16 The history of selected Australian taxa

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In examining the fossil record of the Australian flora since the arrival of angiosperms, several taxonomic groups loom large, either because they have an extensive and informative fossil record, or because they are prominent in the living vegetation and are selectively sought in the fossil record. The aim here is to consider some taxa that cover each of these areas in order to complement the vegetation reconstructions discussed in earlier chapters. There are several candidates that fall into the category of having an extensive fossil record, but the outstanding one is *Nothofagus*, which dominates many palynofloras, and is also well represented in the macrofossil record. The Podocarpaceae, Araucariaceae, Proteaceae and Casuarinaceae are also considered here because they have a mixture of good pollen and macrofossil records, and important evolutionary arguments can be based on these records. The prime example of a taxon that is prominent in the living vegetation and is actively sought in the fossil record is *Eucalyptus*, and its pollen and macrofossil record will also be considered, although it is much smaller than those of the other taxa. In choosing these taxa, several other notable groups have been excluded. In most cases this is because the record is biassed to either pollen (e.g. *Acacia*, Chenopodiaceae) or macrofossils (e.g. Lauraceae, cycads) and a combined data set cannot be supplied. There is no doubt that the greatest weakness lies with the macrofossil record, especially for those taxa that produce entire-margined, medium-sized leaves. Taxonomic research on these groups should be a priority for the future.

NOTHOFAGUS

Nothofagus has been described as the key genus in the study of southern hemisphere plant evolution and biogeography (van Steenis, 1971, 1972). There are a number of reasons for this.

1. It has a completely southern hemispheric distribution, whereas its closest relatives are, and probably always have been, northern hemispheric.
2. It occurs in all the major Gondwanic land masses except Antarctica, where it has an extensive fossil record, and Africa and India, where it has never been recorded as an autochthonous fossil.
3. Fruits are extremely poorly dispersed (Rodway, 1914) and cannot survive long periods in sea water (Preest, 1963). It is generally agreed that long-distance fruit dispersal is unlikely to have been an important agent for *Nothofagus* dispersal, although Macphail *et al.* (Chapter 10) provide important data suggesting that long-distance dispersal has operated in *Nothofagus*.
4. Its fossil record is extensive and well studied.

It is only recently that the fossil record has been properly exploited in reconstructing the past his-

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Table 16.1. Nothofagus *subgenera as defined by Hill & Read (1991) and pollen types as defined by Dettmann* et al. *(1990). Subgeneric names are used in the text in place of pollen-type names to avoid confusion*

Nothofagus			
Subgenus *Nothofagus*	Subgenus *Fuscospora*	Subgenus *Lophozonia*	Subgenus *Brassospora*
Five species in South America; *N. fusca* type b pollen	Five species in South America, New Zealand and Australia; *N. fusca* type a pollen	Six species in South America, New Zealand and Australia; *N. menziesii*-type pollen	Nineteen species in New Guinea and New Caledonia; *N. brassii*-type pollen

tory of *Nothofagus*. Earlier attempts at determining the centre of origin and migration routes of *Nothofagus* often relied heavily on the distribution and interrelationships of extant species, and the literature contains an array of possible options, with almost every conceivable centre of origin being invoked at one time or another (e.g. Cranwell, 1963; Darlington, 1965; van Steenis, 1971, 1972; Raven & Axelrod, 1972; Hanks & Fairbrothers, 1976; Schuster, 1976). A recent revision of the vast fossil pollen record (Dettmann *et al.*, 1990) and descriptions and reviews of macrofossils (e.g. Romero & Dibbern, 1985; Tanai, 1986; Hill, 1991) have allowed a far more detailed interpretation of the past distribution and evolution of *Nothofagus*, although some problems remain. In order fully to integrate the pollen and macrofossil record, a brief description of the current infrageneric classification of *Nothofagus* is required.

Infrageneric classification

Nothofagus is usually assigned to the Fagaceae, although some recent evidence supports the erection of the monogeneric family Nothofagaceae (e.g. Nixon, 1989). Furthermore, Nixon concluded that *Nothofagus* is more closely related to Betulaceae than to Fagaceae, although there is other conflicting evidence, summarised by Hill, (1993).

There have been three different infrageneric classifications proposed for *Nothofagus* (van Steenis, 1953; Philipson & Philipson, 1988; Hill & Read, 1991). A major difficulty with the earlier classifications was that palynologists recognised three distinct pollen morphologies amongst the

extant and fossil species, only one of which correlated with formal infrageneric groupings. In van Steenis' classification, the primary infrageneric division was based on the dichotomy created by the deciduous or evergreen habit. Recognition of four distinct vernation patterns in *Nothofagus* (Philipson & Philipson, 1979, 1988), in conjunction with several other characteristics of leaf and cupule morphology, led Hill & Read (1991) to hypothesise that the evergreen habit is polyphyletic. This may explain the lack of correlation between classifications based primarily on the deciduous–evergreen dichotomy and the pollen groupings. The most recent infrageneric classification (Hill & Read, 1991) correlates well with the established but recently revised pollen groupings (Dettmann *et al.*, 1990; Table 16.1). With the infrageneric taxonomy and pollen groupings now in harmony, more order is apparent in the fossil record of *Nothofagus*.

Origin, dispersal and diversification

The centre of origin and migration routes of *Nothofagus* must be compatible with that of related taxa in Fagaceae and Betulaceae, which are regarded as the most closely related families. Burger (1981, 1990) and Truswell *et al.* (1987) recently focussed attention on the possible interchange of plants between Southeast Asia and Australia during the Late Cretaceous–early Tertiary. They suggest that a complex of continental fragments probably provided a kind of stepping stone path since the Early Cretaceous, and especially in the Late Cretaceous and early Tertiary. Truswell *et al.* (1987) reported several floral examples from

the fossil pollen record as probable exploiters of this route in both directions, but they explicitly excluded *Nothofagus*, since its highly distinctive pollen has not been recorded in the appropriate sediments. However, recent macrofossil records from the southern hemisphere provide another option. As well as an abundance of *Nothofagus* macrofossils, there are leaves and wood in Late Cretaceous–early Tertiary sediments that are regarded as fagaceous, but not *Nothofagus* (Romero, 1986; Romero & Dibbern, 1985; Birkenmajer & Zastawniak, 1989a; M. S. Pole, personal communication). Furthermore, a leaf from the Late Cretaceous Winton Formation in Queensland (R. S. Hill, unpublished data) appears to be fagaceous, and Pole (1992) has recorded Late Cretaceous leaves from New Zealand that are morphologically similar to Betulaceae. This suggests that a Cretaceous fagalean complex may have existed in Gondwana during the early history of *Nothofagus*, and possibly preceded the origin of *Nothofagus*.

This fagalean complex, with a generalised pollen type, may have existed in the Southeast Asian–Australian region during the Cretaceous, giving rise to the Betulaceae and Fagaceae in the northern part of this region, where the fossil record of the Betulaceae at least is both early and diverse (Crane, 1989). Part of the complex may have migrated into high southern latitudes, via the route suggested by Burger (1981) and Truswell *et al.* (1987; Figure 16.1), there to evolve into *Nothofagus*. Such an hypothesis is compatible with the presence of Late Cretaceous–early Tertiary 'fagaceous–betulaceous-like' macrofossils in the southern hemisphere, explains the lack of previous geographical links between *Nothofagus* pollen and that of closely related taxa, and is also compatible with the hypothesis of Dettmann *et al.* (1990) that *Nothofagus* arose at high southern latitudes. Although it seems clear from the extensive fossil pollen record that *Nothofagus* had a high latitude southern origin during the Late Cretaceous (early Campanian) within the Weddellian province (Dettmann *et al.*, 1990; see below), the sparse Cretaceous pollen record from the northern Australian–Southeast Asian region may mask a possible centre of origin for *Nothofagus* there. Clearly more fossil evidence is required to test this hypothesis rigorously.

Case (1988, 1989) extended the Weddellian Zoogeographic Province (Figure 16.2) to a 'biogeographic province' and hypothesised that it was a centre of diversification during the Late Cre-
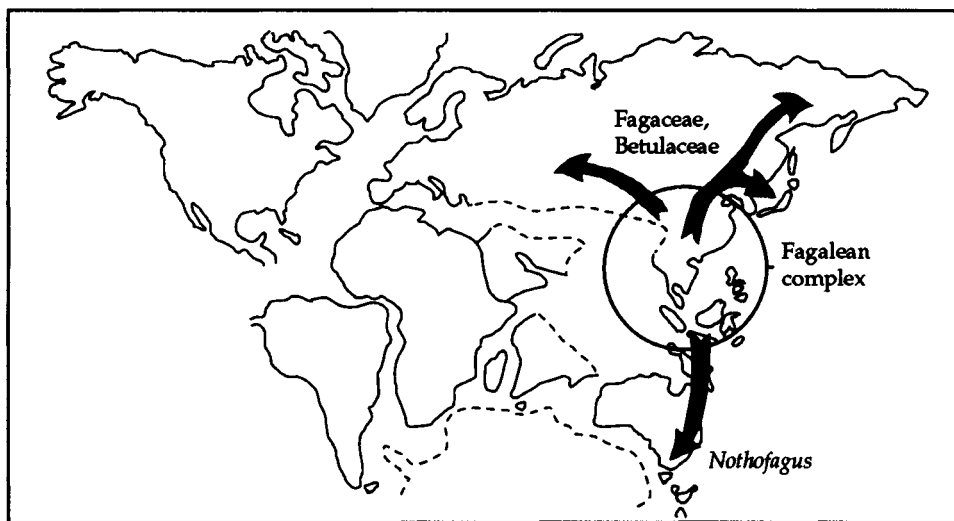

Figure 16.1 Map of possible Early Cretaceous route of Fagalean lineages from a centre of origin in Southeast Asia. (Adapted from Truswell *et al.*, 1987.)
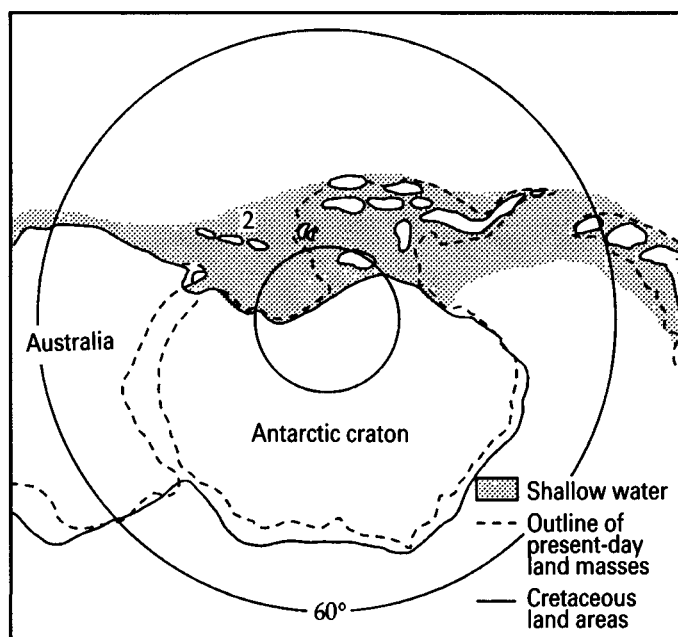
Figure 16.2 Reconstruction of the Weddellian Zoogeographic Province (stippled area), during the Late Cretaceous and early Tertiary. The numbered land masses are: 1, South America; 2, New Zealand. (Adapted from Case (1988), who considers that the stippled area should represent a continuous, coastal environment bordered by shallow seas.)

taceous and Tertiary, and that part of the evolving biota included *Nothofagus*. The region extends from southern South America, along the Antarctic Peninsula and West Antarctica to Tasmania and southeastern Australia and New Zealand. Case hypothesised that many novel species arose and survived in this region, primarily due to the low extinction rates that characterise high latitude environments (Hickey *et al.*, 1983; Jablonski *et al.*, 1983). Such an hypothesis is consistent with the *Nothofagus* pollen record for the region.

