Climate is the primary framework within which plant populations grow, reproduce and, in the longer time frame, evolve. However, reconstructions of palaeoclimate are often based on the marine record (e.g. Quilty, 1984 and Chapter 3, this volume) or on computer modelling (Sloan & Barron, 1990). The latter type, in particular, suffer from their dependence on simplified scenarios and must be tested against the terrestrial palaeontological record. Individual species and whole plant communities are morphologically and physiologically adapted to their physical environment, most strongly to climate, and so plant macrofossils are a proxy record of past climates (Wolfe, 1971, 1985; Upchurch & Wolfe, 1987). Several studies have indicated that plant macrofossils provide a potentially accurate record of Tertiary terrestrial palaeotemperatures (Wolfe, 1979, 1990; Read et al., 1990). Interpretation of the climatic signal preserved in plant fossil assemblages is dependent on understanding (1) how plants (and vegetation) interact with climate, (2) how plant fossil assemblages were formed, and (3) how these assemblages relate to the original vegetation.

The use of terms such as tropical, subtropical and temperate in palaeoclimatic discussions is potentially confusing, as these terms are rarely defined climatically and have geographical (latitudinal) connotations that are inapplicable for much of the Tertiary. Following Wolfe (1979, 1985; Upchurch & Wolfe, 1987), the terms megathermal, mesothermal and microthermal are used here to describe the temperature characteristics of the vegetation of the main climatic zones. The definitions of Nix (1982; Kershaw & Nix, 1988) are used here, although Wolfe’s (1979, 1985) vegetation classification uses slightly different definitions.

This discussion is restricted to the Tertiary, since pre-Tertiary floras are dominated by plant groups with no or few modern analogues and so palaeobotanical indices of climate are (as yet) unreliable. Numerous accounts of the Tertiary climate history of Australia based on palaeobotanical evidence have been published (Kemp, 1978, 1981; Christophel, 1981, 1988; Nix, 1982; Truswell & Harris, 1982; Christophel & Greenwood, 1989), in some cases as part of global accounts (Axelrod, 1984; Wolfe, 1985). Many of these interpretations have been based solely on nearest-living-relative analogy (NLR) and provide qualitative reconstructions of climate.

Many North American studies have used a strong correlation between the proportion of woody plant species with entire leaf margins and mean annual temperature (MAT) in modern mesic forests (leaf margin analysis, Wolfe, 1979, 1990), and other aspects of foliar morphology, to

* Modified from Nix (1982): megathermal, > 24 °C (MAT); meso-megathermal interzone, 20–24 °C; mesothermal, 14–20 °C (14–24 °C if the interzone is included); microthermal, < 14 °C.
Palaeobotanical evidence for Tertiary climates

reconstruct both the regional distribution of physiognomically defined vegetation types and palaeoclimates for the Late Cretaceous and Tertiary (e.g. Wolfe, 1985; Upchurch & Wolfe, 1987; Parrish & Spicer, 1988). Wolfe (1971, 1979, 1985) has argued that foliar physiognomic approaches are preferred to NLR methodologies, primarily due to inaccurate systematic treatments for many Tertiary floras. However, foliar physiognomic analysis is used here according to the methodology proposed by Greenwood (1991a; Christophel & Greenwood, 1988, 1989), in combination with recent quantitative analyses of key NLRs, of Tertiary taxa (Nix, 1982; Kershaw & Nix, 1988; Read & Hope, 1990; Read et al., 1990) to interpret early Tertiary macrofloras from Australia (Figure 4.1). Wood anatomy (Frakes & Francis, 1990) and epiphyllous fungi found on leaf cuticle (Lange, 1978, 1981, 1982) are other sources of climatic information from plant fossil assemblages. These approaches provide quantitative estimates for critical components of climate that can be tested against estimates from the marine record and climatic models.

THE NATURE OF THE PLANT MACROFOSSIL RECORD

Leaf accumulations in streams or lakes constitute a biased, but nevertheless detailed, record of the parent vegetation. This bias results from a number of processes acting on the plant parts (primarily leaves) from the time of abscission or traumatic loss to their eventual entombment in sediment and lithification (Ferguson, 1985; Spicer, 1989; Greenwood, 1991a):

1. Deciduous and evergreen trees may have different representation in an assemblage if leaf-fall is asynchronous with periods of maximum sedimentation.
2. Different plant species may have leaves that are dehiscent or nondehiscent (e.g. many palms, herbs and forbs). Nondehiscent leaves are less likely to be fossilised than are dehiscent leaves.
3. Plant organs may have varying capacities for transport from the plant body. For example, leaves with a low weight per unit area tend to travel further in air than do denser leaves.
4. Leaves of individual species (e.g. sun versus shade leaves) and different species decay at different rates.
5. The varying productivity of the plants is significant, with canopy trees producing copious amounts of leaves, swamping the litter-fall.

Fossil leaf accumulations therefore reflect only a subset of the original surrounding vegetation, and in most situations represent only the local plant communities (Greenwood, 1991a). Furthermore, smaller plant macrofossil accumulations may represent geologically instantaneous records of past vegetation. Individual sedimentary facies often reflect different components of the local vegetational mosaic (see e.g. Christophel et al.,

Figure 4.1 Location map of Australian Tertiary macrofloras discussed in the text, and modern thermal regimes (adapted from Nix, 1982; Christophel & Greenwood, 1989): 1, Stuart Creek (silcrete floras); 2, Nelly Creek; 3, Golden Grove; 4, Maslin Bay; 5, Nerrija; 6, Bacchus Marsh; 7, Anglesea; 8, Latrobe Valley (Yallourn & Morwell); 9, Pioneer; 10, Cethana; 11, Monpeelyata.
Table 4.1. Foliar physiognomic characteristics of leaf-litter from modern Australian rainforest

