**Table 4.1** Leaf margin equations for Australia and Global calibrations.

| **Equation** | **Region** | **SE** | **Author** |
|---|---|---|---|
| MAT = 1.32 + 22.0 x P | Australia | ± 2.20 °C | Greenwood et al. 2004 |
| MAT = 4.6 + 20.4 x P | Global calibration | ± 4.8°C | Peppe et al. 2011 |

**Table 4.2** Nearest living relatives of Brandy Creek and other Eocene flora. M= leaf macrofossils and P =pollen/spores.

**Table 4.3** Key for identification of Germlings (adapted from Lange 1976) modified by Wells and Hill (1993).

| | **Description** | **Grade** |
|---|---|---|
| 1a | Undulating or entire margin, 5-15µm in diameter | 2 |
| 1b | Invaginations present on margin, 8-15 (-20) µm in diameter | 3 |
| 2a | Simple, entire margin, no (or barely any) undulations | Grade 1 |
| 2b | Margin undulate | Grade 2 |
| 3a | Invaginations present on only part of the margin, usually extending less than one third of the way to the centre | Grade 3 |
| 3b | Invaginations present all the way around the margin, with (0-1)1-3 deep (extending more than half way to the centre), invaginations irregularly interspersed among shallower ones. If invaginations are more regular , then the depth of penetration is reduced to less than half way to the centre | 4 |
| 4a | (0- ) 1-3 deep invaginations irregularly interspersed among shallower ones. Invaginations are more regular, then the depth of penetration is reduced to less than half to less than half way to the centre | Grade 4 |
| 4b | Usually more than 3 deep invaginations, regularly interspersed among shallower ones. Outline tending towards circular or elliptical | Grade 5 |

**Table 4.4** Leaf Margin Analysis and Bioclimatic climate estimates for south-eastern Australian Eocene Floras

| **Brandy Creek** | **Number** | **LMP** | **MAT** | **Error** |
|---|---|---|---|---|
| LMA Australia | 18 | 83.3% | 19.7 | ±1.9 |
| Bioclimatic | | | 18.7 | ±1.8 |
| LMA Global | 18 | 83.3% | 21.8 | ±1.8 |

**Table 4.5** Comparison between Brandy Creek and other Eocene LMA estimates

| **Macroflora** | **Number of spp.** ***(r)*** | **% spp. no teeth** ***(P)*** | **LMA (σ)** |
|---|---|---|---|
| Brandy Creek 2003 | 18 | 83 | 19.7(1.9) |
| Deans Marsh | 34 | 28 | 5.5(2.9) |
| Hotham Heights | 26 | 74 | 17.9(2.3) |
| Nerriga | 24 | 79 | 19.2(2.25) |
| Golden Grove | 21 | 71 | 17.1(2.68) |

**Table 4.6** Palaeoclimate estimates based on bioclimatic analysis of south eastern Australian Eocene Floras. Modified from Greenwood et al. (2003a) with updated estimates based on additional climate profiles for NLRs.

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. †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.

| **Fossil flora** | **MAT (C°)** | **WQMT (C°)** | **CQMT (C°)** | **MAP (cm/yr)** | **CQMP (cm/yr)** | **WQMP (cm/yr)** |
|---|---|---|---|---|---|---|
| Brandy Creek (14)* | 15.7– 21.7 (18.7) | 21.0-24.4 (22.5) | 9.0- 21.5 (15.2) | 107-320 (213) | 8 – 48 (28) | 40-162 (107) |
| Deans Marsh (11) | 16.6-22.3 (19.4) | 20.0-24.6 (22.3) | 7.0-21.2 (14.3) | 103-350 (186) | 10-51 (30) | 39-166 (103) |
| Hotham Heights () | 16.6 –22.5 (19.5) | 20.1-24.4 (22.3) | 9.6-21.9 (15.7) | 115-342 (228) | 7-48 (28) | 46-169 (108) |
| Nerriga (14) | 16 –23.9 (19.6) | 21.0-23.2 (21.9) | 9-21.3 (15.1) | 110-366 (238) | 9-47 (28) | 41-156 (98) |
| Golden Grove (15) | 15.5 –21.7 (18.7) | 20.0-24.6 (22.5) | 8-20.9 (14.4) | 117-402 (259) | 9-52 (30) | 44-165 (105) |

**Table 4.7.** Percentage of each grade of epiphyllous fungi found at Brandy Creek.

| | **Grade 1** | **Grade 2** | **Grade 3** | **Grade 4** | **Grade 5** |
|---|---|---|---|---|---|
| **Count** | 6% | 28% | 39% | 21% | 4% |

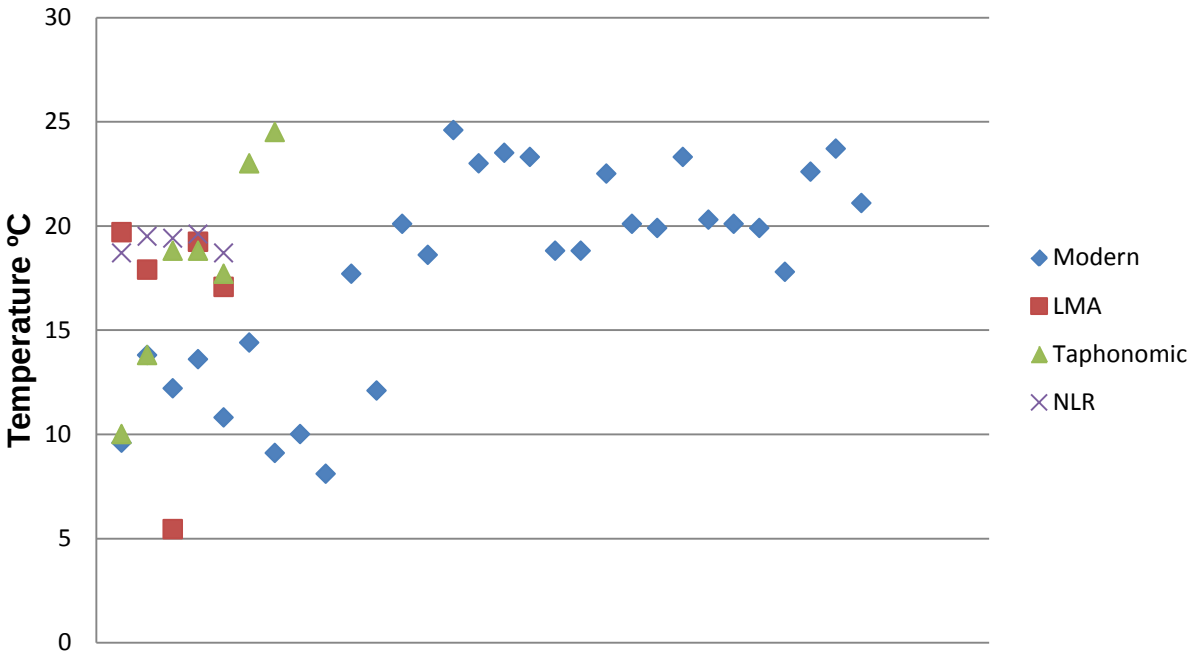


**Figure 4.1**. Comparison of Eocene localities, taphonomic localities, and observed MAT for modern rainforest in eastern Australia.

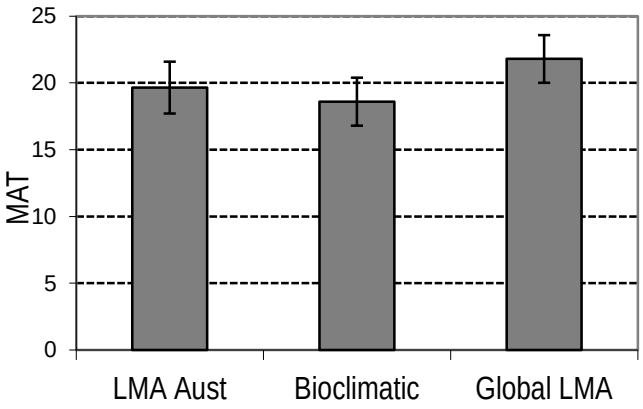


**Figure 4.2** Comparison of estimates of Mean Annual Temperature (MAT) with associated errors of the estimate, for the Brandy Creek Eocene flora based on 3 different climate proxies.

# Chapter 5 Palaeoecological reconstruction of the Brandy Creek Eocene locality, Bogong High Plains, Victoria, Australia

## 5.1 Introduction.

Chapter 5 brings together the taxonomic analysis of the macrofossil record determined in Chapter 2 and the pollen and spores fossil record determined in Chapter 3, with the climate analysis in Chapter 4. Collectively, the data and taxonomic determinations from these chapters are used to reconstruct the palaeoecology of the Brandy Creek Eocene locality. Key elements of the chapter include: 1) a review of the floristic composition of the flora, using both the leaf macrofossil and pollen and spore record; and 2) analysis of trends in community dynamics and diversity by comparing the 17 units that have been sampled vertically at the Brandy Creek locality.

Additional data afforded by the Brandy Creek leaf macrofossil and microfossil records contribute to the understanding of the regional (i.e. south eastern Australia) community dynamics during the Eocene. Comparison is made between Brandy Creek and the other Eocene fossil localities from south eastern Australia as well as New Zealand that represent the same or slightly older time frames to determine regional trends in both floristic composition and diversity. This chapter therefore discusses Brandy Creek in the global context, looking at the common elements of floristic composition, diversity and climate as well as how the Brandy Creek flora compares to regional and global landscapes during this time.

### 5.1.1 Australia during the Eocene

During the Eocene the southern margin of Australia lay at high southern latitudes at approximately 60°S (Wilford and Brown 1994). Despite this, Australia was warmer and more humid than it is currently; reflecting globally warm conditions (Barlow and Hyland 1986; Martin 1990; Greenwood and Wing 1995; Zachos et al. 2001; Huber and Caballero 2011). The Eocene (55.8 – 33.9mya) was a period of

transformation during which the worlds biota modernised and the northern hemisphere continents adopted their current position. Australia lay adjacent to Antarctica but separated from that continent by a seaway, although with a land connection through what is now Tasmania for part of the Eocene (Wilford and Brown 1994). The Eocene is recognised from a variety of climate proxies as having globally highly equable climates and low latitudinal temperature gradients between the equator and the poles (Greenwood and Wing 1995; Marwick 1998; Zachos et al. 2001; Huber and Caballero 2011). During the Eocene there is a peak in temperature and diversity at the early Eocene known as the Early Eocene Climatic Optimum (53 -50 mya), which was the result of long term warming during the mid Paleocene (Zachos et al. 2001 and 2008). The long term cooling that occurs after the EECO is briefly interrupted by the Middle Eocene Climatic Optimum (MECO) (~ 40my), lasting for approximately 400,000 yrs (Bijl et al. 2010; Pearson 2010). After the MECO and during the late Eocene there is continued drop in temperature and carbon dioxide levels across the globe, particularly at high latitudes (Pagani et al. 2005; Lear et al. 2008; Eldrett et al. 2009; Pross et al. 2012).

Prior to the Paleogene Australia was part of the great southern landmass, Gondwana. Australia and Antarctica began to separate in the middle Cretaceous (approximately 110 Ma) but a narrow ocean did not form between the two continents until the late Eocene/ Oligocene approximately 38 Ma (Wilford and Brown 1994). Ocean currents were prevented from coming up from the south by shallow water between Tasmania and the mainland (Kemp 1978; Veevers et al. 1991). Throughout the Paleogene Australia gradually moved north, increasing deep sea circulation between Australia and Antarctica. Circum-polar circulation gradually led to the cooling of Antarctica and a decrease in ocean temperatures resulting in the cooler climates in the south of the Australian continent today (Kemp 1978; Wilford and Brown 1994; Quilty 1994).

Although globally the world was cooling during the late Eocene, equable climates remained as Australia gradually moved north. The seaway between Australia and Antarctica had begun to widen, but was still shallow and the south Tasman rise was a barrier to westerly circulation. Oxygen isotope and palaeobotanical proxy data

indicate a shallow ocean and terrestrial temperature gradient from equator to high latitudes (Greenwood and Wing 1995; Pagani et al. 2005; Huber and Caballero 2011).

### 5.1.2 Australian Eocene Climates and Vegetation

Throughout the Paleogene, much as it is now, Australia lacked a substantive tall mountain range (i.e., greater than 3000m asl; Jones and Veevers 1982). The main mountainous area in Australia today is in the southeast, with the highest peaks near Mt. Kosciuszko (2228m asl.) in New South Wales, and Mt. Hotham (1862m asl.) and Mt. Bogong (1986m a.s.l.) in the Bogong High Plains of Victoria (Groves 1994). However, there is some doubt that the Bogong High Plains were at the same elevation then as now. The timing of the uplift events that created the Highlands varies, with some authors suggesting late Mesozoic or mid Cretaceous uplift (O'Sullivan et al. 1999; Nott 2005), whilst others suggest uplift occurred during the Late Paleogene (Oligocene) to Late Neogene (Jones and Veevers 1982; Ollier 1986; Ollier and Pain 1994; Holdgate et al. 2008). Holdgate's analysis of the palynology in the mudstone that the elevation was a maximum of 600m asl. This is consistent with other authors that place the Eocene, Mt. Hotham at lower elevation than today, approximately 400 - 600m asl and supporting a very different type of vegetation than it currently does (Carpenter et al. 2004; Greenwood et al 2003 and 2004; Orr 1999; Holdgate et al. 2008).

Plant fossils provide consistent evidence of a much warmer Australia during the Eocene. The Eocene plant fossil record of south eastern Australia indicates that temperatures were warm, with MAT ranging from 16 to 22°C, low seasonality with cold quarter mean temperatures > 13°C, and warmest quarter mean temperature < 25°C. MAP during this time was high with MAP ~170 – 190cm/yr and mean cold quarter precipitation <30cm and mean warmest quarter precipitation >50cm (Greenwood et al. 2003).

***Brandy Creek in a global context***

Eocene fossil floras from Brandy Creek have nearest living relatives that are endemic to rainforests of northeast Queensland (Greenwood et al 2003), which have considered to be relictual containing some of the oldest families of rainforest plants in the world (Australian Heritage Commission 1986; Adam 1992; Crisp et al. 1999). Many of these rainforest taxa have also been found at Eocene localities outside Australia in both the Northern and Southern Hemisphere. These include Cupressaceae, Casuarinaceae, and Proteaceae at Laguna del Hunco, Argentina; and Lauraceae, including *Litsea, Endiandra*, and *Beilschmeidia* from the London Clay flora and the late Eocene Pikiplko fossil forest New Zealand (Collinson 1983 in Carpenter et al. 2004; Wilf 2000; Lee et.al 2012). All these floras are characteristic of closed mesothermal and /or megathermal rainforests with high diversity. The Eocene fossil record of Africa shows no shared genera with Australia. The interior of the African continents was becoming dryer during the Eocene with the vegetation reflecting woodland and savannah genera (Jacobs, 2004).

During the Eocene, Australia, South America and South Africa were situated at high southern latitudes. Consequently, Australia and South America in particular share a number of families of fossils, and many fossil taxa found in South American localities have nearest living relatives found in the Humid Wet Tropics of north eastern Queensland (Dettmann 1989; Thornhill et al. 2012b).

The presence of fossil taxa from the same family found on different continents provides clues to past plant distributions when the southern continents were connected via 'pathways' provided by Antarctica (Barlow 1981; Crisp et al. 1999). Fossils document the presence of South American fossil Myrtaceae taxa dispersing into Australia where the family now occupies multiple climate ranges. Similarly, *Casuarina* species were dispersed into South America from Australian origins (Morley 2000).

### *5.1.3 Reconstructing Ancient Plant Communities*

The use of quantitative sampling for Australian Eocene fossil sites has been limited in the past. North American researchers, by contrast, have largely adopted the use of quantitative palaeobotanical data for analysis of plant diversity, abundance and palaeoclimate (e.g., Wing and Greenwood 1993; Wing et al. 1995; Wing 1998; Wing 2000; Wing and Harrington 2001; Wilf et al. 2003; Smith et al. 2012). This approach is limited to a few Eocene sites in Australia with large taxonomic counts recorded for Anglesea (2250 specimens), Golden Grove (greater than 800 specimens), Maslin Bay (2700 specimens) and Nerriga (600 specimens (Hill 1982; Christophel et al. 1978, 1987). These counts have been used mainly to estimate floral diversity rather than abundance, however Christophel and Greenwood (1987) and Greenwood et al. (2003 and 2004) used leaf margin data for climate analysis of Australian Paleogene floras. The limited nature of the quantitative data has meant that regional Australian environmental trends, which have been shown to be different to Northern Hemisphere environmental trends, have provided only a partial picture of Eocene climates and environments (Carpenter 1994; Greenwood and Basinger 1994; Greenwood and Wing 1995; Greenwood et al. 2000). Prior to the current study, no quantitative data were produced from the Bogong High Plains Eocene macrofossil sites in Australia. This has prevented a comprehensive reconstruction of the Eocene environment of south eastern Australia.

#### *The nature of the plant fossil record*

Leaves, pollen and spores all have important roles to play in the reconstruction of ancient plant communities and environments (Kemp 1978; Truswell 1990, 1993; Macphail et al. 1994; Martin 1994; Greenwood et al 2003 and 2004; Smith et al. 2012). Accounts of climate and vegetation in Australia during the Eocene are based on both microfossil and macrofossil evidence (e.g., Kemp 1981; Macphail et al. 1994; Martin 1994, 1998 Christophel and Greenwood 1989; Carpenter 1994; Greenwood and Basinger 1994; Greenwood and Wing 1995; Greenwood et al. 2000 and 2003; Carpenter et al. 2004 and 2012; Thornhill et al. 2012(a)).

The contributions of macrofossils and microfossils differs. Macrofossils generally travel short distances before deposition, and provide an account that is more accurate than microfossils of plant diversity, dominance and relative abundance in the local community (Burnham 1989; Greenwood 1991, 1992).

In comparison to macrofossils, microfossils generally present a regional rather than local picture of vegetation, with pollen tending to travel comparatively longer distances from source vegetation prior to deposition. In a closed forest environment spores and pollen mainly reflect the local trees, but even in these settings pollen from wind-pollinated trees (e.g. Causarinaceae, *Nothofagus* and most conifers) may be over-represented, distorting measures of their relative importance and presenting a 'bias' in the fossil record (Greenwood 1991; Kershaw and Bulman 1994; Walker and Sun 2000; Rowe 2012).

Of greater concern is the lack of information on some plant families reflected by the pollen record. For example, Lauraceae pollen are not usually preserved in the fossil record due to their thin walls (Macphail 1980), yet Lauraceae leaf fossils are very common in Australian Palaeogene floras (Christophel and Rowett 1996; Keefe 2000; Vadala and Greenwood 2001; Greenwood et al. 2003). Conversely, *Nothofagus* pollen is present in many Paleogene sediments across southeastern Australian fossil localities such as Hotham Heights, Anglesea, Nerriga, and Golden Grove (Carpenter et al. 2004; Christophel and Blackburn 1978, Christophel and Greenwood1987; Hill 1982). However, the macrofossil record of *Nothofagus* has been largely restricted to Oligocene and Miocene sites in Tasmania such as Cethana, Little Rapid River, Monpeelyata and Pioneer (Hill 1992; Hill and Scriven 1997). There are relatively few reliably identified *Nothofagus* macrofossils on mainland Australia, where they are largely restricted to Early Miocene sediments of Victoria (Bacchus Marsh), New South Wales (Kiandra and Vegetable Creek) and Western Australia (West Dale). These sites have produced only one species and few specimens (Christophel 1985; Hill 1988; Hill and Merrifield 1993; Scriven and Hill 1995; Paull and Hill 2003).

Combining leaf, pollen and spore data allows for assessment of both local and extra-local species richness, as taxa not encounted in the macroflora may be detected

in the spore and pollen sum, and vice-versa. Additional data afforded by this combined approach reflect the differential preservation potential of spores and pollen compared to leaves and other macrofossils. This study has provided the necessary quantitative data for proposing a reconstruction of the paleoecology of Brandy Creek.

Preservation of leaf fossils depends on the nature of their transport and the depositional environment. Numerous factors determine whether a leaf becomes fossilised, including abscission, transport, decay and deposition. Collectively the study of variations in these processes and how they affect representational bias in the fossil record is called taphonomy. Transport of the leaves to a depositional environment can depend on the height of the trees, presence or absence of wind and the time taken for a leaf to fall to the ground (Ferguson 1985; Gastaldo 1988, Spicer 1989, 1991; Greenwood 1991, 1992). Shape, size, structure and density of leaves can also determine the rate and distance of transport (Spicer 1991). In aerial and water transport, smaller leaves can travel farther than larger leaves (Greenwood 1991 and 1992; Steart et al. 2006), and water energy can contribute to the presence of whole, partial or fragmented leaves (Rich 1989). Deposition must occur in anoxic, stable conditions, such as a lake or creek bed allowing for fossilisation.

## 5.2 Materials and Methods

Plant macrofossils were collected from the late Eocene Brandy Creek locality, Bogong High Plains, north east of Melbourne, (37° 01’ S, 147° 13’ E; Map reference 8323 Dargo 55HEV 030188), at an altitude of 1500 m asl (above sea level). Holdgate et al. (2008) place the age of the Brandy Creek flora as Middle *Nothofagidites asperus* zone (late Eocene) based on the presence of *Cyathidites splendens* (Figure 5.1).

Four metres of outcrop were sampled vertically from base upwards to determine site variability in species richness and diversity through time. The outcrop represents a period of 1000 -4000 year based on 10cm representing 0 – 30 years (Alison, Moeller and Davis, 1986) (figure 5.2). Sample locations are described in the lithologic log on figure 5.2 as units. These samples of sediment were cut away from the outcrop and taken back to the laboratory for both macro floral and palynological

processing. Leaf macrofossils were observed *in situ* to be preserved mostly as compressions with organically preserved mesophyll and cuticle – that is, 'mummified' – with a small number of poorly preserved impressions towards the top of the outcrop, the latter of which were not included in the analysis. Mummified leaves were freed from the mudstone matrix in the laboratory by maceration using dilute (20%) $H_2O_2$ (hydrogen peroxide) using the method of Christophel (1980*)* as modified by Rowett (1991). Palynological processing is outlined in Chapter 3.

Quantitative sampling provided greater than 500 partial or entire leaves which were assessed for taxonomic assignment (Chapter 2) and ecological information, such as species dominance and diversity. Field census data from laterally continuous fossiliferous sediments, and studies based on present day leaf litter, have shown that large numbers of specimens (greater than 350) can closely approximate patterns of dominance and overall floristic richness of the original floral community and multiple samples from the same stratigraphic origin provide greater representation of both local and regional floras (e.g., Burnham et al. 1989; Burnham et al. 1992; Burnham et al. 1993; Greenwood 1991, 1992; Greenwood and Basinger 1994; Wing et al. 1995; Wilf et al.1998 and 2008; Smith et al. 2012).

1702 pollen and spore grains were counted from three samples at Brandy Creek. From these samples 36 different palynomorphs (i.e., spores and pollen) were identified. Pollen and spore analysis provided additional information of the floristic character of the site (Chapter 3). Presented here are count data from the sampled section (figure 5.2), analysed to provide richness and diversity information. Counts up to 500 grains are more likely to catch rare pollen, i.e. palynomorphs less than 1% of the sum (Farley 1988), although Weng et al.(2006) suggest counts of more than 1000 are required to capture rare palynomorphs. Of all the plant fossil records available to palaeobotanists, fossil palynomorphs are the most abundant. This abundance allows for both local and regional assessment of vegetation over both short and long periods of time (Martin 1998; Soepboer et al. 2010; Tuffs et al. 2012).

Abundance diagrams of the Brandy Creek palyno flora provide information on composition within and between samples and are used to characterise the abundance

of individuals of a given species in a community in relation to the abundance of other species (Kent and Coker 1992). Abundance is graphically represented here using histograms, a spindle diagram (macrofloras) and a TILIA diagram for pollen/spores (Hammer et al. 2001; Grimm, 2011).

Hierarchical clustering is a top down clustering method showing the relationship between individual members and clustering them based on the level of similarity or distance using a distance metric (Krebs 1989). Hierarchical clustering is used at Brandy Creek to determine the level of similarity between each sample based on presence/absence of leaf specimens and palynomorphs. The analysis was conducted using PAST software version 2.16 using Bray Curtis association metric, with group average linkages weighting all samples equally (Krebs 1989; Hammer et al. 2001).

A Spindle diagram is used to show all morphotypes present at Brandy Creek and to show the changes in floristic composition of the flora over time. Spindle diagrams were generated using PAST version 2.16 (Hammer et al. 2001).

A number of statistical methods and diversity measures were used to analyse trends in species richness and diversity within the sampled outcrop at Brandy Creek. Alpha diversity for all samples is measured as species richness (abundance) as well as using diversity indices.

Diversity indices to measure species evenness include Simpson's Diversity Index (Simpson, 1949):

$$D=\Sigma_i \left(\frac{n_i}{N}\right)^2$$

Where D equals species diversity, N is the total number of individuals and *n* is the number of individuals of a species.

The Shannon- Wiener index (H) is calculated as:

$$H = -\sum pi \ \log_e pi$$

Where *n* is the sample size, and $f_i$ is the number of observations in category $i$ where $i$ equals the number of specimens of each morphotype and number of specimens for each palynomorph (Shannon, 1948).

The evenness of diversity is assessed by using Pielou's evenness index:

$$J = \frac{H}{H_{max}}$$

Where H is derived from the Shannon diversity index and $H_{max}$ is the log of the number of morphotypes/palynomorphs (Mulder et al. 2004).

Species composition and hence community structure across the 17 units at Brandy Creek is analysed using SHE (Buzas and Hayek 1998). Developed by Buzas and Hayek (1998), originally for the analysis of benthic foraminiferal assemblages, SHE analysis is based on three diversity indices; species richness (In S), species diversity (H) and evenness (E)(H =InS +InE). The premise is that the results will produce a linear pattern if the samples are the same. Changes in slope reflect changes in species composition and therefore community structure. High evenness shows that there is no single species dominating the flora, low evenness generally indicates a community is species poor (Osterman, Buzas and Hayek 2002).

Rarefaction has been used widely in palaeoecology for microfossil and macrofossil analysis and is used here to identify trends within the Brandy Creek flora, comparison with Brandy Creek and other Eocene flora as well as comparison with modern equivalents (Raup 1975; Harrington and Kemp 2001; Wilf et al. 2003 and Wilf et al. 2005; Peppe 2010; Smith et al. 2012).

Rarefaction works by estimating the expected number of species in a random sample of individuals from a larger collection. By standardising the samples, a rarefaction curve is generated. The shape of the rarefaction curve is determined by the number of individuals of each species and the evenness of the abundance distribution (Raup 1975; Collins and Simberloff 2009; Colwell et al. 2012).

Rarefaction analysis was performed using software PAST version 2.16 (Hammer et al. 2001). Variability of fossil material due to difference in preservation and production of specimens leads to different sample sizes, rarefaction standardises these samples so they are equal. Rarefaction estimates the species richness (E ($S_n$)) expected based on all specimen counts being equal for all samples (Tipper 1979; Krebs 1989; Birks and Line 1991; Koellner et al. 2004). The equation is as follows:

$$E(S_n) = \sum_{i=1}^{S} \left[ 1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right]$$

where:

$E(S_n)$ = Expected number of species in a random sample of *n* individuals;

*S* = Total number of species in the entire collection;

$N_i$ = Number of individuals in species *i;*

*N* = Total number of individuals in collection = $3\ N_i$;

*n* = Value of sample size (number of individuals) chosen for standardisation ($n \leq N$); and

*(N/n)* = Number of combinations of *n* individuals that can be chosen from a set of N individuals.

For comparison among rarefaction analyses to be successful a number of assumptions are made: the samples need to be taxonomically similar; the sampling method must be the same for each sample and samples must be from the same or similar habitat. If these assumption are not meet than the rarefaction curve will be skewed (Raup 1975; Tipper 1979; Krebs 1989, Newton, 1999). Brandy Creek is compared to other Eocene sites that have similar taxonomic composition provided through both leaf macrofossil and palynological sampling. Depositional environments for all localites are considered fluvio - lacustrine mudstone deposits and previous palaeoclimate analysis shows that palaeotemperature and palaeoprecipitation are similar across the region (Greenwood et al. 2003 and 2004).

## 5.3 Results

### 5.3.1 Overview of the Brandy Creek Fossil Flora

The Brandy Creek leaf macroflora is moderately diverse with 18 leaf morphotypes (Table 5.1). The leaf macrofossils are dominated by Lauraceae with 15 morphotypes, including leaves that have affinity to the extant genera, *Cryptocarya, Endiandra* and *Litsea*, each having 5, 8 and 2 morphotypes respectively. Cunoniaceae/Elaeocarpaceae are also present in the flora (Figure 5.3).

A total of 36 palynomorphs were recognised in the Brandy Creek microflora, represented by angiosperms, gymnosperms, and pteridophytes (Table 5.2). The angiosperms represent 41.9% of the flora, with *Nothofagus* type pollen representing 19.1% of the angiosperm total. Most noticeably is the absence of Lauraceae which rarely preserves as fossil pollen (Macphail 1980). *Cyatheacidites spp* dominates the pollen/spore counts (40%) indicating that the fern may have been close to the point of deposition. The dominance of *Cyatheacidites spp* in the palynomorphs count is consistent with the Brandy Creek count in 2000, with *Cyatheacidites spp* aff. Dicksoniaceae represented 68% of the total count (Keefe 2000). Numerous other pteridophytes are present in the flora although with less prominence including *Ischyosporities sp*. *Baculatisporites* sp. and *Foveotriletes* sp. Not surprisingly gymnosperms represent only a small percentage of the population 6.2% with *Araucariacites australis* being the most abundant (Figure 5.4).

There are a number of palynomorphs that are rare, occurring in trace amounts representing less than 1 % of the total sum. These include *Cupanieidites sp. aff*. Sapindaceae, *Haloragacidiites harrisii* aff. Casuarinaceae, *Podosporites sp.* aff. Podocarpaceae and *Verrucosisporites kopukuensis aff.* Schizaeaceae. These rare palynomorphs are important to capture as they contribute to the diversity of the flora.

The families represented in the Brandy Creek leaf macroflora are reflected in Eocene fossil localities across south eastern Australia including nearby Hotham

Heights, Nerriga, Golden Grove and Deans Mash. Lauraceae was dominant in the local landscape and prominent across the region (Figure 5.5). There are high proportions of Cunoniaceae/ Elaeocarpaceae at Brandy Creek (16%) and Golden Grove (27%), but these taxa comprise a minor component at the other localities. Only two families were recorded as Brandy Creek macrofossil compared to the other localities which record the presence of Proteaceae, Gymnosperms, ferns and Gymnostoma (figure 5.5).

There are a number of shared palynomorphs recorded at Brandy Creek and other Eocene localities (Figure 5.6). The close proximity of the Hotham Heights locality to Brandy Creek allows for a comparison of the two microfloras. Comparison between the Brandy Creek 2000, and 2003 counts and the Hotham Heights counts show the two locations have 20 palynomorphs in common (Table 5.3). The comparison gives some clarification to the over representation of some genera in the pollen and spore sum at Brandy Creek particularly *Cyatheacidites spp.* Although *Cyatheacidites spp.* represents 13% of the total count, at Hotham Heights locality this is much less of the total count that *Cyatheacidites* spp. at Brandy Creek which represented approximately 68% of the total count for Brandy Creek 2000 or approximately 41% of the total count for Brandy Creek 2003. The high percentage at the Brandy Creek locality suggests that the sampling represents a localised presence of *Cyatheacidites spp.* at the Brandy Creek during the Eocene or secondly a sampling bias.

Extending beyond the localised flora, comparison with regional localities found that there is crossover of palynomorphs between localities. For example Golden Grove shares 20 palynomorphs with Brandy Creek, Deans Marsh 18 and Nerriga 14, (Table 5.3). A cluster analysis shows the relationships among the Eocene site (Figure 5.7). The dendogram shows that Brandy Creek and Hotham Heights are similar; this is not surprising given their close proximity of the 2 locations. Holdgate et al. (2008) concludes that Brandy Creek and Hotham Heights localities belong to the same stratigraphic layer and facies. The localities share many of the same macrofossils and palynomorphs. The Dendogram also shows that Deans Marsh and Golden Grove are also closely related. The two floras are found at coastal localities, however Deans

Marsh is in Victoria and Golden Grove is in South Australia (Christophel and Greenwood 1987; Rowett and Sparrow 1994). The commonality between the floras found at Deans Marsh, Golden Grove, Nerriga, Hotham Heights, and Brandy Creek suggest the flora at these localities are characteristic of the flora that dominated large parts of southeastern Australia during the Eocene. Although the age of the floras represent the breath of the Eocene period, there is no obvious differences in the floristic composition of the floras (Rowett and Sparrow 1994; Greenwood et al. 2003).