The most complete fossil record of *Nothofagus* is supplied by pollen. Of the eight pollen types now recognised in fossil and living *Nothofagus*, two are nominated as 'ancestral' and appear first in the fossil record (Dettmann *et al.*, 1990). Ancestral type a, represented by the single fossil species *Nothofagidites senectus*, occurs over wide areas of southern Gondwana in sediments as old as early Campanian. Two other fossil species, *Nothofagidites endurus* (from southeastern Australia) and *N.*

kaitangensis (from New Zealand), are assigned to ancestral type b and first occur in the mid-Campanian. Ancestral pollen types a and b are considered to be most closely related to pollen of *Nothofagus* subgenera *Fuscospora* and *Nothofagus*, respectively (Dettmann *et al.*, 1990).

Following the appearance of *Nothofagus* in the fossil record, there were spatially and temporally distinctive events of rapid diversification. The oldest known occurrences of the pollen types belonging to the extant subgenera are from the late Campanian of the Antarctic Peninsula and from the Maastrichtian of southern South America, a region that was a centre of Late Cretaceous diversity for *Nothofagus* (Dettmann *et al.*, 1990). The significantly younger occurrences in southern Australia and New Zealand of *Nothofagus* subgenus *Nothofagus* (Paleocene), *Nothofagus* subgenus *Lophozonia* (Eocene) and *Nothofagus* subgenus *Brassospora* (Eocene in New Zealand, late Maastrichtian in Australia) imply a

migrational lag and routes involving western Antarctica (Dettmann *et al.*, 1990). Since pollen of *Nothofagus* subgenus *Brassospora* spp. first appears in the west Antarctica–southern South America region, the subgenus probably originated there. However, there is a restricted diversity of this pollen type in that region and it is unknown post-Oligocene (Dettmann *et al.*, 1990). Rapid diversification of *Nothofagus* subgenus *Brassospora* occurred during the Eocene–Oligocene in the Australian–New Zealand region (Dettmann *et al.*, 1990) and its pollen type dominates pollen assemblages, particularly in southeastern Australia during this time (Martin, 1978; Macphail *et al.*, Chapter 10, this volume; Kershaw *et al.*, Chapter 13, this volume). Most species producing *Nothofagus* subgenus *Brassospora*-type pollen became extinct in southern Australia and New Zealand during the late Tertiary, presumably in response to climatic change, although some species remained in Tasmania until the Pleistocene (Hill & Macphail, 1994).

The most common *Nothofagus* macrofossils are leaves, which represent both deciduous and evergreen forms (Romero & Dibbern, 1985; Tanai, 1986; Birkenmajer & Zastawniak, 1989*a,b*; Hill, 1991). Outside of Tasmania, and to some extent southeastern mainland Australia, good organic preservation of *Nothofagus* leaves is rare. This is unfortunate because the infrageneric affinities of *Nothofagus* leaves are difficult to determine on gross leaf morphology and venation pattern alone (Hill, 1991). Reproductive structures are generally uncommon macrofossils, and the woody cupules, sometimes containing fruits, have been recovered only from Tasmania (Hill, 1987, 1991) and one site on mainland southeastern Australia (Christophel, 1985).

By far the most informative macrofossil record of *Nothofagus* comes from Tasmania. Two of the four extant subgenera (*Lophozonia* and *Fuscospora*) now occur in Tasmania, with the others restricted to New Guinea–New Caledonia (*Brassospora*) and southern South America (*Nothofagus*), respectively. However, all subgenera occur in Tasmanian Oligocene sediments, and apparently coexisted, since they are found in small sedimen-

tary units with spatially restricted catchments (Hill, 1991). Biogeographically, the most significant Tasmanian macrofossils are:

1. Leaves of *N. cethanica* (Hill, 1984).
2. Leaves, cupules and fruits of subgenus *Nothofagus* (Hill, 1987, 1991).
3. Leaves and cupules of more than one species of subgenus *Brassospora* (Hill, 1987, 1991).

Nothofagus cethanica is very similar to *N. fusca*, currently a New Zealand endemic, and unlike *Nothofagus* spp. on any other land mass. Prior to the discovery of the Tasmanian fossils of subgenus *Nothofagus* there was only limited pollen evidence for the past existence of this subgenus far outside its current range. The macrofossils of subgenus *Brassospora* are virtually unique and provide the only substantial evidence of the gross morphology of the plants that produce the most abundant pollen. Tasmanian Oligocene *Nothofagus* macrofossils expose several formidable palaeoecological problems, including the reasons for:

1. The extinction of *N. cethanica* in Tasmania, coupled with the survival of *N. fusca* in similar latitudes in New Zealand.
2. The extinction of *Nothofagus* subgenus *Nothofagus*, coupled with its survival in similar (?or more southerly) latitudes in South America.
3. The co-occurrence of species in all four subgenera within very close proximity, and possibly within the same vegetation. This includes such apparently bizarre mixtures as *Nothofagus* subgenus *Brassospora* (now in tropical montane vegetation) with *N. gunnii* (an extant Tasmanian subalpine or alpine deciduous shrub or small tree), which has been recorded at Cethana (Hill, 1984; Carpenter, 1991).
4. The apparent ability of evergreen members of subgenus *Lophozonia* to evolve substantially (in leaf form at least) and remain in the region to the present, coupled with the extinction of most other species.
5. The survival to the present, with unchanged gross leaf morphology, of the winter deciduous *N. gunnii*, while numerous evergreen species

in the same and two other subgenera have become extinct, and members of the fourth subgenus have survived only after substantial change in leaf morphology.

The great enigma of the *Nothofagus* record is the mid-Tertiary abundance of *Nothofagus* subgenus *Brassospora*-type pollen in southern Australia and New Zealand, coupled with the paucity of associated macrofossils. Two distinct types of cupule and leaf of subgenus *Brassospora* have been described from a small sedimentary unit in northwestern Tasmania (Hill, 1987, 1991), and probable leaves and a single cupule from a more diverse suite of fossils in north-central Tasmania (Carpenter, 1991), but they are the only conclusive nonpollen record of the subgenus. Their co-occurrence with all other *Nothofagus* subgenera has led to analyses of prevailing palaeoclimates and experiments on the physiological tolerances of living species (Read & Hill, 1989; Read & Hope, 1989; Read, 1990; Read *et al.*, 1990), resulting in the hypothesis that the Oligocene climate in Tasmania had several features with no modern analogue (Hill, 1990*a*; Read *et al.*, 1990). This climate included mild temperatures with severely compressed extremes, which led to a relatively frost-free environment, and year-round rainfall with very high humidity. The high humidity is evidenced by the diverse and dense epiphytic fungal populations on many of the leaves (Hill, 1990*a*). This climate probably allowed compression of ecological zonation, in a manner similar to that described by Hyndman & Menzies (1990) for the extant rainforests of the Ok Tedi headwaters in New Guinea. Within the Oligocene Tasmanian rainforests, *Nothofagus* subgenus *Brassospora* probably occurred in the canopy, so that juvenile individuals of this type matured with protection against any climatic extremes provided by adult trees. *Nothofagus* spp. in other subgenera occurred in more exposed areas such as ridgetops and lake and river margins, where both juvenile and adult plants were exposed to any prevailing climatic extremes and had to be tolerant of them to survive. With climatic deterioration later in the Tertiary, and in particular a widening of tempera-

ture extremes and a decrease in rainfall, which became markedly seasonal, *Nothofagus* subgenus *Brassospora* spp. were gradually eliminated from the region and were replaced in the canopy by more tolerant *Nothofagus* spp. from other subgenera. Continuing climatic change forced the extinction of some of these species, whereas others, notably in subgenus *Lophozonia*, evolved in response to the changing conditions (Hill, 1991). An alternative hypothesis is that extinction of *Nothofagus* subgenus *Brassospora* from southeastern Australia resulted from its failure to keep pace with the climatic fluctuations that became more pronounced in the region from the mid-Miocene (Read *et al.*, 1990), which was first proposed to account for the extinction of the subgenus from New Zealand (Wardle, 1968). These hypotheses will undoubtedly be refined as future research provides more palaeobotanical and ecophysiological data, but they are consistent with results of past physiological research on extant species from across the latitudinal range. Another possibility is that the frequency of wide-scale disturbance was relatively high during the Oligocene, favouring *Nothofagus* spp. (Hill, 1987), many of which have a disturbance-based ecology (e.g. Veblen & Ashton, 1978; Veblen *et al.*, 1981; Read *et al.*, 1990). The later decrease in disturbance frequency may have forced the demise of these species. Finally, changes in atmospheric CO_2 levels may have altered the competitive abilities of the component taxa in Tasmanian Oligocene rainforests, but data are absent.

There is little macrofossil evidence for evolution in *Nothofagus*, probably because the bulk of the record occurs in the Cenozoic. Pollen evidence (e.g. Dettmann *et al.*, 1990) demonstrates that most major evolutionary events within the genus were complete by the end of the Cretaceous and the common early Tertiary macrofossils support this, in that they are often morphologically similar to extant species. The earliest known species of subgenus *Brassospora* (Oligocene) had serrate-margined leaves and cupule valves that enclosed the fruits (Hill, 1991), although a recently discovered cupule has much reduced valves (R. S. Hill, unpublished data). Serrate-

margined leaves and large cupule valves may represent the condition ancestral to the extant species in the subgenus that have finely serrate or entire-margined leaves and cupules that range from robust valves fully enclosing the fruits to those where cupule valves are absent. However, these fossils substantially postdate the origin of the subgenus and may represent derived forms peculiar to the Tasmanian region. More widespread and conclusive fossil evidence suggests that in southeastern Australia (including Tasmania) and probably also in New Zealand, evergreen species in subgenus *Lophozonia* responded to Cenozoic climate change by significantly reducing their leaf area, forming the characteristic microphyllous species that dominate microthermal rainforest in the regions (Hill, 1991; Figure 16.3). *Nothofagus moorei*, which has a leaf form very similar to the widespread early Tertiary broad-leaved ancestral species in Australia and possibly New Zealand (it may even have dispersed to New Zealand from Australia over the Tasman Sea in the early Tertiary), is extant in isolated high altitude microthermal rainforest at mid-latitudes on the eastern Australian coast. In contrast, the only extant deciduous species outside South America, the high altitude Tasmanian endemic *N. gunnii*, has not altered its general leaf morphology since the Early Oligocene at least (Hill, 1991). This may be because leaves of this species were and are absent during the rigours of the increasingly severe Tasmanian winters.