**A. Mean % leaves**

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Micro-</th>
<th>Noto-</th>
<th>Mesophylls</th>
<th>% entire leaf margins</th>
</tr>
</thead>
<tbody>
<tr>
<td>CMVF</td>
<td>6–25</td>
<td>50–70</td>
<td>11–39</td>
<td>90.0–98.3</td>
</tr>
<tr>
<td>CNVF</td>
<td>16–55</td>
<td>35–77</td>
<td>2–22</td>
<td>34.3–57.0</td>
</tr>
<tr>
<td>SNVF</td>
<td>59–85</td>
<td>14–36</td>
<td>0–11</td>
<td>87.0–95.3 (Qld)</td>
</tr>
<tr>
<td>MV-FF</td>
<td>74–80</td>
<td>19–24</td>
<td>1–2</td>
<td>56.7–96.4</td>
</tr>
<tr>
<td>MFF</td>
<td>90–96</td>
<td>4–10</td>
<td>0</td>
<td>1.0–13.0</td>
</tr>
<tr>
<td>NMF</td>
<td>96–99</td>
<td>1–4</td>
<td>0</td>
<td>not available</td>
</tr>
</tbody>
</table>

**B. % taxa**

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Micro-</th>
<th>Noto-</th>
<th>Mesophylls</th>
<th>LSI</th>
<th>% entire leaf margins</th>
</tr>
</thead>
<tbody>
<tr>
<td>CMVF</td>
<td>11–18</td>
<td>58–78</td>
<td>11–30</td>
<td>47–59</td>
<td>82.4–95.0</td>
</tr>
<tr>
<td>CNVF</td>
<td>30–46</td>
<td>14–63</td>
<td>0–36</td>
<td>33–43</td>
<td>50.0–81.8</td>
</tr>
<tr>
<td>SNVF</td>
<td>40–75</td>
<td>25–50</td>
<td>0–20</td>
<td>13–38</td>
<td>84.2–90.0 (Qld)</td>
</tr>
<tr>
<td>MFF</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>14.3–25.0 (NSW)</td>
</tr>
</tbody>
</table>

*CMVF, complex mesophyll vine forest; CNVF, complex notophyll vine forest; SNVF, simple notophyll vine forest; MV-FF, microphyll vine-fern forest; MFF, microphyll fern forest; LSI, leaf size index (from Webb, 1959; Tracey, 1982). *Based on a single site (four samples). *Based on Macphail et al., 1991, Table 3 (Lake Dobson and Precipitous Bluff). Data from Greenwood, 1991a (Table 1, in part) and 1992.

1987). However, stratigraphically correlated macrofloras may be separated in time (as a record of the original vegetation, and hence climate) by tens of thousands of years.

**Palaeobotanical evidence of climate**

Terrestrial plant fossil assemblages record local climate usually over small time intervals. Each plant assemblage represents a single datum of climate, with separate assemblages from a single flora providing information about local variation. However, continuous deposition of terrigenous sediments within a single basin (e.g. the Latrobe Valley) preserve climate records spanning millions of years.

The present analysis uses a dataset derived from modern Australian rainforest leaf-litter and fluvially deposited beds (Christophel & Greenwood, 1987, 1988, 1989; Greenwood, 1992; Table 4.1). A multivariate foliar physiognomic analysis for the Australian Middle Eocene macrofloras is in preparation (D. R. Greenwood, unpublished data), however, here temperature characteristics are derived primarily from univariate comparisons (e.g. Figure 4.2). Other Australian Tertiary macrofloras are discussed qualitatively using leaf size and margin data only, as full data are not available. These analyses are supplemented by quantitative and qualitative estimates based on NLR analyses from Read et al. (1990; Read, 1990) and Nix (1982; Kershaw &
Palaeobotanical evidence for Tertiary climates

M. Nix, 1988). Forest nomenclature and typology in this discussion follows those of Webb (1959, 1968), Tracey (1982; Table 4.1) and Wolfe (1979).

Figure 4.2 Relationship (least-squares regression) between leaf size index of forest-floor leaf-litter from Australian rainforests and mean annual temperature (MAT), $r = 0.94$. (Adapted from Greenwood, 1992.)

Foliar physiognomy and climate

Greenwood (1992; Greenwood & Christophel, 1990, unpublished data) suggests that the relationship between leaf margin type and MAT for Australian forests is different from, and more complex than, that derived by Wolfe (1979) for east Asian forests. Leaf size is strongly correlated with MAT in Australian rainforest canopies (Webb, 1968), and, since the leaf size bias between the canopy and forest floor litter is consistent (Greenwood, 1991a), modern leaf-litter from humid vegetation shows a strong relationship between leaf size, calculated as the leaf size index (LSI = (% microphylls + 2% notophylls + 3% mesophylls − 100)/2; Wolfe, 1978; Burnham, 1989), and MAT (Greenwood, 1991a, 1992; Figure 4.2). Mean leaf length (specimens) is also strongly correlated with MAT (Greenwood, 1992).

The LSI of the Tertiary macrofloras (where applicable) has been used to calculate the prevailing MAT using a linear regression equation from modern litter (Figure 4.2). These MAT values must be considered to be minimum estimates; the actual values are likely to be 1–3 °C higher, as the taphonomic size bias is always towards smaller leaves than are found in the parent vegetation. The spread of MAT values in Figure 4.2 indicates the uncertainty of this magnitude. New data from the Australian rainforest litter are also used here to calculate MAT using leaf margin analysis. The use of separate foliar physiognomic indices to
calculate MAT provides a check on the fidelity of the estimates.

AUSTRALIAN TERTIARY MACROFLORAS AND PALAEOCLIMATES

This discussion is restricted to a small group of macrofloras and is not a general review of the Australian Tertiary climate. The macrofossil sites (Figure 4.1) represent a few key points in time: Middle–Late Eocene (Anglesea, Maslin Bay, southern Lake Eyre Basin silcrete and Nelly Creek, Nerriga), Oligocene (Cethana), Late Oligocene–Early Miocene (Pioneer, Monpeelata) and the Early–Middle Miocene (Bacchus Marsh, Latrobe Valley), and can be considered to be individual ‘snapshots’, where climate can be inferred for local areas. Late Tertiary macrofloras are scarce in Australia, and, apart from Bacchus Marsh and the Latrobe Valley, are not considered here.