### 5.3.2 Trends in Diversity and Plant Community Composition.

#### *Species Richness, Diversity and Evenness.*

Both leaf macrofossils and palynomorphs samples were used to assess species evenness. The data set includes 530 leaf macrofossil specimens and 1702 palynomorphs specimens taxonomically sorted into 18 leaf morphotypes and 36 palynomorphs, respectively. Figures 5.8a and b show the three measures of evenness; species abundance (ln S) species diversity (H) and evenness (E) (ln $E = H - \ln S$) for macrofossils. As expected, as the number of specimens (lnS) increases as each unit is sampled sequentially, there is a corresponding increase in the diversity (H) of the flora. There is a jump from 0.8 to 2.0 for both abundance and diversity, after which they level off. The evenness across the samples trends downwards from 0.0 to - 0.8 indicating that the number of dominant species declines with increased sampling. There is little difference in species diversity and dominance in the Brandy Creek palynomorphs between the three samples.

#### *Rarefaction Analysis: Brandy Creek and other Australian Eocene floras.*

Rarefaction analysis accounts for the difference in sample sizes – if 2 samples have the same species richness but significantly different sample sizes, is their diversity the same? Correcting for sample size is particularly important when sampling fossils, because taphonomic constraints can result in low species richness simply due to the omission of rare taxa (Raup 1975; Collins et al. 2009; Colwell et al. 2012). The sampling criteria for the Brandy Creek flora was for the selection of specimens with

either a margin, apex or base or entire leaves resulting in different sample sizes between layers.

The rarefaction curve for combined Brandy Creek samples (Figure 5.9a) shows a steep rise in the number of morphotypes found in the first 200 specimens. At approximately 300 specimens the curve begins to flatten suggesting a saturation point were sampling is unlikely to deliver new morphotypes. At 500 specimens no new morphotypes are recorded suggesting that a sample size greater than 200 but less than 500 is sufficient to capture the richness of local vegetation.

There is a direct relationship between palynological richness and the number of palynomorphs counted at a single site (Wing and Harrington, 2001; Weng et al. 2006). Most pollen counts are usually 300 grains or less; if the pollen count is low then the most common palynomoprhs are likely to be detected, with the rare palynomorphs only found by chance (Weng et al. 2006). Weng et al. (2006) has shown that if the frequency of an individual pollen taxon is greater than 5% then it is most likely to have been found in the first 100 grains counted. As the frequency falls, the likelihood of detection will increase as the counts increase. Weng et al. (2006) found that rare taxa (i.e., <1%) had an 80% chance of being detected if 1000 or more grains were counted in the sample.

The results shown in Figure 5.9b. are consistent with Weng et al. (2006). The rarefaction curve shows that most palynomorph taxa were recorded within the first 500 counts, whilst the remaining rare taxa were added with additional counts of over 1000 specimens. The rarefaction curve shows a gradual levelling off (saturation point) were the chance that additional counts will result in additional taxa are unlikely. Weng et al. (2006) notes that this saturation point can vary depending on vegetation. In temperate ecosystems, the saturation point can occur with low pollen counts; this is the opposite for high diversity tropical rainforest were the saturation point will occur only after large pollen counts.

Comparisons between Brandy Creek and other Eocene localities in southeastern Australia showed most sites sampled had up to 500 specimens with the

exception of Deans Marsh where over 1000 specimens had been collected. The rarefaction curve (Figure 5.10) shows that the sampling at Brandy Creek and Golden Grove reach saturation point with the curve flattening out . For Nerriga and to a greater extent Deans Mash the rarefaction curve continues to trend upwards suggesting that saturation point has not been achieved. The results show that large sample size can result in greater detected diversity.

***Comparison of the Eocene floras and extant floras.***

With the exception of the Eocene Deans Marsh, diversity of extant rainforests was greater than the Eocene fossil localities analysed (Figure 5.11). Brandy Creek and the other fossil localities are most similar to the extant Ella Bay locality with 800 specimens counted. The number of species at Ella Bay is 26, compared to 26 at Nerriga, 18 at Brandy Creek, 22 at Golden Grove, and 34 at Deans Marsh. The other extant sites were samples from water bodies; Ella Bay River, Windsor upstream (upper) and Windsor downstream (lower) have 37, 43 and 38 species respectively. A rarefaction analysis was conducted to compare Eocene localities and the modern forest floor leaf litter of Ella Bay, Ella Bay River (stream-bed), Windsor upstream and Windsor Down stream (Figure 5.11.). From the rarefaction analysis, the Brandy Creek Eocene macroflora, based on the curve and 95% confidence interval falling below the curves and 95% CI of the other sites, has the lowest diversity of all of the Australian Eocene macrofloras with count data. The diversity at Brandy Creek is also lower than recorded for leaf litter from the Ella Bay forest floor samples, the stream-bed samples from Ella Bay River, and the Mt. Windsor samples. Smith et al. (2012, Fig. 9) provided rarefaction curves of forest floor litter from temperate deciduous and tropical forests sites in their analysis of the diversity of North and South American Eocene macrofloras. The Brandy Creek macroflora rarefaction curve and 95% CI fall between the least diverse modern tropical forest sample in their analysis, and the temperate deciduous forest sample from Harvard Forest in Massachusetts, USA.

**Plant Community Dynamics over Time**

***Cluster Analysis***

Vertical sampling (representing time) of the Brandy Creek locality allows for changes in community composition to be assessed. A hierarchical cluster was performed to determine if there were any patterns in species abundance and sample composition. The results for the cluster analysis for the 17 macrofossil samples and the three palynomorph samples are shown in figures 5.12 a and b. The macrofossil dendogram shows the samples are clustered into seven groups. The clusters do not show any clear similarities between stratigraphically adjacent sample , with the exception of samples 1 and 2. The remaining clusters contain samples that are mixed stratigraphically. The dendogram indicates that there are no significant changes in floristic composition over time at Brandy Creek.

A Spindle diagram (figure 5.13) is used to illustrate the most common taxa across the samples. The width of the blocks represents the number of specimens for each morphotypes. The greatest concentration of macrofossil are from layer 8 to 14, with BC010 aff. Lauraceae *Endiandra* a dominant feature of the Brandy Creek flora. The diagram also shows that taxa peak in abundance between layers 8 and 14 including aff. Cunoniaceae/Elaeocarpaceae (BC017 and BC016) aff. Lauraceae *Cryptocarya* (BC002, BC009) and aff. Lauraceae Endiandra **(**BC014) From Bed 4 to 6 there is minimal representation among the taxa with the exception of BC017 aff. Cunoniaceae/ Elaeocarpaceae which remains a constant feature of the flora through the sequential sampling. The absence of many morphotype in these beds and their reappearance in bed 8 is more likely due to taphonomic bias than actual absence from the landscape at this time.

The Palynomorphs dendogram shows that sample 1 (unit 1) and sample 2 (unit 3) are closely related, whilst sample 3 (unit 11) is different (figure 5.12b). Although the specimen counts are similar for all three samples, there is a large proportion of palynomorphs found in samples 1 and 2 that are absent or in low numbers (trace) for sample 3 (Table 5.4) The TILIA diagram (figure 5.14) shows no obvious shifts in

floristic composition over time. *Cyatheacidities* spp.< 45µm is present across the three samples, although is most prominent in sample three, whilst *Cyatheacidities* spp. >45µm is more prominent in samples 1 and 2. Among the Angiosperms, *Nothofagus* type pollen occurs across the three samples, showing greater abundance in sample 2.

***Rarefaction Analysis***

Rarefaction analysis was conducted to determine differences in diversity over time. Samples were group based on the results of the cluster analysis (figure 5.12a). Figure 5.15a shows that samples 5 and 8 had the greatest number of specimens, yielding the greatest number of morphotypes. The decline in specimen numbers between layers could possibly be a taphonomic issue with preservation conditions not supporting whole or partial leaf preservation, or secondly a shift in floristic composition, with the morphotypes recorded in the macroflora becoming less dominant over time, possibly as a result of forest succession.

Rarefaction of the three palynomorphs samples (Figure 5.15b) shows that sample 2 has the least number of specimens however is the most diverse of the three samples. Sample 1 has similar diversity to sample 2, despite having a greater number of specimens to achieve similar diversity. Sample three is the least diverse of the samples.

## 5.4 Discussion

### 5.4.1 Brandy Creek during the Eocene

The Brandy Creek flora is moderately diverse with 18 leaf morphotypes and 36 pollen and spore taxa recorded at the locality. Many have affinity with extant families and genera found in rainforests of northeastern Queensland including the Lauraceae genera,*Cryptocarya*, *Endiandra* and *Litsea*; and Proteaceae, Sapindaceae, Arcauariaceae and Podocarpaceae,Restionaceae, Dicksoniaceae and Cyatheaceae; Leaf litter sampling of modern forests shows that depositional sites close to or within streams can give results of high diversity that are, reflective of the local plant population (Greenwood 1992 and Greenwood and Christophel 2005). The fine siltstone and sandstone found at Brandy Creek, plus the presence of partial and entire leaves suggest that the Brandy Creek depositional environment was likely to have been a small lake or oxbow with the flora reflective of the local area (Greenwood, 1991).

The results document a peak in macrofossil diversity near the middle of the stratigraphic sequence. Lauraceae expands its dominance in both abundance and diversity. There is also an increase in abundance of Cunonicace/Elaeocarpaceae, which maintains its presence throughout the outcrop, whilst many Lauraceae genera disappear and then reappear at different times.

Selective sampling of partial or entire leaves at Brandy Creek may have resulted in a bias towards families whose leaf material is more robust or of families more prominent in the landscape, increasing the chances of partial or entire leaves being fossilised. The selective sampling may have unintentionally limited diversity of the Brandy Creek macroflora. Many of the families that are recorded at the other Eocene localities are recorded as palynomorphs at Brandy Creek (figure 5.6).

The cluster analysis shows adjacent strata at the locality are not usually more similar to each other than to other strata. This is interpreted as the outcrop representing a single community type that did not experience significant shifts in composition for the time interval represented by the outcrop. Nevertheless relative

abundances varied.

The palynomorph results show that there is no movement in species composition over time. *Cyatheacidities* spp, maintains it dominance throughout the outcrop and *Nothofagus* type pollen counts remain fairly stable through the section. Palynomorphs have been shown to reflect both local flora and regional vegetation depending upon depositional type. For example, pollen sequences from soil profiles tend to record population changes within a radius of less than 50 m (Odgaard 1999), however if the depositional environment is a medium to large lake then this can represent an area up to 5km from the depositional site (Odgaard 1999).

The Brandy Creek pollen and spore results show that *Cyatheacidities spp.* was present on the landscape, which can be said with some certainty. However, the abundance of *Cyatheacidities* spp. Spores could have more to do with the large volumes produced by a single frond, and not indicative of plant abundance on the landscape (Page, 1979). Other families may be under -representation in the palyoflora.

Pollen with affinity to Proteaceae was documented at Brandy Creek. It is likely that the Proteaceae pollen reflects local rather than regional presence, particularly as it occurs in the macrofossil samples from nearby Hotham Heights (Carpenter et al. 2004). Analysis of Proteaceae modern pollen rain has shown that Proteaceae can often be under represented in the pollen counts. Martin (1978) records 4% Proteaceae pollen from a modern study site having 13 Proteaceous species, and Hassell (2000) had similar results with less than 3% Proteaceae making up the pollen count. These low counts do not reflect the dominance of Proteaceae on the landscape today.

Under-representation in the pollen count can be attributed to its structural position in the plant community. For example, Proteaceae is typically an understory plant leading to low dispersal of pollen. Proteaceae pollen is large and heavy making transport difficult. Furthermore the family are also pollinated by insects, birds or other animals and do not produce large amounts of pollen which contributes to under-representation in the palynological count (Itzstein – Davey 2003).

Rare taxa are important elements in the vegetation and should be considered part of any plant community analysis. In most cases the occurrence of rare taxa in the pollen count is a result of the pollination mechanism and pollen productivity rather than rarity in the community. Some taxa produce few pollen grains to be carried by animal vectors rather that wind and water. Entomophilous taxa with low pollen productivity are more likely to reflect local vegetation (Weng et al. 2006; Metlsov et al. 2011). Large numbers of rare taxa among a few dominant taxa may signal a recent change in floristic composition, with the conditions favouring the dominant and common genera. These changes may include rainfall, temperature or competition for ground space to allow the expansion of the population.

The absence of *Nothofagus* from the macrofossil record of mainland Australia until the early Miocene indicates that the high proportion of *Nothofagus* pollen *(Nothofagidites*) at the Brandy Creek flora is more likely to reflect regional rather than local vegetation (Paull and Hill 1993; Christophel and Greenwood1989). Pollen from regional sources can dominate a pollen sum without contributing substantially to the local vegetation (Walker and Sun 2000; Rowe 2012). *Nothofagus* macrofossil have been recorded from Tasmania during the Eocene and it is likely that the presence of *Nothofagus* pollen in fossil localities from southeastern Australia, including Brandy Creek, is a result of long distance dispersal (Hill 1991, 1994; Hill et al. 1999 and Jordan and Hill 1999).

### 5.4.2 Eocene Regional Diversity

There are similarities in the floristic composition of Brandy Creek and other Eocene flora from southeastern Australia (Figure 5.5 and 5.6). Rarefaction analysis of Brandy Creek and the other localities confirm a moderately diverse flora across the region during the Eocene. Diversity is greatest in the floras that are early to middle Eocene in age, such as the early Eocene Deans Marsh and the middle Eocene Golden Grove, and Nerriga. This corresponds to a period of high carbon dioxide levels and high temperatures (Figure 5.1) (Bijl et al. 2010; Pearson 2010), whilst the late Eocene was a period of cooling (Pagani et al. 2005; Lear et al. 2008). The slightly lower

diversity of the Brandy Creek flora compared to the other Eocene floras is likely the result primarily of a biased approach of sampling of partial or complete leaves.

Temperature estimates of the Brandy Creek flora based on Leaf Margin Analysis and Bioclimatic Analysis are not reflective of late Eocene cooling of Brandy Creek is reconstructed as having a MAT 15.7– 21.7°C and a MAP of 107 – 320cm/yr. These temperature estimates are comparable to the early and middle Eocene localities of Nerriga, Golden Grove and Deans Marsh, which have a MAT range between 15.5 °C and 23.9 °C and a MAP 103 -402 cm/yr . Equability (frost free environments with CMMT greater than 10 °C) is more likely to play a role in changes in diversity (Wing and Greenwood 1993, Wing and Greenwood 1995, Archibald et al 2010).

### 5.4.3 Brandy Creek vs. modern flora

The diversity of the Brandy Creek flora is comparable to the diversity of the modern flora in northeastern Queensland today. Comparison of fossil assemblages with nearest living relatives suggest that the floristic composition of the Brandy Creek flora is representative of a simple notophyll - microphyll vine forest (SNMVF). These forests include families such as Lauraceae, Cunonicaeae, Araucariacae, Dicksoniaceae, Proteaceae, Podocarpacae, and Sapindaceae. The climate profile of Brandy Creek is indicative of modern mesothermal rainforest of northeastern Queensland (Nix 1982; Kershaw and Nix 1988). These mesothermal conditions are represented by of all the Eocene floras in southeastern Australia during the Eocene when there was little or no seasonal variation.

There are a number of taxa present in the Brandy Creek flora that have no modern counterparts living in Australia today, including *Nothofagus* s.g. *Brassaspora,* found today in New Guinea and New Caledonia, where it was likely to have retreated as the climate cooled during the Oligocene (Hill 2001). Others such as *Podocarpus* and *Prumnopitys,* which have modern analogs with restricted ranges in Australia (as canopy dominants in northeastern Queensland rainforest), occur in greatest numbers

in tropical New Guinea and New Caledonia (Christophel and Greenwood 1989; Williams and Adams 2010).

With the dominance of angiosperms and climate change resulting in dryer conditions in southeastern Australia, Araucaria and Agathis gradually protracted north during the late Cenozoic (Kershaw and Wagstaff, 2001). Additional factors such as biomass burning and European settled has meant that nearest living relatives of *Araucaria* and *Agathis* are in small number and restricted to the complex rainforest of northeastern Australia today, where the dense canopy provides too much shade for regeneration (Williams and Adam 2010). *Araucaria* and *Agathis* are most diverse in New Caledonia (Hill 1995).

The under representation of Proteaceae in the pollen sum at Brandy Creek is consistent with Proteaceae found in closed forests today. *Orites* and other Proteaceae are understory trees in rainforests of northeastern Queensland, but they are not dominant, as they are out competed for light canopy trees and other shrubs and ferns in the undergrowth (Christophel and Greenwood 1989).

## 5.5 Conclusions.

The Brandy Creek flora is moderately diverse with 18 leaf morphotype taxa and 36 palynomorphs, respectively. The flora at Brandy Creek is representative of the flora that was present in south eastern Australia during the Eocene, with many taxa at Brandy Creek also present at other localities in the region, including nearby Hotham Heights. The diversity of the Brandy Creek flora is comparable to the modern day forests of northeastern Queensland, is characterised by simple notophyll – microphyll vine forest with an MAT of 15.7– 21.7°C and a MAP of 107 – 320cm/yr, and is indicative of mesothermal conditions (Nix 1982; Kershaw and Nix 1989).

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**Table 5.1** List of Brandy Creek leaf morphotypes and their Botanical affinity.

| Morphotype | Identification |
|---|---|
| BC 001 | Lauraceae *aff*. *Cryptocarya* |
| BC 002 | Lauraceae *aff. Cryptocarya* |
| BC 003 | Lauraceae *aff. Cryptocarya* |
| BC 004 | Lauraceae *aff. Endiandra* |
| BC 005 | Lauraceae *aff. Endiandra* |
| BC 006 | Lauraceae *aff. Endiandra* |
| BC 007 | Lauraceae *aff. Endiandra* |
| BC 008 | Lauraceae *aff. Endiandra* |
| BC 009 | Lauraceae *aff*. *Cryptocarya* |
| BC 010 | Lauraceae *aff. Endiandra* |
| BC 011 | Lauraceae *aff. Litsea* |
| BC 012 | Lauraceae *aff. Litsea* |
| BC 013 | Lauraceae *aff. Endiandra* |
| BC 014 | Lauraceae *aff. Endiandra* |
| BC 015 | Lauraceae *aff. Cryptocarya* |
| BC 016 | c.f. Elaeocarpaceae |
| BC 017 | c.f. Elaeocarpaceae |
| BC 018 | c.f. Elaeocarpaceae |

Table 5.2 Percentage count of pollen and spores palynomorphs at Brandy Creek

| *Species list pollen and spores* | *Botanical Affinity* | *count* | *category* |
|---|---|---|---|
| *Cyathidites sp. (<45µm)* | Dicksoniaceae | 27% | P |
| *Cyathidites sp. (>45µm)* | Dicksoniaceae | 13% | P |
| *Ischyosporites sp.* | Dicksoniaceae? | 3.70% | P |
| *Foveotriletes sp.* | Lycopodiaceae | 1.50% | P |
| *Baculatisporites* | Hymenophyllaceae | 1.30% | P |
| *Cyatheacidites annulatus* | Dicksoniaceae | <1% | P |
| *Cyathidites subtilis* | Cyatheaceae | <1% | P |
| *Gleicheniidites sp.* | Gleicheniaceae | <1% | P |
| *Laevigatosporites sp.* | Numerous monolete ferns | <1% | P |
| *Matonisporites sp.* | Dicksoniaceae | <1% | P |
| *Polypodiidites sp.* | Polypodiaceae | <1% | P |
| *Polypodiisporites sp.* | Polypodiaceae | <1% | P |
| *Rugulatisporites sp.* | Thyrospteridaceae | <1% | P |
| *Verrucosisporites kopukuensis* | Schizaeaceae | <1% | P |
| *Araucariacites australis* | Araucariaceae | 3.70% | G |
| *Dilwynites granulates* | Wollemia (Araucariaceae) | <1% | G |
| *Ephedra sp.* | Ephedraceae | <1% | G |
| *Podocarpidites sp.* | Podocarpus | <1% | G |
| *Podosporites sp.* | Podocarpaceae | <1% | G |
| *Nothofagidites emarcidus* | Nothofagaceae: Nothofagus subgenus Brassospora | 7.70% | A |
| *N. brachyspinulosus* | Nothofagaceae: Nothofagus subgenus Fuscospora | 5.90% | A |
| *N. flemingii* | Nothofagaceae: Nothofagus. subgenus Brassospora | 5.50% | A |
| *Tricolporites sphaerica* | | 4.10% | A |
| *Tricolp(or)ites spp.* | unidentified angiosperm | 3.90% | A |
| *Proteacidites pachypolus* | Proteaceae | 2.90% | A |
| *Malvacipollis sp.* | Euphorbiaceae | 2.70% | A |
| *Proteacidites sp.* | Proteaceae | 2.50% | A |
| *Concolplites sp.* | Cunoniaceae | 1.40% | A |
| *Cupanieidites orthoteichus* | Sapindaceae | <1% | A |
| *Ericipites scabratus* | Ericaceae | <1% | A |
| *Milfordia sp.* | Restionaceae | <1% | A |
| *Myrtaceidities spp.* | Myrtaceae | 1.60% | A |
| *Parvisaccites sp.* | Podocarpaceae: Dacrydium bidwillii type | <1% | A |
| *Triporopollenites spp.* | Proteaceae | <1% | A |
| *Haloragacidites harrisii* | Casuarinaceae | <1% | A |
| *Polycolpites sp.* | | <1% | A |
| *Tricolpities reticulates* | Gunneraceae | <1% | A |
| | Total count | 1702 | grains |

**Table 5.3** Comparison of pollen and spore count for Brandy Creek and other Early to Middle Eocene localities in south eastern Australia (Partridge, 1998). Note total count for Golden Grove was not available.

| *Pollen and Spore species* | Brandy Creek 2000 | Brandy Creek 2003 | Hotham Heights | Nerriga | Golden Grove | Deans Marsh |
|---|---|---|---|---|---|---|
| *Araucariacites australis* | * | * | * | * | * | |
| *Baculatisporites sp.* | * | * | * | * | * | * |
| *Concolplites sp*. | | * | | | | |
| *Cupanieidites orthoteichus* | * | * | | | * | * |
| *Cyatheacidites annulatus* | | * | | | | |
| *Cyatheacidites spp. (<45µm)* | * | * | * | | | |
| *Cyatheacidites spp. (>45µm)* | * | * | * | * | * | * |
| *Cyathidites subtilis* | | * | | | | |
| *Dilwynites granulatus* | * | * | * | | * | * |
| *Ephedra sp.* | | * | | | | |
| *Ericipites scabratus* | | * | * | | | |
| *Foveotriletes sp*. | | * | | | | |
| *Gleicheniidites sp.* | | * | | * | | * |
| *Haloragacidites harrisii* | * | * | * | * | * | * |
| *Ischyosporites sp.* | * | * | * | | | * |
| *Laevigatosporites spp.* | * | * | * | | * | * |
| *Malvacipollis sp*. | * | * | | * | * | * |
| *Matonisporites sp.* | * | * | * | | | |
| *Milfordia sp*. | | * | | | | |
| *Myrtaceidites spp*. | * | * | * | * | * | |
| *Nothofagidites emarcidus/heterus* | | * | * | * | * | * |
| *N. flemingii* | * | * | | * | | * |
| *N. brachyspinulosus* | * | * | * | * | * | |
| *Parvisaccites sp.* | | * | | | | |
| *Podocarpidites sp.* | * | * | * | * | * | * |
| *Podosporites sp*. | | * | | | | |
| *Polycolpites sp.* | | * | | * | * | |
| *Polypodiidites/Verrucatoporites spp*. | | * | | | * | |
| *Polypodiisporites sp*. | | * | | | | |
| *Proteacidites pachypolus* | | * | | | * | |
| *Proteacidites spp*. | * | * | * | * | * | * |
| *Rugulatisporites sp*. | * | * | | | * | * |
| *Tricolp(or)ites spp.* | * | * | * | * | * | * |
| *Tricolpities reticulatus* | | * | | | | |
| *Tricolporites sphaerica* | * | * | * | | | * |
| *Triporopollenites spp*. | | * | | | * | * |
| *Verrucosisporites kopukuensis* | * | * | * | | * | * |
| **Total count** | **252** | **1702** | **201** | **113** | **N/A** | **116** |

**Table 5.4** Fossil palynomorphs at Brandy Creek. List shows total count and count for individual layer (x equals absent from the sample).

| Species list | Total count | Sample 1 | Sample 2 | Sample 3 |
|---|---|---|---|---|
| *Araucariacites australis* | 3.7% | 4.5% | 2.2% | 3.6% |
| *Baculatisporites sp.* | 1.3% | x | 2.9% | x |
| *Concolplites sp*. | 1.4% | 1.8% | 2.2% | x |
| *Cupanieidites orthoteichus* | <1% | 1.8% | x | x |
| *Cyatheacidites annulatus* | <1% | x | 1.8% | x |
| *Cyatheacidites s spp. (<45µm)* | 27% | 21% | 17.6% | 46% |
| *Cyatheacidites spp. (>45µm)* | 13% | 18% | 14% | 5.7% |
| *Cyathidites subtilis* | <1% | x | 2.9% | x |
| *Dilwynites granulatus* | <1% | <1% | 1.3% | x |
| *Ephedra sp*. | <1% | x | <1% | x |
| *Ericipites scabratus* | <1% | <1% | x | x |
| *Foveotriletes sp*. | 1.5% | 1.3% | 3.4% | x |
| *Gleicheniidites sp.* | <1% | x | <1% | x |
| *Haloragacidites harrisii* | <1% | <1% | x | x |
| *Ischyosporites sp*. | 3.7% | 3.5% | 2.7% | 4.9% |
| *Laevigatosporites spp.* | <1% | 1.1% | <1% | x |
| *Malvacipollis sp*. | 2.7% | 3% | 2.9% | 2.1% |
| *Matonisporites sp.* | <1% | <1% | 2% | x |
| *Milfordia sp*. | <1% | <1% | <1% | x |
| *Myrtaceidites spp*. | 1.6% | 1.5% | 1.5% | 1.9% |
| *Nothofagidites emarcidus/heterus* | 7.7% | 8.4% | 9.5% | 4.9% |
| *N. flemingii* | 5.5% | 5.1% | 1.3% | 10% |
| *N. brachyspinulosus* | 5.9% | 3.0% | 12.9% | 4.2% |
| *Parvisaccites sp.* | <1% | x | <1% | x |
| *Podocarpidites sp.* | <1% | <1% | <1% | x |
| *Podosporites sp*. | <1% | <1% | x | x |
| *Polycolpites sp.* | <1% | x | 1.1% | x |
| *Polypodiidites/Verrucatoporites spp*. | <1% | <1% | <1% | 1.2% |
| *Polypodiisporites spp*. | <1% | 1.6% | <1% | x |
| *Proteacidites pachypolus* | 2.9% | 6.4% | X | x |
| *Proteacidites spp*. | 2.5% | 2.5% | 2.4% | 2.7% |
| *Rugulatisporites sp*. | <1% | <1% | 1.3% | x |
| *Tricolp(or)ites spp.* | 3.9% | 3% | 1.1% | 8.3% |
| *Tricolpities reticulatus* | <1% | x | <1% | x |
| *Tricolporites sphaerica* | 4.1% | 2.6% | 7.9% | 3.2% |
| *Triporopollenites spp*. | <1% | x | <1% | x |
| *Verrucosisporites kopukuensis* | <1% | 1.5% | <1% | <1% |
| **Total Count** | **1702** | **793** | **441** | **468** |

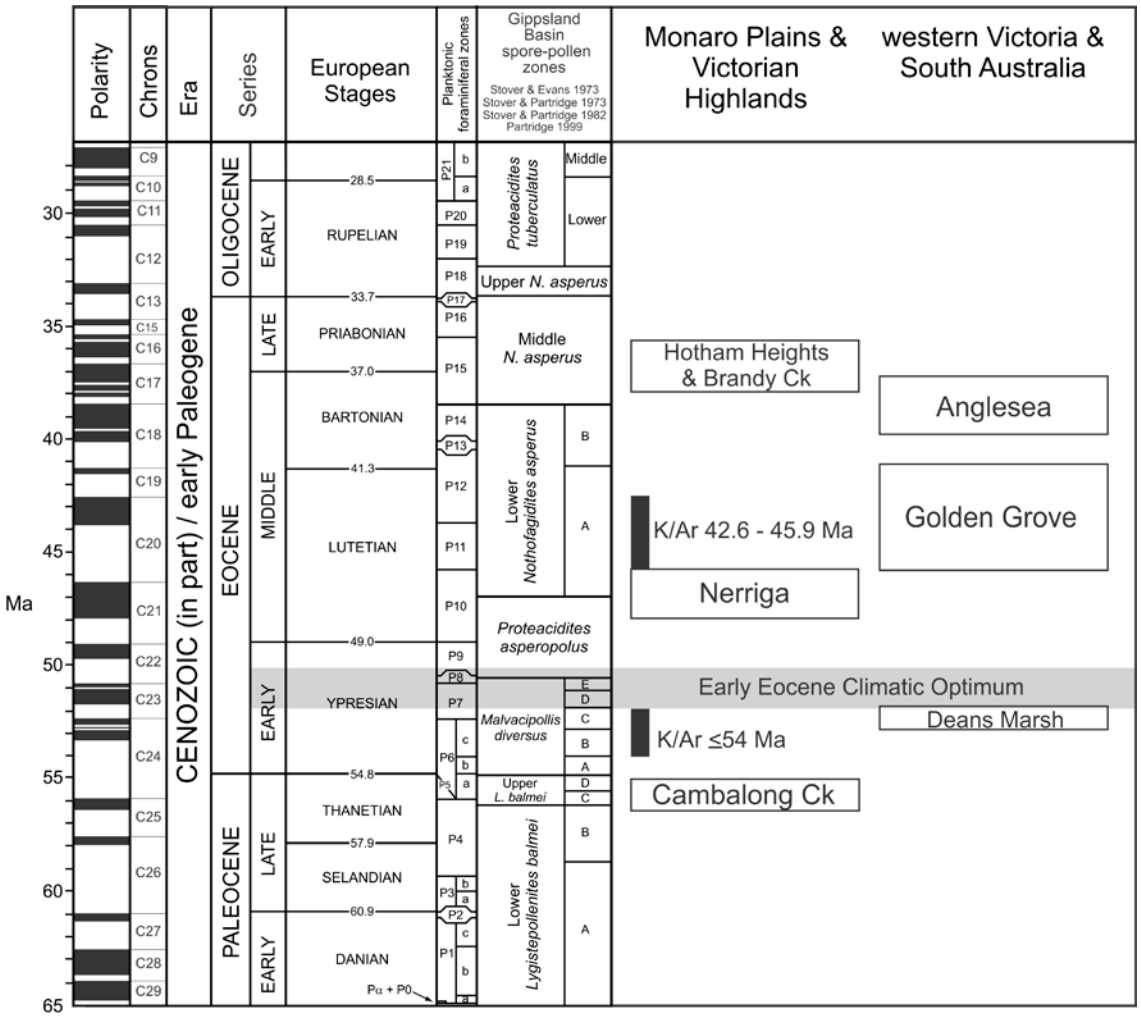



**Figure 5.1** Early Paleogene palynostratigraphic schema for southeastern Australia, showing the updated placement of Brandy Creek and Hotham Heights as late middle to late Eocene (adapted from Greenwood et al. 2003).