Thus, the fossil record of *Nothofagus* has proved to be extremely useful for reconstructing past distributions of the genus and, to a lesser extent, major evolutionary events. Perhaps the major contribution that research on this genus will make in the future is in the reconstruction of past climates and vegetation types because it appears to be extremely conservative, especially in the Cenozoic, and modern physiological data can be applied to the past with reasonable confidence.

PODOCARPACEAE

The family Podocarpaceae consists of 18 extant genera and more than 150 species. By far the largest genus is *Podocarpus*, with more than half the total number of species, with the next largest being *Dacrydium* with 16. Only six of these genera are now present in Australia, with most species restricted to Tasmania and northeast Queensland. This is only a small remnant of a once highly diverse podocarpaceous flora, which has left an extraordinary fossil record.

The origins and relationships of the Podocarpaceae are obscure, although Miller (1988) notes that Podocarpaceae and Cephalotaxaceae consistently occur close to one another in his cladograms. The genus *Rissikia*, from the Triassic of Madagascar, South Africa, Australia and Antarctica (Townrow, 1967a), indicates that the family had evolved by the onset of the Mesozoic (Miller, 1988). Other early far-southern conifers, such as the Jurassic *Nothodacrium* (Townrow, 1967b) and *Mataia* (Townrow, 1967a) are probably podocarps, but their relationship to extant genera requires clarification (Stockey, 1990). Podocarps were still prominent in the Cretaceous, although in Australia they are assigned to extinct genera, e.g. *Bellarinea barklyi* from the Early Cretaceous of Victoria (Drinnan & Chambers, 1986). The pollen record at this time is more useful. For example, Dettmann & Jarzen (1990) documented the Cretaceous pollen records of the extant genera *Dacrycarpus*, *Dacrydium* and *Podocarpus* from the Antarctic/Australian rift valley. They note that *Dacrycarpus* pollen occurs in Late Cretaceous sediments in southern Australia, where it ranges into the Pliocene. This is the earliest known occurrence of this pollen type and probably the earliest fossil record, as *Dacrycarpus* macrofossils reported by Florin (1940) from the Jurassic of India must be considered extremely unlikely. '*Dacrydium*' pollen, as defined by Dettmann & Jarzen (1990), is produced by more than one extant genus. One morphotype, with fossils designated as *Lygistepollenites*, is consistent with extant *Dacrydium* and is widely dispersed in Late Cretaceous sediments of southern Gondwana, with the oldest occurrences in the Coniacian–Santonian of southern Australia and the Antarctic Peninsula. The other '*Dacrydium*' pollen type, which is consistent with extant genera such
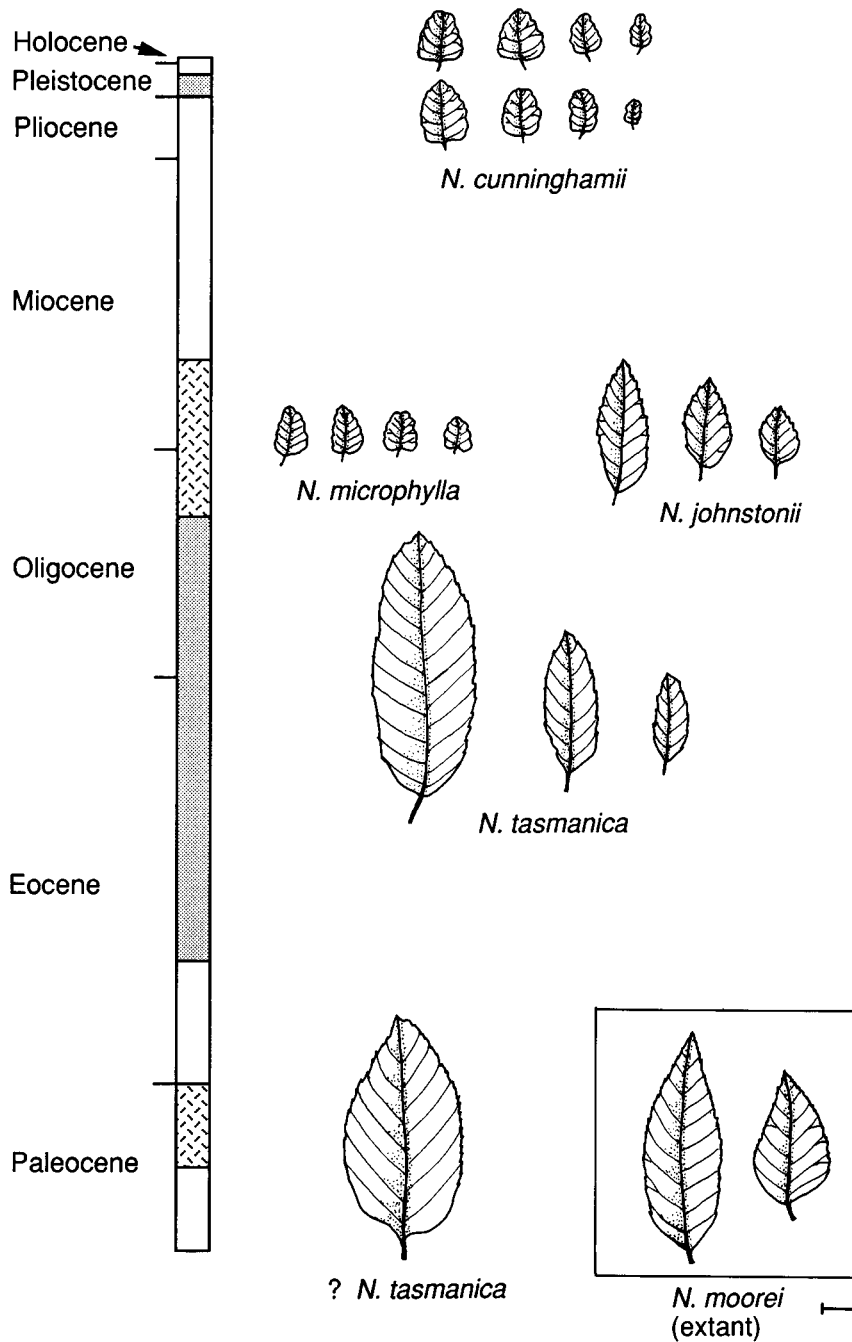
Figure 16.3 Fossil and extant species of *Nothofagus* subgenus *Lophozonia* in southeastern Australia. The shaded areas next to the time scale show the approximate stratigraphic ranges of the fossils. The two rows of *N. cunninghamii* leaves at the top represent the extant species (top row) and Early to mid-Pleistocene leaves (bottom row). Scale bar represents 1 cm.

as *Halocarpus* in New Zealand, is similar to *Podocarpus* pollen and has fossil counterparts in Jurassic sediments. *Podocarpidites ellipticus* 'is similar in general form to, but not diagnostic of, that shed by *Podocarpus* and some species of *Dacrydium*' (Dettmann & Jarzen, 1990). Thus, Dettmann & Jarzen note that the Early Jurassic to Recent range of this species in Australia cannot be taken as indicating *Podocarpus* and/or '*Dacrydium*'.

The Australian Cenozoic pollen record of the Podocarpaceae is abundant and diverse and some taxa warrant special mention. Playford & Dettmann (1979) noted that the fossil species *Phyllocladidites mawsonii* was produced by plants identical with, or very closely related to, *Lagarostrobos franklinii*, which is currently restricted to riverine communities in southwest Tasmania. This pollen type has been prominent in many vegetation and climatic reconstructions (e.g. Kemp, 1978). It is therefore of particular interest that the macrofossil record of *Lagarostrobos* is so sparse. Wells & Hill (1989) assigned one specimen from the Oligocene of northwest Tasmania to a new species of *Lagarostrobos*, but it is not particularly similar to *L. franklinii*, and similarly Carpenter (1991) has suggested an affinity to *Lagarostrobos* for a specimen from Oligocene sediments in northern Tasmania. In other instances the lack of *Lagarostrobos* macrofossils is difficult to explain. For instance, Macphail *et al.* (1991) recorded 45% *P. mawsonii* pollen at the Late Oligocene–Early Miocene Monpeelyata flora in central Tasmania and noted that many grains were apparently immature or aberrant, suggesting a very local source. However, despite the presence of hundreds of podocarpaceous macrofossils, none has so far been related to *Lagarostrobos*, and all have affinities with genera with well-known and distinctive pollen types. Given that *L. franklinii* today is a riverine species, it must be assumed that the ecology of at least one of the species that produced this pollen type in the past was quite different, since *L. franklinii* twigs are common in extant water bodies and are found frequently in Tasmanian Quaternary sediments (e.g. Wells & Hill, 1989; Jordan *et al.*, 1991).

A similar case is presented by the pollen species *Microcachrydites antarcticus*, first described by Cookson (1947). This pollen type, which ranges in Australia from the Jurassic to Miocene, is considered to have affinities with extant *Microcachrys tetragona*, a Tasmanian endemic alpine shrub. There can be no doubt that the taxon (?taxa) that produced *M. antarcticus* pollen had a much wider ecological range than *M. tetragona*, but that does not mean it was morphologically distinct. Blackburn (1985) described a leafy twig from the Latrobe Valley coal as having affinities to *Microcachrys*, and it certainly has more than a superficial resemblance to that genus. If this fossil is *Microcachrys*, then it provides evidence of a plant very similar in leaf arrangement and morphology to the extant alpine shrub, but which must have had a quite different ecological niche. A similar situation occurs in the lowland Early to mid-Pleistocene Regatta Point sediments in western Tasmania, where *M. tetragona* twigs are relatively common (G. J. Jordan, personal communication) in what is interpreted as a predominantly lowland closed-forest vegetation. Perhaps the extant species is the result of compression towards one end of a formerly much broader ecological niche as the result of increased competition, perhaps in response to climatic change or changes in atmospheric CO_2 (maybe as recently as the Quaternary glaciations) or evolution of more specific niches in the expanding angiosperm flora. A similar ecological compression may have occurred in the genus *Microstrobos*. The two extant species are morphologically distinct from one another, and one, *M. niphophilus*, is an endemic alpine shrub or small tree in Tasmania. Macrofossils virtually identical with this species have been recovered from the Monpeelyata sediments in Tasmania (Wells & Hill, 1989), in a region that is considered to have supported a cool climate flora (Hill & Gibson, 1986; Macphail *et al.*, 1991). However, another specimen of the same species has been recovered from lowland Oligocene sediments in northwestern Tasmania in a complex rainforest association (Wells & Hill, 1989; Carpenter *et al.*, Chapter 12 this volume). This suggests a much broader ecological niche during the Oligocene for a species with foliage very similar to extant *M. niphophilus* and a subsequent compression of this niche towards the cooler end.

Many other extant podocarpaceous genera are recorded as macrofossils in Australia during the early Tertiary. Most of them, e.g. *Podocarpus, Falcatifolium, Acmopyle, Dacrycarpus, Dacrydium, Lepidothamnus* and *Phyllocladus*, occur in southeastern Australia, but *Retrophyllum* has been recovered from the southwest. There are also some extinct genera, e.g. *Coronelia* (Townrow, 1965), *Smithtonia* and *Willungia* (Hill & Pole, 1992). Two of these genera, *Acmopyle* and *Dacrycarpus*, contain fossil species that exhibit convergent evolution in response to climate change during the course of the Tertiary.