Middle Eocene

Axelrod (1984) concluded that thermal regimes in southern Australia in the Late Paleocene–Eocene were comparable to the present regime. Nix (1982) depicted a latitudinal zonation of thermal regimes across Australia in the Middle Eocene similar to that of the present, although with MAT values in southern Australia 2°–4 °C warmer than at present. Wolfe (1985), however, suggested a more southerly latitudinal extension of tropical rainforest (megathermal), with paratropical rainforest (mesothermal–megathermal interzone sensu Nix (1982)), in the southern half of Australia, and notophyllous forest (mesothermal) on the adjacent part of Antarctica, in contrast to Nix’s (1982) suggestion of microthermal climates in southernmost Australia and Antarctica. Early–Late Eocene macrofloras from the Antarctic Peninsula suggest that either cool temperate Nothofagus and podocarp rainforest (nanophyll mossy forest, NMF) or deciduous forests were dominant over much of Antarctica at that time (Tokarski et al., 1987; Case, 1988).

A common element in Nix’s (1982), Axelrod’s (1984) and Wolfe’s (1985) interpretations is for uniformly low seasonality (equable) climates in the Eocene. More recently, Sloan & Barron (1990) have suggested that the Eocene mean annual range of temperature (MART) in continental interiors should have been high. The new synthesis presented here differs from Axelrod’s (1984) and Wolfe’s (1985) interpretations in some important details, and provides a quantitative comparison with the estimations of Nix (1982) and of Sloan & Barron (1990).

The Middle Eocene Maslin Bay (North Maslin Sands; McGowran et al., 1970), Anglesea (Eastern View Formation; Abeles et al., 1976) and Golden Grove (North Maslin Sands: Alley, 1987) macrofloras (Figure 4.1) occur in mudstone lenses within fluvial sands (Christophel & Blackburn, 1978; Christophel & Greenwood, 1987, 1989; Christophel et al., 1987). Each clay lens is interpreted as an infilled abandoned channel (oxbow) in a meandering stream sequence. A diverse Middle Eocene macroflora also occurs in well-laminated lake sediments (Titringo Siltstone) at Nerriga (Hill, 1982). These macrofloras provide a record of vegetation at near sea level (Maslin Bay and Anglesea) and at moderate elevations (Golden Grove and Nerriga) for the continental margin from which climate can be inferred (see Table 4.4, below). Eocene macrofloras from the Lake Eyre Basin provide information on vegetation and climate in the continental interior (Lange, 1982; Greenwood et al., 1990; Christophel et al., 1992).

The continental margin Middle Eocene macrofloras have many taxa in common at the generic level (Christophel & Greenwood, 1989) and are typified by abundant leaf remains of Lauraceae. A distinctive feature of the Nerriga macroflora compared to other Australian Eocene macrofloras is the common presence of hastate vine leaves of Menispermaceae (Hill, 1989). This may reflect disturbance in the local vegetation as vines are commonly enriched in modern tropical rainforest canopies after canopy disruption (Tracey, 1982), or it may reflect vine-rich lake-edge vegetation. Many of the identified common plants from these Eocene macrofloras have NLRs with
Table 4.2. The foliar physiognomic characteristics of the macrofloras (specimen-based observations)

<table>
<thead>
<tr>
<th>Site*</th>
<th>No. of leaves°</th>
<th>% entire leaf margins</th>
<th>Leaf size (%)</th>
<th>Mean length (mm)</th>
<th>No. of taxa°</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Micro-</td>
<td>Noto-</td>
<td>Mesophylls</td>
</tr>
<tr>
<td>Middle Eocene</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anglesea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1)</td>
<td>81</td>
<td>73.0</td>
<td>32.0</td>
<td>46.0</td>
<td>22.0</td>
</tr>
<tr>
<td>(2)</td>
<td>1548</td>
<td>79.7</td>
<td>82.9</td>
<td>16.1</td>
<td>0.9</td>
</tr>
<tr>
<td>Maslin Bay</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1)</td>
<td>1046</td>
<td>84.0</td>
<td>25.0</td>
<td>54.0</td>
<td>21.0</td>
</tr>
<tr>
<td>(2)</td>
<td>90</td>
<td>76.7</td>
<td>43.2</td>
<td>41.1</td>
<td>15.7</td>
</tr>
<tr>
<td>(3)</td>
<td>210</td>
<td>70.0</td>
<td>24.0</td>
<td>53.0</td>
<td>23.0</td>
</tr>
<tr>
<td>Golden Grove</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(6)</td>
<td>338</td>
<td>47.4</td>
<td>52.6</td>
<td>40.9</td>
<td>6.5</td>
</tr>
<tr>
<td>Nerriga</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1)</td>
<td>129</td>
<td>66.0</td>
<td>24.0</td>
<td>55.0</td>
<td>21.0</td>
</tr>
<tr>
<td>(4)</td>
<td>112</td>
<td>44.1</td>
<td>22.7</td>
<td>59.2</td>
<td>18.1</td>
</tr>
<tr>
<td></td>
<td>576</td>
<td>39.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(including fragmented leaves)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deane's Marsh</td>
<td></td>
<td></td>
<td>100.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Nelly Creek (5)</td>
<td>160</td>
<td>88.0</td>
<td>80.0</td>
<td>20.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Oligocene</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cethana</td>
<td>267</td>
<td>13.0</td>
<td>95.0</td>
<td>5.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Pioneer</td>
<td>308</td>
<td>9.7</td>
<td>100.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Early Miocene</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bacchus Marsh</td>
<td></td>
<td></td>
<td>100.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Monpeelyata</td>
<td>630</td>
<td>57.5</td>
<td>100.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

*Cethana, Pioneer and Monpeelyata data; R. S. Hill & R. J. Carpenter, personal communication.