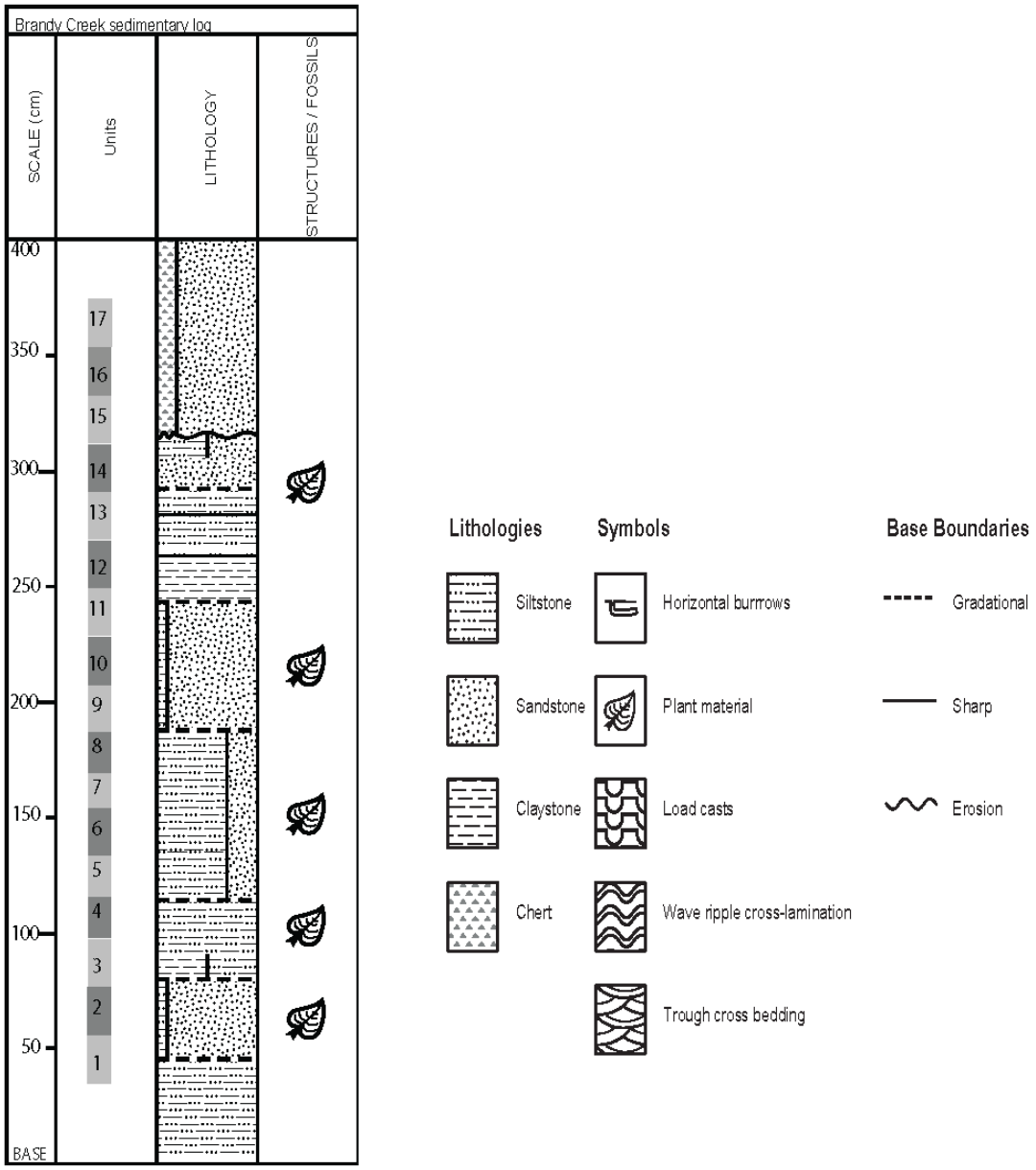



**Figure 5.2** Stratigraphic log of the Brandy Creek outcrop showing scale, units, lithology, and fossil structures present and key.

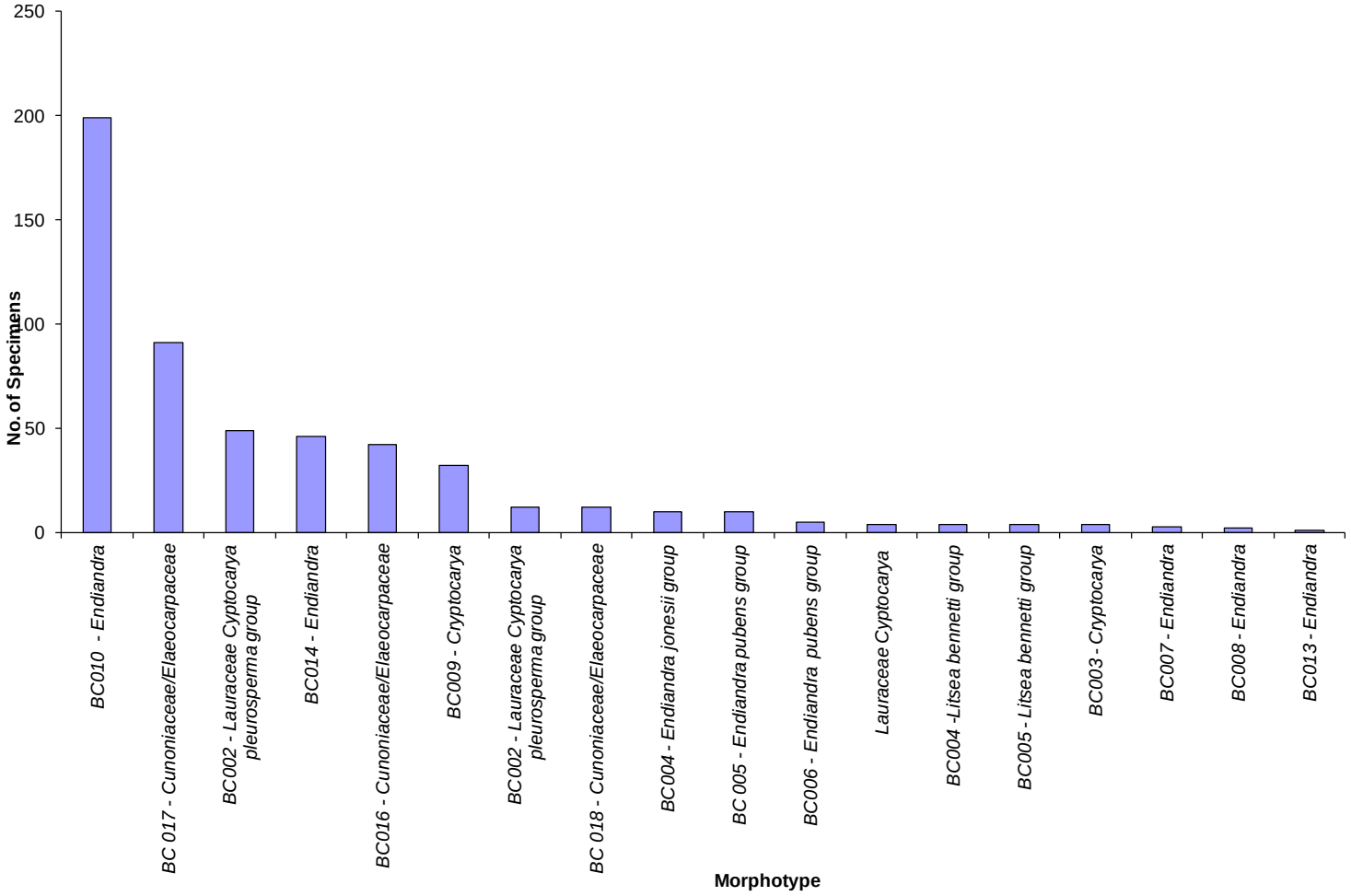



**Figure 5.3** Brandy Creek leaf morphotype rank abundance plot.

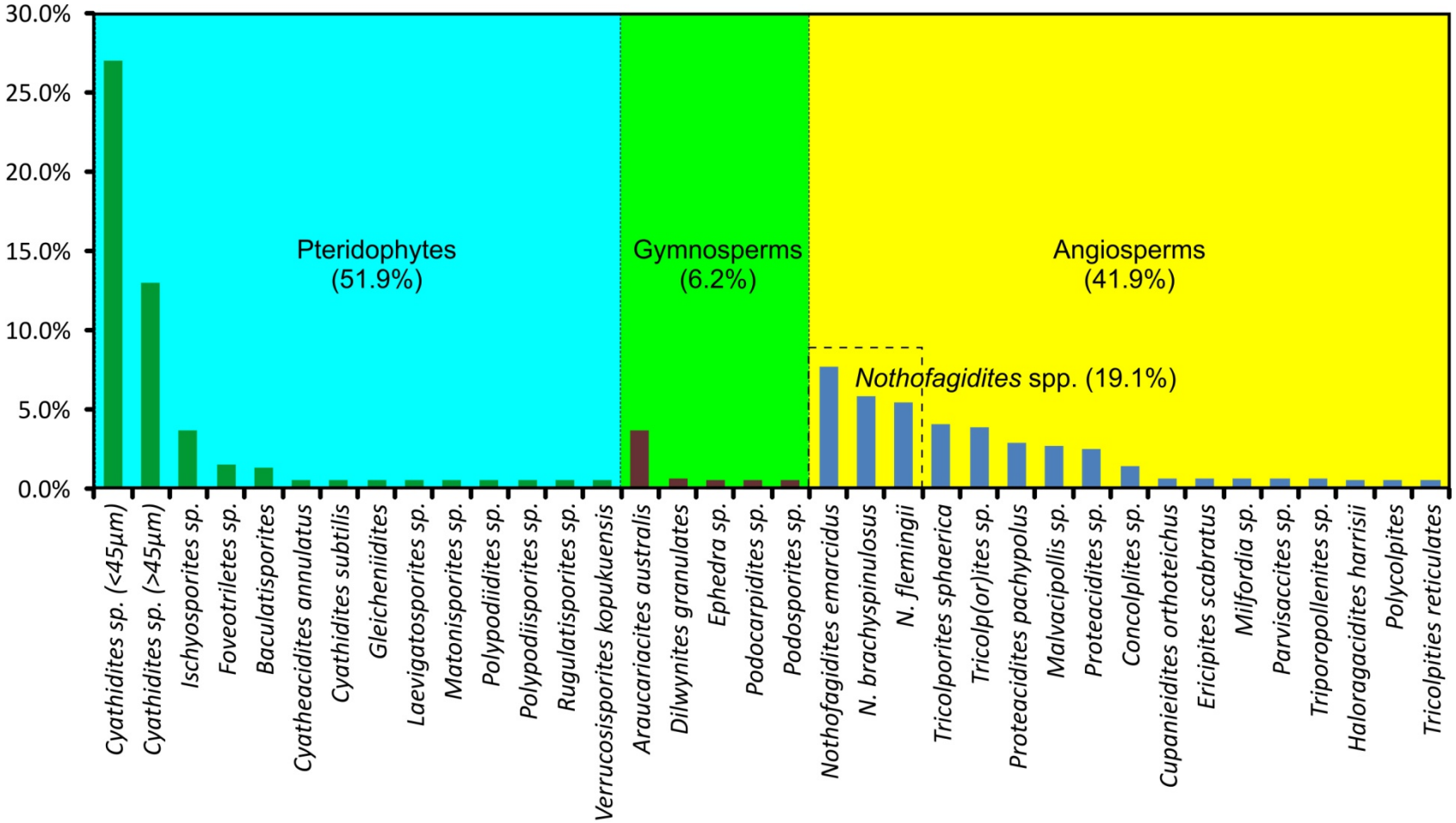



**Figure 5.4** Brandy Creek (all samples summed) palynomorph rank abundance plot with palynomorphs grouped by major plant group.

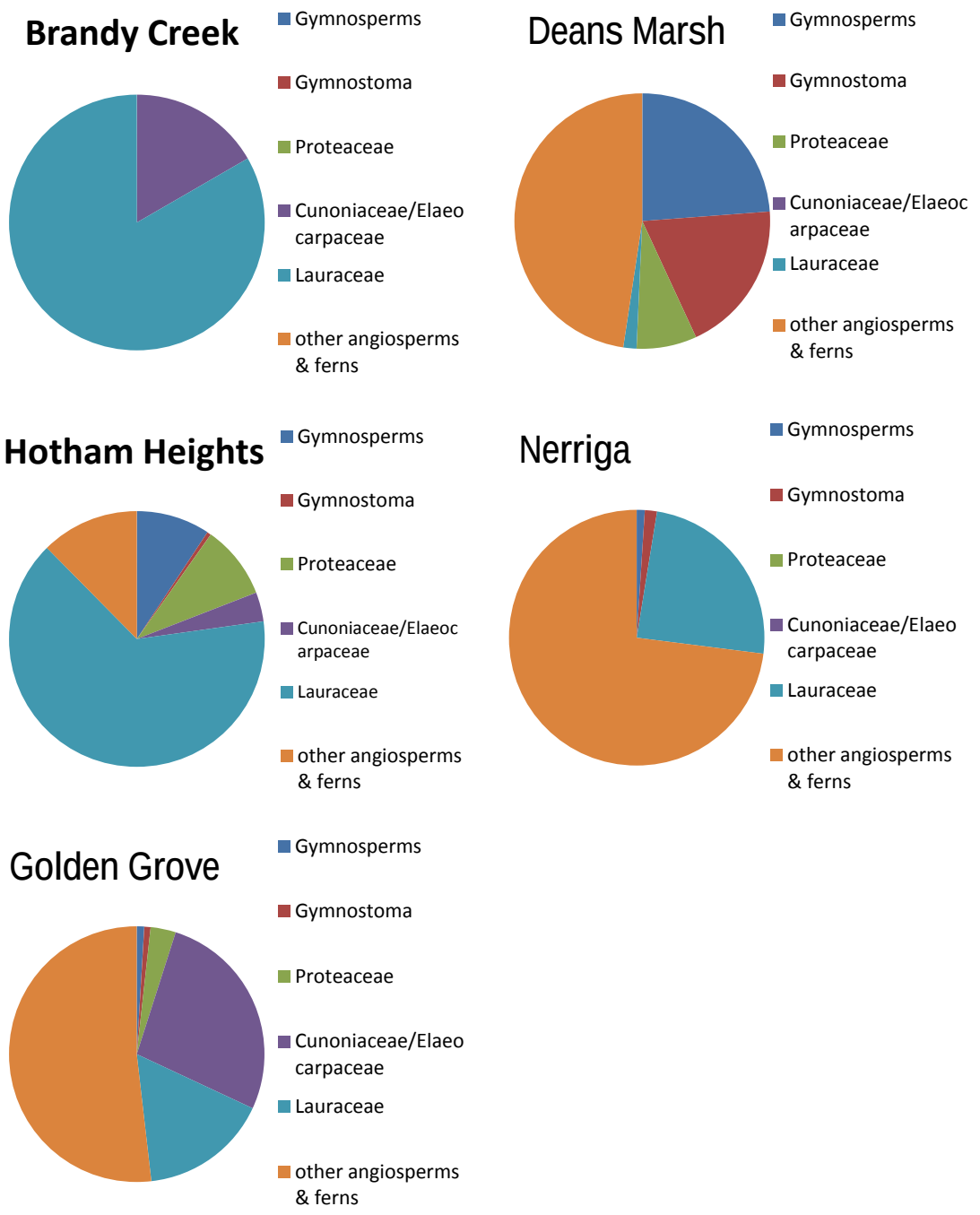



**Figure 5.5** Floristic composition of Eocene localities based on the macrofloral record (data from Greenwood et al. 2003).

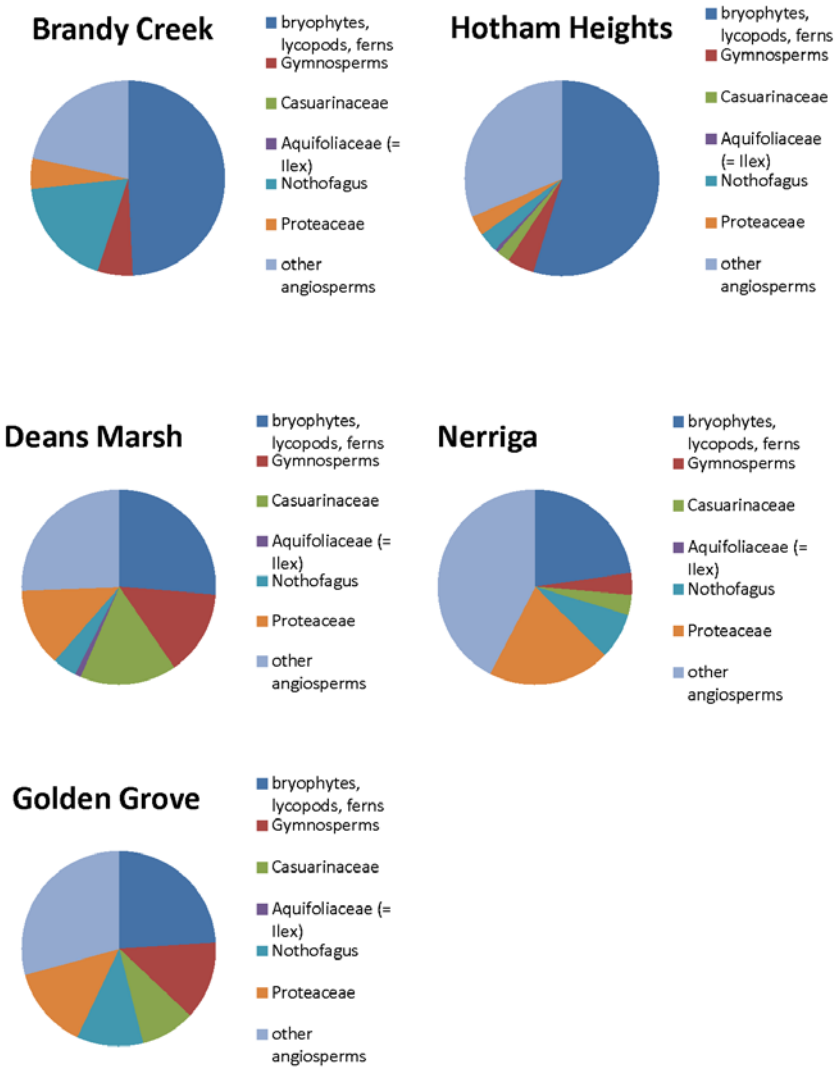



**Figure 5.6** Floristic composition of Eocene localities based on palynomorphs (data adapted from Partridge, 1998 (Hotham Heights, Dean Marsh, and Golden Grove ); Hill, 1982 (Nerriga).

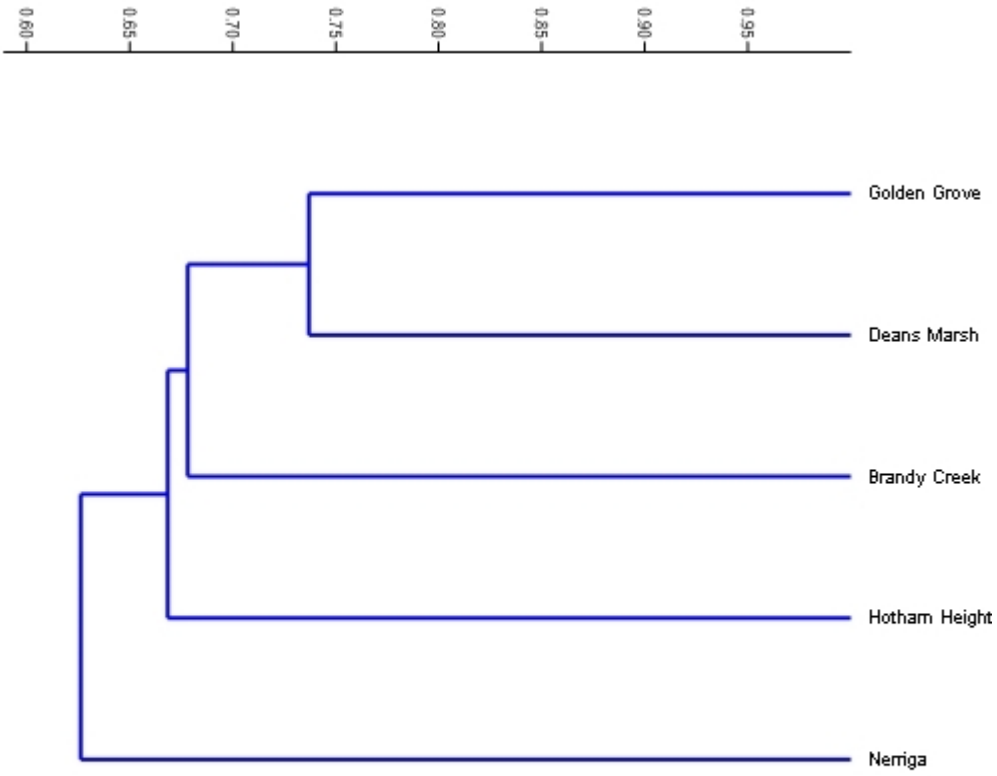
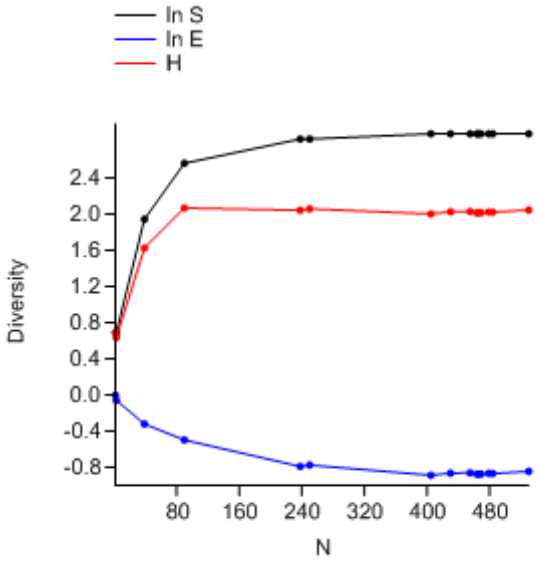
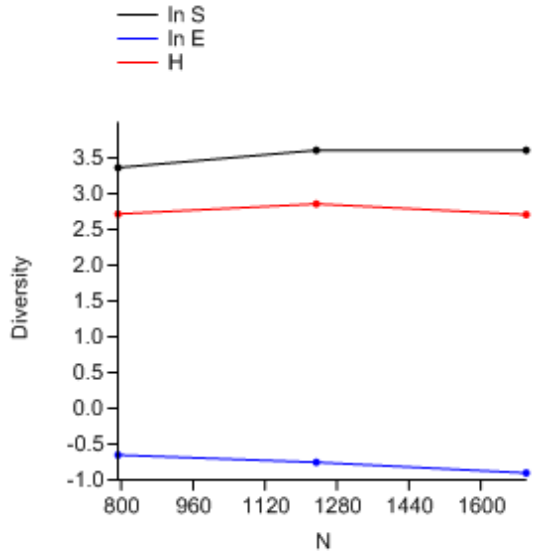



**Figure 5.7** Dendogram showing the relationship between Brandy Creek and other early and middle Eocene localities based on the presence or absence of palynomorphs using Bray Curtis association metric with group average link fusion. Numbers along the base represent dissimilarity values.

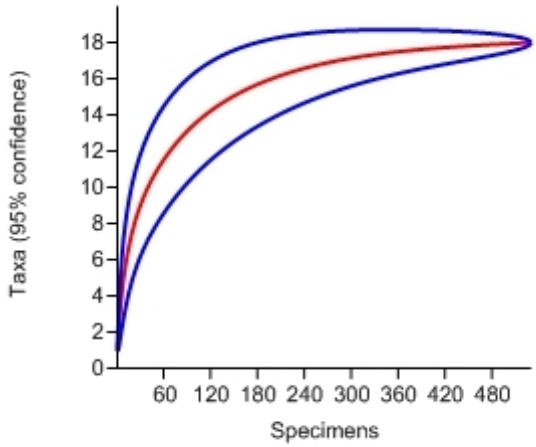



**(a)**

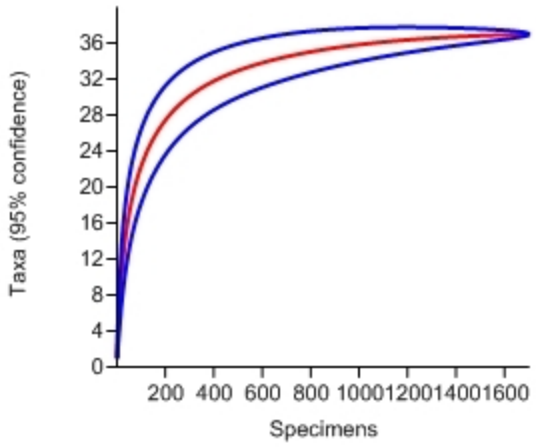



**(b)**

**Figure 5.8a –b** SHE diagram showing relationship between species abundance (ln S), diversity (ln E) and (H) evenness for (a) macro fossil and (b) pollen/spores.




**a)**




**b)**

**Figure 5.9** Rarefaction curves of summed plant leaf morphotypes (A) and palynomorphs (B) from the sampled section at Brandy Creek.

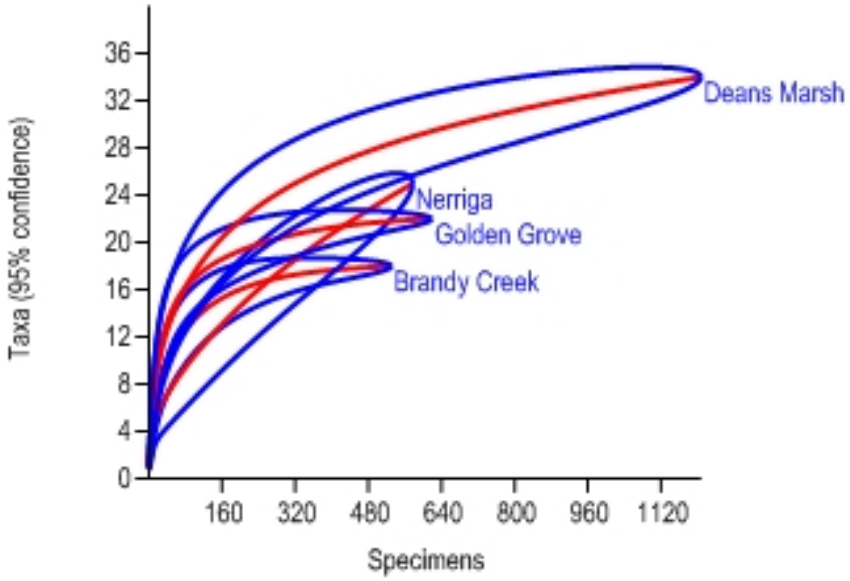



**Figure 5.10** Rarefaction curves of leaf morphotypes for Brandy Creek and other Australian Eocene localities. Data sources: compilation by D.R. Greenwood (pers. comm.), derived from; Christophel and Greenwood (1987), Greenwood (1991), Hill (1982), Rowett (1991), Rowett and Sparrow (1994), Greenwood et al. (2003), and Greenwood and Christophel (2005).

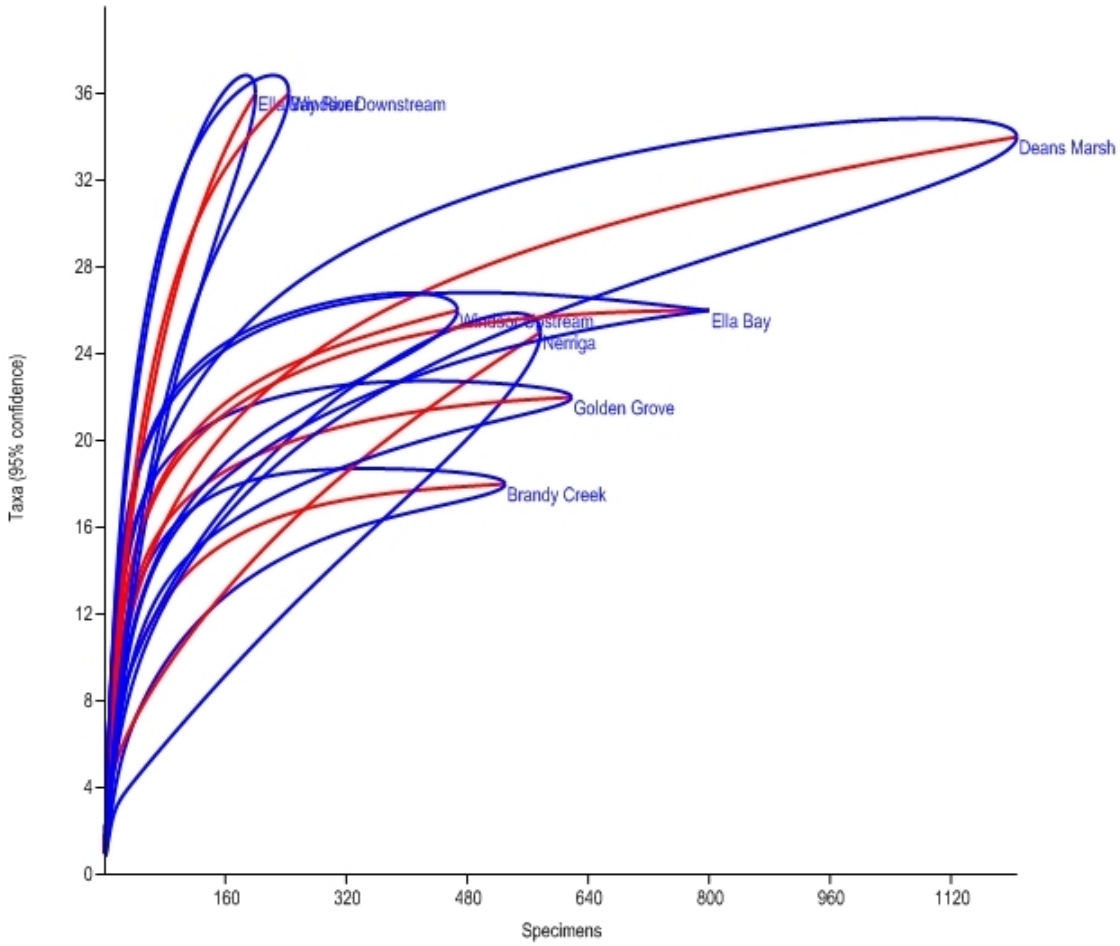
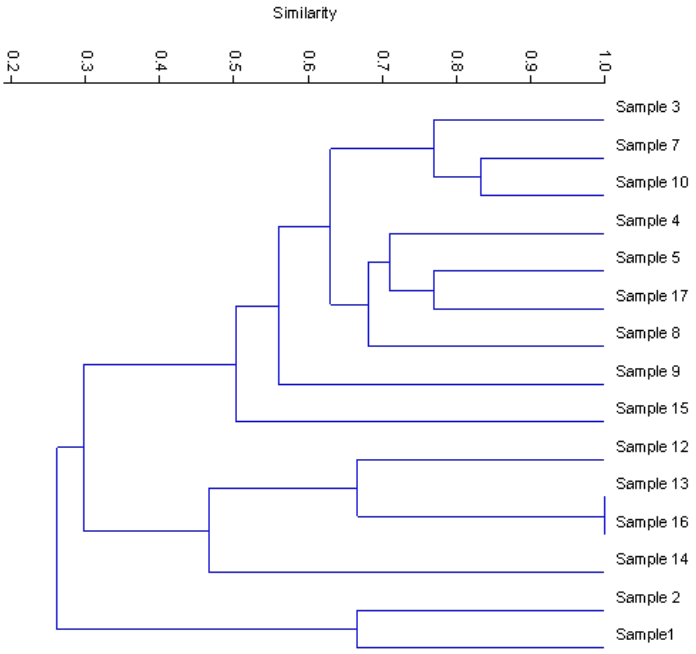
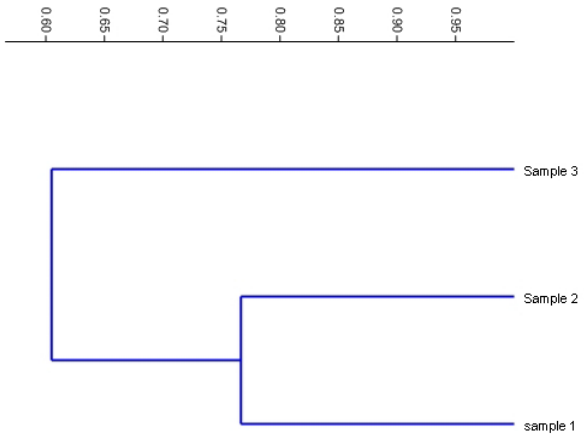



**Figure 5.11** Rarefaction curves comparing Eocene to modern tropical rainforest leaf assemblages from the Wet Tropics region of north eastern Queensland. Data from Ella Bay, Ella Bay River, Windsor upstream and Windsor Down Stream based on leaf litter counts by Greenwood (1988, 1992, 2005; & unpublished; Smith et al. 2012).




**a)**




**b)**

**Figure 5.12** (a) Dendogram showing the relationship between the samples at Brandy Creek. Beds (units) listed correspond with the stratigraphic log described in figure 5.1(b) relationship between palynomorph samples sample 1(unit 1) sample 2 (unit 3) and sample 3 (unit 11) of stratigraphic log. Level of dissimilarity is indicated on the x-axis.