Acmopyle is very restricted today, with one species in New Caledonia and the other in Fiji. However, it is known as a macrofossil from several early Tertiary sites in southeastern Australia and demonstrates an elegant pattern of evolution, presumably in response to declining water availability (Figure 16.4). The oldest *Acmopyle* macrofossils (Late Paleocene, southern New South Wales) are fully amphistomatic, with stomata equally distributed over both leaf surfaces. This suggests that water was plentiful throughout the year for this species and that water loss was never a serious problem (Hill & Carpenter, 1991). Therefore the plant has maximised its stomatal distribution in an attempt to maximise photosynthesis and growth. By the Early Eocene *Acmopyle* had begun to lose stomata on one leaf surface (Regatta Point and Buckland in Tasmania), suggesting that control of water loss was developing as a serious problem; the species had also adapted morphologically by reducing their stomatal distribution, presumably with the consequence that net photosynthesis was also reduced (Hill & Carpenter, 1991). The plant was clearly adapting to a harsher environment but at a cost in terms of potential growth. This trend continued throughout the Eocene, and by the Late Eocene one species of *Acmopyle* had evolved to the point where stomata were reduced to one leaf surface (Loch Aber, Tasmania). The last record of *Acmopyle* in southeastern Australia is from the Early Oligocene, and it can be assumed that at about this time the climate changed to such a degree that *Acmopyle* was no longer able to evolve a competitive response to it, and thus became extinct in the region. The two living species of *Acmopyle* both have a stomatal distribution similar to that of the Early Eocene species in Tasmania – there are stomata on both leaf surfaces, but they are relatively restricted on
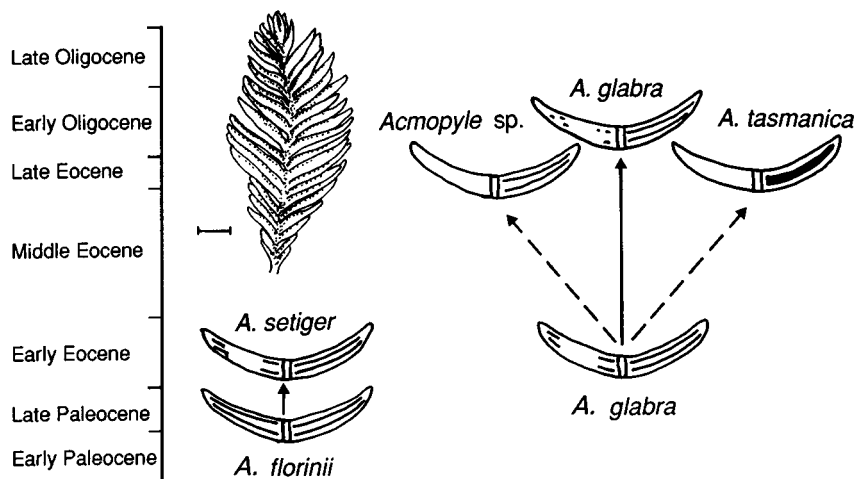

Figure 16.4 Stomatal distribution on leaves of fossil species of *Acmopyle* from southeastern Australia. The leaf 'pair' in each drawing represents the functional 'upper' surface (left-hand side) and 'lower' surface (right-hand side) of a single leaf. The stomatal distribution is shown in black on the leaf surfaces. Broken lines represent uncertain phylogenetic relationships. The entire short shoot, which illustrates the general leaf arrangement, belongs to *A. florinii*. Scale bar represents 5 mm.

one of them. This suggests that the prevailing climate over the range of living *Acmopyle* is suboptimal, but that it is not as severe as the genus can withstand.

Dacrycarpus illustrates an interesting combination of morphological changes that are probably responses to both temperature and rainfall changes. *Dacrycarpus* has two foliage types. In one type, the leaves are bilaterally flattened, so that each functional leaf surface is composed of both adaxial and abaxial leaf surfaces. Furthermore, the whole short shoot (a single season's growth) is flattened into two dimensions, so that the short shoot probably functions like a single broad angiosperm leaf. As well as this, *Dacrycarpus* produces small, scale-like, bifacially flattened leaves that are arranged spirally around the axis in an imbricate arrangement. In most living species these two foliage forms appear apparently at random on the plant, although the bilaterally flattened foliage is often considered to represent a juvenile phase.

Dacrycarpus macrofossils are particularly abundant in early Tertiary sediments in southeastern Australia (Cookson & Pike, 1953; Wells & Hill, 1989; Hill & Carpenter, 1991), and demonstrate a clear trend in foliage evolution (Figure 16.5). In Early Eocene sediments, both foliage types are very common, and in each stomata occur all over both leaf surfaces. However, in progressively more recent sediments there is a trend in two aspects of leaf morphology. Firstly, the bilaterally flattened foliage becomes less common, and by the end of the Oligocene is no longer present as a macrofossil. Secondly, in the bifacially flattened foliage, stomates become progressively more restricted to the inner (adaxial) leaf surface, and by the end of the Oligocene are only found in that position. No *Dacrycarpus* macrofossils have been found in Tasmania after the earliest Miocene, but pollen is recorded up until the Early to mid-
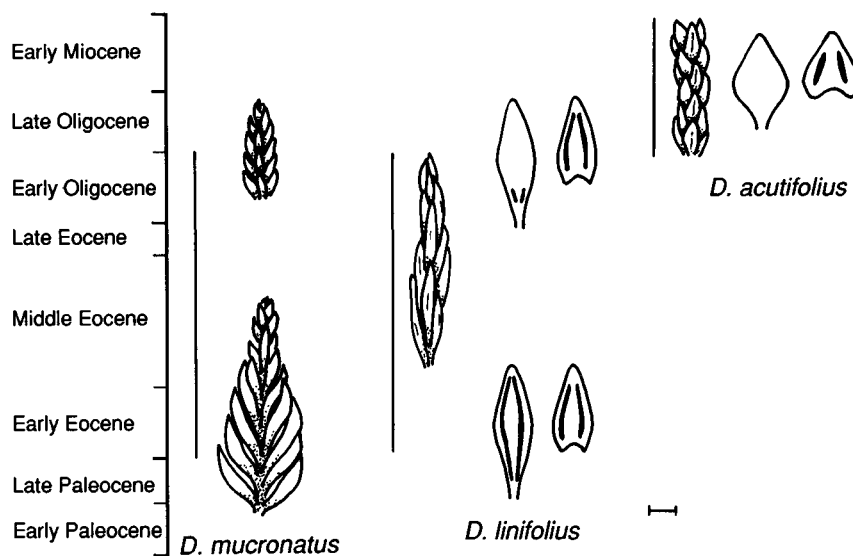

Figure 16.5 Stratigraphic distribution of selected fossil *Dacrycarpus* spp. in southeastern Australia. The line to the left of each species shows the approximate stratigraphic range. *Dacrycarpus mucronatus* shows the change from a combination of bilaterally and bifacially flattened foliage (Early Eocene) to predominantly bifacially flattened foliage (Early Oligocene). *Dacrycarpus linifolius* has been recovered only as bifacially flattened foliage, but the stomatal distribution varies through time. To the right of the short shoot are stylised drawings of leaves, showing the abaxial surface (left-hand side) and adaxial surface (right-hand side). The stomatal distribution is shown in black on the leaf surface. Note the reduction in stomata on the abaxial surface from the Early Eocene to the Early Oligocene. *Dacrycarpus acutifolius* has a more restricted stratigraphic range, but is typical of several Late Oligocene–Early Miocene species in having only bifacially flattened leaves and stomates restricted to the adaxial surface. Scale bar represents 1 mm.

Pleistocene (Hill & Macphail, 1985, 1994), suggesting that *Dacrycarpus* may have been a victim of the Quaternary glacial cycles in Australia. Thus, in this genus we see reduction in leaf area similar to that noted earlier for *Nothofagus*, presumably in response to declining mean annual temperature, as well as a restriction in the distribution of stomata, which is interpreted as a response to the onset of seasonal rainfall and possibly a decrease in total annual rainfall as well. The other interesting feature of *Dacrycarpus* is that these trends are seen in more than one phylogenetic line, suggesting that these were general convergent trends in foliage in response to common external factors (Hill & Carpenter, 1991).

The fossil record of the Podocarpaceae is very productive. There is no doubt that further work will improve our understanding of phylogenetic relationships among fossil and extant species, and this will allow refinement of evolutionary studies on the response of these taxa to climatic change. The Podocarpaceae appears to be a particularly important family for study of the effect of very long-term climate change on leaf morphology and, ultimately, on vegetation form and taxonomic make-up during the Cenozoic.

ARAUCARIACEAE

The two extant genera in the Araucariaceae, *Agathis* and *Araucaria*, are confined to the southern hemisphere, where they occur as trees sometimes reaching 60 m or more (Florin, 1963; Stockey, 1982). There are 13 extant species of *Agathis*, three of which occur in northeastern Australia (Whitmore, 1980). *Araucaria* is divided into four sections containing 22 species, 2 of which occur in northeastern Australia and 1 on Norfolk Island (Hill & Bigwood, 1987). The current centre of diversity for both genera is New Caledonia, with 5 *Agathis* and 14 *Araucaria* spp.

The family was more diverse and widespread during the Mesozoic, and extended into the northern hemisphere during the Jurassic (Stockey, 1982). A large number of fossils have been assigned to the Araucariaceae, many of which must be regarded as extremely doubtful. The pol-

len record is extensive and widespread, but, because of its uniformity, is not helpful in tracing particular phylogenetic lines within the family (Martin, 1978; Stockey, 1982). In this brief review only some of the more certain and relevant records are considered.

Araucaria has a much more extensive fossil record than *Agathis*. However, this record is difficult to interpret because of the number of conifers with superficially similar foliage and the proliferation of generic names used to encompass them. The pre-Jurassic record is particularly uncertain and is not considered reliable (Stockey, 1982). Stockey (1982) considered that *Araucarites phillipsii*, the cone and cone scale associated with *Brachyphyllum mamillare* from the Yorkshire Jurassic, is part of the same species, which has strong affinities to *Araucaria* section *Eutacta*. Stockey described several other *Araucarites* spp. from widespread Jurassic and Cretaceous localities, which have less certain affinities to this section of *Araucaria*.

Drinnan & Chambers (1986) described an *Araucaria* sp. from the Early Cretaceous Koonwarra fossil bed, which they compared with *A. heterophylla*, and assigned to section *Eutacta*. Species that can be assigned to section *Eutacta* are widespread across South America–Antarctica–Australia–New Zealand during the Tertiary (Florin, 1940) and are particularly prominent in southeastern Australia (summarised by Hill & Bigwood, 1987; Hill, 1990*b*). Organically preserved specimens have been described from the Early Eocene of Tasmania (Hill & Bigwood, 1987), Oligocene of Victoria (Cookson & Duigan, 1951) and Oligocene – earliest Miocene of Tasmania (Hill, 1990*b*). There are also several undescribed species in Tasmania from Eocene and Oligocene sediments (R. S. Hill, unpublished data). One of the interesting features of the Tertiary *Araucaria* section *Eutacta* record in Tasmania is that in several deposits up to three species apparently co-occurred. The overall species diversity in Tasmania during the Oligocene is comparable with New Caledonia today, and suggests that the current concentration of species there may be due to the extant climate–vegetation associations rather than to any historical centre of origin.