(3), L. J. Scriven, personal communication.
(4), Hill, 1982, and personal communication.
(6), D. Barrett, personal communication; Greenwood, 1991a.
°Number of whole leaves used to calculate the values.
°Number of leaf taxa encountered in sample used; whole macroflora may be higher.


Christophel (1981; Christophel & Blackburn, 1978) originally considered the Anglesea, Nerriga and Maslin Bay macrofloras analogous to modern complex notophyll vine forest (CNVF) or simple mesophyll vine forest (SMVF). The initial analysis of Maslin Bay was based on a large sample (1046 leaves); however, only the tallies presented by Christophel & Blackburn (1978) were available here. The Anglesea analysis was based on a small sample (81 leaves) and Christophel’s interpretations of all of the macrofloras were based on direct comparisons with canopy values (from Webb, 1959). Burnham (1989; Burnham et al., 1992) and Greenwood (1991a, 1992) suggested that sample sizes in excess of 200–350 leaves are required to sample leaf assemblages adequately. Subsequent analysis of the Anglesea and Golden Grove macrofloras used much larger samples (267–1548 leaves; Tables 4.2, 4.3) and a more
Table 4.3. The foliar physiognomic characteristics of the macrofloras (taxon-based observations)

<table>
<thead>
<tr>
<th>Site*</th>
<th>No. of leaves</th>
<th>No. of taxa</th>
<th>% entire leaf margins</th>
<th>Leaf size (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Micro- Noto- Mesophylls</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>60.0 40.0 0</td>
</tr>
<tr>
<td>Middle Eocene</td>
<td></td>
<td></td>
<td></td>
<td>23.0 50.0 27.0</td>
</tr>
<tr>
<td>Anglesea (1)</td>
<td>793</td>
<td>30</td>
<td>70.0</td>
<td>25.0 47.0 28.0</td>
</tr>
<tr>
<td>(2)</td>
<td>81</td>
<td>41</td>
<td>78.0</td>
<td>53.3 46.7 0</td>
</tr>
<tr>
<td>Maslin Bay (2)</td>
<td>1046</td>
<td>57</td>
<td>79.0</td>
<td>25.0 45.0 30.0</td>
</tr>
<tr>
<td>Golden Grove (5)</td>
<td>338</td>
<td>24</td>
<td>—</td>
<td>60.0 40.0 0</td>
</tr>
<tr>
<td>Nerriga (1)</td>
<td>129</td>
<td>38</td>
<td>66.0</td>
<td>25.0 45.0 30.0</td>
</tr>
<tr>
<td>(4)</td>
<td>116</td>
<td>25</td>
<td>80.0</td>
<td>56.5 39.1 4.3</td>
</tr>
<tr>
<td>Nelly Creek (3)</td>
<td>160</td>
<td>16</td>
<td>75.0</td>
<td>60.0 40.0 0</td>
</tr>
<tr>
<td>Oligocene</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cethana</td>
<td>267</td>
<td>—</td>
<td>—</td>
<td>100 0 0</td>
</tr>
<tr>
<td>Late Oligocene–Early Miocene</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pioneer</td>
<td>308</td>
<td>5</td>
<td>60.0</td>
<td>100 0 0</td>
</tr>
<tr>
<td>Monpeelyata</td>
<td>630</td>
<td>&gt;7</td>
<td>&gt;60.0</td>
<td>100 0 0</td>
</tr>
<tr>
<td>Early Miocene</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bacchus Marsh</td>
<td>—</td>
<td>6</td>
<td>66.7</td>
<td>90.0 10.0 0</td>
</tr>
</tbody>
</table>

*Cethana, Pioneer and Monpeelyata data; R. S. Hill & R. J. Carpenter, personal communication. 
(2), Christophel, 1981. 
(4), Hill, 1982, and personal communication. 
All other data: Christophel & Greenwood, 1987, 1988, 1989 and unpublished data. 
bLSI, leaf size index.

detailed comparison with modern leaf-litter (Christophel & Greenwood, 1987, 1988, 1989). In these later analyses, the Anglesea Site II macroflora (Christophel et al., 1987) matched simple notophyll vine forest (SNVF) litter, and the Nerriga, Golden Grove and Maslin Bay macrofloras compared most closely to CNVF litter; however, in this instance the Maslin Bay analysis was based on a sample of only 90 leaves (Tables 4.3, 4.4).

The Middle Eocene continental margin macrofloras are dominated by simple, narrowly elliptic (length: width > 2.0), microphyllous to notophyllous leaves (Anglesea) or notophylls (Christophel & Greenwood, 1988), with entire margins more common than nonentire (Tables 4.2, 4.3). The leaves in litter from SNVF, CNVF and complex mesophyll vine forest (CMVF) from Queensland are typically wider and there are fewer leaf specimens and leaf species with nonentire margins present than the leaves from the fossil macrofloras (Christophel & Greenwood, 1988; Tables 4.1–4.3). Leaves from New South Wales SNVF and CNVF are as narrow as the Anglesea and Golden Grove leaves, but the proportion of leaves and species with nonentire margins is much higher in the New South Wales SNVF than in the Anglesea macroflora. A significant number of hastate-base and broad leaves (mostly Menispermaceae) gives the Nerriga macroflora a unique foliar physiognomic signature compared to the other Eocene macrofloras; however, narrowly elliptic leaves also dominate this flora. The tend-
ency towards narrower leaves in the Eocene macrofloras versus analogous modern Queensland mesic vegetation (SNVF, CNVF and CMVF) may reflect latitudinally controlled climatic differences, as indicated by the narrower leaves found in New South Wales CNVF and SNVF; however, the exact relationship is unclear.