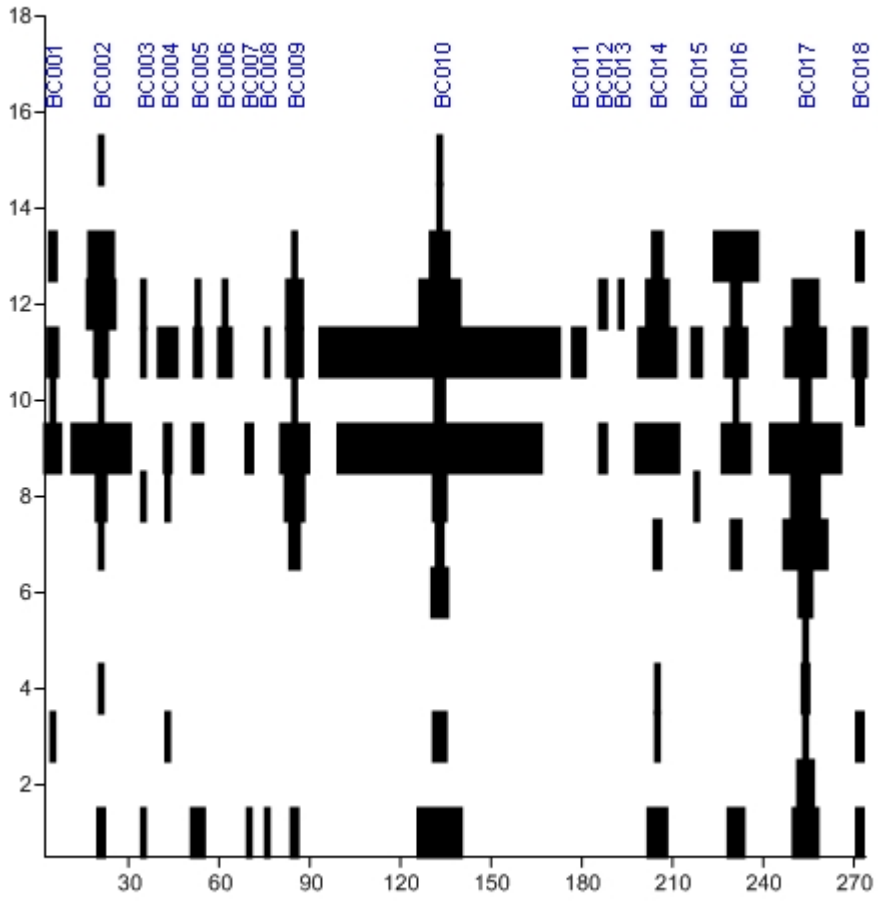



**Figure 5.13** Spindle diagram of the Brandy Creek macrofossils showing the relative contribution (width of horizontal bar) of each macrofloral taxon (leaf morphotype) with depth in the sampled section.

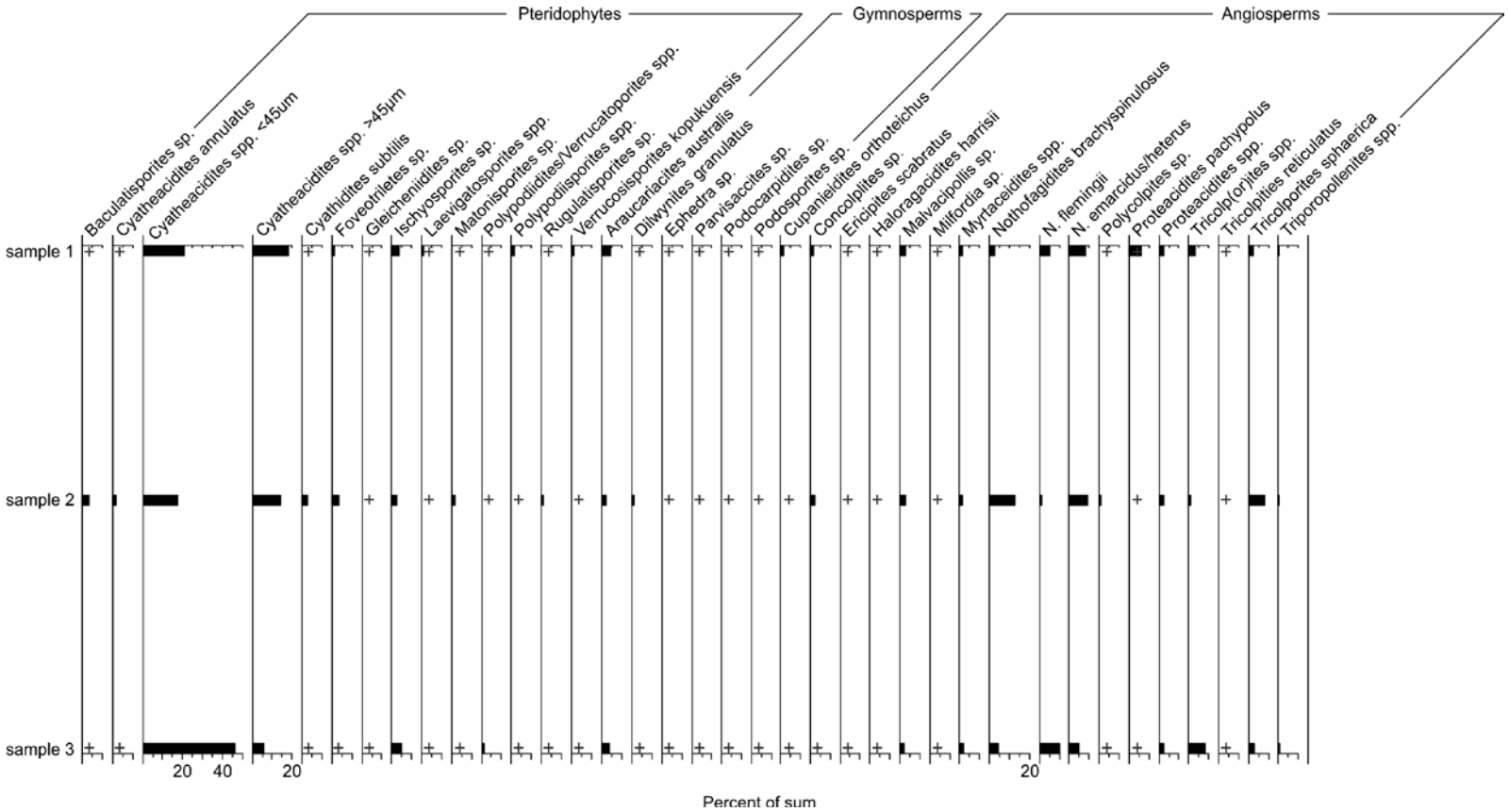



**Figure 5.14** Spore-pollen abundance diagram generated using the Tilia program (Grimm 2011) showing the palynomorph floristic composition for the three samples and differences in their abundance between the 3 samples.

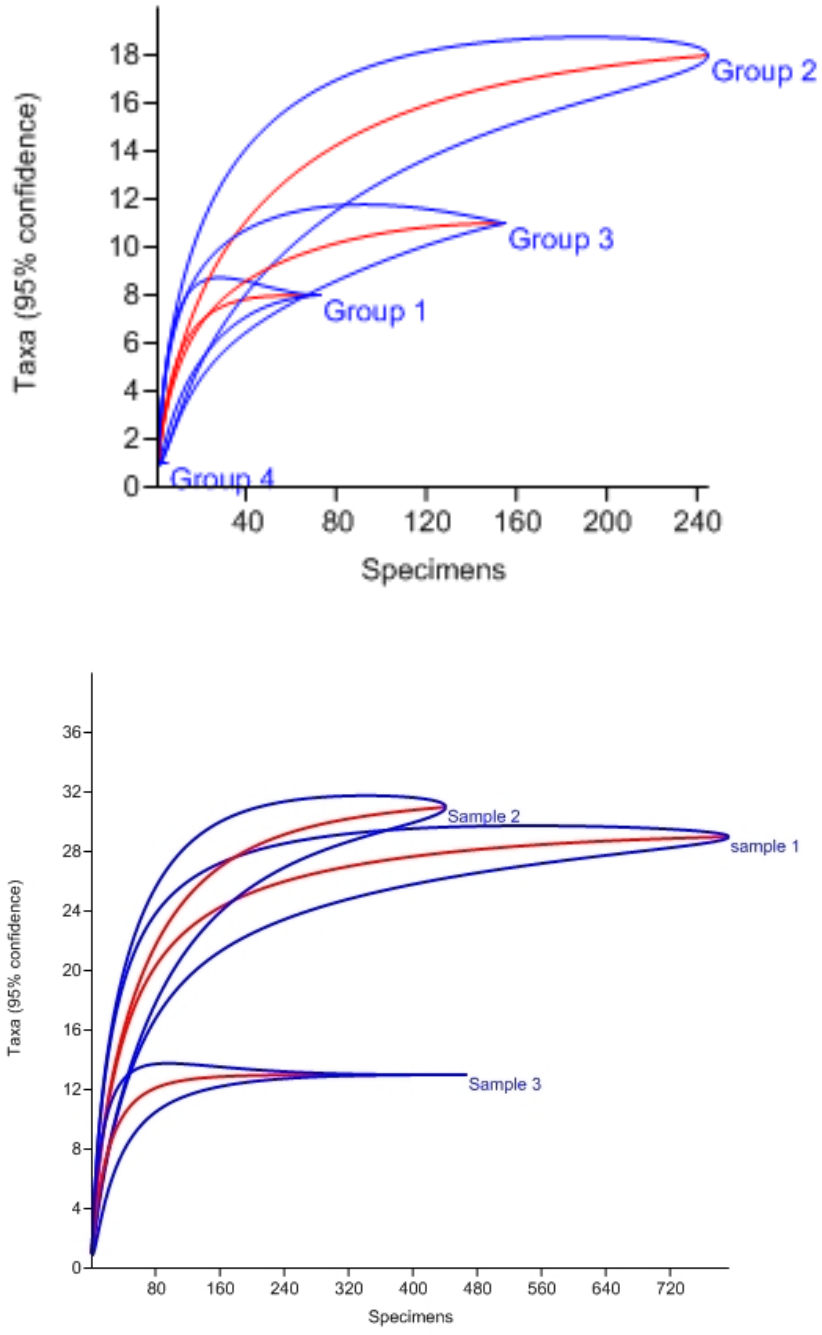



**Figure 5.15** (a) Rarefaction curves for all macrofossil samples at Brandy Creek grouped according to the cluster analysis (0.7 similarity; Fig. 5.12a). Group 1 (samples 3, 7 & 10); Group 2 (samples 4, 5 & 17); Group 3 (sample 8); Group 4 (samples 12, 13 &16). (b)Rarefaction curve for all palynomorphs samples at Brandy Creek.

# Chapter 6. Conclusions.

## 6.1 Major findings of the study.

The research presented in this thesis provides an account of the Eocene Brandy Creek fossil flora, a site located on the Bogong High Plains, in the Victorian Alps of Australia. These data are then used to reconstruct the palaeoecology and palaeoclimate of the site in the late middle Eocene to late Eocene. The Bogong High Plains today is at 1700m a.s.l. and is above the winter snowline and supports subalpine plant communities, but 40-45 million years ago, the fossil data presented in this thesis paints a very different picture. The major results of the study are:

1. Leaf macrofossil assemblages from Brandy Creek reveal 18 morphotypes that have affinity with nearest living relatives from modern Australian tropical rainforests. The Lauraceae genera *Cyptocarya, Endiandra* and *Litsea* were a major component of the Brandy Creek flora, with additional contributions by Cunonicaceae/Elaeocarpaceae. Comparison with regional floras show that Lauraceae was dominant in the landscape across south eastern Australia during the Eocene and also has a presence outside of Australia including New Zealand.

2. 36 pollen and spores species were identified at Brandy Creek representing pteridophytes (ferns and other spore-producing plants), gymnosperms (principally conifers) and angiosperms. The pollen and spores represent both a regional (e.g., *Nothofagus*) and local flora (e.g., Dicksoniaceae, Araucariaceae and Proteaceae). Comparison with Eocene localities in south eastern Australia show that these families and others were widespread across the region.

3. The two methods used in this study to reconstruct palaeoclimate at Brandy Creek are in general agreement, with Leaf Margin Analysis and Bioclimatic analysis giving a Mean Annual Temperature (MAT) of 19.7 °C and 18.7 °C respectively. Although a slightly younger site (late Eocene), the MAT at Brandy Creek is similar to other Eocene localities from the early and middle Eocene of southern Australia and New Zealand.

4. The climate profile of Brandy Creek sits within the mesothermal range of MAT 14 - 20 °C as described by Nix (1982), with the Warm Quarter Mean Temperature range (21.0 - 24.4°C) and Cold Quarter Mean Temperature range 9.0 -21°C, with a Mean Annual Precipiation estimates as 107 -320cm/yr. These mesothermal conditions are indicative of the palaeoclimate across south eastern Australia during the Eocene.

5. The presence of epiphyllous fungi at Brandy Creek and drip tips of some of the leaf macrofossils supports bioclimatic evidence of warm, wet environment with high rainfall.

6. The Brandy Creek flora is moderately diverse with 18 leaf morphotypes and 36 palynomorphs represented in the flora.

## 6.2 Further work.

No individual study can accomplish all of the goals set at the initiation of the project, and all studies uncover new questions that need to be answered. In addition, new methodologies are developed, offering additional insights but often time requiring different approaches to data gathering. This thesis reports on a study that was initiated in 2000, with a significant hiatus in the mid 2000s. Since 2000, interest in the climates of the Eocene, and in particular the warm intervals of this epoch, has increased, as has understanding of the factors driving Eocene global warmth (e.g., Huber and Caballero 2011), and the biological implications of Eocene climate (e.g., Wilf et al. 2003; Archibald et al. 2011; Smith et al. 2012). The following additional areas of inquiry are identified:

1. *Further sampling to obtain additional leaf fossils.*

A small area of outcrop was sampled as part of this study, and reported in this thesis. The proximity of the Hotham Heights locality to the Brandy Creek site, and reports of additional fossil sites in the area (Greenwood et al. 2000) imply that other outcrops exist. The Brandy Creek mine area includes additional outcrop to that sampled as part of this study. Additional reconnaissance of this area, and further sampling at the quarry site that was the source of the

fossil reported in this thesis will likely yield better quality leaf fossils (i.e., more leaves with intact lamina) and additional plant taxa.

2. *Analysis of the remaining pollen samples.*

Palynology was not considered a major part of the study, and so only limited effort was expended on this area of the study, with only 3 samples from 7 available samples counted for spore-pollen counts. This decision was made to allow continued focus on the leaf macroflora, but also in recognition that the microflora differed in only minor ways between samples dispersed vertically within the sampled section. Nonetheless, further analysis will likely yield additional palynomorph taxa if for no other reason than increased count size. The discrepancy between the original analyses of the Brandy Creek and Hotham Heights microfloras (Greenwood et al. 2003; Carpenter et al. 2004), and the Holdgate et al. (2008) analysis, suggests further exploration of the causes of this difference.

3. *Application of additional palaeobotanical climate proxies based on refined taxonomic assessment and collection of additional intact leaf fossils.*

The general fragmentary character of the leaf morphotypes collected as part of this study, restricted application in this thesis of leaf physiognomy approaches to climate reconstruction to the use of Leaf Margin Analysis as only leaf margin characters were available. Should further collecting and analysis yield a suite of intact leaves, multivariate approaches such as CLAMP become possible, offering estimation of a broader range of climate variables, as well as direct estimation of the palaeoelevation of the site (e.g., Forrest et al. 1999). Furthermore, additional sampling and taxonomic analysis will add to the potential list of NLRs for bioclimatic analysis.

## 6.3 References.

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# Appendix 1

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2003

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

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## 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.**

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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 $CO_2$. Recent studies however, suggest early Paleogene $pCO_2$ <500 ppm, concentrations similar to those of the last few decades when $pCO_2$ has been 340–360 ppm, but much lower than those determined using geochemical proxies and modeling (Royer et al., 2001). At these $pCO_2$ 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 ($7° \times 10°$ 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

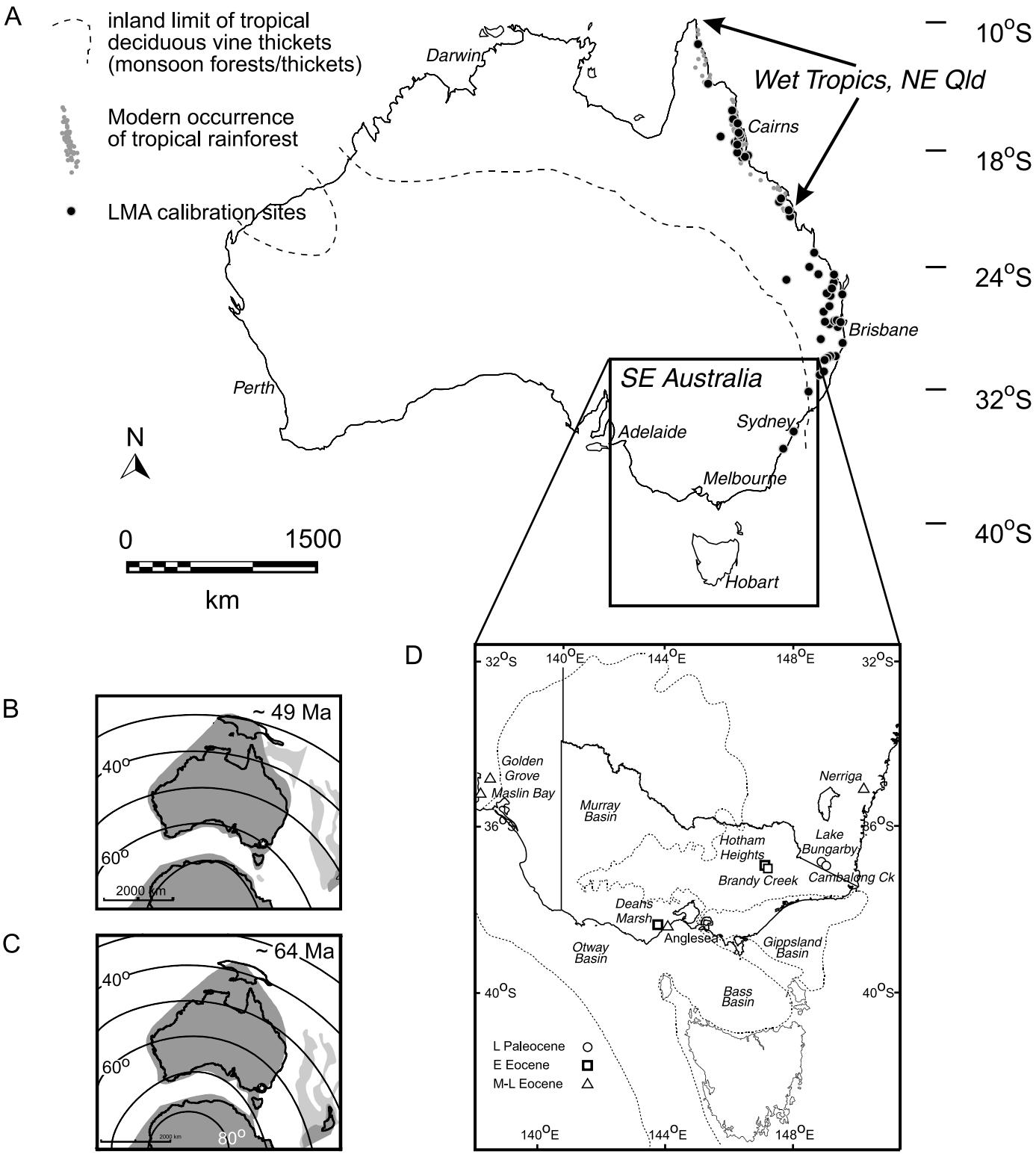


Figure 1. Location and paleogeographic setting for study area. A: Map of Australia showing location of southeastern Australia study area and other locations mentioned in the text, the modern distribution of tropical rainforests, and the location of the LMA calibration sites (Greenwood et al., 2001, personal 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 (Titringo siltstone) that crops out to the north of the Monaro Plains (Hill, 1982). Microfloras in the Titringo 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 $H_2O_2$. Ex-

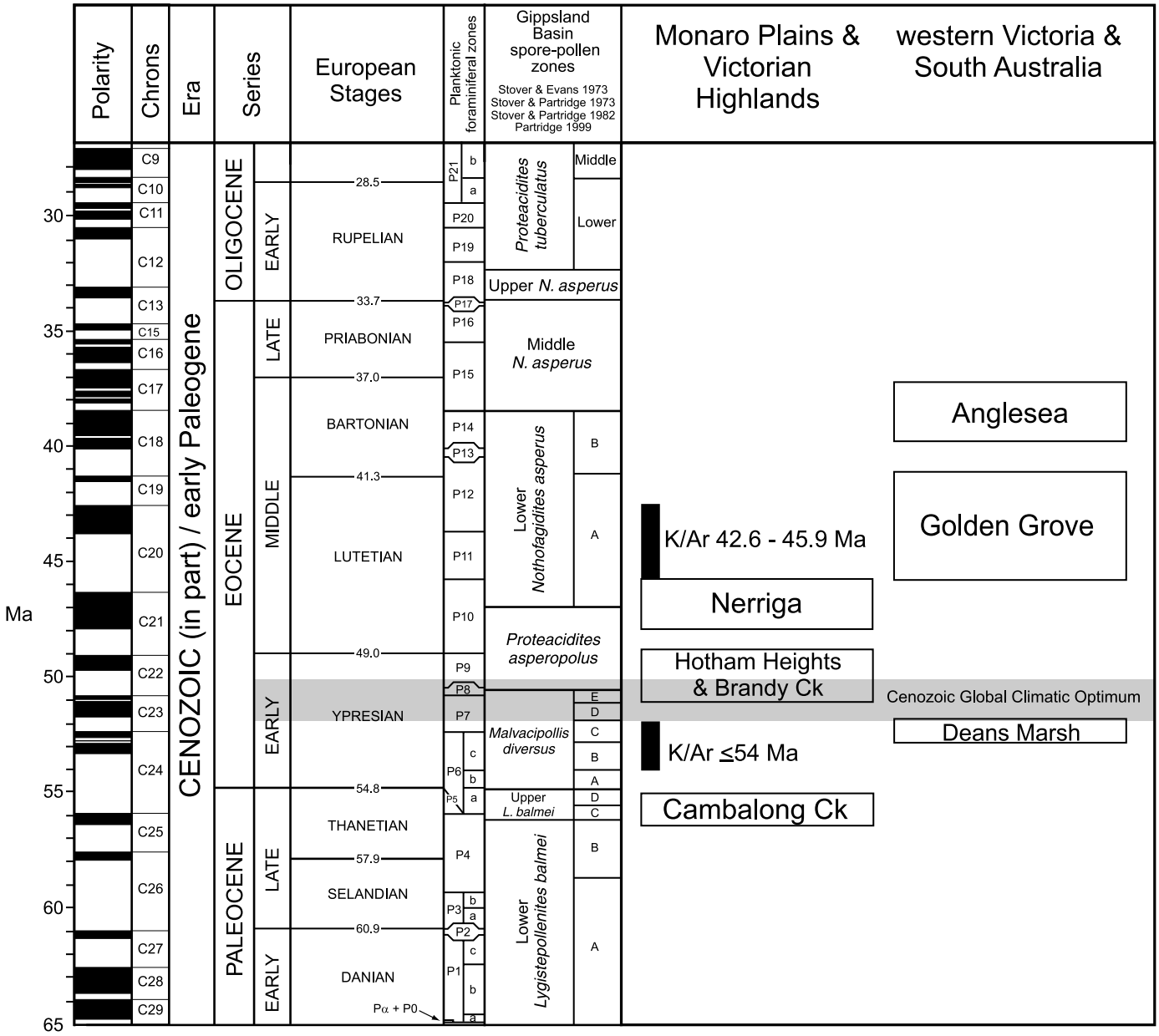


Figure 2. Early Paleogene palynostratigraphic schema for southeastern Australia showing the stratigraphic arrangement of the macrofloras discussed in the text (adapted from Greenwood et al., 2000b). Stratigraphy adapted from Macphail et al. (1994) and Chaproniere et al. (1996), to the geochronometric 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 PALYNOMORPHS 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 | *Cyathea* | | p† | p | p | p | p | p |
| Matonisporites ornamentalis | Dicksoniaceae | Dicksonia | | | p | p | | | |
| | Stangeriaceae | *Bowenia* | | | | | m† | | m |
| Phyllocladidites mawsonii | " | *Lagarostrobos* | p | p | | | p | p | p |
| *Podocarpidites* spp. | " | *Podocarpus* | p | m | p | | p | m | m |
| *Araucariacites australis* | Araucariaceae | *Agathis* | p | | m | m | p | m | m |
| " | " | *Araucaria* | p | m | | | p | | |
| Banksieaeidites arcuatus | Proteaceae | Musgraveinae | | | | | | m | m |
| *Proteacidites* spp. | Proteaceae | *Orites* | m | | m | m | | | |
| " | Proteaceae | *Helicia* | m | | m | m | | m | |
| | Elaeocarpaceae | *Aceratium* | | | m | m | | | |
| | " | *Elaeocarpus* | m | | m | m | | | |
| | " | *Sloanea* | | | | | | m | m |
| Not preserved | Lauraceae | *Beilschmiedia* | m | | m | m | | m | m |
| " | " | *Cryptocarya* | m | m | m | m | m | m | m |
| " | " | *Endiandra* | m | m | m | m | m | m | m |
| " | " | *Litsea* | m | | m | m | m | | m |
| Haloragacidites harrisii | Casuarinaceae | *Gymnostoma* | p | m | p | m | m | m | m |
| | Ebenaceae | *Diospyros* | | | | | m | m | m |
| | Grossulariaceae | *Quintinia* | | | | | | | m |
| Nothofagidities heterus-emarcidus | Nothofagaceae | *Nothofagus* sg *Brassospora* | p | p | p | | p | p | p |
| N. asperus | " | *Nothofagus* sg *Lophozonia* | | | | | | p | p |
| | Eucryphiaceae | *Eucryphia* | m | | | | | | |
| Cupanieidites orthoteichus | Sapindaceae | Cupanieae (aff. *Cupaniopsis*) | | p | | p | p | p | p |
| *Ilexpollenites* sp. | Aquifoliaceae | *Ilex* | p | p | p | p | | | |
| | Sterculiaceae | *Brachychiton* | | | | | 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 vegetational 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 (*Haloragicidites 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).

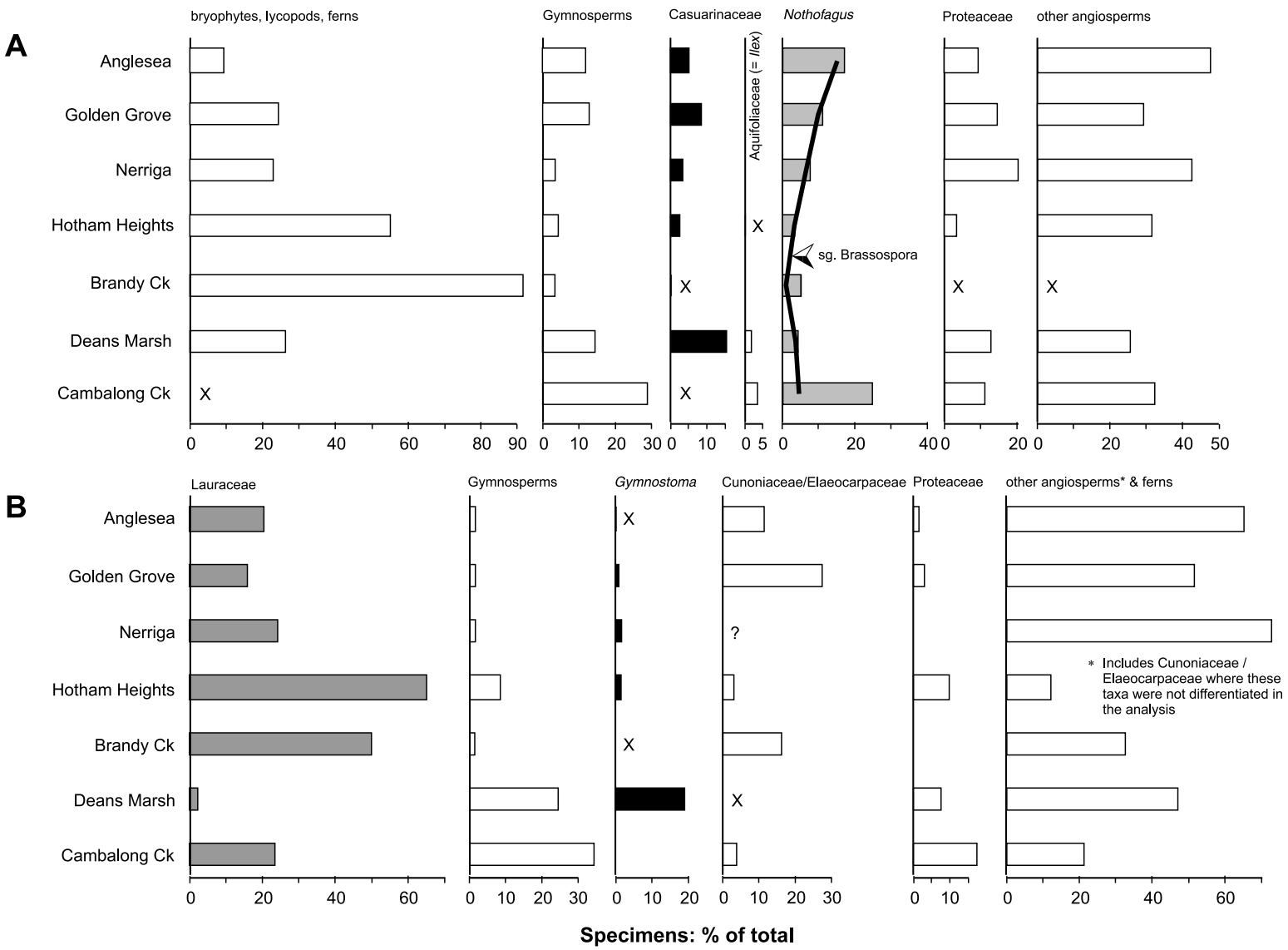


Figure 3. Changes in the relative abundance (spore-pollen grains, and macrofloral specimen counts) of the principal taxa for southeastern Australia over the late Paleocene to middle Eocene, based on microfloras (A) and macrofloras (B) from the fossil floras. *Nothofagus* sg. *Brassospora* differentiated 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), Keefe (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 *Acmopyle, 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.