Tasmania in the early Tertiary may have been similarly conducive to a high species diversity in this section of *Araucaria*.

Section *Intermedia* of *Araucaria*, which is currently restricted to New Guinea, is represented in the fossil record by the ? Late Cretaceous *A. haastii* from New Zealand (Ettingshausen, 1891; Stockey, 1982; Hill & Bigwood, 1987). Section *Columbea*, with two extant species in South America, is represented in the fossil record by *A. balcombensis* from the Tertiary of Victoria, and *A. hastiensis* from the Middle–Late Eocene of Tasmania (Hill, 1990*b*). *Araucaria nathorstii*, from the Tertiary of Argentina (Menendez & Caccavari, 1966) may also belong to section *Columbea*, although this has not been determined with certainty (Hill & Bigwood, 1987).

Section *Bunya* of *Araucaria* is restricted to a single extant species, *A. bidwillii*, in Queensland. This section was more widespread during the Mesozoic, even into the northern hemisphere, and more diverse, and remains indicate that the cone morphology in this section was similar to *A. bidwillii* by the Jurassic (Stockey, 1982). Stockey noted that *A. bidwillii* represents the last species of a very distinctive group of araucarians that is of major significance in determining evolutionary relationships within the genus.

The fossil record of *Agathis* is restricted to the southern hemisphere, and more particularly to Australia and New Zealand (Florin, 1963). The oldest record of *Agathis* in this region is *A. jurassica* from the Jurassic Talbragar Fish Bed Flora in New South Wales (White, 1981). This fossil species consists of leaf impressions and associated cone scales. However, Stockey (1982) noted that the cone scales also show close similarities with *Araucaria* section *Eutacta*, and there must be considerable doubt about the taxonomic connection between the leaves and these reproductive structures; later, Stockey (1990) suggested that the foliage of *A. jurassica* may in fact be podocarpaceous. Florin (1940) noted the possible presence of *Agathis* in the Late Cretaceous of Australia, but his record requires confirmation. Christophel (1981; Chapter 11, this volume) recorded the presence of *Agathis* in the Middle Eocene Maslin Bay sediments, but this taxon has not yet been

described. The Late Eocene Vegetable Creek sediments in northern New South Wales contain leaf and cone scale impressions that are certainly *Agathis*, although there is no confirmatory cuticular preservation. Well-described and organically preserved *Agathis* leaves have been described from probable Oligocene sediments in Victoria (Cookson & Duigan, 1951) and Tasmania (Hill & Bigwood, 1987; Carpenter, 1991), and Middle Eocene–Oligocene sediments in southwestern Australia (Hill & Merrifield, 1993).

Bigwood & Hill (1985) described leaves from Early Eocene sediments in Tasmania and placed them in the genus *Araucarioides*. These leaves were considered to have features of both *Agathis* and *Araucaria*. Stockey (1990) hypothesised that this genus, coupled with the large number of 'araucarian' cone scales in northern hemisphere localities, 'suggests that the Araucariaceae may have included an additional genus in the past'. Cantrill (1991) described *Podozamites taenioides* from mid–late Albian sediments in Victoria. This species, based on foliage, is very similar to the Tertiary species assigned to *Araucarioides*, and may represent an older record of the same genus. Cantrill (1991) noted that some Australian *Podozamites* spp. were similar in gross morphology to *Agathis*. It may be that this group of taxa, which extended into the Early Eocene in Tasmania, included the taxon ancestral to *Agathis*, which probably evolved in the Australia–New Zealand region sometime in the Jurassic–Cretaceous.

Clearly, the present diversity of the Araucariaceae, with the exception of New Caledonia, is only a small fraction of the past, but it represents a family that figured largely during the formative stages of the extant Australian vegetation. Although many fossils in the Araucariaceae are yet to be described or fully understood, there is no doubt of the importance of Australia in unravelling the phylogenetic history of this important family of currently southern hemisphere conifers.

PROTEACEAE

The Proteaceae is one of the major Australian families. Worldwide there are about 75 genera of

evergreen trees and shrubs, with a strong representation in tropical and subtropical closed forests, as well as in sclerophyllous heaths and woodlands on oligotrophic soils (Johnson & Briggs, 1981). The family has been divided into five subfamilies (Johnson & Briggs 1975), all of which occur in Australia. The extant species of the Proteaceae have been extremely well studied and, primarily due to the efforts of Johnson & Briggs (1963, 1975, 1981), the phylogeny of the family is well understood. Given its mostly southern hemispheric distribution, and its strong centres of diversity in Australia (east coast and southwest corner) and the southern tip of Africa, the Proteaceae is an extremely interesting family in terms of both its evolution and past distribution. The fossil record is invaluable in reconstructing this history.

Johnson & Briggs (1975) undertook an extremely detailed analysis of the living species and proposed several hypotheses relating to the evolution and past distribution of parts of the family. Although the fossil record at the time was not particularly useful for testing these hypotheses, more recent fossil data have proved to be strongly supportive of some of these hypotheses. The intention here is to concentrate on the Australian fossil history of the family, but some examples of the value of fossil data in testing well-established hypotheses are worth mentioning. For example, Johnson & Briggs (1975) noted that 'The ancestors of Cenarrheninae, Dilobeiinae, Proteeae, Hicksbeachiinae, Gevuininae, Macadamiinae and Roupalinae . . . must have evolved by the early Upper Cretaceous.' Furthermore, they considered that *Dilobeia*, Hicksbeachiinae, Gevuininae and Macadamiinae were probably distributed by land in the mid-Cretaceous rather than by distance dispersal over marine barriers at a later date. More recently, Dettmann (1989) noted that during the Campanian–Maastrichtian an array of Proteaceae were introduced into Antarctica, including possible *Macadamia* (Macadamiinae), *Gevuina/Hicksbeachia* (Gevuininae/Hicksbeachiinae), *Knightia, Xylomelum* and *Beauprea* (Cenarrheninae). She considered that southeastern Australia may have been the site of evolution of the New Caledonian and New Zealand *Knightia* and the *Gevuina/Hicksbeachia* alliance, which today has a disjunct distribution between northeastern Australia and Chile. Furthermore, she suggested an introduction of *Macadamia* into Antarctica and southern Australasia by the Campanian. Dettmann & Jarzen (1990, 1991) proposed this region as a source area for *Beauprea* as well. Thus, Johnson & Brigg's hypothesis has, in large part, been substantiated by fossil evidence.

Cretaceous pollen data provide vital evidence for the time and place of appearance of proteaceous groupings (Dettmann, 1989; Dettmann & Jarzen, 1990, 1991), and led to the hypothesis that the family originated in northern Gondwana (Dettmann, 1989). Furthermore, Dettmann & Jarzen (1991) have reported pollen of both rainforest and sclerophyllous types of Proteaceae in the Late Cretaceous of the Otway Basin in southeastern Australia, strengthening the argument for a diversification of the family at that time. However, in the early Tertiary the pollen and macrofossil record of the family expanded enormously.

Martin (1978, 1982) noted the major increase in diversity and abundance of Proteaceae during the Late Paleocene–Eocene. Although the familial affinity of some of these fossil pollen types is in doubt (Martin, 1973; Martin & Harris, 1974), many 'are undoubtedly true Proteaceae' (Martin & Harris, 1974). The abrupt disappearance of many of these pollen species at about the end of the Eocene is apparent from stratigraphic range charts (e.g. Stover & Partridge, 1973). This high diversity and abundance of proteaceous pollen has been treated with some suspicion for two reasons:

1. Relatively low percentages of proteaceous pollen are retrieved from surface samples in extant dry Australian forests where the family is abundant and diverse (Martin, 1978). Martin (1982) considers that it is possible that the early Tertiary species were trees that would produce more pollen than a comparable extant sclerophyllous shrub layer, but notes that Kershaw (1970) has recorded low pollen counts from extant proteaceous trees in Queensland rainforests. Martin further suggested that many of the taxa may

have dominated the vegetation, but see (2), below.

2. Christophel & Blackburn (1978) noted that the Middle Eocene Maslin Bay flora contained 35–40% *Proteacidites* spp., but relatively few proteaceous macrofossils. They and Christophel (1981), who noted the same trend at Nerriga, considered that one factor that may be contributing to this discrepancy is the difficulty experienced in identifying the pollen, but this is unlikely to be of major significance.

There is little doubt that the majority of the great diversity and abundance of pollen assigned to 'Proteaceae' in the early Tertiary came from proteaceous plants, but there is at present no reasonable explanation for their demise or the paucity of proteaceous macrofossils in the deposits that yield the pollen.

One possibility that has not been fully investigated is a shift in pollination strategies. Extant Proteaceae rely on biotic pollination, by insects (which is considered to be the ancestral state), birds or animals (Johnson & Briggs, 1975). However, it is possible that wind pollination may have been significant in an early Tertiary group of proteaceous species that are now extinct. The evidence for this is circumstantial. About half the proteaceous species that became extinct in southeastern Australia by the end of the Eocene had pollen grains with diameters in the range 20–40 μm, which Muller (1979) considered optimal for wind pollination. The other species all had much larger grains (some over 100 μm in diameter), which may reflect early animal pollination strategies. The smaller proteaceous species are often quite abundant, comparable with other, well-known wind-pollinated taxa in the same sediment, e.g. species of *Nothofagus* or Casuarinaceae. Faegri & van der Pijl (1979) give some examples of species, in families that are basically entomophilous, that have apparently become secondarily anemophilous; the same may have occurred in the Proteaceae. This goes some way to explaining the abundance of pollen but paucity of associated macrofossils. An even more convincing demonstration of the phenomenon of pollen dominance and paucity of associated macrofossils is supplied by *Nothofagus* subgenus *Brassospora* (see earlier discussion). The reason for the extinction of a large number of Proteaceae by the end of the Eocene is uncertain, but may be tied to climatic change, either directly, due to the climatic tolerances of the species involved, or indirectly. Indirect effects of climatic change include either a change in pollination strategies due to an increase in animal and/or bird pollinators, or a change in vegetation type, which made wind pollination a less competitive strategy. For example, if the Proteaceae were not canopy trees, wind pollination would be a viable method only if the vegetation was relatively open. The development of closed vegetation would mean that canopy or forest edge taxa (e.g. *Nothofagus*, Casuarinaceae and the conifers) could still utilise wind pollination, but subcanopy taxa (the now extinct Proteaceae) would become extinct. Faegri & van der Pijl (1979, p. 48) noted that in dense forest vegetation 'wind is so slight and infrequent that anemophily is contra-indicated'.

Another hypothesis to explain the reduction in wind pollination in understorey plants is that during the very early Tertiary the southern Australian vegetation was at very high latitudes (Wilford & Brown, Chapter 2, this volume), and the vegetation existed under polar photoperiods. With the sun at a low angle in the sky during summer, and tracking an almost circular path around the horizon during the day, it is likely that the structure of forests was quite different from that observed in wet regions of Australia today. It is probable that relatively widely spaced conical trees dominated, and thus wind pollination was a viable strategy for understorey plants below the open canopy. As Australia moved into lower latitudes, the sun angle increased and a closed-forest structure would have developed as the most efficient way to utilise the incoming solar radiation. This may have been critical for the loss of wind pollination as a viable strategy in understorey plants. This hypothesis is tentative at present, but is the first that explains the observed data.