The leaf size index for Anglesea (Table 4.3; Figure 4.2) suggests a MAT of 15–18 °C. Using leaf margin analysis (Wolfe, 1979, 1985; data from Greenwood, 1992) the MAT is estimated to be 17 °C. The LSI values for Maslin Bay and Golden Grove suggest MAT values of 23–26 °C and 17–20 °C respectively (Figure 4.2). Modern SNVF has a range of MAT of 12–18 °C (mesothermal), CNVF MAT of 17–22 °C (mesothermal) and CMVF MAT of 20–27 °C (mesothermal–megathermal interzone to megathermal). Fungal epiphyllous germlings recorded on Anglesea leaf cuticles are of type V, and type 6 manginuloid hyphae are also present, which indicate a humid climate of the type restricted to modern montane tropical rainforest (Lange, 1981, 1982). The floristic character of the Anglesea macroflora is consistent with this interpretation (Christophel & Greenwood, 1989; Christophel, Chapter 11, this volume). Leaf cuticles from Golden Grove and Maslin Bay have high grade fungal epiphyllous germlings (A. I. Rowen, personal communication) indicative of warm humid climates (Lange, 1978, 1982).

The leaf size index (Table 4.3) of the Nerriga macroflora using Hill’s (1982, and personal communication) data suggests a MAT of 16–21 °C (mesothermal). If Christophel’s (1981) data are used, the LSI is much higher, giving a MAT of 25–28 °C. Christophel’s (1981) original figures were preliminary and probably overestimate

<table>
<thead>
<tr>
<th>Site</th>
<th>Sedimentary environment</th>
<th>Modern elevn (m)</th>
<th>% entire leaf margins</th>
<th>LSI</th>
<th>MAT °C</th>
<th>Vegetation type*</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Middle Eocene</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Anglesea</td>
<td>Oxbow pond</td>
<td>50</td>
<td>70</td>
<td>20.0</td>
<td>15–18</td>
<td>SNVF</td>
</tr>
<tr>
<td>Maslin Bay</td>
<td>Oxbow pond</td>
<td>65</td>
<td>79</td>
<td>51.5</td>
<td>23–26</td>
<td>CMVF</td>
</tr>
<tr>
<td>Golden Grove</td>
<td>Oxbow pond</td>
<td>120</td>
<td>—</td>
<td>25.0</td>
<td>17–20</td>
<td>CNVF</td>
</tr>
<tr>
<td>Nerriga</td>
<td>Lake</td>
<td>535–570</td>
<td>66</td>
<td>23.8</td>
<td>16–21</td>
<td>CNVF</td>
</tr>
<tr>
<td>Nelly Creek</td>
<td>River channel</td>
<td>8</td>
<td>75</td>
<td>20.0</td>
<td>&gt;20</td>
<td>ScF/MVF</td>
</tr>
<tr>
<td><strong>Oligocene</strong></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>Cethana</td>
<td>Lake</td>
<td>300</td>
<td>—</td>
<td>?0</td>
<td>10–12</td>
<td>MVFF</td>
</tr>
<tr>
<td><strong>Late Oligocene–Early Miocene</strong></td>
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<tr>
<td>Pioneer</td>
<td>Alluvial fan</td>
<td>Sea-level</td>
<td>60</td>
<td>0</td>
<td>10–12</td>
<td>MFF/SNVF</td>
</tr>
<tr>
<td>Monpeelyata</td>
<td>Lake</td>
<td>920</td>
<td>&gt;60</td>
<td>0</td>
<td>4–8</td>
<td>NMF/T</td>
</tr>
<tr>
<td><strong>Early Miocene</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bacchus Marsh</td>
<td>Oxbow pond</td>
<td>400</td>
<td>67</td>
<td>10</td>
<td>12–14</td>
<td>MFF</td>
</tr>
</tbody>
</table>

elevn, elevation; LSI, leaf size index; MAT, mean annual temperature.

*MVFF, (?semideciduous) mesophyll vine forest (monsoon forest)
ScF, sclerophyllous forest (?marked dry season)
CNVF, complex notophyll vine forest (mesothermal rainforest)
SNVF, simple notophyll vine forest (mesothermal rainforest)
MVFF, microphyll vine–fern forest (microthermal rainforest)
MFF, microphyll fern forest (microthermal Nothofagus rainforest)
NMF/T, nanophyll mossy forest (subalpine rainforest or wet thicket).
species number (Hill, 1982; 38 versus ca 20 species) and LSI is sensitive to both species number and the proportion of mesophylls (Wolfe & Upchurch, 1987; Greenwood, 1992). Leaf margin analysis of the Nerriga macroflora based on Hill's data indicates a MAT of 21 °C. The Nerriga macroflora sediments outcrop today at moderate elevation (Hill, 1982; Table 4.4). If this modern elevation is indicative of the Eocene elevation the Nerriga macroflora can be expected to indicate a lower MAT than do lowland Middle Eocene sites at similar palaeolatitude (e.g. Maslin Bay). The MAT estimate for Nerriga (16-21 °C) compared to Golden Grove and Maslin Bay (Table 4.4) is slightly higher than would be expected on the basis of their present elevations.

Lake sediments may be enriched with the smaller sun-leaves of the upper canopy (Roth & Dilcher, 1978; Spicer, 1981) and so the MAT for Nerriga based on LSI may be an underestimate. However, the significant number of entire-margined vine leaves may also bias the leaf margin analysis, producing a MAT estimate that is too high. Greenwood (1992; Greenwood & Christophel, 1990) has demonstrated that taphonomic and ecological factors introduce a significant uncertainty in leaf margin analysis estimates of MAT. The actual MAT value for Nerriga probably lies between the estimates derived from the LSI (Hill, 1982) and from leaf margins. In either case, a mesothermal humid climate is indicated.

There are several explanations for the relatively high estimated MAT for Nerriga, and the apparent discrepancy between Maslin Bay and Golden Grove values. The Nerriga macroflora is older than the other Middle Eocene macrofloras, so climatic change over this interval may be the cause. However, there is debate over the timing and degree of uplift of the Great Dividing Range (Ollier, 1986), including the upland area of the Nerriga macroflora. It is possible that the Nerriga macroflora was deposited at a lower elevation than at present, as significant uplift in the area may have occurred during and since the Oligocene (Ollier, 1986). If this is so, the apparent similarity between the Nerriga and Golden Grove MAT estimates relative to Maslin Bay (Table 4.4) can be explained.