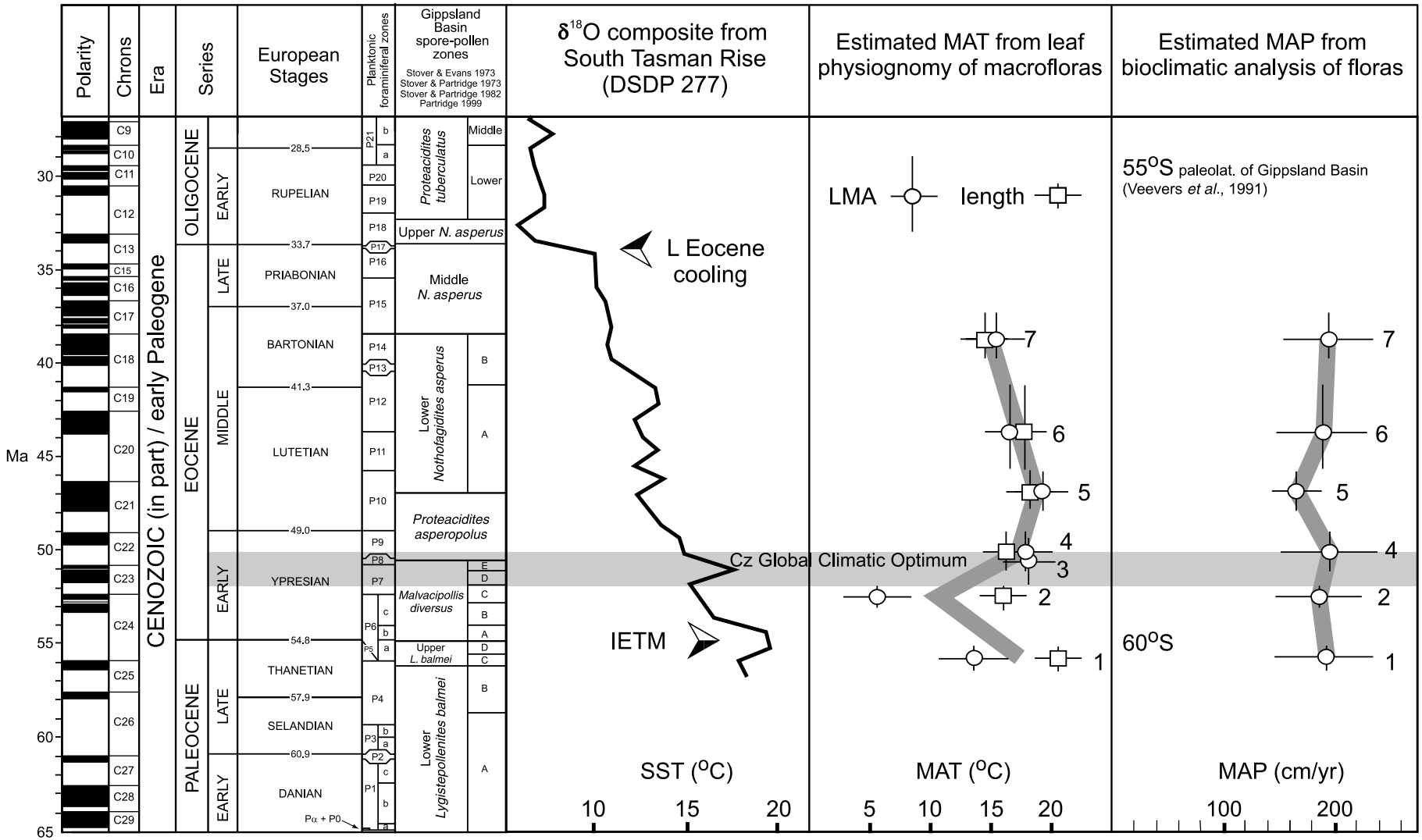


Figure 4. Summary chart of climate change over the early Paleogene for southeastern Australia. Sea surface temperatures for the South Tasman Rise (Shackleton and Kennett, 1975, diagrammatic only, adjusted to Berggren et al., 1995, time scale) are given to show the regional expression of the global Paleogene 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

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

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

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

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

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

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

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 Christophel (2003) found that leaf size and the proportion of dicot species with entire leaf margins for southeastern Australia late Paleocene to middle Miocene florasvaried 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 | 20.4–24.3 | 12.6–17.6 | 155–240 | 14–31 | 51–93 |
| | (18.5) | (22.4) | (15.1) | (198) | (23) | (72) |
| Deans Marsh (11) | 16.9–20.6 | 21.5–24.7 | 13.3–18.2 | 146–226 | 14–29 | 51–88 |
| | (18.8) | (23.1) | (15.7) | (186) | (21) | (70) |
| Hotham Heights (16) | 16.8–21.3 | 20.9–25.1 | 13.1–18.3 | 150–195 | 13–28 | 54–101 |
| | (19.0) | (23.0) | (15.7) | (240) | (21) | (77) |
| Brandy Creek (14) | 17.2–22.1 | 20.8–25.2 | 12.9–18.5 | 148–234 | 14–30 | 53–98 |
| | (19.6) | (23.0) | (15.7) | (191) | (22) | (76) |
| Nerriga (14) | 16.8–19.4 | 21.3–23.4 | 12.9–15.9 | 143–190 | 13–23 | 54–75 |
| | (18.1) | (22.3) | (14.4) | (166) | (18) | (64) |
| Golden Grove (15) | 16.8–21.1 | 21.0–24.9 | 12.7–18.1 | 148–231 | 13–30 | 54–95 |
| | (18.9) | (23.0) | (15.4) | (190) | (22) | (74) |
| Anglesea (17) | 17.3–21.2 | 21.1–24.6 | 12.8–17.8 | 153–237 | 15–32 | 59–98 |
| | (19.3) | (22.8) | (15.3) | (195) | (23) | (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; CQMT—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 proportion 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 (*r*) | % spp. no teeth (*P*) | Mean length (*ML*, 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 growing 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 ±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).

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# Cenozoic uplift history of the Southeastern Highlands, constrained by palaeobotanical and geomorphological analyses of the Bogong Plateau, Victoria

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On the high elevation, low relief Bogong plateau, within the southeastern Highlands in Victoria, well-preserved diverse macrofloras and microfloras have been recovered from early to late Eocene sediments at two sites underlying Eocene-Oligocene basalts. Estimates of mean annual temperature (MAT) were made from the floras at each site, using the overlap of climate envelopes of the nearest living relatives of multiple fossil taxa, and the proportion of non-toothed rather than toothed leaf margins of all fossil leaves. The most likely scenario is an Eocene MAT at Bogong Plateau of 18°C; from this, the Eocene palaeoelevation of the plateau, calculated using the 'lapse rate' method, was about 800 m (700-1000 m lower than at present). This is consistent with the cloudy mesothermal montane environment indicated by the abundance of tree ferns in the Bogong Plateau floras. The palaeoelevation was also reconstructed from the elevation of the base of the basalt and the sub-basaltic sediments, along with the maximum elevation of peaks in the area and the identification of the Eocene river level from fluvial terraces. The results show that in the Eocene, the Bogong Plateau had a low relief of 100-200 m and lay at an elevation of around 700 m, with peaks to 900 m. Therefore both the palaeobotanical and geomorphological evidence indicate that there was substantial post-Eocene uplift of the Southeastern Highlands by 700-1000 m, accompanied by disruption and elevation along faults. This uplift probably coincided with a major period of tectonism that affected most of southern Victoria in the Late Miocene – Early Pliocene. The initial uplift of the Southeastern Highlands occurred in the mid-Cretaceous, so the Neogene event proposed here involves additional uplift of an already elevated plateau, in contrast to earlier suggestions that a single event, the Kosciuszko Uplift, created the Southeastern Highlands during the Plio-Pleistocene.

KEY WORDS: palaeoelevation, Eocene, Australia, palaeobotany, uplift, palaeoclimate.

## INTRODUCTION

The Australian Alps are a dominant feature of the present landscape of southeastern Australia. They represent the highest part of the Southeastern Highlands, and contain all mountains in Australia over 1650 m above sea level, including Australia's highest point, Mount Kosciuszko at 2228 m asl. This elevated region extends from southeastern New South Wales well into eastern Victoria, and can be divided into two broad areas: the subdued topography of the high plains, and the deeply incised valleys of the northern and southern slopes. The high plains comprise a number of separate small plateaux and broad ridges with a low undulating relief of only 100–250 m, and usually lie at elevations of over 1200 m. Alpine grasslands, snow-

covered in winter, cover the highest areas, with some development of peat swamps; immediately below the tree line are stunted snow gums (*Eucalyptus pauciflora*).

In Victoria, the largest of the high plains is the Bogong–Cobungra–Dargo plateau, hereafter called the Bogong Plateau, which appears to have been a single extensive surface before dissection by rivers and minor disruption by Tertiary faulting (Neilson 1962; Crohn 1949; Orr 1999). This high plains area rises to over 1700 m at its northern margin, which includes Mount Hotham and Mt Bogong, Victoria's highest point at 1986 m, and slopes gradually to the south. It has developed on Ordovician sediments and high-grade metamorphics, with a capping of Eocene to Oligocene basaltic lavas (Older Volcanics; Wellman 1974).

## UPLIFT HISTORY OF THE SOUTHEASTERN HIGHLANDS

The creation of the Southeastern Highlands is believed to date to the mid-Cretaceous (90±5 Ma), when subduction along the eastern margin of the Australian Plate ceased (Gallagher *et al.* 1994; Veevers 2000), and a major phase of uplift and denudation caused cooling of the upper crustal rocks, recorded in apatite fission track data from throughout southeastern Australia (Dumitru *et al.* 1991; Kohn *et al.* 1999). The high plains have frequently been interpreted as remnants of an (Early) Mesozoic peneplain/palaeosurface uplifted at this time (e.g. Gregory 1903; Hills 1975; Hill 1999). The fission track studies conflict strongly with this hypothesis, and instead suggest that the high plains underwent at least 1.5 km of denudation in the mid-Cretaceous, so that the present land surface of the high plains was created in the Paleogene (O'Sullivan *et al.* 1999). The fission track results need further reconciliation with the geomorphological interpretations, as it is possible that the amount of denudation calculated from the fission track data has been overestimated (Joyce *et al.* 2003).

During the Cenozoic, there was additional uplift and denudation of the Southeastern Highlands and this may have been responsible for much of the dissection of the high plains surface, forming the adjacent deeply incised valleys. Fission track data from Mt Feathertop show that rocks now at the surface cooled rapidly between about 70 Ma and 50 Ma (O'Sullivan *et al.* 1999), and this was interpreted as indicating that Mt Feathertop underwent 1–2 km of rapid denudation in the Paleogene, so that the present surface was not exposed until some time after the Eocene, when the basalts covering the adjacent high plains were erupted. Periods of uplift in the late Paleogene to late Neogene have also been proposed (e.g. Jones & Veevers 1982; Ollier 1986; Ollier & Pain 1994). The Gippsland Basin, lying immediately to the south of the uplands, does not record a major influx of sediment,

particularly coarse material, until the Pliocene-Pleistocene, when the Haunted Hills Formation was deposited (Jenkin 1988). This has been attributed by some geomorphologists (Andrews 1911; Brown 1969; Jenkin 1988) to a major Plio-Pleistocene uplift of the highlands called the Kosciuszko Uplift, although the relative importance of this event is now disputed (e.g. Hill 1999). Substantial Late Miocene - Pliocene uplift occurred in the Victorian Southern Uplands (Joyce *et al.* 2003), but the effect of this on the Southeastern Highlands is uncertain. Thus there is little agreement on the amount and timing of uplift of the high plains.

To constrain the Cenozoic history of the Southeastern Highlands, two additional lines of evidence are available. Firstly, Eocene-Oligocene macrofloras are known from multiple sites in sub-basaltic sediments on and near the Bogong Plateau, particularly near Mt Hotham (Greenwood *et al.* 2003; Carpenter *et al*. 2004). Palaeobotanical methods have been used to reconstruct the palaeoelevation of macrofloral and microfloral sites and resolve questions on the timing and rate of uplift of the Rocky Mountains and the Andes (Gregory & Chase 1992; Gregory-Wodzicki *et al.* 1998; Gregory 2000; Smith *et al*. 2009). Applying similar methods to macrofloras from the Bogong Plateau will provide insight into the palaeoelevation of this area in the mid-Tertiary, placing constraints on the timing and rate of uplift of the area that are truly independent of the geomorphological evidence.

Secondly, two geomorphic studies of the Bogong Plateau have provided detailed understanding of the relationship between the drainage evolution and the amount of fault movement (Orr 1999; Holdgate *et al*. 2008), and the resulting interpretations of palaeoelevation can be cross-checked against the palaeobotanical conclusions to resolve the conflicting hypotheses on the age and nature of uplift of the high plains.

Furthermore, because the high plains around Mt Hotham and Mt Kosciuszko are the only truly alpine areas in southeastern Australia (Fig. 1A), and lie above the climatic treeline (i.e. warmest monthly mean temperature <10°C), they support a biota that is unusual in the Australian context as it is adapted to seasonal freezing, e.g. the winter hibernating mountain pygmy possum, *Burramys*. The uplift history of the high plains is intrinsically linked to the origin of this biota, as without the mountains there could be no alpine climate (Costin *et al.* 2000), and the geomorphic evolution of extensive mountain areas like the Southeastern Highlands probably also substantially influenced the regional climate, as has been shown in the Bolivian Andes (Gregory-Wodzicki *et al.* 1998).

## PALAEOELEVATION OF BOGONG PLATEAU FROM FOSSIL FLORAS

### Fossil floras

Plant fossils were collected at two localities on the Bogong Plateau (Fig. 1); a road cut at Hotham Heights (elevation 1783 m), and at the Brandy Creek mine (~1500 m). At both sites small exposures of fluvio-lacustrine Paleogene sand/siltstones unconformably overlie weathered, steeply-inclined Palaeozoic strata and are capped by basalt (Fig. 2). At Brandy Creek Mine the Paleogene sediments are essentially flat lying, however at Hotham Heights the sediments have a strike of 150º and dip at 15º west. The fossiliferous sediments sampled for macroflora at Brandy Creek Mine crop out 100 m west of the site sampled for microflora by Holdgate *et al*. (2008), and consists of unlithified carbonaceous mudstones. The sediments at both localities contain abundant fossil leaves, with >30 dicot taxa recognised at each site from compression leaf fragments (Keefe, 2001; Greenwood *et al.* 2003; Carpenter *et al.* 2004). Leaf fossils were freed from the mudstone by maceration with dilute $H_2O_2$ and cleaned with HF before mounting; they were identified to genus level using published accounts of diagnostic cuticle characters for extant Australian plant families (e.g. Carpenter *et al.* 2004).

The Gippsland Basin zonation includes independent age dating based on marine microfossils and radiometric dates, and has become the primary basis for dating terrestrial sediments in southeastern Australia (Macphail *et al.* 1994; Partridge 1999; Holdgate & Clarke 2000). The least weathered basalts near Mt Hotham have been K/Ar dated as Late Eocene to Late Oligocene (36.3 ± 0.6 and 33.1 ± 0.8 Ma; Wellman 1974). The underlying sediments at Hotham Heights and Brandy Creek contain somewhat older early Eocene microfloras assigned to the upper *Malvacipollis diversus* Zone to lower *Proteacidites asperopolus* Zone within the palynological zonation developed for the adjacent Gippsland Basin (Greenwood *et al.* 2003; Carpenter *et al.* 2004). An alternative late Eocene age assignment is given to the Hotham Heights sediments based on correlation with the Middle *Nothofagus asperus* Zone, consistent with the older age noted for the overlying basalts (Holdgate *et al*. 2008). Based on the photo of the Brandy Creek site provided by Holdgate *et al*. (2008) however, their late Eocene microflora was sampled from a different location and lithology to the Brandy Creek Mine macroflora, so reassignment of this flora to a late Eocene age is considered tentative in this report.

For the palaeoelevation analysis, the Bogong Plateau Eocene macrofloras must be compared to a flora of the same age from a nearby locality known to have been close to sea level at the time. For this purpose and in recognition of the two alternative age assignments,

the Regatta Point and Anglesea floras were chosen (Fig. 1). The Regatta Point flora contains the mangroves *Nypa* (Arecaceae) and *Brownlowia*, and hence grew at sea level, and the microflora at the site belongs to the early Eocene Upper *M. diversus* Zone (Pole & Macphail 1996; Pole 200?). The Anglesea flora outcrops in the Alcoa open-cut coal mine and has been dated to the Bartonian stage (i.e., late Middle Eocene) based on correlation with the Middle *N. asperus* Zone (Holdgate & Clarke 2000).

**Palaeoelevation analysis**

Mean annual temperature (MAT) varies with elevation. As a result, the palaeoelevation of an inland site with known MAT (e.g. by macrofloral analysis) can be calculated by comparison with a nearby coeval site at sea level, also with known MAT, using the 'lapse rate' method (Meyer 1992):

$$\text{Palaeoelevation}_{\text{inland site}} = (\text{MAT}_{\text{sealevel site}} - \text{MAT}_{\text{inland site}}) / \text{lapse rate} \quad (1)$$

where lapse rate is the change in temperature with elevation (°C / 100 m). This is not a 'lapse rate' in the meteorological sense (Forest *et al.* 1995). If the sea level site is no longer at sea level, then its present elevation must be subtracted from the calculated palaeoelevation of the inland site.

Three corrections must be applied to derive palaeoelevation by this method (Meyer 1992; Gregory & Chase 1992): continentality, elevated base level and latitude. Continentality refers to the fact that the altitudinal temperature gradient is less in continental interiors than at coastlines (Meyer 1992; Greenwood & Wing 1995). As a result, inland and coastal sites at the same latitude and similar elevation will have different MAT values. Furthermore, in continental interiors the base level (lowest elevation) is generally elevated above sea level, and this can also decrease the lapse rate. The global mean lapse rate is 0.59°C / 100 m ± 0.1°C (Meyer 1992), but the western North American 'mean regional average' lapse rate is only 0.3°C / 100 m (Wolfe 1992); this shallower temperature gradient reflects the combined effects of continentality and an elevated base level. Finally, if the sea level and inland sites being compared are not close together, a latitudinal correction must be applied, because MAT varies with latitude as well as elevation.

All three sites considered in this study are within 150 km of the coast, and none are on the inland side of the drainage divide, so continentality and base level are unlikely to influence the lapse rate. The present lapse rates for the Mt Hotham and Mt Kosciuszko areas, calculated from the MAT and elevation for local meteorological stations, are very similar (0.52°C / 100

m and 0.63°C / 100 m respectively; Fig. 3A). The mean rate of 0.58°C / 100 m for southeastern Australia approximates the global mean of 0.59°C / 100 m (Meyer 1992).

Because the sea level site (Regatta Point) is 5.3° south of Bogong Plateau, a latitudinal correction is required. The latitudinal temperature gradient for eastern Australia is 0.47°C / 1° latitude, using data from meteorological stations at <200 m a.s.l. elevation throughout the region (Fig. 3B). Global meridional temperature gradients were shallower in the early Eocene than at present (Greenwood & Wing 1995), but the globally averaged gradient was 0.4-0.6°C / 1° latitude, similar to that currently observed in eastern Australia. No latitudinal correction is required for the Anglesea flora.

**Palaeotemperature analysis**

Two palaeobotanical methods for estimating MAT were applied in this study. Firstly, in bioclimatic analysis the palaeoclimate is inferred from the climate preferences of the nearest living relative of each fossil taxon, using either the 'threshold approach' based on key plant taxa (e.g. the 'palm line' in Greenwood & Wing 1995) or the 'assemblage approach' where the climate envelope of a fossil site is calculated from the overlap of the climate profiles for multiple fossil plant taxa (e.g. Kershaw 1996; Greenwood *et al.* 2003, 2005). A library of 'climate profiles' for present-day Australian and some New Guinea rainforest genera has been developed that encompasses the nearest living relatives (i.e. 'NLRs') of important Australian Paleogene plant taxa (Kershaw 1996; Moss & Kershaw 2000; Gallagher *et al.* 2003; Read *et al*. 2005). The mean annual temperature and error for each site were calculated from the climate profiles of the NLRs using the method of Greenwood *et al*. (2003, 2005). Using key taxa (e.g. Greenwood & Wing 1995) provides only threshold values (i.e. 'no colder than').

Secondly, MAT can be calculated from leaf physiognomy. Two calibrations were used, both based on leaf margin analysis, where the percentage of woody dicot species in the flora is determined by the proportion of non-toothed rather than toothed leaf margins (leaf margin proportion or '*LMP*' as a percentage): (i) calibrated for modern Australian vegetation (Equation 2), and (ii) a calibration based on the CLAMP 'warm sites' dataset based on 114 modern forest sites worldwide (Equation 3).

$$MAT = 27.0 \cdot LMP - 2.12 \text{ (Greenwood } et\ al. \text{ 2004)} \quad (2)$$

$$MAT = 24.4 \cdot LMP + 3.25 \text{ (Wilf 1997; Greenwood } et\ al. \text{ 2005)} \quad (3)$$

Applying the method of Wilf (1997), the error of the estimate for leaf margin analysis is

expressed here as the binomial sampling error (Equation 4) where *c* is the slope from the leaf margin analysis regression equation, *LMP* as defined in (2), and *r* is the number of species scored for leaf margin type for the individual flora.

$$\sigma[\mathrm{LMA}] = c\sqrt{\frac{LMP \cdot (1 - LMP)}{r}} \quad \text{(Wilf, 1997)} \qquad (4)$$

For the early Eocene sea level flora at Regatta Point, the MAT calculated from LMA is ?? ± 2.0°C (Table 1). Pole (2007) reported 11 species of Lauraceae for Regatta Point as well as *Gymnostoma* (Casuarinaceae), *Ilex* (Aquifoliaceae), *Telopea* (Proteaceae), Rhizophoraceae (mangroves) and a diverse suite of conifers, and interpreted the floras as reflecting a mesothermal rainforest with MAT 12-20°C. The presence of the mangrove palm *Nypa* (Arecaceae) in the flora (Pole & Macphail 1996) can be used to constrain MAT independently, using the key taxa bioclimatic method. Palms (Arecaceae) are limited to areas with MAT >10°C (Greenwood & Wing 1995). However the northern and southern limits of the only extant *Nypa* species, *N. fruticans*, are the mouth of the Herbert River in Queensland (MAT 23.8°C, Fig. 1) and the Ryukyu Islands (MAT 22.1°C, Jones 1995) respectively. For the purposes of this analysis, a conservative lower MAT limit for *Nypa* at Regatta Point was set at 20°C (Table 1), which corresponds to the worldwide lower limit of mangrove forests (Odum & McIvor 1990). Climatic estimates for the Anglesea floras have been previously reported (Greenwood *et al*. 2003) but are updated here using equations 2 and 3 and bioclimatic analysis (Table 1).

For the Bogong Plateau Eocene floras, the MAT calculated from the leaf margin analysis (74-75% non-toothed margins) is 17.9-18.2 ± 2.2°C (Table 1). The bioclimatic analysis of these floras combined the available climate profiles of the nearest living relatives ('NLRs') of identified macroflora and microflora (Greenwood *et al*. 2003; Carpenter *et al*. 2004). The climate profiles for multiple NLRs for Hotham Heights are shown in Fig. 4, including also the calculated climate envelope (shaded box) and mean value of MAT for this site (bold dashed line). Although the NLRs *Cnemidaria* (a tree fern) and *Acmopyle* (a conifer) lacked climate profiles and so could not be used in the calculation, Carpenter *et al*. (2004) noted that both of these taxa are indicative of MAT approximately 16–20°C. For the purposes of the calculation of MAT the climate profile of North American species of *Ilex* (Greenwood *et al*. 2005) was substituted for the Australian *Ilex* climate profile. In Australia *Ilex* is represented by a narrowly distributed single megathermal species, whereas in North America there are several

widely distributed mesothermal *Ilex* species. Both the Australian and North American climate profiles for *Ilex* are shown on Fig. 4. The calculated climate envelopes for Hotham Heights and Brandy Creek Mine give MAT values of 18.7 ± 2.6°C and 18.6 ± 2.7°C respectively, values slightly warmer than the estimates of MAT derived using leaf margin analysis, but within the error of both sets of estimates. The estimates for Hotham Heights provided here are a little cooler than that previously given by Greenwood *et al*. (2003), due to the use in the present analysis of a more refined systematic analysis of that flora (Carpenter et al. 2004).

The bioclimatic estimates of MAT are consistent with the species-rich and diverse nature of the Bogong Plateau floras (>50 species of dicots); extant wet forests in Australia at MAT <14°C are species poor (i.e. <20 species of dicot and conifers). The canopy of the Eocene floras was dominated by nine or more species of Lauraceae, including *Cryptocarya*, *Endiandra* and *Litsea* (Greenwood *et al.* 2003; Carpenter *et al.* 2004); extant forests with diverse Lauraceae are restricted to sites with MAT >16°C. The combined palynological and macrofossil evidence indicates that conifers either contributed to the canopy or emerged from it (e.g. Araucariaceae, *Agathis* and *Wollemia*; and Podocarpaceae incl. aff. *Podocarpus*, *Acmopyle* and *Dacrydium*). Several other dicots (*Gymnostoma*, aff. *Diospyros*, Musgraveinae, *Darlingia* and likely *Ilex* and *Nothofagus* subgenus *Brassospora*) contributed to the tree layers or other woody synusiae (e.g. vines, Vitaceae cf. *Cissus*). Palynological evidence indicates that the Bogong Plateau forest understorey was rich in ferns, especially tree ferns (aff. *Cnemidaria*, *Cyathea* and *Dicksonia*), consistent with a cloudy mesothermal montane environment (Greenwood *et al.* 2003; Carpenter *et al.* 2004).

**Elevation of Bogong Plateau in the early Eocene**

The Eocene elevation of the Bogong Plateau macrofloral localities was determined from the MAT values at Regatta Point, Hotham Heights and Brandy Creek (Table 1), using the calculated lapse rate and latitudinal correction for the area (Table 2). The current elevation of Regatta Point is only 50 m, which is well within the uncertainties of the lapse rate calculation, so no correction for this elevation was applied. From the maximum and minimum MAT values at each site, taking into account the uncertainties, the elevation of the Bogong Plateau in the early Eocene was between 70 and 1200 m (Table 2). This range overestimates the uncertainty in the calculations, because although MAT and lapse rate covary, the total error is less than the sum of the errors in the components (Gregory & Chase 1992), and the standard error based on the lapse rate for south-eastern Australia is 430 m. For the most likely scenario, an MAT at Regatta Point of 20°C and an MAT at Bogong Plateau of 18°C, the

palaeoelevation was about 800 m. This is consistent with the cloudy mesothermal montane environment indicated by the rich presence of ferns, particularly tree ferns, in the Bogong Plateau floras (Greenwood *et al.* 2003; Carpenter *et al.* 2004). Thus the palaeobotanical evidence, even under the 4°C warmer global temperatures of the early Eocene (the upper limit of most palaeoproxy evidence, Greenwood & Wing 1995), indicates that the elevation of the Bogong Plateau in the Eocene was 700-1000 m lower than at present (1500-1800 m). The area now has a subalpine to alpine climate (Mt Hotham MAT 4.7°C), and is partially above the climatic treeline, so the possibility that the early Eocene elevation of the Bogong Plateau approximated that of today is unsupportable from a palaeoecological perspective.

## PALAEOELEVATION OF BOGONG PLATEAU FROM GEOMORPHIC ANALYSIS

The landscape of the Bogong Plateau prior to eruption of the Eocene to Oligocene basaltic lavas can be reconstructed from the elevation of the base of the basalt and the sub-basaltic sediments, and had a low relief of 100-200 m (Fig. 5), but was not necessarily at a low elevation. The high plains' rivers had broad open valleys with low gradients, and are floored by sands and quartz-rich (occasionally lithic) gravels, overlain by finer sediments. Following the extrusion of the basalts, this landscape was tectonically disrupted and elevated by fault block displacements, in particular along the Tawonga Fault, which bounds the Bogong Plateau to the northwest (Fig. 1). The land surface southeast of this fault was uplifted and tilted to the southeast to form the Bogong Plateau (Crohn 1949; Orr 1999). Minor displacements occurred across the intra-block Kiewa Fault and a mid-block warp (Orr 1999). The Tawonga and Kiewa Faults originated in the Paleozoic, but were reactivated in the Tertiary. Both the local fault displacements and general highlands uplift caused a significant increase in relief, and the resultant stream erosion formed the deeply incised valleys of the northern and southern slopes of the Southeastern Highlands. The extent of deep stream incision into the high plains was restricted by the development of major knickpoints at the edges of the high plains, where streams fall 300–600 m into the adjacent deeply incised valleys. Tectonic uplift occurred after eruption of the basalts, because the basalt lavas did not flow into these steep-sided valleys, and the base of the basalt is displaced by the Kiewa Fault.

Thus it is clear that the Eocene landscape of the Bogong Plateau, before the tectonic disruption, was at a lower elevation than at present. To reconstruct its palaeoelevation, the pattern of stream incision can be used. Under a stable tectonic regime, a river will establish a graded stream profile that is concave upwards and increases in gradient upstream. After a sudden regional tectonic uplift, a river will attempt to re-establish its graded profile by

incising downward; in general, the incision initiates at the downstream limit of uplift and migrates upstream as a knickpoint. Some of the incision that has affected the Bogong Plateau originated at the highland margins, suggesting general uplift of the entire highlands region. The amount of down-cutting reflects the amount of uplift; in the Bogong Plateau area the magnitude of stream incision increases upstream, because the uplift was greatest along the crest of the highlands, as a result of local fault displacements as well as general highlands uplift (Orr 1999). Faulting is evident from changes in both watershed elevations and stream incision; the most notable increases are across the Tawonga Fault. The amounts by which incision increased can determine the fault displacements, and as a result the palaeoelevation of the area.

Determining the land surface before fault development requires deconstruction of the height changes across the faults. As the maximum fault-related uplift was accommodated along the Tawonga Fault, the reconstruction is based on the displacement across this fault.

A north-south transect (Fig. 1) was constructed showing the present height of the highest peaks (all formed of Paleozoic basement) within 3 km of the transect; these peaks have undergone the least erosion during the Tertiary, and will therefore approximate the high points of the pre-basalt Eocene land surface. Outcrops of sub-basaltic sediments mark the river valleys of the Eocene landscape, so their elevations, including the Hotham Heights and Brandy Creek sample sites, were also projected onto the transect (Fig. 5). In addition, the long profiles of adjacent present-day rivers were projected onto the transect line (Fig. 5). The data were derived from topographic maps using spot heights and 20m contours, and the locations of all data points are their positions perpendicular to the transect line.

To reconstruct the pre-basalt land surface, the displacements across the Tawonga and Kiewa Faults and the mid-block warp were subtracted. The present heights of the peaks and sub-volcanic sediments on the downthrown sides of the Kiewa Fault and mid-block warp (eastern and southern sides respectively) were elevated by 80 m and 110 m respectively, as the base of the basalt is displaced by that amount across these structures (Orr 1999). The Tawonga Fault caused both uplift and tilting of the Eocene land surface. To remove these effects, the peak height profile on the upthrown (southeastern) side of the fault was rotated to horizontal, and then reduced in elevation so that the heights of the highest peaks immediately north and south of the fault were the same, giving a total maximum displacement of around 750 m across the Tawonga Fault, decreasing to the southeast. After this procedure, some outcrops of sub-volcanic sediments were higher than the peaks (Fig. 5), so the peak height profile was locally raised to the level of these points. The difference in elevation between the

peak heights and the sub-basaltic sediments represents the minimum local relief of the Eocene land surface (~200m; Fig. 5).

Had no general highlands uplift accompanied the fault displacements, the higher parts of the Eocene landscape would have been at or above an elevation of 1200 m, i.e. the present height of the highest peak on the northern side of the Tawonga Fault (Fig. 5). However there was also uplift of the entire highlands area, because on the northern side of the fault, which would not have been uplifted by fault movement, the Kiewa River has incised 500 m below the likely river level in the Eocene (identified from a prominent terrace level in the Kiewa valley by Orr 1999; Fig. 5). The overall elevation of the profile was therefore reduced by 500 m, which represents the cumulative amount of Cenozoic stream incision due to regional uplift of the highlands. The higher relief nearer to the margins is consistent with a 'normal' (undisplaced) highlands distribution.

The results (Fig. 5) indicate a low relief Eocene landscape at an elevation around 700 m, with peaks to 900 m. This is a slightly lower elevation than most of the present New South Wales southern tablelands, for example. River valleys occurred at a general level of 600 m to 700 m, with tributaries rising to higher elevations, e.g. the Hotham Heights site, which would have had a palaeoelevation of about 800 m (Fig. 5).

## AMOUNT AND TIMING OF TERTIARY UPLIFT IN THE SOUTHEASTERN HIGHLANDS

Both the palaeobotanical and geomorphological evidence presented here indicate that the Bogong Plateau was only moderately elevated in the Eocene, and there was substantial uplift of 700-1000 m after eruption of the mid-Cenozoic basalts. However, the amount of uplift through the Southeastern Highlands, as shown by the depth of fluvial incision below the basalt flows, is variable. To the east along the Snowy River the post-basalt down-cutting has been less. Oligocene basalt flows on the Nunniong Plateau rest on Palaeozoic bedrock at 1100–1200 m elevation, whereas 25–30 km to the east at Deddick they occur on the flanks of the Snowy River valley at only 700–900 m asl, with the present river some 600 m below (Hills 1975). This shows that a valley with 200-500 m of relief had already been cut by Eocene time, and subsequently it has been deepened another 600 m. Some 50 km to the south of Deddick, near Buchan, the post-basaltic incision is considerably less; Eocene basalts occupy a broad abandoned valley that lies only about 200 m above present river level (Webb *et al.* 1991).

The timing of the post-basalt uplift is not well constrained. Periods of uplift in the late

Paleogene to late Neogene have been proposed by several authors (e.g. Jones & Veevers 1982; Ollier 1986; Ollier & Pain 1994), but there is little direct evidence on timing. The uplift may coincide with a major period of tectonism that affected most of southern Victoria in the Late Miocene – Early Pliocene, causing several hundred meters of uplift in the Southern Victorian Uplands (Joyce *et al.* 2003) and fault displacements of up to 180 m and overall uplift of as much as 300 m in western Victoria (Paine *et al.* 2004). Tectonic activity was concentrated at ~6 Ma, and produced a regional unconformity at around the Miocene–Pliocene boundary within the successions in the southeastern Australian Tertiary basins (Dickinson *et al.* 2001; Sandiford 2003). The Late Miocene- Early Pliocene tectonism is probably also reflected in the deposition of the Haunted Hills Formation across the onshore Gippsland Basin at this time, as alluvial fan gravels and sheet sands of Pliocene- Pleistocene age flanking the Southeastern Highlands (Bolger 1991). The tectonic activity probably resulted from the compression of the entire Australian continent due to collision of the Australian plate with the plates of Southeast Asia along the Melanesian and Timor Arcs, and/or to a change in relative plate motion between the Australian and Pacific plates (Hill *et al.* 1995; Sandiford 2003).