It should be noted that there were probable bird-pollinated Proteaceae present in Australia by

the Eocene. McNamara & Scott (1983) described a *Banksia* infructescence from Early Eocene silcretes in the Stirling Ranges of northwestern Australia and noted that one follicle had apparently been removed from the infructescence in a fashion similar to that employed by parrots today. This suggests a plant–animal interaction that may have extended to pollination; given the current pollination strategies of *Banksia* (Hopper, 1980; Hopper & Burbidge, 1982; Turner, 1982), either bird or small mammal pollination is indicated. Christophel (1984) described an inflorescence closely related to the extant genera *Musgravea* and *Austromuellera* from the Middle Eocene Anglesea sediments that again suggests animal (?probably bird) pollination.

Some Oligocene macrofloras differ from the preceding Eocene macrofloras in containing diverse and numerous proteaceous remains. The best examples are the Latrobe Valley coal in Victoria (Cookson & Duigan, 1950; Blackburn, 1985; Hill & Christophel, 1988; Hill, 1990c; Blackburn & Sluiter, Chapter 14, this volume), Cethana in Tasmania (Hill & Christophel, 1988; Carpenter & Hill, 1988; Carpenter, 1991; Carpenter *et al.*, Chapter 12, this volume), and West Dale in southwestern Australia (Hill & Merrifield, 1993). Many of the proteaceous taxa in these deposits can be assigned to extant genera, and in particular the *Banksia/Dryandra* group (fossils are assigned to *Banksieaephyllum* or *Banksieaeformis* depending on the preservation or otherwise of cuticle). Leaves of this type are first recorded in the Late Paleocene of southern New South Wales (R. S. Hill & J. G. Jordan, unpublished data) and are present in several Eocene sites in southeastern Australia (Hill & Christophel, 1988). However, the number of species, and the diversity in single deposit peaks in the Oligocene, may also be related to a change in pollination mechanisms (see Carpenter *et al.*, Chapter 12, this volume).

Hill (1990a) has hypothesised that the *Banksieaephyllum* fossils demonstrate the probable pathway for the development of the sclerophyllous heath flora that is prominent in Australia today in areas with oligotrophic soils and a mediterranean climate (hot, dry summers and mild, wet winters).

The first *Banksieaephyllum* leaves in the fossil record have several typically sclerophyllous characters (thick, highly vascularised leaves etc.), suggesting that they occurred on oligotrophic soils. However, they occur in typical rainforest associations and have relatively few morphological adaptations for stomatal protection. This suggests that water was always plentiful, which is in keeping with the climatic reconstruction for that time (Quilty, Chapter 3, this volume). However, Hill (1990a) suggested that such leaves may have been pre-adapted to xeromorphic conditions that increased in intensity and spread geographically later in the Tertiary. For example, the *Banksieaephyllum* spp. in the Latrobe Valley coal show a mixture of leaf morphologies. According to Blackburn (1985) those associated with rainforest species still show little or no stomatal protection, whereas those associated with more open (xerophytic) vegetation show some adaptations for stomatal protection (e.g. dense trichomes, stomata in pits between the veins, revolute leaf margins). Such adaptations must be associated with reduced water availability, since they must substantially reduce the CO_2 uptake (and hence photosynthesis) and must be advantageous to the plant if protection against excessive transpirational loss was of particular importance. Among modern *Banksia* and *Dryandra* spp., several extreme forms of stomatal protection occur, including those mentioned above, although often developed to a much greater degree (Figure 16.6). While it is tempting to suggest that this represents an evolutionary progression from the early Tertiary forms, which were pre-adapted to some extent to xeromorphic conditions, through to the extant forms, with their often extreme adaptations, there has been no phylogenetic analysis of fossil *Banksieaephyllum* leaves to test this hypothesis. As with the Casuarinaceae (see later), we cannot discount an alternative hypothesis, that extremely xeromorphic *Banksia/Dryandra* spp. evolved at a relatively early stage in restricted dry microsites, or in remote areas in central Australia and later expanded into southern and eastern Australia, replacing the less xeromorphic forms. In either case, this group offers an excellent opportunity to
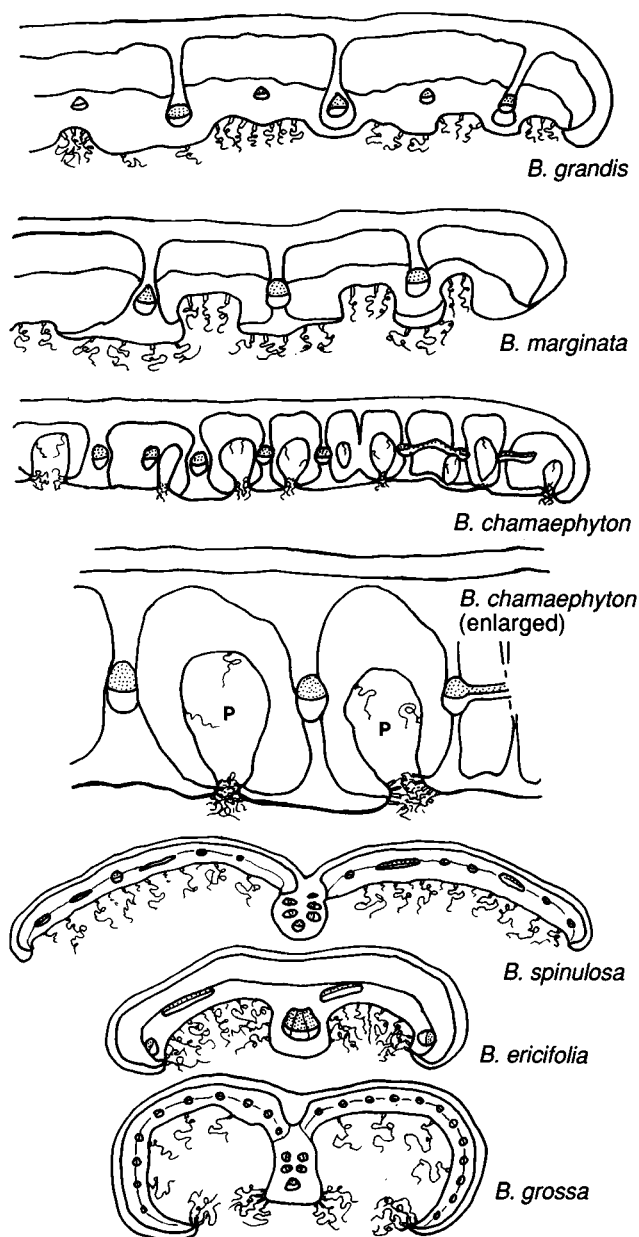
Figure 16.6 Drawings of transverse sections of leaves of several extant *Banksia* spp. In all cases the stomatal surface (abaxial) is the lower surface. The top three species show a range among broad-leaved species from those with minor depressions containing stomata and trichomes (*B. grandis*) to those with more deeply developed pits (*B. marginata*) to the extreme case of stomatal pit development (*B. chamaephyton*). In *B. chamaephyton* the stomata occur in large balloon-shaped pits (P), which extend more than half way through the leaf. The opening of the pit is protected by tufts of trichomes. The lower three species are examples of relatively narrow leaves that protect the stomata by means of revolute margins. These species range from only slightly revolute (*B. spinulosa*) to an intermediate phase (*B. ericifolia*) to the extreme case of highly revolute leaves (*B. grossa*) with dense bands of trichomes along the mid-vein and leaf margins protecting the opening of the grooves in the leaf containing the stomata. This is a similar strategy to the tufts of trichomes in *B. chamaephyton*.

study the response of a restricted taxon to major climatic change over a long period.

The fossil record for most other proteaceous genera is more restricted, but overall this record is very impressive. The pollen record is well known, but still in need of revision in order to determine the true affinities of some species (Dettmann & Jarzen, 1990). The leaf record is also impressive, has grown considerably over the last few years and promises further expansion in the near future. Reproductive structures are fewer but offer a particularly important source of phylogenetic information. There are still undescribed taxa of proteaceous reproductive structures (e.g. Hill & Macphail, 1983; Christophel, 1984) and we can expect further progress in this direction over the next few years. A detailed analysis of this record will undoubtedly lead to a much greater understanding of the past history of this major Australian family.

CASUARINACEAE

The family Casuarinaceae comprises 96 extant species in four genera that are confined to the Malesian–Australian–Melanesian region, except for the essentially littoral species *Casuarina equisetifolia* (Johnson & Wilson, 1989). The family is widespread in Australia, and ranges through most vegetation types, although it is restricted to one small population in rainforest. The affinities of the family are obscure, but it has an impressive fossil record. Pollen of the Casuarinaceae is readily identifiable, but unfortunately the generic affinities cannot be determined. According to Johnson & Wilson (1989) fossil pollen has been reliably reported from South Africa (Coetzee & Muller, 1984, Coetzee & Praglowski, 1984), Argentina (Archangelsky, 1973) and on the suboceanic Ninetyeast Ridge in the Indian Ocean (Kemp & Harris, 1977). It is also common in Australia and New Zealand from the Paleocene onwards (Martin, 1978; Mildenhall, 1980). The latest occurrence of Casuarinaceae pollen in New Zealand is Early Pleistocene (Mildenhall, 1980).
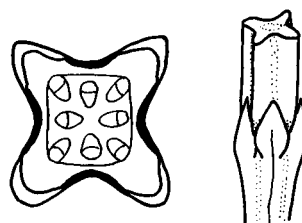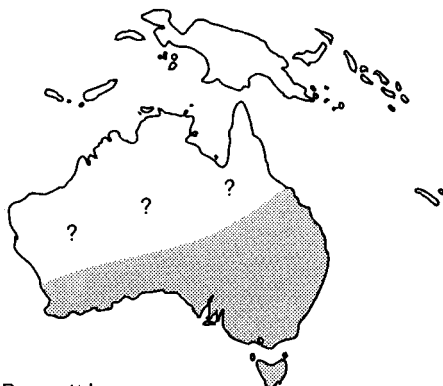
Macrofossils of Casuarinaceae are relatively abundant, and convey much more taxonomic information than does pollen. In Australia the macrofossil record extends from the Early Eocene onwards (although a specimen described by Douglas (1978) from Victoria may extend the record into the Paleocene, according to Blackburn (1985)) and demonstrates some interesting trends. The earliest records (Eocene–Oligocene) are all *Gymnostoma*. Three species have been described in detail (Scriven & Christophel, 1990), although none of the fossil *Gymnostoma* species has yet been named. *Gymnostoma* extends into the Miocene in the Latrobe Valley coal (Blackburn, 1985) and the Etadunna Formation in central Australia (Greenwood *et al.*, 1990), but it has not been recorded as a macrofossil after that time. *Gymnostoma australianum* still occurs in Australia, in a small patch of rainforest on the Atherton Tableland (Fig. 16.7).
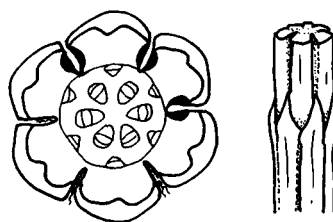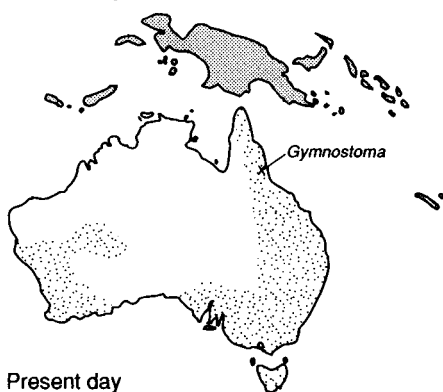
Macrofossil records of other casuarinacean genera in Australia are sparse. Blackburn (1985) described cladodes and female cones from the Yallourn and Morwell coal seams as *Casuarina*, and suggested that they were similar to extant species such as *C. equisetifolia*. Patton (1936) noted the presence of cladodes and females cones of Casuarinaceae from the possibly Miocene siliceous sandstones at Limestone Reserve in Victoria. These specimens appear most likely to belong to *Allocasuarina*, although a reinvestigation is nececessary to confirm this. Blackburn (1985) also noted the presence of cladodes and cones that he considered to be almost certainly *Allocasuarina* in the Pliocene of Victoria (Deane, 1904) and the ?Miocene of South Australia. Greenwood *et al.* (1990) noted the presence of what are probably *Allocasuarina* cones in Miocene sediments in central Australia, where they co-occur with *Gymnostoma*.