The MAT values and elevation of the Maslin Bay and Golden Grove macrofloras suggests that either two distinct and climatically controlled vegetation types occurred within only a short distance, or that taphonomic bias is causing a significant reduction in mean leaf size, resulting in an underestimate of MAT for Golden Grove (an overestimate for Maslin Bay is highly unlikely; Christophel & Greenwood, 1988). Christophel & Greenwood (1987) have suggested that there may be a significant collection bias towards smaller curated leaves for the Golden Grove macroflora. The Maslin Bay macroflora is based solely on compressions and impressions in situ on the mudstone matrix, whereas all of the other macrofloras are based on mummified leaves that have been isolated from the matrix. It is possible that this preservational difference may enhance leaf size taphonomic biases. Casual inspection of compression—impression facies of the Golden Grove macroflora (see Christophel & Greenwood, 1987) was equivocal on this point. These factors act to underscore the degree to which taphonomic biases influence resolution of quantitative variables.

The Lake Eyre Basin contains extensive fluvial and fluvio-lacustrine sequences of Tertiary sediments (Wopfner et al., 1974; Ambrose et al., 1979). An outcrop of the Paleocene—Eocene Eyre Formation (Sluiter, 1991) within the southern margin of present Lake Eyre (e.g. Nelly Creek site, Figure 4.1) contains leaf and fruit macrofloras (Wopfner et al., 1974). These macrofloras are usually silicified and abundant capsular myrtaceous fruits, including putative Eucalyptus (Lange, 1978, 1982), have been recorded from correlated sediments in the same region (Ambrose et al., 1979; Greenwood et al., 1990). Middle Eocene sediments of the Eyre Formation at Nelly Creek contain mummified leaves and fruits (Christophel et al., 1992).

A significant number of taxa in the Lake Eyre silcretes have leaves with broad lamina, large size and entire margins, suggesting that they grew in mesic environments; other taxa have very narrow,
small leaves, with coarse serrations (to spinose),
or narrow-lobed leaves, which suggest dry or
seasonally dry climates (Givnish, 1984; Wolfe,
1985). The silcrete floras suggest a mosaic of
sclerophyllous vegetation and broad-leaved gal-
tery forests (Greenwood et al., 1990; Greenwood,
suggested that adaption to low soil fertility during
the Tertiary may have produced sclerophyllous
plants, pre-adapting many lineages of Australian
plants to seasonally dry and arid climates. It is
plausible therefore, that the sclerophyllous
elements in the Lake Eyre Basin floras do not
represent dry climate vegetation, but low fertility
soils.

The foliar physiognomy of the Nelly Creek
macroflora partly matches the silcrete macro-
floras; however, the presence of sunken stomata
and thick cuticles (Christophel et al., 1992) on
the leaves of this mummified macroflora emphasise
the sclerophyllous and/or xerophyllous character.
The floristic composition of both the silcrete
floras and the Nelly Creek macroflora also support
this interpretation, with some taxa commonly
associated with seasonally dry environments (e.g.
*Brachychiton*) and others associated with mesic–
humid environments (Christophel, Chapter 11,
this volume). Only scarce, low grade (types I and
II), epiphyllous fungal germlings occur on Nelly
Creek leaf cuticles (Christophel et al., 1992), indicat-
ing that rainfall was low (Lange, 1978, 1982)
or markedly seasonal. The common presence of
both *Gymnostoma* and *Brachychiton* in some
exposures of Eyre Formation (Greenwood et al.,
1990; Greenwood, 1991b) indicate low seasonal
and diurnal temperature variation in central Aus-
tralia in the Eocene as these genera today are
restricted to frost-free mesotherm–megatherm
areas (data from Webb & Tracey, 1982). On the
basis of MAT estimates for more southerly
Middle Eocene macrofloras (e.g. Maslin Bay,
Golden Grove) and the common presence of
mesotherm–megatherm taxa (e.g. *Gymnostoma*),
the Lake Eyre Basin macrofloras probably reflect
a MAT of $> 20$ °C.

The foliar physiognomy of the Nelly Creek
macroflora is distinct from the Middle Eocene
macrofloras at continental margin sites
(Christophel et al., 1992). Nelly Creek leaves are
significantly smaller overall (Tables 4.2, 4.3), with
a different assortment of leaf types. Important
floristic differences are discussed by Christophel
(Chapter 11, this volume). Lobed leaves and
species with toothed leaf margins are common in
both disturbed environments (early succession),
and in strongly seasonal environments (Givnish,
1984; Upchurch & Wolfe, 1987). The foliar
physiognomy of the Nelly Creek and silcrete
macrofloras compared to the other Eocene
macrofloras suggests the presence in central Aus-
tralia of seasonally dry (?monsoonal) palaecli-
nates where mesic broad-leaved vegetation
occurred in riparian corridors (Greenwood et al.,
1990; Greenwood, 1991b; Christophel et al.,
1992). This interpretation is supported by sedi-
mentological evidence that suggests periods of
aridity in central Australia in the early Tertiary
(Quilty, 1984).

**Oligocene**

The best-documented Early Oligocene macro-
flora occurs at Cethana in Tasmania (Hill & Car-
penter, 1991; Figure 4.1) in ?slumped lake
sediments at a present altitude of 300 m (R. J.
Carpenter, personal communication). The Late
Oligocene–Early Miocene Pioneer macroflora
occurs in lenses of organic-rich clays in coarse
braided fan (alluvial) deposits close to sea level in
north-eastern Tasmania (Hill & Macphail, 1983).
This macroflora represents the lowland vegetation
of the area at that time (Table 4.4). The Late
Oligocene–Early Miocene Monpeelyata macro-
flora occurs at 920 m above sea level and it is
probable that the original palaeovegetation
occurred at this or a higher elevation (Hill &
Gibson, 1986; Macphail et al., 1991).