Some geomorphologists (e.g. Andrews 1911; Brown 1969; Jenkin 1988) attributed the creation of the Southeastern Highlands to a major event called the Kosciuszko Uplift, which was generally believed to have occurred in the Plio-Pleistocene. The relative importance of this event has been disputed (e.g. Hill 1999), and earlier concepts of highland uplift were different and not based on the Davisian model of cyclic landscape evolution from mountain range to peneplain. Howitt (1877) interpreted the Victorian high plains region as an elevated plateau continuous with the Monaro Tablelands of New South Wales, before being dissected when post-Miocene uplift produced increased stream erosion. The evidence from the present study supports this earlier interpretation and implies that a substantial uplift did occur during the Miocene to Early Pliocene, somewhat earlier than the Kosciuszko Uplift proposition. Because the initial uplift of the Southeastern Highlands occurred earlier still in the mid-Cretaceous (Gallagher *et al.* 1994; Veevers 2000), the Late Tertiary event caused additional uplift of an already elevated plateau, in contrast to the concept of the Kosciuszko Uplift as a single Plio-Pleistocene event.

There may also have been additional periods of uplift. The fission track data from Mt Feathertop on the northern margin of the Bogong plateau show that rocks now at the surface cooled rapidly between about 70 Ma and 50 Ma, and this was interpreted as indicating that Mt Feathertop underwent 1–2 km of rapid denudation in the Early Tertiary (O'Sullivan *et al.*

1999). This would represent an intermediate phase of uplift and erosion, between the widely documented episodes in the mid-Cretaceous and Late Tertiary.

If the interpretations of this study are correct, then the Southeastern Highlands did not reach their current elevation until the Late Miocene – Early Pliocene. Therefore the high plains have been alpine areas for only 6 Ma or less, and the high altitude biota that is adapted to seasonal freezing must have evolved in this time frame.

## CONCLUSIONS

(1) Early to Late Eocene palaeofloras, preserved beneath Late Oligocene – Early Eocene basalts on the northern edge of the Bogong plateau, can be used to estimate the palaeoelevation of the area prior to basalt eruption. Estimates of mean annual temperature (MAT) at each site were made using the climate preferences of the mangrove *Nypa*, the overlap of climate envelopes for multiple taxa, leaf margin analysis (proportion of non-toothed rather than toothed leaf margins) and the mean length of all leaves. The Eocene MAT at Bogong plateau was most likely 18°C. The palaeoelevation of the Bogong plateau sites, calculated by comparison with the early Eocene Regatta Point site at sea level in Tasmania using the 'lapse rate' method, was about 800 m (700-1000 m lower than at present); a similar estimate – indistinguishable allowing for the error of the estimates – is derived using the late Middle Eocene Anglesea flora. This is consistent with the cloudy mesothermal montane environment indicated by the rich presence of tree ferns in the Bogong Plateau floras (Carpenter *et al*. 2004).

(2) The palaeoelevation was also reconstructed using the elevation of the base of the basalt and the sub-basaltic sediments, as well as the maximum elevation of peaks in the area and the identification of the Eocene river level from fluvial terraces, to determine displacement across the Tawonga Fault and uplift of the entire highlands area. The results indicate that in the Eocene, prior to eruption of the Eocene- Oligocene basaltic lavas, the Bogong Plateau had a low relief of 100-200 m and lay at an elevation of around 700 m, with peaks to 900 m.

(3) Both the palaeobotanical and geomorphological evidence therefore indicate that the Bogong Plateau was only moderately elevated in the Eocene, and that there was substantial uplift of 700-1000 m after eruption of the mid-Cenozoic basalts. The uplift probably coincided with a major period of tectonism that affected most of southern Victoria in the Late Miocene – Early Pliocene. Because the initial uplift of the Southeastern Highlands occurred earlier still in the mid-Cretaceous, the Tertiary event proposed here involves additional uplift

of an already elevated plateau, in contrast to earlier suggestions that a single event, the Kosciuszko Uplift, created the Southeastern Highlands during the Plio-Pleistocene.

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**Fig. 1.** Map of the Victorian High Plains showing main localities. Transects for cross sections in Fig. 5 shown (A - B). Fossil sites, (1) Hotham Heights and (2) Brandy Creek Mine. The location of the Kiewa and Tawonga faults shown in 1C are based on Fig. 1.9 (p. 20) in Gray *et al*. (1988).

**Fig. 2.** Diagrammatic lithological logs for the two early Eocene fossil flora localities. Examples of fossil leaves from each flora are shown. **2A** Hotham Heights. **2B** Brandy Creek Mine. Images of leaf fossils provided by R. Carpenter and R. Keefe.

**Fig. 3.** **3A** Plots of MAT vs. elevation for the Mt Kosciuszko and Mt Hotham areas used to derive lapse rates. **3B** Plots of MAT vs. latitude for sites < 200m a.s.l. along the Australian east coast used to derive the meridional gradient. Data from Australian meteorological station averages.

**Fig. 4.** Bioclimatic analysis of the Hotham Heights Eocene flora. Vertical lines are the 5-95% range of MAT for the nearest living relative for each fossil taxon, and the boxes show the 25-75% range, except for *Nothofagus* s.g. *Brassospora* where one standard deviation (box) is shown (Read *et al*. 2005). The horizontal shaded box is the calculated climatic envelope for this site, with the calculated mean value shown as a bold dashed line. Primary Australia modern distribution data used for the bioclimatic analysis was from the Australian National Herbarium database, with permission.

**Fig. 5.** Cross sections of: (A) present elevations across the Tawonga Fault in the High Plains; and (B) reconstructed Eocene elevations. Surface thrust interpretation of the Tawonga Fault is based on Beavis (1960). Adapted from Orr (1999).

**Table 1.** Calculation of MAT for Bogong Plateau (upland) and both Regatta Point and Anglesea (sea level) floras in the Early and late Middle Eocene (see text for equations used).

| Locality | LMP | MAT from LMA | MAT from bioclimatic analysis |
|---|---|---|---|
| Regatta Point | N/A | N/A | 12-20°C[1] |
| Anglesea[2] | 65 | 15.5 (± 2.4°C) | 19.3 (± 1.9°C) |
| Brandy Creek | 75 | 18.2 (± 2.2°C) | 18.6 (± 2.7°C) |
| Hotham Heights | 70 | 16.7 (± ??°C) | 18.7 (± 2.6°C) |

[1] range from Pole (2007)

[2] estimates from Greenwood *et al*. (2003)

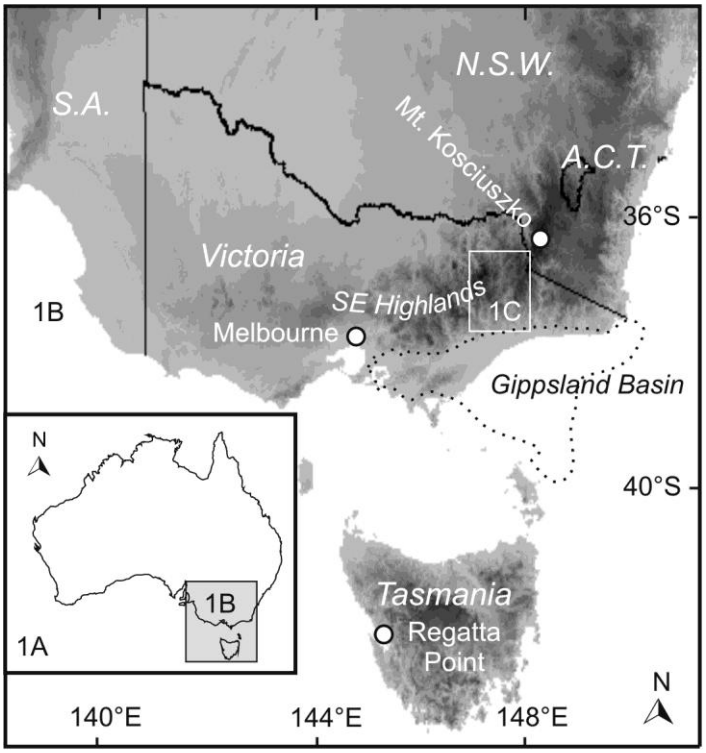
**Table 2.** Calculation of early Eocene palaeoelevation of Bogong Plateau (BP). Latitude of Regatta Point is 5.3° S of Bogong Plateau.

| Regatta Point MAT (°C) (from Table 1) | East Aust latitudinal temp. gradient (ΔT°C / 1° latitude) | Regatta Point MAT adjusted to BP latitude (°C) | Bogong Plateau MAT (°C) (from Table 1) | MAT difference (Regatta Point - BP) | Present SE Australian lapse rate (ΔT°C / 100 m) | Bogong Plateau palaeoelevation (m) |
|---|---|---|---|---|---|---|
| 16.3 | 0.47 | 18.8 | 22.1 max | -3.3 | 0.58 | |
| 16.3 | 0.47 | 18.8 | 15.6 min | 3.2 | 0.58 | 550 |
| 20 | 0.47 | 22.5 | 22.1 max | 0.4 | 0.58 | 70 |
| 20 | 0.47 | 22.5 | 15.6 min | 6.9 | 0.58 | 1200 |

**?revised Table 2.** Calculation of late Eocene palaeoelevation of Bogong Plateau (BP). Latitude of Regatta Point is 5.3° S of Bogong Plateau.

| Anglesea MAT (°C) (corrected for latitude from Table 1) | Bogong Plateau MAT (°C) (from Table 1) | MAT difference (Anglesea - BP) | Present SE Australian lapse rate (ΔT°C / 100 m) | Bogong Plateau palaeoelevation (m) |
|---|---|---|---|---|
| 16.2 | 16.7 | -0.5 | 0.58 | 0 |
| 16.2 | 18.2 | -2.0 | 0.58 | 0 |
| 20.0 | 18.7 | 1.3 | 0.58 | 216 |
| 20.0 | 18.6 | 1.4 | 0.58 | 233 |

**Figure 1.**


N.S.W.
S.A.
Mt. Kosciuszko
A.C.T.
36°S
Victoria
1B
SE Highlands
1C
Melbourne
Gippsland Basin
N
40°S
1B
1A
Tasmania
Regatta
Point
N
140°E
144°E
148°E

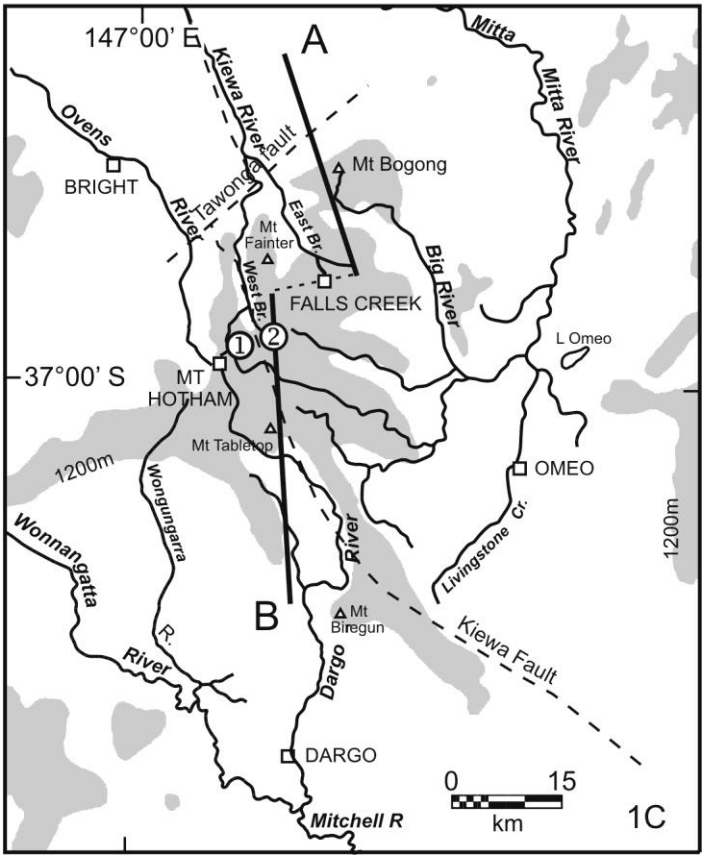

147°00' E
A
Mitta
Mitta River
Kiewa River
Ovens
Kiewa Fault
BRIGHT
Mt Bogong
Tawonga
River
East Br.
Mt
Fainter
West Br.
Big River
FALLS CREEK
L Omeo
1
2
37°00' S
MT
HOTHAM
Mt Tabletop
1200m
OMEO
Wongungarra
River
Livingstone cr.
1200m
Wonnangatta
R.
River
B
Mt
Biregun
Kiewa Fault
Dargo
River
DARGO
0
15
km
Mitchell R
1C

**Figure 2.**

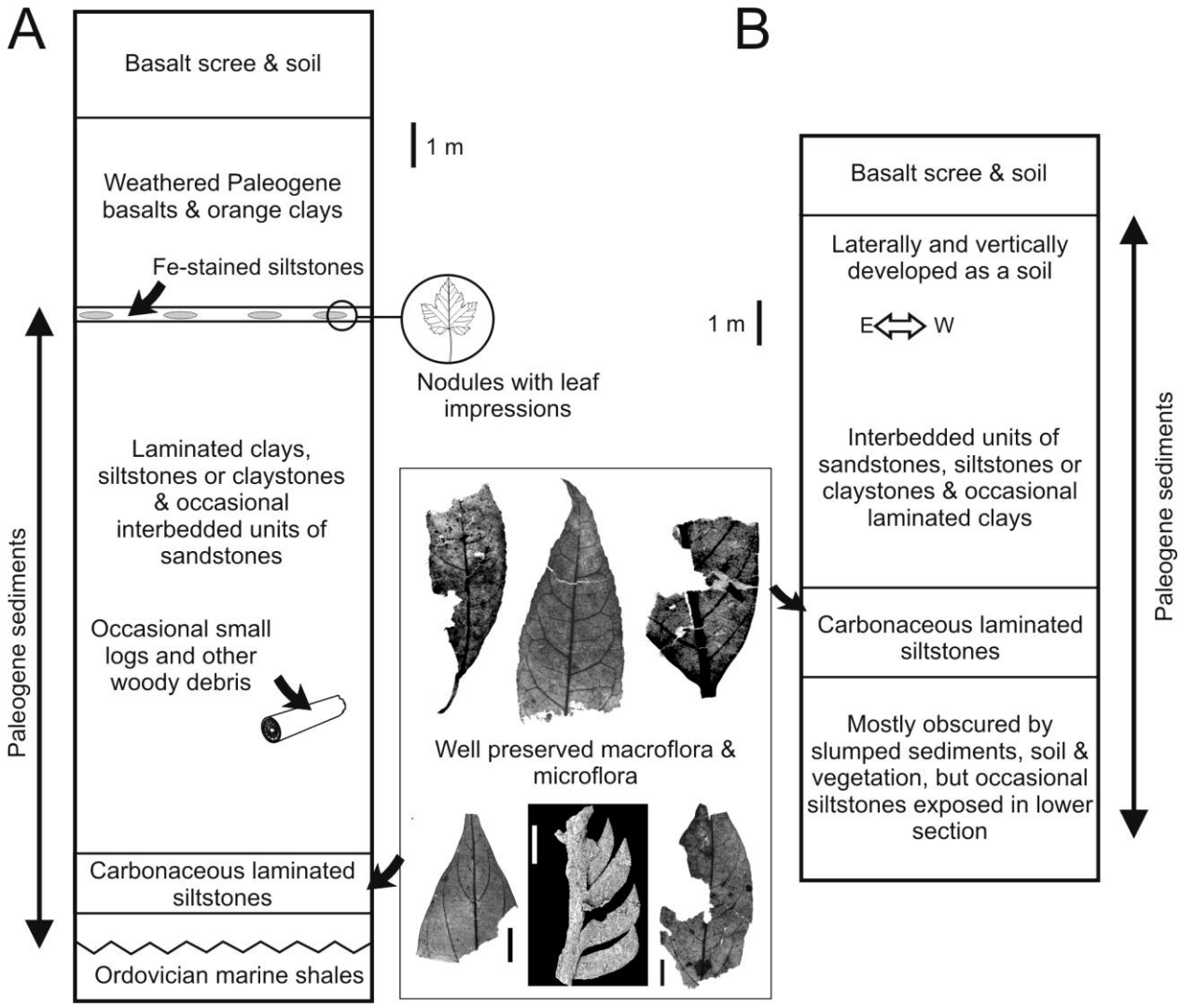

A
Basalt scree & soil
Weathered Paleogene basalts & orange clays
Fe-stained siltstones
Laminated clays, siltstones or claystones & occasional interbedded units of sandstones
Occasional small logs and other woody debris
Carbonaceous laminated siltstones
Ordovician marine shales
Paleogene sediments
1 m
Nodules with leaf impressions
Well preserved macroflora & microflora
B
Basalt scree & soil
Laterally and vertically developed as a soil
E W
1 m
Interbedded units of sandstones, siltstones or claystones & occasional laminated clays
Carbonaceous laminated siltstones
Mostly obscured by slumped sediments, soil & vegetation, but occasional siltstones exposed in lower section
Paleogene sediments

**Figure 3.**

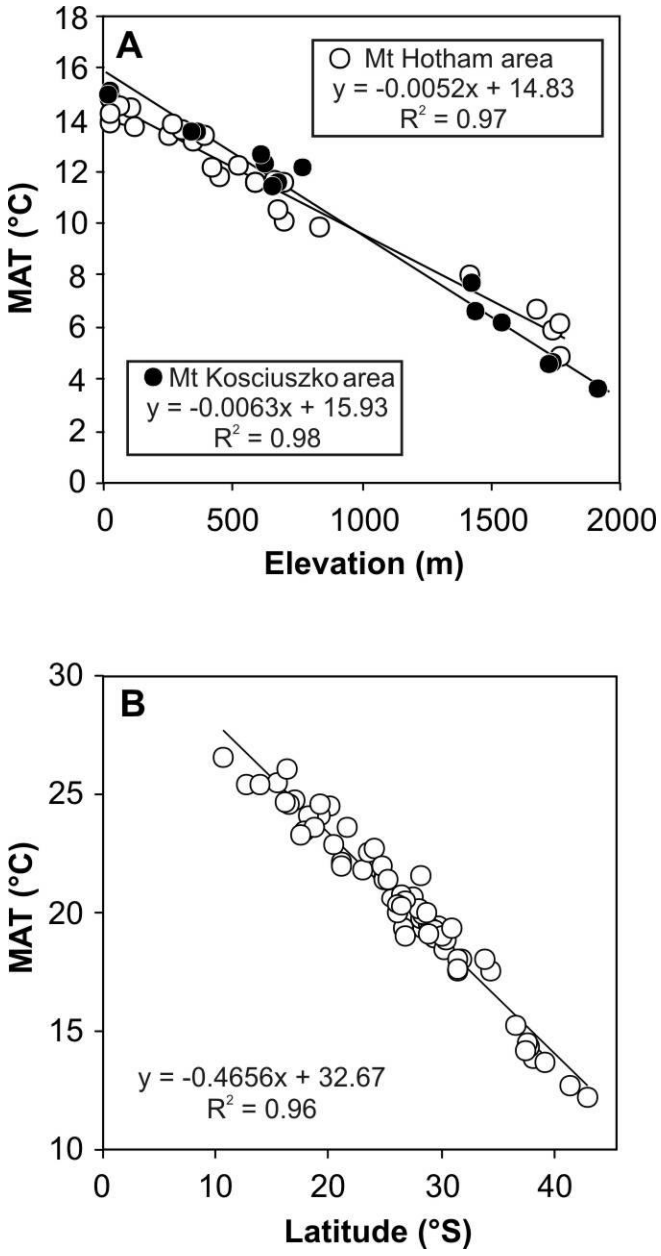

A
Mt Hotham area
y = -0.0052x + 14.83
R2 = 0.97
Mt Kosciuszko area
y = -0.0063x + 15.93
R2 = 0.98
MAT (°C)
Elevation (m)
0
2
4
6
8
10
12
14
16
18
0
500
1000
1500
2000
B
y = -0.4656x + 32.67
R2 = 0.96
MAT (°C)
Latitude (°S)
10
15
20
25
30
0
10
20
30
40

**Figure 4.**

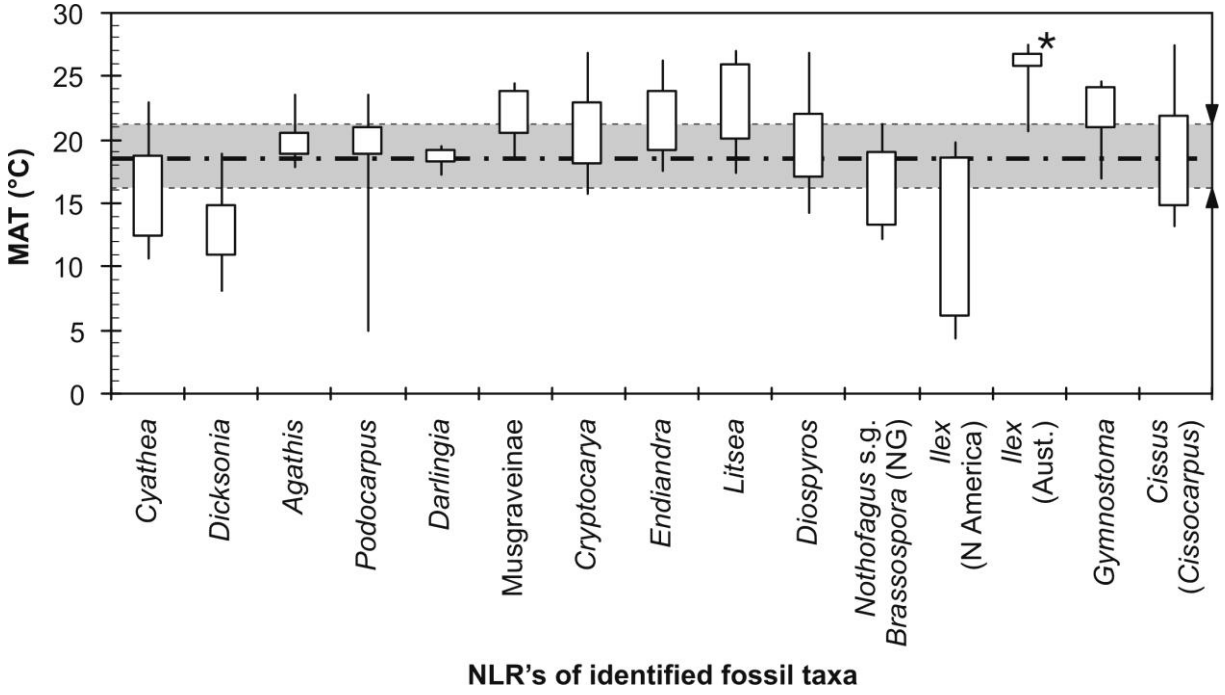
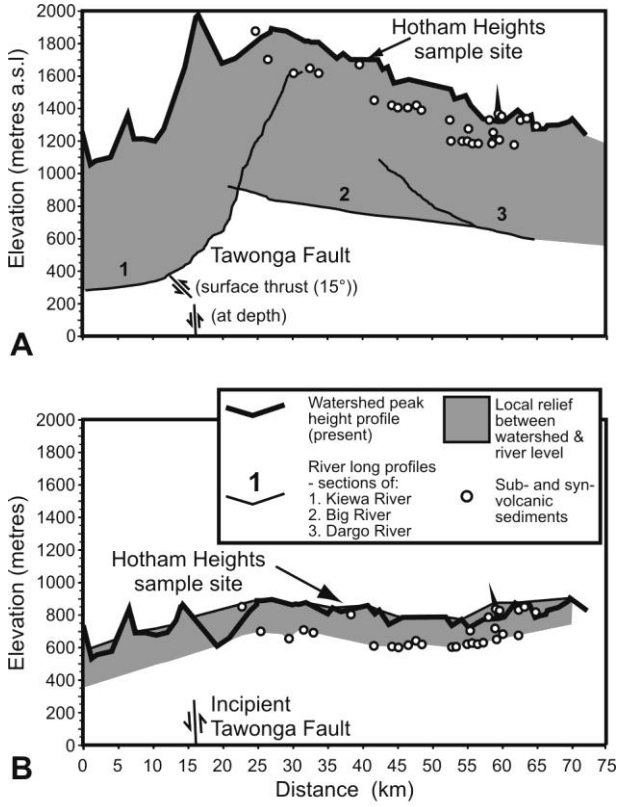

MAT (°C)
30
25
20
15
10
5
0
*
Cyathea
Dicksonia
Agathis
Podocarpus
Darlingia
Musgraveinae
Cryptocarya
Endiandra
Litsea
Diospyros
Nothofagus s.g. Brassospora (NG)
Ilex (N America)
Ilex (Aust.)
Gymnostoma
Cissus (Cissocarpus)
NLR's of identified fossil taxa

**Figure 5.**


Elevation (metres a.s.l)
Hotham Heights
sample site
1
2
3
Tawonga Fault
(surface thrust (15°))
(at depth)
A
Watershed peak
height profile
(present)
Local relief
between
watershed &
river level
River long profiles
- sections of:
1. Kiewa River
2. Big River
3. Dargo River
Sub- and syn-
volcanic
sediments
Elevation (metres)
Hotham Heights
sample site
Incipient
Tawonga Fault
B
Distance (km)

# Appendix 2

**Appendix 2.** Data matrix for binary character scoring of fossil morphotypes at Brandy Creek. '1' denotes the presence of character, '0' denotes absence of character, '999' denote character unable to be scored.

Upper epidermis

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **BC001- 1390** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| **BC002 - 1608** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| **BC003- 1205** | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| **BC004- 1335** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC005- 1401** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC006- 1364** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| **BC007- 1526** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC008- 1260** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC009- 1613** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC010- 1305** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC011- 1240** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC012- 1336** | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC013- 1051** | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 | 999 |
| **BC014- 1245** | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC015- 1580** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC016- 1532** | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC017- 1080** | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| **BC018- 1183** | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |

Lower epidermis

| | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BC001- 1390 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| BC002 - 1608 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| BC003- 1205 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| BC004- 1335 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| BC005- 1401 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| BC006- 1364 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| BC007- 1526 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| BC008- 1260 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| BC009- 1613 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| BC010- 1305 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| BC011- 1240 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| BC012- 1336 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| BC013- 1051 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| BC014- 1245 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BC015- 1580 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| BC016- 1532 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| BC017- 1080 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| BC018- 1183 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

# Appendix 3

# Appendix 3 Scores for leaf margin analysis and other leaf attributes.

| TABLE 2 | | | margin type | | | | | | leaf size | | | | | apex | | | | base | | | L:W | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TAXON | | specimens | lobed | no-teeth | compound | ligto 1 | ligto 2 | micro 1 | micro 2 | micro 3 | meso 1 | meso 2&3 | emarginate | rounded | acute | attenuate | cordate | round | acute | <1.00 | >1.00 | 2.00 | 3.00 | >4.00 |
| *BC001* | 2.3% | 12 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *BC002* | 9.2% | 49 | 0 | 1 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *BC003* | 0.8% | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0.5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *BC004* | 1.9% | 10 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *BC005* | 1.9% | 10 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *BC006* | 0.9% | 5 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 0 |
| *BC007* | 0.6% | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *BC008* | 0.4% | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *BC009* | 6.0% | 32 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0 | 1 |
| *BC010* | 37.5% | 199 | 0 | 1 | 0 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0.33 | 0.33 | 0.33 | 0 | 0.5 | 0.5 | 0 | 0 | 0.33 | 0.33 | 0.33 |
| *BC011* | 0.8% | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *BC012* | 0.8% | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *BC013* | 0.2% | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *BC014* | 8.7% | 46 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *BC015* | 0.8% | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *BC016* | 7.9% | 42 | 0 | 0 | 1 | 0 | 0 | 0 | 0.5 | 0.5 | 0 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 0 | 1 | 0 | 0 | 0.33 | 0.33 | 0.33 |
| *BC017* | 17.2% | 91 | 0 | 0 | 1 | 0 | 0 | 0.33 | 0.33 | 0.33 | 0 | 0 | 0 | 0.33 | 0.33 | 0.33 | 0 | 0.5 | 0.5 | 0 | 0 | 0.33 | 0.33 | 0.33 |
| *BC018* | 2.3% | 12 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Simpson's Ds | 100% | 530 | 0% | 83% | 17% | 0% | 0% | 0% | 22% | 78% | 0% | 0% | 0% | 80% | 0% | 20% | 0% | 0% | 100% | 0% | 33% | 22% | 22% | 22% |

# Appendix 4

# Appendix 4

**Appendix 4** Climate profiles for Nearest Living Relatives of Eocene floras discussed in this thesis. MAT ( Mean Annual Temperature), CQTrT (Coldest quarter temperature), WQtrT ( Warmest quarter temperature), MAP ( Mean annual precipitation), WQtrP ( Warmest quarter precipitation), CQtrP (Coldest quarter precipitation).