Thus the macrofossil record from central, coastal southern and eastern Australia suggests that *Gymnostoma* was dominant from the Early Eocene (or ?Paleocene) until the Oligocene and then there was a relatively short transition during the Miocene to dominance by *Casuarina* and *Allocasuarina*. Blackburn (1985) noted this transition in the Latrobe Valley coal, where *Gymnostoma*
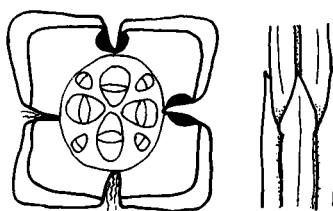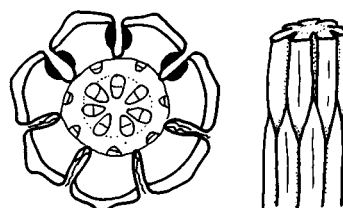
Figure 16.7 Distribution of the three major Casuarinaceous genera during the Eocene–Oligocene and present day. The population of *Gymnostoma* shown in northeastern Australia in the present day is *G. australianum*. Examples of transverse sections through cladodes of species from each genus are shown on the right-hand side. Stomatal distribution is shown by thick black lines on the surface. Trichomes are shown in some stomatal pits. Note the relatively superficial stomata in *Gymnostoma* compared with the other genera.

dominates over *Casuarina* at Morwell, but the reverse is true at Yallourn.

Hill (1990a) considered that the Casuarinaceae family was an excellent illustration of the effect of developing aridity in southern Australia during the Tertiary. In the early Tertiary, when the climate was uniformly wet, *Gymnostoma* was the only Casuarinaceae identified, and it occurs in many macrofossil deposits. Although *Gymnostoma* is quite scleromorphic in its reduced and virtually nonfunctional leaves and woody photosynthetic stem, it is not particularly adapted to prevent water loss. The very name of the genus describes its unprotected stomata (Figure 16.7), which are present in rows on the usually glabrous stem surface. Thus *Gymnostoma* can be considered to be a genus that may be adapted to oligotrophic soils, and in particular the characteristically phosphorus-poor Australian soils, but is not particularly xeromorphic. In contrast, both *Casuarina* and *Allocasuarina* have well-protected stomata, in deep grooves along the stem, which are often filled with trichomes (Figure 16.7). These genera are not only scleromorphic, but xeromorphic as well, i.e. they have morphological adaptations to prevent excessive water loss. These adaptations must surely have evolved in response to continually dry conditions, since they must severely disrupt the entry of CO_2 into the stems. Such an adaptation must therefore confer a great benefit to the plant in order to overcome the disadvantage in terms of lost productivity.

The apparent changeover in dominance during the Miocene is therefore readily explainable in terms of climatic change. As the climate dried in southern Australia, *Gymnostoma* was no longer competitive and its niche was taken over by *Casuarina* and *Allocasuarina*. It is tempting to consider that *Gymnostoma* may have been ancestral to *Casuarina* and/or *Allocasuarina*, but there is no evidence for this. When *Casuarina* and *Allocasuarina* first appear in the Australian macrofossil record they are recognisable as the extant genera, and, although Christophel (1980) has suggested that some of the fossils from the Latrobe Valley coal may be intermediate, there has been no further report of this nature; Blackburn (1985)

confidently assigned all specimens from that locality to extant genera.

There are two options to explain this rapid change in dominant casuarinacean genera in southern Australia during the Miocene. It is possible that *Casuarina* and *Allocasuarina* evolved relatively late in the Tertiary, especially in comparison with *Gymnostoma*, and rapidly exploited new niches as they became available during the Miocene spread of aridity. However, I consider it more likely that *Casuarina* and *Allocasuarina* are also ancient genera, perhaps as old as *Gymnostoma*, but without the associated macrofossil record. During the early Tertiary, or perhaps even earlier, *Gymnostoma* was common in the vast tracts of rainforest that occurred around coastal southern and eastern Australia. However, even during this period of high water availability there must have been dry microsites in this coastal belt (e.g. ridgetops, sand dunes), and in these xeric microsites it is possible that the more xeromorphic *Casuarina* and *Allocasuarina* became established. Even if this occurred, it is unlikely that plants in such microsites would leave a macrofossil record, being remote from sedimentary environments. However, such plants would have been very well placed to expand rapidly when the climate dried later in the Tertiary. There may also have been more extensive areas suitable for these genera in inland Australia during the early Tertiary, but the only reliable macrofossil record of the family from central Australia is a report of two species of *Gymnostoma* from the Middle Eocene Nelly Creek flora (Christophel *et al.*, 1992).

Extra-Australian records

There is a small but very significant extra-Australian macrofossil record of the Casuarinaceae. Frenguelli (1943) described *Casuarina patagonica* from Miocene sediments in southern South America (since revised to 59 million years (Early Eocene), E. J. Romero, personal communication). The illustrated specimen consists of a short branch bearing four female cones. Christophel (1980) considered that it was possible that this specimen belonged to a non-*Gymnostoma*

form of Casuarinaceae, but it was 'equally if not more likely' to have affinities with *Gymnostoma*. Johnson & Wilson (1989) unequivocally assign this species to *Gymnostoma*. E. J. Romero (personal communication) has collected two more specimens of Casuarinaceae female cones, from Early Eocene sediments in South America, that are about twice the size of *C. patagonica* and have several other distinguishing features. Romero concludes that these specimens represent a new species of *Gymnostoma* that is distinct from *C. patagonica*.

Campbell & Holden (1984) have described two casuarinacean species from Miocene sediments in the South Island of New Zealand. They considered that the characteristics of the female cone of *Casuarina stellata* are consistent with *Gymnostoma*, a conclusion supported by Johnson & Wilson (1989). However, the fruiting cones of *C. avenacea* clearly do not belong to *Gymnostoma*. Johnson & Wilson (1989) considered that this specimen should be assigned to *Allocasuarina*, but Johnson (1991) has revised this opinion and the generic affinities of this species are less certain. Some specimens of *C. avenacea* clearly have more than four pairs of bracts in a whorl of the female fructification, but one specimen appears to have only four, and superficially resembles *Gymnostoma*. This has implications when we consider the affinities of *C. patagonica*. Although the parts of that specimen all appear to be in whorls of four, there is at least the possibility that this is only part of the range exhibited by the species and that it was, in fact, not *Gymnostoma*.

Thus the extra-Australian macrofossil record of Casuarinaceae demonstrates that *Gymnostoma* was present in South America during the Early Eocene and New Zealand during the Miocene. Non-*Gymnostoma* Casuarinaceae was also present in New Zealand in the Miocene, and possibly also in South America in the Early Eocene. The presence of Casuarinaceae pollen in New Zealand since the Paleocene suggests a long history in that land mass. Thus we can be sure that *Gymnostoma* at least was widespread across the southern hemisphere during the early Tertiary and it is probable that its origin precedes the separation of Australia

and New Zealand from Antarctica. There is less convincing evidence to suggest that at least one other genus (possibly *Casuarina*) has a similarly long history, although more recent long-distance dispersal from Australia may play a role here. This fossil record makes a particularly interesting comparison with *Eucalyptus* (discussed below), especially its apparently contemporaneous extinction in New Zealand during the Early Pleistocene.

EUCALYPTUS

Eucalyptus has justifiably been called the 'universal Australian' (Pryor & Johnson, 1981), with its more than 500 species, which are nearly all endemic to Australia. In form, the species range from low shrubs to the tallest flowering plants in the world. Lange (1980) noted that eucalypts have been estimated to contribute 75% of Australian vegetation, and at the wetter margins of the continent they dominate nearly all vegetation except rainforest and allied mesic types. Only in the arid Australian interior are eucalypts generally lacking in dominance.

The macrofossil record

The genus is highly diversified (Johnson, 1972; Pryor & Johnson, 1981) and, in conjunction with its current dominance, it would be expected to yield a complex and challenging fossil record. That this is not the case has been well documented, most notably by Lange (1978, 1980, 1982), who made a detailed but futile search for organically preserved eucalypt remains among coastal Tertiary dispersed cuticles. However, *Eucalyptus* has a macrofossil record, and it is more detailed than is usually acknowledged. The widespread ignorance of this record is as much a commentary on the mystique surrounding this genus in Australia as a sign of scientific rigour. When Maiden (1922) produced his *Critical Revision of the Genus* Eucalyptus, he included descriptions of 19 macrofossil species, as well as four records of sub fossils that were assigned to extant species. In stark contrast, Lange (1980) believed there was 'no Tertiary record of *Eucalyptus* that could with-

stand close taxonomic scrutiny' and Christophel (1989) considered that the only macrofossil records of *Eucalyptus* worth mentioning were 'definitely eucalyptoid' Miocene leaf and fruit impressions from Chalk Mountain in New South Wales. Christophel also noted that, by the Pliocene, *Eucalyptus* 'is well represented', although to my knowledge there is only one macrofossil record of this age (*E. pluti*; McCoy, 1876).

Clearly, after the promising start reported by Maiden (1922), something went seriously wrong with the Australian *Eucalyptus* macrofossil record. Part of the problem extends from the general view of the quality of taxonomic work on Australian Tertiary plant macrofossils undertaken during the late nineteenth and early twentieth centuries. In Australia, Deane (1896, 1900) launched a vigorous attack on the taxonomic work of von Ettingshausen (1888), noting for instance in 1896 that von Ettingshausen 'has expressed views as to the origin of the vegetation of Australia, and of the rest of the world, which appear to be entirely erroneous'. E. W. Berry (in Maiden, 1922), in an apparent defence of von Ettingshausen, noted that, apart from the work of that taxonomist and of Mueller, 'There have been more worthless articles written about the Cretaceous and Tertiary floras of Australia than any other equal area of the earth's surface'. These two examples represent only a small fraction of the criticism aimed at Australian macrofossil palaeobotany at that time. This ongoing criticism, from both within and without, did enormous damage to Australian palaeobotany. Although there was undoubtedly some poor taxonomic work done during these pioneer days, there was much good work carried out as well. The strength of criticism seems to have brought research almost to a halt from the 1920s until the 1950s, when Cookson resurrected macrofossil research. It is not surprising that few people wished to become involved in a field associated with such a stigma. Furthermore, living plant taxonomists lost confidence in palaeobotany.