The Cethana macroflora is species rich and
contains a diverse association of microthermal lin-
geages including three of the four modern
Many of the taxa found in the Cethana assemblage
are today restricted to the montane tropical rain-
forests of New Guinea and New Caledonia (Hill,
1990a). Physiognomically, these modern forests are analogous to Australian (microthermal) microphyll vine-fern forest (MV-FF) of upland areas (>1000 m) in the northeast Queensland Humid Tropical Region, and New Guinea montane forests.

The Pioneer macroflora is dominated by leaves of *Nothofagus*, with abundant conifer material and several species of angiosperm. The single site used for this analysis is less diverse than the Cethana macroflora.

Initial analysis of the foliar physiognomy of the Cethana and Pioneer macrofloras suggested a match with Australian microphyll fern forest (MFF) (Hill & Macphail, 1983; Christophel & Greenwood, 1989). MFF in south eastern Australia and Tasmania is species poor relative to the tropical microthermal rainforests (MV-FF) and appears physiognomically distinct (Webb, 1959, 1968; Tracey, 1982). Hill & Macphail (1983) recorded grade V germlings (Lange, 1976) from Pioneer and thus suggested that rainfall was in excess of 1500 mm annually. The relative frequency of the three main leaf size categories (Tables 4.1–4.3) in both macrofloras matches MFF. These Tasmanian macrofloras have a higher frequency of species with entire leaf margins than do modern Australian MFF, and SNVF from New South Wales, and reflect more the situation seen in modern MV-FF. Important floristic differences contribute to these discrepancies which in part reflect extinction events (Hill & Read, 1987; Carpenter et al., Chapter 12, this volume), and in part may reflect climatic differences (such as a change in MART).

Leaf sizes are predominantly microphyllous in both macrofloras, although leptophyllous conifers are also prominent. The LSIs of the Cethana and Pioneer macrofloras are not meaningful as both are zero. On the basis of modern leaf-litter studies (Greenwood, 1992), mesic vegetation above 12 °C MAT will have a LSI value > 0, and a LSI of zero below 10–12 °C MAT (Figure 4.2). Modern MFF in Australia ranges from a MAT of 4–15 °C, with *Nothofagus moorei* occurring over the range 8.9–16.1 °C (Read, 1990). The presence of leaves similar to those of modern *N. moorei*, and the predominance of microphylls in both macrofloras, suggest a MAT of 10–12 °C. On the basis of analogous modern forests (MFF and MV-FF) and particularly key taxa such as *Nothofagus* (Read, 1990), the MART of the Oligocene paleovegetation (particularly at Cethana) was probably low, < 10 °C. The presence of climatically sensitive taxa (e.g. *Nothofagus* subgenus *Brassospora*) in the Cethana macroflora suggests that freezing temperatures were unlikely (Hill, 1990a; Read et al., 1990).

The Monpeelyata macroflora is characterised by entire-margined leaves (Table 4.2) and imbricate foliage conifers, including *Araucaria* (Hill & Gibson, 1986; Hill, 1990b). Significant numbers of small-sized toothed *Nothofagus* leaves (*N. microphylla*) related to *N. cunninghamii* are present (Hill, 1991), in addition to leaves of the modern deciduous species, *N. gunnii*. Overall leaf size is very small, with nanophylls dominant (< 25 mm length). This macroflora may represent alpine shrub vegetation or low alpine woodland (Hill & Gibson, 1986). Macphail et al. (1991) have suggested that the macroflora represents local cool temperate rainforest (nanophyll mossy forest, NMF) or rainforest scrub (nanophyll mossy thicket, NMT), with a lakeside coniferous microphyllous–angiosperm shrubby vegetation. Significantly also, Macphail et al. (1991) suggested that the Monpeelyata flora was deposited below the alpine treeline. On the basis of the small size of the *N. microphylla* leaves and the modern tolerances of *N. gunnii* (Read, 1990), a MAT of 4–8 °C is indicated, and a MART of ca 15 °C. The presence of subalpine vegetation at Monpeelyata reflects the elevation at the time (Hill & Gibson, 1986; Macphail et al., 1991).

**Miocene**

An Early Miocene macroflora occurs at Bacchus Marsh in Victoria (Figure 4.1) in a single clay lens in fluvial sands (Werribee Formation; Abele et al., 1976). It is likely this site was at an elevation similar to the present situation (400 m) in the Miocene (Christophel, 1985). The macroflora is poorly known but is dominated by leaves from only a few
species (Christophel, 1985). Leaf sizes range from microphyllous to nanophyllous, with toothed leaves (Nothofagus) dominating, although the second most common leaf type (Myrtaceae) has an entire margin. Some nanophyllous conifers are present, including Araucaria and Dacrycarpus (Christophel, 1985, and personal communication). Today, Araucaria may be found in association with N. moorei in the SNVF–MFF ecotone at Mt Lamington in southeast Queensland under microthermal regimes (Webb & Tracey, 1982), and in Chile and Argentina with a winter deciduous species of Nothofagus under winter snow climates (Veblen & Schlegel, 1982). Comparison of the macroflora with modern leaf assemblages indicates a match with N. moorei – MFF (Tables 4.2–4.3). This vegetation type (although with N. cunninghamii, not N. moorei) is found today near to the Bacchus Marsh site, implying a similar climate in the Miocene. The Bacchus Marsh macroflora LSI value indicates a MAT of 12–14 °C.