| | MAT | N | MEAN | S.D. | 2.5% | 5% | 10% | 25% | 50% | 75% | 90% | 95% | 97.5% | MAX | MIN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cyatheaceae | Cyathea | | 15.8 | 3.9 | 9.7 | 10.2 | 11.0 | 12.3 | 15.9 | 18.9 | 20.7 | 23.2 | 24.6 | 25.7 | 9.2 |
| Dicksoniaceae | Dicksonia | 210 | 13.4 | 3.4 | 7.7 | 8.8 | 9.5 | 11.0 | 12.8 | 15.7 | 18.6 | 19.8 | 20.5 | 21.9 | 5.7 |
| Gleicheniaceae | Dicranopteris, Diplopterygium, Gleichenia, & Sticherus | 437 | 17.5 | 5.2 | 10.5 | 10.7 | 11.3 | 13.8 | 16.0 | 22.8 | 24.8 | 25.8 | 26.5 | 26.9 | 10.2 |
| | Gleichenia | | 10.7 | 3.4 | 5.2 | 5.6 | 6.2 | 7.6 | 11.0 | 13.7 | 15.6 | 16.1 | 16.3 | 16.3 | 4.8 |
| Pteridaceae | Acrostichum aureum + A. speciosum | 65 | 24.4 | 2.7 | 19.2 | 19.5 | 20.0 | 22.3 | 24.3 | 27.0 | 27.8 | 28.0 | 28.1 | 28.1 | 19.0 |
| Salviniaceae | Azolla filiculoides | | 15.6 | 4.9 | 11.1 | 11.2 | 11.4 | 12.1 | 16.0 | 19.2 | 25.3 | 25.3 | 25.3 | 25.3 | 11.0 |
| Schizeaceae | Lygodium | 183 | 24.3 | 2.1 | 21.4 | 21.5 | 21.6 | 23.1 | 25.4 | 26.2 | 26.8 | 26.8 | 26.8 | 26.8 | 21.4 |
| Cycadaceae | Cycas | 84 | 24.8 | 2.6 | 19.0 | 19.4 | 19.8 | 24.9 | 25.9 | 26.5 | 26.8 | 26.9 | 26.9 | 26.9 | 18.6 |
| Stangeriaceae | Bowenia serrulata, B. spectabilis | | 22.1 | 2.2 | 17.6 | 18.2 | 18.9 | 20.6 | 22.8 | 24.0 | 24.4 | 24.5 | 24.5 | 24.5 | 17.1 |
| Zamiaceae | Lepidozamia | | 22.1 | 2.3 | 16.9 | 17.0 | 17.4 | 21.3 | 23.2 | 23.8 | 24.3 | 24.4 | 24.5 | 24.5 | 16.7 |
| | Macrozamia | | 17.2 | 2.2 | 13.3 | 13.6 | 14.2 | 15.8 | 17.1 | 19.1 | 20.6 | 21.1 | 21.7 | 22.1 | 12.9 |
| Araucariaceae | Agathis atropurpurea, A. microstachya, A. robusta | | 20.0 | 1.6 | 17.6 | 17.8 | 18.1 | 18.9 | 19.8 | 20.7 | 22.6 | 23.9 | 24.3 | 24.4 | 16.0 |
| | Araucaria bidwillii, A. cunninghamii | | 20.7 | 2.8 | 15.2 | 16.3 | 17.8 | 18.9 | 20.5 | 22.9 | 24.8 | 25.3 | 25.6 | 25.7 | 14.1 |
| Cupressaceae / Taxc | Athrotaxis (A. cupressoides, A. laxifolia, A. selaginoides) | | 5.6 | 0.4 | 5.1 | 5.1 | 5.2 | 5.4 | 5.6 | 5.8 | 6.4 | 6.9 | 7.0 | 7.0 | 5.0 |
| | Callitris | 175 | 15.5 | 3.2 | 10.2 | 11.1 | 11.8 | 13.2 | 15.2 | 16.9 | 19.5 | 21.9 | 25.2 | 26.8 | 7.5 |
| Podocarpaceae | Dacrycarpus NZ, NG & Fiji | | | | | | | 10.0 | | 16.0 | | | | 8.0 | 25.0 |
| | Lagarostrobos franklinii | | 9.0 | 2.4 | 5.4 | 5.5 | 5.6 | 7.8 | 10.5 | 10.7 | 10.8 | 10.8 | 10.8 | 10.8 | 5.3 |
| | Microcachrys | | 4.3 | 0.4 | 4.0 | 4.0 | 4.0 | 4.1 | 4.3 | 4.5 | 5.2 | 5.2 | 5.2 | 5.2 | 3.9 |
| | Phyllocladus asplenifolious | | 8.9 | 2.8 | 5.7 | 5.8 | 6.0 | 6.4 | 8.8 | 11.4 | 14.4 | 14.6 | 14.6 | 14.6 | 5.7 |
| | Podocarpus (Aust. spp.) | | 18.4 | 5.5 | 4.3 | 4.9 | 6.5 | 18.2 | 20.0 | 21.2 | 23.1 | 24.2 | 25.5 | 25.8 | 3.7 |
| | Prumnopitys amara (Sundacarpus amara) | 41 | 20.6 | 1.0 | 19.1 | 19.3 | 19.5 | 20.0 | 20.6 | 21.0 | 21.8 | 23.5 | 24.0 | 24.0 | 18.9 |
| | Prumnopitys ladei | | 18.3 | 0.5 | 17.3 | 17.3 | 17.7 | 18.2 | 18.3 | 18.9 | 18.9 | 18.9 | 18.9 | 18.9 | 17.3 |
| Agavaceae | Cordyline | | 19.5 | 2.4 | 12.7 | 13.4 | 15.6 | 19.5 | 20.1 | 20.6 | 21.2 | 22.8 | 24.7 | 24.7 | 11.9 |
| Arecaceae | Calamus | | | | | | | | | | | | | | |
| | Livistona | | 21.9 | 5.1 | 13.6 | 14.3 | 15.0 | 17.2 | 24.7 | 26.4 | 27.3 | 27.3 | 27.3 | 27.3 | 12.8 |
| Araliaceae | Polyscias | | 13.1 | 4.5 | 6.7 | 7.0 | 7.6 | 9.4 | 12.5 | 16.7 | 20.6 | 21.6 | 22.0 | 23.8 | 6.3 |
| Bombacaceae (subf. | Adansonia gregorii | 26 | 27.2 | 0.7 | 25.9 | 26.1 | 26.4 | 26.6 | 27.3 | 27.6 | 28.5 | 28.7 | 28.7 | 28.7 | 25.7 |
| Nothofagaceae | Nothofagus sg. Brassospora | | | | | | | | | | | | | 23.5 | 10.6 |
| | Nothofagus sg. Lophozonia (N. cunninghamii, N. moorei) | | 9.7 | 3.1 | 4.6 | 4.8 | 5.3 | 7.3 | 10.2 | 11.4 | 14.1 | 15.2 | 18.1 | 18.1 | 4.4 |
| Epacridaceae | Richea | | 5.8 | 1.5 | 3.4 | 3.8 | 4.1 | 4.8 | 5.5 | 6.7 | 8.0 | 9.3 | 10.0 | 11.8 | 2.8 |
| Eucryphiaceae | Eucryphia | | 10.2 | 2.8 | 5.8 | 6.0 | 6.5 | 8.9 | 10.7 | 12.5 | 14.1 | 15.7 | 16.4 | 16.4 | 5.6 |
| Casuarinaceae | Allocasuarina | | 14.4 | 3.3 | 8.5 | 9.4 | 10.5 | 11.8 | 14.0 | 16.1 | 18.9 | 20.2 | 22.7 | 26.1 | 6.3 |
| | Casuarina | | 18.2 | 3.5 | 12.2 | 12.5 | 13.2 | 15.8 | 17.8 | 21.1 | 23.4 | 24.9 | 26.8 | 27.3 | 10.5 |
| | Gymnostoma australianum | 60 | 23.7 | 2.4 | 18.4 | 18.7 | 19.2 | 23.1 | 24.9 | 25.3 | 25.5 | 25.6 | 25.6 | 25.6 | 17.8 |
| Cunoniaceae | Acsmithia | 61 | 20.0 | 2.6 | 16.5 | 16.6 | 16.7 | 17.1 | 20.7 | 21.4 | 24.0 | 24.4 | 24.5 | 24.5 | 16.4 |
| | Aphanopetalum | 82 | 15.9 | 2.0 | 12.0 | 12.6 | 13.4 | 14.4 | 15.8 | 17.1 | 18.6 | 20.4 | 20.8 | 21.9 | 11.3 |
| | Anodopetalum biglandulsoum | 98 | 9.8 | 1.6 | 6.7 | 7.1 | 7.9 | 8.5 | 9.9 | 11.2 | 11.7 | 12.0 | 12.1 | 12.1 | 6.4 |
| | Bauera | 400 | 11.8 | 3.7 | 5.6 | 6.4 | 7.0 | 9.3 | 11.7 | 13.9 | 17.2 | 18.6 | 19.8 | 21.3 | 4.6 |
| | Caldcluvia | 253 | 18.8 | 2.8 | 13.4 | 13.8 | 14.4 | 16.2 | 19.3 | 20.8 | 21.7 | 23.4 | 24.5 | 25.4 | 13.0 |
| | Callicoma serratifolia | 30 | 14.3 | 1.7 | 11.1 | 11.3 | 11.7 | 13.9 | 14.6 | 15.5 | 16.6 | 17.6 | 17.6 | 17.6 | 11.0 |
| | Ceratopetalum | 410 | 19.9 | 2.9 | 13.2 | 14.3 | 15.7 | 18.2 | 20.2 | 21.5 | 23.8 | 24.7 | 25.2 | 25.6 | 10.7 |
| | Geissois | 118 | 19.9 | 2.0 | 15.2 | 15.7 | 16.5 | 19.2 | 20.6 | 21.1 | 21.8 | 22.6 | 23.3 | 24.3 | 14.6 |
| | Gillbeea | 132 | 21.6 | 1.6 | 19.1 | 19.5 | 20.0 | 20.6 | 21.1 | 22.6 | 24.3 | 24.9 | 25.3 | 25.5 | 18.4 |
| | Pseudoweinmannia lachnocarpa | 82 | 20.9 | 2.6 | 15.6 | 16.0 | 16.6 | 19.7 | 20.9 | 23.4 | 24.5 | 24.8 | 25.0 | 25.1 | 15.3 |
| | Pullea stutzeri | 151 | 20.9 | 1.7 | 18.3 | 18.7 | 19.0 | 19.8 | 20.7 | 21.7 | 23.9 | 24.8 | 25.2 | 25.5 | 16.9 |
| | Schizomeria | 171 | 19.3 | 2.3 | 13.9 | 14.5 | 15.9 | 17.9 | 19.9 | 20.8 | 21.7 | 22.2 | 22.7 | 24.0 | 13.4 |
| | Vesselowskya | 46 | 13.9 | 2.4 | 10.7 | 10.8 | 11.0 | 11.7 | 13.7 | 16.2 | 16.8 | 17.5 | 19.5 | 19.7 | 10.6 |

| | mean temp Cold Qtr | N | MEAN | S.D. | 2.5% | 5% | 10% | 25% | 50% | 75% | 90% | 95% | 97.5% | MAX | MIN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cyatheaceae | Cyathea | | 11.2 | 4.3 | 4.4 | 5.2 | 6.0 | 7.6 | 10.7 | 14.4 | 17.0 | 20.0 | 21.7 | 23.0 | 3.6 |
| Dicksoniaceae | Dicksonia | | 8.6 | 3.5 | 3.4 | 4.0 | 5.0 | 6.2 | 7.9 | 10.2 | 14.5 | 15.7 | 16.3 | 18.0 | 1.7 |
| Gleicheniaceae | Dicranopteris, Diplopterygium, Gleichenia, & Sticherus | | 13.2 | 5.8 | 6.3 | 6.6 | 7.2 | 8.5 | 10.6 | 19.8 | 21.9 | 23.9 | 24.8 | 24.8 | 6.0 |
| | Gleichenia | | 6.3 | 3.7 | 1.2 | 1.4 | 1.7 | 3.0 | 6.8 | 9.7 | 11.5 | 12.1 | 12.2 | 12.2 | 1.0 |
| Pteridaceae | Acrostichum aureum + A. speciosum | | 20.6 | 3.3 | 14.7 | 15.0 | 15.5 | 18.7 | 21.1 | 23.5 | 24.7 | 25.4 | 26.1 | 26.9 | 14.5 |
| Salviniaceae | Azolla filiculoides | | 9.7 | 5.8 | 5.0 | 5.1 | 5.3 | 5.9 | 10.5 | 13.1 | 22.1 | 22.1 | 22.1 | 22.1 | 4.9 |
| Schizeaceae | Lygodium | | 20.7 | 3.1 | 14.4 | 15.1 | 16.0 | 18.7 | 21.4 | 23.0 | 24.0 | 24.8 | 25.2 | 26.8 | 12.7 |
| Cycadaceae | Cycas | | 20.8 | 3.1 | 13.5 | 14.1 | 15.7 | 19.9 | 21.9 | 23.0 | 24.0 | 24.3 | 24.5 | 24.5 | 13.0 |
| Stangeriaceae | Bowenia | | 18.7 | 2.4 | 14.4 | 14.7 | 14.9 | 16.9 | 19.6 | 20.7 | 21.1 | 21.2 | 21.2 | 21.2 | 13.8 |
| Zamiaceae | Lepidozamia | | 18.3 | 2.8 | 11.9 | 12.1 | 12.5 | 17.4 | 19.6 | 20.0 | 20.3 | 20.5 | 21.1 | 21.3 | 11.7 |
| | Macrozamia | | 11.5 | 2.5 | 7.3 | 7.7 | 8.2 | 9.7 | 12.0 | 12.9 | 15.4 | 16.1 | 17.0 | 17.0 | 7.0 |
| Araucariaceae | Agathis atropurpurea, A. microstachya, A. robusta | | 16.1 | 1.8 | 13.0 | 13.5 | 14.1 | 14.8 | 16.0 | 16.9 | 19.1 | 20.1 | 20.6 | 21.2 | 12.1 |
| | Araucaria bidwillii, A. cunninghamii | | 16.4 | 3.8 | 9.4 | 10.9 | 11.7 | 13.2 | 16.3 | 19.7 | 22.3 | 23.2 | 23.6 | 23.6 | 8.0 |
| Cupressaceae / Taxodiaceae | Athrotaxis | | 1.8 | 0.5 | 1.1 | 1.2 | 1.3 | 1.5 | 1.8 | 2.0 | 2.7 | 3.1 | 3.1 | 3.1 | 0.9 |
| | Callitris | | 9.6 | 3.6 | 4.5 | 4.9 | 5.6 | 7.2 | 9.1 | 11.3 | 14.1 | 17.7 | 21.8 | 23.5 | 2.4 |
| Podocarpaceae | Dacrycarpus NZ, NG & Fiji | | | | | | | | | | | | | | |
| | Lagarostrobos franklinii | | 5.2 | 2.3 | 1.8 | 1.9 | 2.1 | 4.1 | 6.6 | 6.9 | 6.9 | 6.9 | 6.9 | 6.9 | 1.8 |
| | Microcachrys | | 0.7 | 0.4 | 0.3 | 0.3 | 0.3 | 0.4 | 0.7 | 1.2 | 1.4 | 1.4 | 1.4 | 1.4 | 0.3 |
| | Phyllocladus asplenifolious | | 5.4 | 3.4 | 1.9 | 2.0 | 2.2 | 2.8 | 4.9 | 7.9 | 12.7 | 13.0 | 13.0 | 13.0 | 1.9 |
| | Podocarpus (Aust. spp.) | | 14.3 | 6.2 | -1.4 | -0.6 | 1.3 | 14.1 | 16.3 | 17.8 | 19.9 | 21.3 | 22.7 | 23.1 | -2.2 |
| | Prumnopitys ladei | | 14.5 | 0.5 | 13.5 | 13.5 | 14.0 | 14.5 | 14.6 | 15.1 | 15.1 | 15.1 | 15.1 | 15.1 | 13.5 |
| | Prumnopitys amara (Sundacarpus amara) | | 16.7 | 1.1 | 15.0 | 15.2 | 15.5 | 16.0 | 16.6 | 17.4 | 18.1 | 20.0 | 20.6 | 20.6 | 14.9 |
| Agavaceae | Cordyline | | 15.5 | 2.7 | 7.7 | 9.0 | 11.0 | 15.3 | 16.2 | 16.8 | 17.3 | 19.6 | 21.9 | 21.9 | 6.4 |
| Arecaceae | Livistona | | 17.8 | 5.7 | 7.2 | 8.2 | 11.8 | 13.2 | 20.1 | 22.9 | 24.3 | 24.7 | 24.7 | 24.7 | 6.3 |
| Araliaceae | Polyscias | | 8.0 | 5.1 | 0.8 | 1.1 | 1.9 | 3.9 | 7.4 | 11.9 | 15.9 | 17.5 | 18.6 | 20.7 | 0.4 |
| Bombacaceae (subf. Bombacoideae of Malvaceae) | Adansonia gregorii | | 22.3 | 1.0 | 19.7 | 20.9 | 21.3 | 21.8 | 22.5 | 22.9 | 23.8 | 24.1 | 24.2 | 24.2 | 19.4 |
| Nothofagaceae | Nothofagus sg. Brassospora | | | | | | | | | | | | | | |
| | Nothofagus Lophozonia (N. cunninghamii, N. moorei) | | 5.2 | 3.0 | 1.0 | 1.2 | 1.5 | 2.6 | 5.1 | 8.0 | 9.5 | 9.9 | 12.1 | 12.3 | 0.8 |
| Epacridaceae | Richea | | 1.7 | 1.7 | -1.1 | -0.7 | -0.3 | 0.7 | 1.5 | 2.7 | 4.2 | 5.2 | 6.4 | 7.4 | -1.8 |
| Eucryphiaceae | Eucryphia | | 5.8 | 2.4 | 2.0 | 2.5 | 2.9 | 3.8 | 5.8 | 7.2 | 9.6 | 12.5 | 12.5 | 12.5 | 1.6 |
| Casuarinaceae | Allocasuarina | | 9.1 | 3.6 | 3.1 | 3.8 | 4.8 | 6.4 | 8.7 | 11.0 | 13.4 | 15.5 | 18.7 | 24.3 | 2.5 |
| | Casuarina | | 12.5 | 4.3 | 5.6 | 6.1 | 7.1 | 9.8 | 11.7 | 16.3 | 18.9 | 20.4 | 23.9 | 24.5 | 5.1 |
| | Gymnostoma australianum | | 20.5 | 2.5 | 15.0 | 15.3 | 15.8 | 19.8 | 21.7 | 22.1 | 22.4 | 22.4 | 22.5 | 22.5 | 14.4 |
| Cunoniaceae | Acsmithia | | 16.2 | 2.6 | 12.7 | 12.7 | 12.9 | 13.3 | 16.7 | 17.6 | 20.0 | 20.6 | 20.9 | 21.0 | 12.6 |
| | Aphanopetalum | | 10.4 | 2.3 | 6.1 | 7.0 | 7.9 | 8.6 | 10.5 | 11.5 | 13.5 | 14.8 | 15.3 | 17.8 | 5.3 |
| | Anodopetalum biglandulsoum | | 6.2 | 1.8 | 2.9 | 3.1 | 3.9 | 4.4 | 6.1 | 8.1 | 8.7 | 8.9 | 9.0 | 9.1 | 2.6 |
| | Bauera | | 7.7 | 3.4 | 1.8 | 2.5 | 3.1 | 5.0 | 7.7 | 9.6 | 12.8 | 14.5 | 15.5 | 16.4 | 0.9 |
| | Caldcluvia | | 14.3 | 3.5 | 7.6 | 8.1 | 9.1 | 11.7 | 15.0 | 16.9 | 18.4 | 20.2 | 21.3 | 22.2 | 7.1 |
| | Callicoma serratifolia | | 9.2 | 1.9 | 5.5 | 5.6 | 5.9 | 8.4 | 9.3 | 10.6 | 11.7 | 12.1 | 12.2 | 12.2 | 5.3 |
| | Ceratopetalum | | 16.0 | 3.6 | 7.7 | 9.0 | 10.8 | 14.1 | 16.4 | 17.9 | 20.3 | 21.5 | 22.1 | 22.5 | 5.5 |
| | Geissois | | 15.8 | 2.3 | 10.7 | 11.1 | 12.0 | 14.9 | 16.4 | 17.3 | 18.1 | 19.2 | 20.4 | 20.8 | 10.4 |
| | Gillbeea | | 17.9 | 1.8 | 15.3 | 15.7 | 16.1 | 16.8 | 17.4 | 19.0 | 21.0 | 21.7 | 22.2 | 22.4 | 14.3 |
| | Pseudoweinmannia | | 16.9 | 3.1 | 11.2 | 11.6 | 12.2 | 14.6 | 17.2 | 19.5 | 21.2 | 21.7 | 21.9 | 22.0 | 10.8 |
| | Pullea stutzeri | | 17.1 | 1.9 | 14.2 | 14.6 | 15.1 | 15.9 | 16.7 | 18.0 | 19.9 | 21.6 | 22.1 | 22.4 | 13.0 |
| | Schizomeria | | 14.9 | 2.7 | 8.8 | 9.5 | 10.5 | 13.2 | 15.8 | 16.9 | 17.9 | 18.5 | 19.1 | 20.6 | 8.2 |
| | Vesselowskya | | 8.4 | 2.1 | 5.3 | 5.5 | 5.9 | 6.6 | 8.1 | 10.3 | 11.0 | 11.7 | 13.6 | 13.8 | 5.1 |
| Elaeocarpaceae | Aceratium | | 17.6 | 2.2 | 15.0 | 15.2 | 15.4 | 15.9 | 17.0 | 19.4 | 21.2 | 22.0 | 22.3 | 22.5 | 14.3 |
| | Elaeocarpus | | 11.1 | 4.4 | 3.1 | 3.6 | 4.6 | 7.8 | 11.7 | 14.3 | 16.6 | 18.9 | 21.7 | 24.0 | 2.6 |
| | Sloanea | | 12.6 | 2.2 | 9.3 | 9.5 | 9.9 | 10.6 | 12.5 | 14.5 | 15.5 | 16.5 | 16.9 | 17.0 | 9.0 |
| Sterculiaceae | Brachychiton | | 14.6 | 6.0 | 5.2 | 5.6 | 6.4 | 9.7 | 14.3 | 20.3 | 22.7 | 24.1 | 25.1 | 25.2 | 4.8 |
| Aquifoliaceae | Ilex arnhemensis | | 22.4 | 1.7 | 17.7 | 18.3 | 20.2 | 21.8 | 22.8 | 23.6 | 24.4 | 24.6 | 24.7 | 24.7 | 17.2 |
| Proteaceae | Banksia | | 9.8 | 4.3 | 2.5 | 3.1 | 4.3 | 6.4 | 10.0 | 12.1 | 14.9 | 17.9 | 20.4 | 24.4 | -0.1 |
| | Carnarvonia araliifolia | | 16.7 | 2.0 | 14.2 | 14.3 | 14.4 | 14.7 | 16.2 | 18.2 | 19.9 | 20.4 | 20.5 | 20.5 | 14.1 |
| | Conospermum | | 11.1 | 2.4 | 5.4 | 6.4 | 7.5 | 9.5 | 11.4 | 12.7 | 14.2 | 14.7 | 15.7 | 16.9 | -3.5 |
| | Darlingia | | 14.5 | 0.9 | 13.1 | 13.2 | 13.3 | 14.1 | 14.7 | 15.2 | 15.7 | 15.7 | 15.7 | 15.7 | 13.1 |
| | Gevuina + Hicksbeachia | | 15.3 | 1.6 | 12.6 | 12.8 | 13.3 | 14.2 | 15.3 | 16.2 | 17.2 | 18.6 | 19.9 | 21.4 | 11.4 |
| | Helicia | | 18.6 | 3.5 | 12.8 | 13.9 | 14.6 | 15.9 | 17.5 | 21.5 | 24.3 | 24.9 | 25.2 | 25.5 | 11.0 |
| | Isopogon | | | | | | | | | | | | | | |
| | Lambertia | | | | | | | | | | | | | | |
| | Musgravea & Austromuellera | | 17.7 | 2.6 | 12.9 | 13.8 | 14.1 | 15.3 | 18.5 | 20.3 | 20.9 | 21.1 | 21.2 | 21.2 | 11.9 |
| | Orites | | 6.5 | 5.8 | -0.8 | -0.5 | 0.1 | 1.6 | 3.8 | 11.8 | 14.5 | 15.8 | 16.4 | 20.9 | -1.1 |
| | Petrophile | | 11.1 | 2.1 | 6.0 | 6.5 | 7.8 | 10.0 | 11.2 | 12.4 | 13.6 | 14.5 | 15.1 | 16.2 | 4.7 |

| | mean temp Warm Qtr | N | MEAN | S.D. | 2.5% | 5% | 10% | 25% | 50% | 75% | 90% | 95% | 97.5% | MAX | MIN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cyatheaceae | Cyathea | | 20.0 | 3.5 | 13.9 | 14.6 | 15.3 | 17.1 | 20.5 | 22.6 | 24.5 | 26.2 | 27.2 | 27.9 | 13.2 |
| Dicksoniaceae | Dicksonia | | 18.1 | 3.3 | 12.1 | 13.2 | 13.8 | 15.3 | 18.2 | 20.7 | 22.6 | 23.7 | 24.6 | 25.2 | 10.1 |
| Gleicheniaceae | Dicranopteris, Diplopterygium, Gleichenia, & Sticherus | | 21.5 | 4.6 | 13.9 | 14.2 | 14.7 | 18.2 | 21.5 | 25.9 | 26.7 | 27.0 | 28.6 | 30.4 | 13.7 |
| | Gleichenia | | 15.2 | 3.3 | 9.2 | 9.7 | 10.3 | 13.6 | 15.8 | 17.8 | 19.7 | 20.1 | 20.2 | 20.2 | 8.3 |
| Pteridaceae | Acrostichum aureum + A. speciosum | | 27.3 | 2.3 | 23.3 | 23.6 | 24.1 | 25.7 | 27.4 | 29.1 | 30.8 | 31.2 | 31.4 | 31.4 | 22.2 |
| Salviniaceae | Azolla filiculoides | | 9.7 | 5.8 | 5.0 | 5.1 | 5.3 | 5.9 | 10.5 | 13.1 | 22.1 | 22.1 | 22.1 | 22.1 | 4.9 |
| Schizeaceae | Lygodium | | 27.1 | 1.9 | 23.1 | 23.5 | 24.2 | 25.9 | 27.6 | 28.3 | 29.6 | 30.3 | 30.7 | 31.0 | 22.3 |
| Cycadaceae | Cycas | | 27.9 | 2.4 | 23.1 | 23.2 | 23.5 | 27.2 | 28.6 | 29.5 | 30.3 | 31.1 | 31.1 | 31.1 | 22.9 |
| Stangeriaceae | Bowenia | | 25.0 | 2.0 | 20.4 | 21.5 | 22.1 | 23.7 | 25.8 | 26.6 | 27.1 | 27.3 | 27.3 | 27.3 | 19.9 |
| Zamiaceae | Lepidozamia | | 25.3 | 1.9 | 20.9 | 21.1 | 21.3 | 23.9 | 26.1 | 26.7 | 27.0 | 27.0 | 27.1 | 27.1 | 20.8 |
| | Macrozamia | | 22.3 | 2.0 | 18.1 | 18.7 | 19.6 | 20.9 | 22.8 | 23.9 | 25.1 | 25.3 | 25.9 | 26.3 | 17.5 |
| Araucariaceae | Agathis atropurpurea, A. microstachya, A. robusta | | 23.2 | 1.5 | 20.8 | 21.0 | 21.4 | 22.2 | 23.0 | 23.8 | 25.4 | 26.6 | 26.8 | 27.0 | 19.3 |
| | Araucaria bidwillii, A. cunninghamii | | 24.3 | 2.0 | 19.9 | 20.5 | 22.0 | 23.1 | 24.2 | 25.7 | 27.0 | 27.4 | 27.6 | 27.6 | 19.4 |
| Cupressaceae / Taxodiaceae | Athrotaxis | | 9.7 | 0.5 | 9.2 | 9.3 | 9.3 | 9.4 | 9.7 | 9.8 | 10.6 | 11.2 | 11.2 | 11.2 | 9.2 |
| | Callitris | | 21.1 | 3.1 | 15.4 | 16.1 | 17.0 | 18.8 | 21.3 | 23.2 | 25.1 | 26.6 | 28.9 | 30.3 | 13.0 |
| Podocarpaceae | Dacrycarpus NZ, NG & Fiji | | | | | | | | | | | | | | |
| | Lagarostrobos franklinii | | 12.8 | 2.4 | 9.3 | 9.3 | 9.5 | 11.7 | 14.2 | 14.6 | 14.7 | 14.7 | 14.7 | 14.7 | 9.2 |
| | Microcachrys | | 8.3 | 0.5 | 7.8 | 7.8 | 7.8 | 7.9 | 8.4 | 8.5 | 9.2 | 9.2 | 9.2 | 9.2 | 7.8 |
| | Phyllocladus asplenifolious | | 12.5 | 2.1 | 9.8 | 9.8 | 9.9 | 10.2 | 12.5 | 14.6 | 16.0 | 16.0 | 16.0 | 16.0 | 9.7 |
| | Podocarpus (Aust. spp.) | | 22.0 | 4.7 | 9.8 | 10.6 | 12.2 | 22.1 | 23.1 | 24.6 | 26.4 | 27.3 | 27.7 | 28.0 | 7.6 |
| | Prumnopitys ladei | | 21.4 | 0.5 | 20.5 | 20.5 | 20.9 | 21.3 | 21.5 | 21.9 | 22.0 | 22.0 | 22.0 | 22.0 | 20.5 |
| | Prumnopitys amara (Sundacarpus amara) | | 23.7 | 0.9 | 22.2 | 22.4 | 22.6 | 23.1 | 23.8 | 24.3 | 24.8 | 26.3 | 26.8 | 26.8 | 22.1 |
| Agavaceae | Cordyline | | 22.8 | 2.0 | 16.9 | 18.3 | 19.2 | 22.7 | 23.1 | 23.6 | 24.7 | 25.8 | 26.7 | 27.1 | 15.9 |
| Arecaceae | Livistona | | 25.9 | 4.3 | 19.4 | 19.6 | 19.8 | 20.5 | 28.6 | 29.7 | 30.9 | 30.9 | 30.9 | 30.9 | 19.3 |
| Araliaceae | Polyscias | | 18.0 | 3.7 | 12.7 | 13.0 | 13.5 | 14.9 | 17.6 | 20.5 | 24.3 | 25.3 | 26.3 | 26.4 | 12.5 |
| Bombacaceae (subf. Bombacoideae of Malvaceae) | Adansonia gregorii | | 30.6 | 0.8 | 29.4 | 29.5 | 29.5 | 30.3 | 30.7 | 31.2 | 31.8 | 32.0 | 32.0 | 32.0 | 29.4 |
| Nothofagaceae | Nothofagus sg. Brassospora | | | | | | | | | | | | | | |
| | Nothofagus Lophozonia (N. cunninghamii, N. moorei) | | 14.2 | 3.2 | 8.7 | 9.2 | 9.9 | 11.9 | 14.3 | 16.6 | 18.1 | 18.6 | 23.2 | 23.2 | 8.3 |
| Epacridaceae | Richea | | 10.1 | 1.7 | 7.7 | 7.9 | 8.3 | 9.0 | 9.9 | 11.1 | 13.0 | 13.7 | 14.4 | 16.3 | 6.8 |
| Eucryphiaceae | Eucryphia | | 14.7 | 3.2 | 9.4 | 9.6 | 10.0 | 12.4 | 15.7 | 17.3 | 19.1 | 19.6 | 19.7 | 19.7 | 9.1 |
| Casuarinaceae | Allocasuarina | | 19.5 | 3.3 | 13.4 | 14.4 | 15.4 | 17.3 | 19.2 | 21.5 | 24.4 | 25.5 | 26.8 | 29.0 | 10.4 |
| | Casuarina | | 23.6 | 2.9 | 18.3 | 19.1 | 19.9 | 21.0 | 23.9 | 26.1 | 27.3 | 27.8 | 28.4 | 29.3 | 15.5 |
| | Gymnostoma australianum | | 26.2 | 2.3 | 21.1 | 21.5 | 21.9 | 25.6 | 27.4 | 27.7 | 27.9 | 28.0 | 28.0 | 28.1 | 20.6 |
| Cunoniaceae | Acsmithia | | 23.0 | 2.6 | 19.5 | 19.6 | 19.7 | 20.2 | 23.7 | 24.7 | 26.9 | 27.2 | 27.3 | 27.4 | 19.5 |
| | Aphanopetalum | | 20.9 | 1.9 | 17.5 | 17.7 | 18.6 | 19.7 | 21.0 | 22.1 | 23.4 | 24.7 | 25.1 | 25.3 | 17.2 |
| | Anodopetalum biglandulsoum | | 13.5 | 1.4 | 10.8 | 11.1 | 11.9 | 12.6 | 13.8 | 14.6 | 15.5 | 15.7 | 15.8 | 15.8 | 10.3 |
| | Bauera | | 15.9 | 3.8 | 9.6 | 10.4 | 11.0 | 13.4 | 15.3 | 18.6 | 21.8 | 23.1 | 23.9 | 25.6 | 8.6 |
| | Caldcluvia | | 22.5 | 2.2 | 18.4 | 18.8 | 19.2 | 21.0 | 23.0 | 23.9 | 24.9 | 26.1 | 26.8 | 27.9 | 17.7 |
| | Callicoma serratifolia | | 19.1 | 1.6 | 16.5 | 16.6 | 16.8 | 18.1 | 19.5 | 20.1 | 21.4 | 22.7 | 22.7 | 22.7 | 16.3 |
| | Ceratopetalum | | 23.3 | 2.3 | 18.3 | 19.2 | 20.0 | 22.0 | 23.4 | 24.2 | 26.5 | 27.3 | 27.7 | 28.0 | 15.8 |
| | Geissois | | 23.2 | 1.7 | 19.0 | 19.4 | 20.1 | 22.8 | 23.7 | 24.2 | 24.5 | 25.6 | 26.3 | 27.2 | 18.3 |
| | Gillbeea | | 24.6 | 1.5 | 22.3 | 22.6 | 23.1 | 23.7 | 24.1 | 25.7 | 27.2 | 27.6 | 27.9 | 28.0 | 21.6 |
| | Pseudoweinmannia | | 24.2 | 2.2 | 19.5 | 19.8 | 20.3 | 23.6 | 24.3 | 26.1 | 27.0 | 27.3 | 27.5 | 27.6 | 19.2 |
| | Pullea stutzeri | | 23.9 | 1.6 | 21.6 | 21.8 | 22.1 | 23.0 | 23.7 | 24.6 | 26.6 | 27.3 | 27.7 | 28.0 | 19.9 |
| | Schizomeria | | 23.0 | 1.8 | 18.7 | 19.5 | 20.1 | 22.2 | 23.4 | 24.1 | 24.9 | 25.4 | 25.8 | 26.8 | 17.6 |
| | Vesselowskya | | 19.0 | 2.7 | 15.3 | 15.4 | 15.6 | 16.4 | 18.7 | 21.6 | 22.6 | 23.4 | 24.6 | 24.7 | 15.2 |
| Elaeocarpaceae | Aceratium | | 24.3 | 1.9 | 21.8 | 21.9 | 22.1 | 22.7 | 23.7 | 26.2 | 27.4 | 27.7 | 28.0 | 28.2 | 21.7 |
| | Elaeocarpus | | 20.1 | 3.2 | 14.4 | 14.7 | 15.4 | 17.9 | 20.5 | 22.2 | 24.2 | 25.6 | 26.2 | 26.3 | 13.1 |
| | Sloanea | | 21.9 | 2.0 | 18.6 | 18.8 | 19.1 | 19.8 | 22.3 | 23.7 | 24.2 | 24.3 | 24.3 | 24.3 | 18.5 |
| Sterculiaceae | Brachychiton | | 24.7 | 4.1 | 17.9 | 18.2 | 18.8 | 21.6 | 24.6 | 28.2 | 30.5 | 30.9 | 31.0 | 31.1 | 17.6 |
| Aquifoliaceae | Ilex arnhemensis | | 28.5 | 1.5 | 24.3 | 24.8 | 25.9 | 28.3 | 28.8 | 29.4 | 30.0 | 30.8 | 31.2 | 31.4 | 23.5 |
| Proteaceae | Banksia | | 19.6 | 3.8 | 13.2 | 13.8 | 15.1 | 17.0 | 19.0 | 22.4 | 25.2 | 26.6 | 27.3 | 31.4 | 11.2 |
| | Carnarvonia araliifolia | | 23.5 | 1.7 | 21.3 | 21.4 | 21.5 | 22.1 | 23.3 | 24.9 | 26.5 | 26.6 | 26.6 | 26.6 | 21.2 |
| | Conospermum | | 21.3 | 2.8 | 16.0 | 17.3 | 17.8 | 19.1 | 21.1 | 23.9 | 25.2 | 25.6 | 26.6 | 27.7 | 6.8 |
| | Darlingia | | 21.8 | 0.7 | 20.6 | 20.6 | 20.7 | 21.5 | 21.8 | 22.4 | 22.6 | 22.6 | 22.6 | 22.6 | 20.6 |
| | Gevuina + Hicksbeachia | | 22.9 | 1.2 | 21.0 | 21.3 | 21.5 | 22.1 | 22.8 | 23.4 | 24.2 | 25.3 | 26.7 | 27.2 | 19.8 |
| | Helicia | | 25.1 | 2.6 | 20.8 | 21.4 | 22.1 | 23.1 | 24.3 | 27.5 | 29.1 | 29.6 | 30.1 | 30.6 | 18.8 |
| | Isopogon | | | | | | | | | | | | | | |
| | Lambertia | | | | | | | | | | | | | | |
| | Musgravea & Austromuellera | | 24.3 | 2.2 | 20.1 | 20.9 | 21.1 | 22.2 | 25.0 | 26.1 | 26.9 | 27.1 | 27.2 | 27.2 | 19.3 |
| | Orites | | 14.3 | 5.7 | 7.4 | 7.6 | 7.9 | 9.1 | 11.5 | 20.1 | 21.9 | 22.6 | 22.9 | 26.9 | 7.2 |
| | Petrophile | | 21.7 | 2.6 | 17.1 | 17.5 | 18.1 | 19.5 | 21.7 | 24.0 | 25.2 | 25.9 | 26.5 | 29.5 | 15.9 |
| | Stenocarpus | | 24.3 | 2.9 | 18.9 | 19.9 | 20.7 | 22.3 | 23.8 | 26.6 | 28.9 | 29.6 | 30.4 | 31.2 | 17.6 |
| | Symphionema | | 17.6 | 1.6 | 15.0 | 15.4 | 15.9 | 16.2 | 17.5 | 19.2 | 20.1 | 20.2 | 20.2 | 20.2 | 14.7 |