In the Latrobe Valley (Figure 4.1), a more-or-less continuous sequence of coal formation from the Eocene to the Pliocene has preserved a record of swamp and terrestrial vegetation (Blackburn & Sluiter, Chapter 14, this volume). In contrast to the Latrobe Valley coal floras, most species from the Middle Miocene Yallourn Clay macroflora show no sclerophyllous features; cuticles are thin with few or no trichomes and possess surficial stomata (D. R. Greenwood, unpublished data). However, there are floristic elements such as Dacrycarpus latrobensis (Hill & Carpenter, 1991) and Agathis common to the Late Miocene coals and the clays. The Clay flora typically contains mainly microphyllous entire-margined leaves. In some samples microphyllous toothed leaves of N. moorei type (aff. N. tasmanica) were common. The cuticle flora is diverse (20–30 cuticle morphotypes) and is dominated by several species in each of the Lauraceae, Myrtaceae (aff. Syzygium), Cunoniaceae and Proteaceae.

The predominantly microphyllous nature of the macroflora of the Yallourn Clays, together with the occasional presence of N. moorei type leaves suggests that the Middle Miocene palaeoclimate was similar to the present climate of the area, although perhaps less seasonal. SNVF dominated by Syzygium and MFF with N. cunninghamii are found in the nearby Strzelecki Ranges. The relatively higher diversity of the Yallourn Clays cuticle and macroflora compared to Victorian MFF and SNVF, and the presence of N. moorei type leaves, however, suggests a better parallel with New South Wales MFF and SNVF, and indicates a MAT of 9–16 °C (see e.g. Read, 1990).

CONCLUSIONS

From the review and new analyses presented here, it is apparent that climates were not uniform across Australia during the Middle Eocene, and that local topography in the Oligocene and the Early Miocene influenced the climate and plant communities in southeastern Australia (Table 4.4). Nix's (1982) conclusion that increasing seasonality in both temperature extremes and rainfall and, less so, marked changes in the thermal regime, was the primary driving force of biotic change within Australia during the early to mid-Tertiary is supported by the palaeobotanical evidence of climate and vegetation patterns (e.g. Christophel & Greenwood, 1989; Read et al., 1990).

The Middle Eocene macrofloras at Maslin Bay, Golden Grove, Anglesea and Nerriga (Figures 4.1 and 4.3) reveal predominantly mesothermal–megathermal humid climates ranging from MAT values of about 16 °C (Anglesea, mesothermal) to perhaps as high as 25 °C (Maslin Bay, megathermal) in the coastal lowlands and at moderate elevations. Climates in the Middle Eocene were markedly warmer in southern Australia than at present. Rainforests analogous to SNVF, CNVF and CMVF grew under these climates (Christophel & Greenwood, 1989). There is evidence that a transitional zone from mesothermal to microthermal climates to the south, and mesothermal to megathermal climates to the north, existed in an irregular band across southeastern Australia (e.g. Nix, 1982; Christophel & Greenwood, 1989); however, this interpretation and the latitudinal position of such a zone remains speculative until more macrofloras are described in
Figure 4.3 Reconstruction of Australia and region for the Middle Eocene showing palaeocoastline superimposed on modern coastline. Based in part on Christophel & Greenwood (1989). NMT, nanophyll mossy thicket or subalpine woodland (microthermal); BDF, broad-leaved deciduous forest (microthermal); MFF, microphyll fern forest (microthermal); SNVF/CNVF, simple/complex notophyll vine forest (mesothermal); CMVF, complex mesophyll vine forest (mesothermal–megathermal); ScF, sclerophyllous forest (?megathermal); MVF, semideciduous mesophyll vine forest (monsoonal megathermal).

detail from a wider geographical area. The Lake Eyre Basin macrofloras indicate a development by the Middle Eocene of seasonally wet/dry ?megathermal climates in the continental interior, and that vegetation physiognomically pre-adapted to aridity was in place in the interior at that time (Greenwood et al., 1990; Christophel et al., 1992).

Wolfe (1985) speculated on the nature of Australian Early Miocene vegetation and climate. However, the limited number of well-documented Oligocene and Miocene macrofloras from southeastern Australia precludes any extraregional synthesis. What is clear is that this region experienced cooler temperatures in the Oligocene than in the Eocene (see e.g. Hill & Gibson, 1986; Hill, 1990a). Microthermal lineages (sensu Nix, 1982), particularly Nothofagus, were of increasing importance, compared to the situation in the Middle Eocene (Hill, 1990a; Read et al., 1990). The foliar physiognomic and floristic character of these macrofloras suggests humid microthermal climates, although modern Australasian tropical montane communities are better analogies for the Cethana Oligocene vegetation than are modern southern Australian humid microthermal forests such as the Nothofagus-dominated MFF (Hill, 1990a; Read et al., 1990). In contrast, the Pioneer and Miocene Bacchus Marsh macrofloras suggest microthermal to modern Nothofagus-dominated MFF, particularly the N. moorei-dominated forests of montane New South Wales. The absence from the Early Miocene macrofloras of some key Oligocene taxa suggests increasing seasonality with perhaps greater temperature extremes during the Early Miocene than in the Oligocene (Hill & Read, 1987; Hill, 1990a). Subalpine woodlands occurred at this time at moderate altitudes in Tasmania (Hill & Gibson, 1986; Macphail et al., 1991).

The Middle Miocene Yallourn Clay macroflora indicates mainly microthermal climates in southeastern Australia. Mesothermal humid vegetation (SNVF) probably persisted in parts of the Latrobe Valley during the Middle Miocene, as it does today. There is anecdotal evidence to suggest that Middle Miocene climates in the Latrobe Valley area were more equable than today, but that seasonal dryness became established by the Late Miocene, and perhaps much earlier in the continental interior (Lange, 1982; Quilty, 1984; Greenwood et al., 1990).

The poor knowledge of macrofloras of suitable age and preservation over much of the continent prevents a continental synthesis at this time. There are further areas of research on palaeobotanical climatic evidence, such as wood anatomy and dispersed cuticle (e.g. Upchurch & Wolfe, 1987), which remain largely untapped. Important information on Australian Tertiary climates can be gained from analyses of macrofloras. Work continues on the well-preserved early to mid-Tertiary macrofloras of southeastern Australia
and Tasmania; however, there is an urgent need to find and analyse macrofloras from outside of these areas and to apply a wider range of approaches.

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