| | MAP | N | MEAN | S.D. | 2.5% | 5% | 10% | 25% | 50% | 75% | 90% | 95% | 97.5% | MAX | MIN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cyatheaceae | Cyathea | | 1558 | 732 | 621 | 666 | 757 | 1028 | 1365 | 1927 | 2648 | 3135 | 3587 | 5086 | 576 |
| Dicksoniaceae | Dicksonia | | 1297 | 689 | 455 | 501 | 592 | 864 | 1159 | 1550 | 2099 | 2727 | 3683 | 5148 | 410 |
| Gleicheniaceae | Dicranopteris, Diplopterygium, Gleichenia, & Sticherus | | 1578 | 1073 | 594 | 623 | 681 | 855 | 1212 | 1905 | 2959 | 4996 | 5476 | 5659 | 565 |
| | Gleichenia | | 1467 | 561 | 918 | 932 | 961 | 1045 | 1217 | 2176 | 2430 | 2579 | 2658 | 2658 | 904 |
| Pteridaceae | Acrostichum aureum + A. speciosum | | 1780 | 957 | 721 | 764 | 849 | 1104 | 1531 | 2288 | 2592 | 3966 | 5425 | 5585 | 678 |
| Salviniaceae | Azolla filiculoides | | 803 | 238 | 571 | 579 | 594 | 639 | 730 | 1145 | 1228 | 1228 | 1228 | 1228 | 564 |
| Schizeaceae | Lygodium | | 1724 | 652 | 710 | 808 | 975 | 1250 | 1668 | 2061 | 2819 | 3180 | 3368 | 4000 | 613 |
| Cycadaceae | Cycas | | 1142 | 348 | 600 | 617 | 651 | 901 | 1180 | 1478 | 1657 | 1737 | 1776 | 1776 | 583 |
| Stangeriaceae | Bowenia | | 1870 | 657 | 1024 | 1076 | 1179 | 1489 | 1774 | 2183 | 3280 | 3821 | 3821 | 3821 | 973 |
| Zamiaceae | Lepidozamia | | 2256 | 694 | 1017 | 1078 | 1200 | 1873 | 2444 | 2654 | 2768 | 3525 | 4015 | 4015 | 956 |
| | Macrozamia | | 1000 | 308 | 608 | 621 | 646 | 722 | 933 | 1314 | 1407 | 1439 | 1956 | 2016 | 596 |
| Araucariaceae | Agathis atropurpurea, A. microstachya, A. robusta | | 2204 | 900 | 933 | 1012 | 1171 | 1601 | 2154 | 2541 | 3107 | 3705 | 6423 | 7025 | 854 |
| | Araucaria bidwillii, A. cunninghamii | | 1399 | 504 | 758 | 790 | 854 | 1046 | 1319 | 1623 | 2310 | 2658 | 2735 | 2770 | 726 |
| Cupressaceae / Tax | Athrotaxis | | 1828 | 363 | 1356 | 1385 | 1445 | 1587 | 1713 | 2101 | 2459 | 2519 | 2519 | 2519 | 1326 |
| | Callitris | | 816 | 492 | 214 | 242 | 297 | 467 | 732 | 1032 | 1541 | 2030 | 2290 | 2469 | 186 |
| Podocarpaceae | Dacrycarpus NZ, NG & Fiji | | | | | 1400 | | | | | | 4500 | | | |
| | Lagarostrobos franklinii | | 1899 | 635 | 1233 | 1243 | 1262 | 1322 | 2012 | 2505 | 2538 | 2538 | 2538 | 2538 | 1223 |
| | Microcachrys | | 2338 | 232 | 1800 | 1815 | 1847 | 2363 | 2442 | 2481 | 2486 | 2486 | 2486 | 2486 | 1784 |
| | Phyllocladus asplenifolious | | 2282 | 1988 | 1211 | 1245 | 1312 | 1513 | 1849 | 2398 | 8406 | 8406 | 8406 | 8406 | 1178 |
| | Podocarpus (Aust. spp.) | | 2126 | 665 | 1071 | 1135 | 1264 | 1534 | 2285 | 2594 | 2815 | 3401 | 3516 | 3601 | 1007 |
| | Prumnopitys ladei | | 2556 | 408 | 2126 | 2141 | 2170 | 2345 | 2418 | 3179 | 3179 | 3179 | 3179 | 3179 | 2111 |
| | Prumnopitys amara (Sundacarpus amara) | | 1724 | 369 | 1284 | 1300 | 1332 | 1433 | 1725 | 1871 | 2319 | 2776 | 2791 | 2791 | 1268 |
| Agavaceae | Cordyline | | 1599 | 463 | 1055 | 1167 | 1202 | 1306 | 1490 | 1742 | 2432 | 2650 | 3437 | 3437 | 910 |
| Arecaceae | Livistona | | 1039 | 343 | 521 | 549 | 605 | 746 | 1196 | 1337 | 1506 | 1618 | 1618 | 1618 | 492 |
| Araliaceae | Polyscias | | 1572 | 1273 | 744 | 769 | 819 | 968 | 1216 | 1635 | 2627 | 5726 | 6748 | 7532 | 719 |
| Bombacaceae (subf | Adansonia gregorii | | 747 | 183 | 550 | 560 | 579 | 626 | 699 | 790 | 1129 | 1129 | 1129 | 1129 | 540 |
| Nothofagaceae | Nothofagus sg. Brassospora | | | | | 1762 | | | | | | 5039 | | 7733 | 1762 |
| | Nothofagus Lophozonia (N. cunninghamii, N. moorei) | | 1798 | 446 | 1031 | 1104 | 1342 | 1461 | 1767 | 2083 | 2646 | 2756 | 2810 | 2818 | 958 |
| Epacridaceae | Richea | | 1689 | 485 | 827 | 903 | 1073 | 1382 | 1597 | 2037 | 2398 | 2468 | 2674 | 2902 | 751 |
| Eucryphiaceae | Eucryphia | | 1634 | 888 | 943 | 968 | 1018 | 1167 | 1424 | 1822 | 2701 | 5424 | 5737 | 5737 | 918 |
| Casuarinaceae | Allocasuarina | | 945 | 452 | 235 | 285 | 385 | 600 | 881 | 1182 | 1560 | 1815 | 1988 | 3093 | 185 |
| | Casuarina | | 809 | 469 | 174 | 199 | 250 | 437 | 706 | 1159 | 1589 | 1720 | 1905 | 2134 | 149 |
| | Gymnostoma australianum | | 3183 | 385 | 2360 | 2397 | 2484 | 3156 | 3366 | 3421 | 3454 | 3465 | 3471 | 3472 | 2323 |
| Cunoniaceae | Acsmithia | | 3921 | 1979 | 1842 | 1894 | 1998 | 2310 | 2923 | 6440 | 6771 | 6882 | 6937 | 6957 | 1253 |
| | Aphanopetalum | | 1034 | 352 | 519 | 617 | 692 | 846 | 967 | 1150 | 1477 | 1795 | 2194 | 2400 | 416 |
| | Anodopetalum biglandulsoum | | 2997 | 478 | 2143 | 2227 | 2357 | 2541 | 3253 | 3350 | 3407 | 3427 | 3436 | 3440 | 1230 |
| | Bauera | | 1374 | 527 | 605 | 674 | 812 | 972 | 1273 | 1650 | 2154 | 2581 | 2747 | 3363 | 536 |
| | Caldcluvia | | 1867 | 826 | 839 | 921 | 1085 | 1450 | 1751 | 2120 | 2527 | 2998 | 4198 | 6957 | 757 |
| | Callicoma serratifolia | | 1398 | 411 | 997 | 1018 | 1062 | 1167 | 1268 | 1555 | 2146 | 2673 | 2673 | 2673 | 975 |
| | Ceratopetalum | | 2126 | 815 | 696 | 913 | 1147 | 1572 | 2089 | 2595 | 3183 | 3671 | 4134 | 6200 | 478 |
| | Geissois | | 1818 | 480 | 1185 | 1218 | 1284 | 1468 | 1704 | 2166 | 2428 | 2515 | 3664 | 3935 | 1152 |
| | Gillbeea | | 2311 | 587 | 1364 | 1414 | 1514 | 1870 | 2319 | 2640 | 3225 | 3513 | 3940 | 4161 | 1315 |
| | Pseudoweinmannia | | 1827 | 645 | 1023 | 1085 | 1207 | 1431 | 1733 | 2164 | 2579 | 3439 | 4040 | 4215 | 962 |
| | Pullea | | 2131 | 787 | 1136 | 1191 | 1302 | 1621 | 1988 | 2464 | 3230 | 3691 | 4254 | 6200 | 1080 |
| | Schizomeria | | 1707 | 377 | 960 | 1061 | 1235 | 1455 | 1679 | 2010 | 2222 | 2299 | 2440 | 3018 | 672 |
| | Vesselowskya | | 1331 | 169 | 1064 | 1114 | 1158 | 1224 | 1302 | 1461 | 1596 | 1646 | 1653 | 1653 | 800 |
| Elaeocarpaceae | Aceratium | | 2223 | 535 | 1228 | 1396 | 1629 | 1914 | 2184 | 2446 | 2994 | 3444 | 3645 | 4013 | 1002 |
| | Elaeocarpus | | 1725 | 1038 | 650 | 693 | 778 | 1033 | 1518 | 2116 | 2607 | 3643 | 6051 | 6281 | 0 |
| | Sloanea | | 1524 | 400 | 908 | 960 | 1064 | 1210 | 1519 | 1792 | 2095 | 2459 | 2490 | 2490 | 724 |
| Sterculiaceae | Brachychiton | | 979 | 781 | 256 | 311 | 421 | 705 | 911 | 1118 | 1532 | 2073 | 4716 | 4972 | 201 |
| Aquifoliaceae | Ilex arnhemensis | | 1302 | 373 | 659 | 735 | 863 | 1080 | 1228 | 1443 | 1705 | 2271 | 2425 | 2885 | 582 |
| Proteaceae | Banksia | | 1006 | 499 | 273 | 314 | 396 | 656 | 921 | 1225 | 1693 | 2173 | 2436 | 2685 | 232 |
| | Carnarvonia araliifolia | | 2076 | 692 | 1094 | 1145 | 1247 | 1734 | 2054 | 2587 | 3081 | 3949 | 4054 | 4054 | 1044 |
| | Conospermum | | 792 | 368 | 232 | 270 | 346 | 492 | 705 | 1070 | 1320 | 1469 | 1607 | 2394 | 194 |

| | pptCold Qtr | N | MEAN | S.D. | 2.5% | 5% | 10% | 25% | 50% | 75% | 90% | 95% | 97.5% | MAX | MIN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cyatheacea | Cyathea | | 267 | 113 | 60 | 94 | 134 | 192 | 258 | 333 | 419 | 475 | 549 | 699 | 20 |
| Dicksoniac | Dicksonia | | 289 | 130 | 113 | 124 | 146 | 188 | 264 | 377 | 491 | 549 | 616 | 692 | 102 |
| Gleichenia | Dicranopteris, Diplopterygium, Gleichenia, & Sticherus | | 249 | 164 | 19 | 37 | 72 | 141 | 219 | 317 | 490 | 650 | 756 | 843 | 2 |
| | Gleichenia | | 411 | 206 | 200 | 205 | 216 | 249 | 323 | 665 | 772 | 794 | 801 | 801 | 194 |
| Pteridacea | Acrostichum aureum + A. speciosum | | 123 | 112 | 7 | 10 | 16 | 35 | 134 | 169 | 295 | 383 | 426 | 440 | 3 |
| Salviniace | Azolla filiculoides | | 146 | 73 | 26 | 32 | 43 | 112 | 153 | 191 | 274 | 274 | 274 | 274 | 20 |
| Schizeacea | Lygodium | | 107 | 93 | 6 | 9 | 15 | 33 | 100 | 151 | 258 | 304 | 347 | 441 | 3 |
| Cycadacea | Cycas | | 38 | 46 | 4 | 4 | 6 | 10 | 18 | 46 | 132 | 148 | 164 | 164 | 3 |
| Stangeriac | Bowenia | | 141 | 101 | 54 | 57 | 61 | 75 | 106 | 174 | 346 | 467 | 467 | 467 | 52 |
| Zamiaceae | Lepidozamia | | 199 | 88 | 46 | 53 | 66 | 155 | 190 | 278 | 324 | 359 | 380 | 380 | 39 |
| | Macrozamia | | 191 | 100 | 95 | 99 | 108 | 133 | 172 | 216 | 369 | 451 | 513 | 532 | 91 |
| Araucariac | Agathis atropurpurea, A. microstachya, A. robusta | | 239 | 144 | 43 | 56 | 84 | 151 | 232 | 295 | 336 | 439 | 946 | 1042 | 29 |
| | Araucaria bidwillii, A. cunninghamii | | 130 | 84 | 18 | 21 | 28 | 55 | 123 | 179 | 279 | 307 | 321 | 321 | 14 |
| Cupressac | Athrotaxis | | 550 | 136 | 408 | 413 | 421 | 449 | 509 | 627 | 799 | 809 | 809 | 809 | 404 |
| | Callitris | | 163 | 84 | 25 | 47 | 64 | 103 | 148 | 207 | 272 | 336 | 409 | 490 | 4 |
| Podocarpa | Dacrycarpus NZ, NG & Fiji | | | | | | | | | | | | | | |
| | Lagarostrobos franklinii | | 585 | 214 | 366 | 370 | 377 | 398 | 599 | 836 | 836 | 836 | 836 | 836 | 363 |
| | Microcachrys | | 712 | 93 | 504 | 510 | 524 | 706 | 739 | 772 | 790 | 790 | 790 | 790 | 497 |
| | Phyllocladus asplenifolious | | 556 | 185 | 386 | 389 | 393 | 406 | 428 | 756 | 857 | 857 | 857 | 857 | 384 |
| | Podocarpus (Aust. spp.) | | 271 | 144 | 31 | 50 | 87 | 187 | 268 | 344 | 454 | 576 | 725 | 762 | 12 |
| | Prumnopitys ladei | | 269 | 59 | 205 | 207 | 212 | 237 | 247 | 357 | 357 | 357 | 357 | 357 | 203 |
| | Prumnopitys amara (Sundacarpus amara) | | 154 | 56 | 86 | 88 | 94 | 111 | 145 | 178 | 241 | 321 | 323 | 323 | 83 |
| Agavaceae | Cordyline | | 152 | 80 | 72 | 75 | 79 | 94 | 121 | 190 | 280 | 367 | 405 | 417 | 70 |
| Arecaceae | Livistona | | 101 | 120 | 4 | 6 | 10 | 20 | 37 | 207 | 326 | 343 | 343 | 343 | 3 |
| Araliaceae | Polyscias | | 297 | 194 | 54 | 80 | 132 | 178 | 250 | 352 | 538 | 829 | 993 | 1118 | 28 |
| Bombacac | Adansonia gregorii | | 14 | 7 | 5 | 5 | 6 | 9 | 14 | 19 | 26 | 26 | 26 | 26 | 4 |
| Nothofaga | Nothofagus sg. Brassospora | | | | | 235 | | 521 | | 521 | | 1073 | | | |
| | Nothofagus Lophozonia (N. cunninghamii, N. moorei) | | 464 | 136 | 243 | 265 | 311 | 365 | 435 | 573 | 654 | 784 | 805 | 805 | 220 |
| Epacridace | Richea | | 508 | 163 | 240 | 263 | 303 | 406 | 497 | 636 | 761 | 800 | 864 | 868 | 217 |
| Eucryphiac | Eucryphia | | 425 | 195 | 202 | 208 | 220 | 258 | 417 | 534 | 790 | 856 | 878 | 878 | 195 |
| Casuarina | Allocasuarina | | 211 | 98 | 49 | 72 | 108 | 140 | 193 | 260 | 328 | 379 | 468 | 826 | 26 |
| | Casuarina | | 132 | 91 | 10 | 16 | 29 | 62 | 109 | 186 | 279 | 321 | 343 | 493 | 4 |
| | Gymnostoma australianum | | 239 | 52 | 149 | 153 | 162 | 223 | 246 | 259 | 291 | 348 | 379 | 379 | 90 |
| Cunoniace | Acsmithia | | 489 | 328 | 140 | 185 | 196 | 230 | 303 | 922 | 979 | 997 | 1004 | 1004 | 93 |
| | Aphanopetalum | | 178 | 54 | 93 | 102 | 120 | 144 | 170 | 206 | 260 | 293 | 333 | 336 | 27 |
| | Anodopetalum biglandulsoum | | 558 | 186 | 289 | 300 | 321 | 398 | 538 | 686 | 844 | 913 | 986 | 1003 | 279 |
| | Bauera | | 390 | 192 | 145 | 158 | 185 | 248 | 336 | 519 | 686 | 813 | 890 | 1045 | 132 |
| | Caldcluvia | | 211 | 128 | 45 | 56 | 79 | 139 | 198 | 269 | 320 | 389 | 475 | 1004 | 33 |
| | Callicoma serratifolia | | 279 | 61 | 187 | 197 | 211 | 236 | 273 | 316 | 368 | 437 | 452 | 452 | 176 |
| | Ceratopetalum | | 226 | 97 | 87 | 100 | 126 | 173 | 222 | 278 | 312 | 384 | 472 | 876 | 74 |
| | Geissois | | 192 | 84 | 79 | 84 | 93 | 123 | 178 | 248 | 304 | 357 | 428 | 490 | 74 |
| | Gillbeea | | 219 | 80 | 83 | 93 | 112 | 149 | 230 | 274 | 300 | 329 | 454 | 512 | 74 |
| | Pseudoweinmannia | | 173 | 74 | 83 | 91 | 107 | 126 | 150 | 230 | 298 | 329 | 430 | 451 | 75 |
| | Pullea stutzeri | | 202 | 111 | 72 | 79 | 91 | 128 | 189 | 257 | 305 | 398 | 487 | 876 | 66 |
| | Schizomeria | | 199 | 65 | 59 | 92 | 108 | 157 | 199 | 247 | 281 | 306 | 335 | 358 | 20 |
| | Vesselowskya | | 209 | 35 | 146 | 160 | 173 | 193 | 206 | 230 | 255 | 276 | 322 | 326 | 99 |
| Elaeocarpa | Aceratium | | 202 | 69 | 84 | 103 | 115 | 149 | 197 | 242 | 288 | 342 | 379 | 446 | 63 |
| | Elaeocarpus | | 275 | 146 | 92 | 107 | 136 | 198 | 251 | 328 | 417 | 529 | 879 | 912 | 0 |
| | Sloanea | | 225 | 77 | 120 | 132 | 144 | 166 | 210 | 272 | 368 | 396 | 414 | 416 | 108 |
| Sterculiace | Brachychiton | | 111 | 91 | 6 | 8 | 14 | 30 | 106 | 166 | 255 | 313 | 351 | 371 | 3 |
| Aquifoliac | Ilex arnhemensis | | 25 | 55 | 3 | 4 | 6 | 11 | 20 | 29 | 63 | 198 | 244 | 304 | 2 |
| Proteaceae | Banksia | | 236 | 101 | 86 | 96 | 116 | 171 | 222 | 285 | 337 | 428 | 533 | 822 | 4 |

| | pptWarm Qtr | N | MEAN | S.D. | 2.5% | 5% | 10% | 25% | 50% | 75% | 90% | 95% | 97.5% | MAX | MIN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cyatheaceae | Cyathea | | 557 | 357 | 120 | 136 | 168 | 264 | 473 | 774 | 1098 | 1274 | 1430 | 1843 | 104 |
| Dicksoniaceae | Dicksonia | | 393 | 312 | 99 | 108 | 127 | 183 | 293 | 518 | 789 | 1093 | 1436 | 1842 | 90 |
| Gleicheniaceae | Dicranopteris, Diplopterygium, Gleichenia, & Sticherus | | 550 | 502 | 107 | 120 | 147 | 225 | 356 | 751 | 1354 | 1757 | 1995 | 2901 | 94 |
| | Gleichenia | | 312 | 79 | 153 | 165 | 217 | 259 | 318 | 378 | 423 | 471 | 471 | 471 | 141 |
| Pteridaceae | Acrostichum aureum + A. speciosum | | 744 | 438 | 244 | 276 | 341 | 454 | 573 | 1070 | 1280 | 1745 | 2102 | 2165 | 212 |
| Salviniaceae | Azolla filiculoides | | 266 | 146 | 167 | 169 | 173 | 185 | 204 | 371 | 599 | 599 | 599 | 599 | 165 |
| Schizeaceae | Lygodium | | 722 | 318 | 269 | 295 | 349 | 463 | 682 | 952 | 1241 | 1354 | 1429 | 1690 | 242 |
| Cycadaceae | Cycas | | 430 | 159 | 228 | 245 | 278 | 318 | 395 | 501 | 747 | 813 | 880 | 880 | 211 |
| Stangeriaceae | Bowenia | | 892 | 247 | 527 | 565 | 626 | 748 | 874 | 995 | 1393 | 1546 | 1546 | 1546 | 489 |
| Zamiaceae | Lepidozamia | | 1032 | 308 | 537 | 553 | 587 | 831 | 1068 | 1282 | 1344 | 1559 | 1666 | 1714 | 520 |
| | Macrozamia | | 357 | 148 | 53 | 74 | 173 | 266 | 349 | 502 | 570 | 603 | 613 | 613 | 33 |
| Araucariaceae | Agathis atropurpurea, A. microstachya, A. robusta | | 938 | 310 | 469 | 501 | 564 | 742 | 917 | 1068 | 1205 | 1605 | 2188 | 2372 | 438 |
| | Araucaria bidwillii, A. cunninghamii | | 609 | 211 | 320 | 336 | 369 | 475 | 581 | 693 | 989 | 1062 | 1185 | 1269 | 303 |
| Cupressaceae / Taxodiaceae | Athrotaxis | | 323 | 53 | 229 | 232 | 237 | 305 | 324 | 362 | 407 | 414 | 414 | 414 | 226 |
| | Callitris | | 268 | 228 | 51 | 58 | 72 | 115 | 202 | 353 | 617 | 842 | 909 | 1133 | 44 |
| Podocarpaceae | Dacrycarpus NZ, NG & Fiji | | | | | | | | | | | | | | |
| | Lagarostrobos franklinii | | 327 | 100 | 221 | 222 | 225 | 235 | 349 | 435 | 435 | 435 | 435 | 435 | 219 |
| | Microcachrys | | 406 | 28 | 359 | 361 | 364 | 390 | 420 | 432 | 434 | 434 | 434 | 434 | 358 |
| | Phyllocladus asplenifolious | | 511 | 734 | 188 | 195 | 211 | 258 | 336 | 415 | 2829 | 2829 | 2829 | 2829 | 180 |
| | Podocarpus (Aust. spp.) | | 837 | 333 | 275 | 305 | 367 | 560 | 920 | 1074 | 1315 | 1456 | 1514 | 1557 | 244 |
| | Prumnopitys ladei | | 1104 | 121 | 970 | 975 | 983 | 1034 | 1056 | 1278 | 1278 | 1278 | 1278 | 1278 | 966 |
| | Prumnopitys amara (Sundacarpus amara) | | 794 | 125 | 638 | 644 | 656 | 703 | 777 | 848 | 991 | 1144 | 1149 | 1149 | 632 |
| Agavaceae | Cordyline | | 741 | 204 | 263 | 447 | 575 | 634 | 731 | 823 | 954 | 1111 | 1469 | 1573 | 139 |
| Arecaceae | Livistona | | 346 | 117 | 200 | 229 | 244 | 288 | 347 | 384 | 406 | 759 | 759 | 759 | 170 |
| Araliaceae | Polyscias | | 511 | 480 | 146 | 156 | 175 | 232 | 327 | 604 | 1065 | 1895 | 2254 | 2529 | 137 |
| Bombacaceae (subf. Bombacoideae of Malvaceae) | Adansonia gregorii | | 259 | 50 | 198 | 203 | 212 | 224 | 254 | 284 | 339 | 400 | 407 | 407 | 193 |
| Nothofagaceae | Nothofagus sg. Brassospora | | | | | 619 | | 887 | | 887 | | 1230 | | | |
| | Nothofagus sg Lophozonia (N. cunninghamii, N. moorei) | | 461 | 259 | 173 | 187 | 214 | 282 | 383 | 636 | 1011 | 1066 | 1093 | 1097 | 159 |
| Epacridaceae | Richea | | 306 | 76 | 178 | 191 | 215 | 245 | 303 | 360 | 420 | 437 | 473 | 513 | 139 |
| Eucryphiaceae | Eucryphia | | 382 | 304 | 189 | 195 | 207 | 243 | 303 | 363 | 507 | 1879 | 1997 | 1997 | 183 |
| Casuarinaceae | Allocasuarina | | 279 | 207 | 42 | 54 | 79 | 152 | 243 | 363 | 557 | 708 | 835 | 1361 | 30 |
| | Casuarina | | 304 | 240 | 48 | 56 | 72 | 121 | 259 | 405 | 675 | 886 | 928 | 951 | 40 |
| | Gymnostoma australianum | | 1256 | 188 | 910 | 960 | 995 | 1079 | 1359 | 1396 | 1419 | 1426 | 1430 | 1431 | 626 |
| Cunoniaceae | Acsmithia | | 1478 | 621 | 811 | 821 | 843 | 909 | 1247 | 2234 | 2344 | 2380 | 2393 | 2393 | 630 |
| | Aphanopetalum | | 351 | 163 | 76 | 126 | 218 | 257 | 331 | 438 | 547 | 676 | 953 | 960 | 28 |
| | Anodopetalum biglandulsoum | | 314 | 101 | 185 | 199 | 215 | 237 | 291 | 373 | 491 | 530 | 563 | 570 | 171 |
| | Bauera | | 286 | 112 | 95 | 119 | 140 | 196 | 275 | 355 | 447 | 495 | 543 | 629 | 57 |
| | Caldcluvia | | 775 | 304 | 356 | 389 | 455 | 593 | 758 | 889 | 1053 | 1310 | 1632 | 2393 | 323 |
| | Callicoma serratifolia | | 469 | 195 | 285 | 290 | 300 | 331 | 399 | 601 | 855 | 988 | 1008 | 1008 | 280 |
| | Ceratopetalum | | 861 | 342 | 192 | 244 | 348 | 693 | 865 | 1038 | 1381 | 1500 | 1560 | 2170 | 140 |
| | Geissois | | 777 | 167 | 503 | 548 | 595 | 672 | 772 | 875 | 955 | 1034 | 1425 | 1663 | 458 |
| | Gillbeea | | 986 | 219 | 679 | 700 | 742 | 835 | 947 | 1105 | 1339 | 1394 | 1497 | 1728 | 658 |
| | Pseudoweinmannia | | 802 | 278 | 415 | 444 | 500 | 671 | 760 | 908 | 1197 | 1439 | 1741 | 1751 | 387 |
| | Pullea stutzeri | | 921 | 278 | 575 | 601 | 655 | 746 | 838 | 987 | 1388 | 1512 | 1781 | 2170 | 548 |
| | Schizomeria | | 710 | 198 | 308 | 357 | 428 | 566 | 754 | 854 | 943 | 1013 | 1159 | 1224 | 237 |
| | Vesselowskya | | 477 | 77 | 349 | 368 | 384 | 408 | 470 | 531 | 606 | 620 | 628 | 629 | 315 |
| Elaeocarpaceae | Aceratium | | 966 | 214 | 617 | 666 | 722 | 812 | 917 | 1045 | 1273 | 1473 | 1561 | 1709 | 529 |
| | Elaeocarpus | | 645 | 414 | 218 | 231 | 259 | 342 | 572 | 867 | 1117 | 1475 | 2158 | 2169 | 0 |
| | Sloanea | | 619 | 167 | 365 | 382 | 414 | 489 | 635 | 760 | 847 | 925 | 1090 | 1104 | 281 |
| Sterculiaceae | Brachychiton | | 364 | 286 | 62 | 78 | 109 | 203 | 312 | 442 | 616 | 735 | 1599 | 1779 | 47 |
| Aquifoliaceae | Ilex arnhemensis | | 442 | 184 | 234 | 261 | 305 | 336 | 387 | 473 | 658 | 1030 | 1127 | 1175 | 206 |
| Proteaceae | Banksia | | 287 | 255 | 38 | 49 | 71 | 136 | 245 | 366 | 603 | 818 | 1177 | 1277 | 28 |
| | Carnarvonia araliifolia | | 937 | 264 | 563 | 583 | 623 | 794 | 912 | 1086 | 1412 | 1692 | 1734 | 1734 | 543 |
| | Conospermum | | 157 | 166 | 29 | 31 | 37 | 53 | 80 | 299 | 416 | 498 | 570 | 721 | 26 |
| | Darlingia | | 965 | 197 | 776 | 781 | 791 | 819 | 914 | 1224 | 1247 | 1247 | 1247 | 1247 | 772 |
| | Gevuina + Hicksbeachia | | 956 | 212 | 603 | 632 | 689 | 793 | 920 | 1088 | 1237 | 1356 | 1468 | 1735 | 574 |
| | Helicia | | 783 | 256 | 366 | 390 | 440 | 582 | 800 | 947 | 1071 | 1264 | 1416 | 1704 | 341 |
| | Isopogon | | | | | | | | | | | | | | |
| | Lambertia | | | | | | | | | | | | | | |
| | Musgravea & Austromuellera | | 1006 | 284 | 602 | 681 | 716 | 821 | 967 | 1110 | 1311 | 1940 | 2097 | 2097 | 524 |
| | Orites | | 741 | 655 | 181 | 193 | 216 | 287 | 409 | 1058 | 2077 | 2243 | 2395 | 2526 | 169 |
| | Petrophile | | 127 | 150 | 28 | 30 | 35 | 48 | 69 | 90 | 379 | 466 | 556 | 671 | 26 |
| | Stenocarpus | | 739 | 226 | 393 | 461 | 507 | 665 | 794 | 956 | 1166 | 1286 | 1552 | 1739 | 83 |