That this stigma endures in the minds of some palaeobotanists is evidenced by the comments of Lange (1980) and Christophel (1989) mentioned earlier. *Eucalyptus* seems to have suffered particularly heavily. Some of the fossil species described by early researchers are clearly not *Eucalyptus*. The oft-cited example is *E. praecoriacea*, which was described by Deane (1902*a*). Deane considered this species to be similar to the extant *E. coriacea* (now *E. pauciflora*). Hill (1980) considered that the type specimen of *E. praecoriacea* is almost certainly part of a frond of a zamioid cycad. However, Christophel's (1981) suggestion that Deane 'had but to glance at the well preserved cuticular structure to realize that he was dealing with a cycad-like plant and not a eucalypt' was unfair, since the organic remains on the fossil are very fragmentary and cell detail has never been successfully observed from attempted preparations. It is instructive to note that Patton (1919), in a paper describing Tertiary *Eucalyptus* leaves, commented that *E. praecoriacea* 'is a very doubtful eucalypt'. This one piece of poor taxonomy should not evince universal contempt. In fact many of the early reports of *Eucalyptus* macrofossils appear to be very convincing, and in the case of the Berwick Quarry fossils described by Deane (1902*b*) a reinvestigation (Pole *et al.*, 1993) has confirmed the generic identity. Thus, the specimens described during the late nineteenth and early twentieth centuries are badly in need of re-examination, and such work may help to resurrect the reputations of some of Australia's pioneer palaeobotanists.

This review is restricted to those reports that are considered to be reliable by modern standards, and consequently many of the previously defined species are disregarded. This should not be taken as a lack of faith in the identity of these fossils, but a lack of sufficient information. In studying the macrofossil record of *Eucalyptus*, there is almost as much to be gained from noting where it does not occur as where it does, and this is also considered.

At present, the oldest reliably dated and described macrofossil associated with *Eucalyptus* is a tree stump, which is probably *in situ* and is enclosed in a 21 million years old basalt in the upper Lachlan Valley of New South Wales. The wood is reasonably well preserved and has been identified by Bishop & Bamber (1985) as 'Myrtaceae with affinities to *Eucalyptus* B' (of Dadswell,

1972). Unfortunately, confirmation of this by identification of diffuse parenchyma cells was not possible. Other wood nearby was identified as *Nothofagus* and *Acacia*, but they were not necessarily closely associated in the source vegetation. Holmes *et al.* (1982) described *Eucalyptus bugaldiensis*, from the Middle Miocene Chalk Mountain Formation in the Warrumbungle Mountains of New South Wales, based on impressions of umbelliferous fruits. They also described two *Eucalyptus* leaf types from impressions and noted that at least two of the phylogenetic lines proposed by Johnson (1972) for *Eucalyptus* were present at the site. They also concluded that the fossils exhibited some features of advanced states in both fruits and leaf venation. The fossils occur in association with predominantly mesophyllous leaves that Holmes *et al.* (1982) interpreted as rainforest, although they cautioned that this should not be used as evidence that eucalypts in the Middle Miocene were adapted to rainforest conditions.

Deane (1902*b*) described seven species of *Eucalyptus* from Middle Miocene sediments at Berwick in Victoria, and Holmes *et al.* (1982) noted the presence of a leaf with *Eucalyptus*-like cuticle and an impression of a eucalypt-like fruit in the flora. This site has recently undergone extensive re-collection, and several leaves with reasonably well-preserved cuticle have been recovered which have clear affinities with *Eucalyptus* (Pole *et al.*, 1993). The remainder of the flora has the character of rainforest. The only other *Eucalyptus* macrofossils from the coastal belt of eastern Australia that are universally accepted are the Pliocene leaves named *E. pluti* from Daylesford in Victoria (McCoy, 1876). McCoy noted that these leaves are almost identical in size and shape with extant *E. globulus*, but he noted some minor differences in the venation pattern. Despite the lack of organic preservation, the generic identity of this species has never been challenged, although that may well be due to its relatively recent age, since similarly convincing but older fossil leaves have been rejected.

The macrofossil record from central Australia casts further light on the history of *Eucalyptus*,

but the evidence is frustratingly uncertain. Lange (1978) described several beautifully preserved casts of eucalypt-like fruits, which are only part of a more diverse collection from Island Lagoon, near Woomera. Unfortunately, there is poor age control on this diverse assemblage of eucalypts, with the suggestion that they have either an Eocene–Oligocene age, or a Miocene age (Ambrose *et al.*, 1979). Greenwood (1991) reported 'the earliest record' of *Eucalyptus* macrofossils from the Middle Eocene silcretes in the Eyre Formation in central Australia. However, he neither described nor illustrated these macrofossils, and his earlier work on the flora (Greenwood *et al.*, 1990) mentioned only leaves assigned to '*Eucalyptophyllum*', about which he concluded 'it is not possible to determine the affinities of this leaf type'. If unequivocal *Eucalyptus* fossils have been found in Middle Eocene sediments in central Australia, their formal description should be a high priority.

It is constructive to consider where *Eucalyptus* macrofossils have not been found in the Australian Tertiary. Lange (1980) systematically searched dispersed cuticle from several near-coastal Eocene or Oligocene floras and found only one cuticle that approached that of a eucalypt on general appearance (among 600 examined from Maslin Bay). Since that time extensive research on coastal Paleocene to Oligocene macrofloras in coastal southeastern Australia (including Tasmania) has failed to uncover a single eucalypt specimen. It is also notable that *Eucalyptus* has not been reported from the Latrobe Valley coal macroflora (Blackburn & Sluiter, Chapter 14, this volume). Allied to this is the argument presented by Archer *et al.* (1991) that the relative rarity of early koalas in Oligo-Miocene rainforests may have been due to the rarity of eucalypts in that vegetation.

Therefore the evidence, sparse as it is, seems to favour the hypothesis proposed by Lange (1980) that in the mid-Tertiary the continental margins of Australia supported only mesic non-eucalypt vegetation, while eucalypts contributed to the more xeric vegetation in the interior. With progressive development of central Australian

aridity, eucalypts were displaced to the continental margins, while most mesic vegetation was eliminated altogether. It is informative that the Miocene coastal sites where *Eucalyptus* has been recorded do seem to contain rainforest vegetation that is less mesomorphic in character and may represent a transition to drier climate forest.

The pollen record

The early pollen record of *Eucalyptus* is even more enigmatic than the macrofossil record. Part of the reason for this is that fossil pollen that has sometimes been referred to *Eucalyptus* is also similar to *Angophora, Syncarpia* and possibly *Metrosideros* (Martin, 1978). Martin (1981) noted that 'It is unfortunate that pollen cannot be used as evidence of the development of the modern *Eucalyptus* flora.' However, since that report there has been an increase in the confidence of assessment of certain types of pollen with *Eucalyptus*.

Cookson & Pike (1954) described the species *Myrtaceidites eucalyptoides* for pollen grains with probable affinities with *Eucalyptus* and they noted its range as Pliocene to Pleistocene. However, this pollen type, which is referred to as the *Angophora/* bloodwood eucalypt type of pollen (Martin, 1989; Chapter 7, this volume) is now recorded from the Late Paleocene of the Lake Eyre Basin in inland Australia (I. R. K. Sluiter & N. F. Alley, unpublished data). Harris (1965) described *M. tenuis* and noted that this species is a very rare form that is similar to forms related to *Eucalyptus* by Cookson & Pike (1954). *Myrtaceidites tenuis* does not extend beyond the Eocene, and its possible affinity with *Eucalyptus* is particularly interesting because the eucalypt-type does not appear again in southeastern Australia until well into the Oligocene.

Although the general type of *Eucalyptus* pollen is difficult to identify at the generic level in the fossil record, there are specific eucalypt pollen types, with distinctive morphology, that offer more hope. An excellent example is *E. spathulata*, which is unique in having distinctive, large verrucae/rugulae (Martin & Gadek, 1988). When similar forms occur in the fossil record their affinity with

Eucalyptus can be assumed with more confidence. Martin & Gadek (1988) have identified *E. spathulata*-like pollen from three Pliocene sites in Australia, one in the southwest and two in the southeast. This species, which is now restricted to southwest Australia, is considered by Martin & Gadek to be the living remnant of a larger group of species that may have filled niches quite different from that of the extant species. Martin (1989) noted that this fossil pollen type is used as a marker of the Miocene/Pliocene boundary in the Gippsland Basin (Victoria), where it extends into the Pleistocene.

In more recent sediments, there is excellent evidence for a dramatic increase in abundance of *Eucalyptus* associated with increased charcoal levels. Although this occurs at different times in different parts of Australia, this is compelling evidence for the influence of Aborigines in artificially increasing the fire frequency (Singh *et al.*, 1980; Kershaw, 1986). The current superdominance of *Eucalyptus* in Australia may therefore be a relatively recent phenomenon, the result of the extraordinary adaptation of the genus to fire (Jackson, 1968) coupled with an artificial increase in ignition associated with the the arrival of humans. A drying climate probably assisted this event, since the vegetation was then much more prone to continue to burn once it was lit.

Extra-Australian records

An intriguing aspect of the fossil record of *Eucalyptus* is its apparent presence in both South America and New Zealand. Frenguelli (1953) described a group of three fruits from Miocene sediments in Patagonia as *Eucalyptus patagonica*. The age of these sediments is currently being revised and is considered to be probably Eocene (E. J. Romero, personal communication). Johnson & Briggs (1984) discussed this fossil and others which had been collected subsequently. They noted that Frenguelli's specimen 'could conceivably belong among the more generalized members of *Symphyomyrtus*', but they did not consider that the other specimens they saw belonged to the *Eucalyptus* alliance. E. J. Romero (personal

communication) has collected further leaf specimens that he believes are *Eucalyptus*, although he considers it possible that they belong to an ancestor or sister group. Future research on these fossils should be of particular importance to those with an interest in the origin and evolution of *Eucalyptus*.

Pole (1989) described leaves from Early Miocene sediments in the South Island of New Zealand that are 'identical to many *Eucalyptus* species', and noted their occurrence with eucalypt-like fructifications. This record is far more reliable at present than that from South America, especially when it is considered in conjunction with the pollen record. Mildenhall (1980) lists the stratigraphic range of *Eucalyptus* pollen in New Zealand as Miocene–Early Pleistocene, suggesting a relatively recent extinction.

These extra-Australian records are of particular significance in tracing the past history of the genus. The New Zealand records can be considered in one of two ways. Either they represent long-distance dispersal from Australia, in the Miocene or earlier, or they represent part of an ancient lineage that was present across at least part of Gondwana prior to separation of New Zealand and Australia but did not assume prominence (and thus appear in the fossil record) until climatic changes favoured its expansion. It is impossible at present to determine between these options, but the South American record will prove crucial. If further work determines a link with *Eucalyptus*, then an ancient (?Cretaceous) Gondwanic distribution for this now characteristically Australian genus would have to be considered the most likely hypothesis. The recent extinction of *Eucalyptus* from New Zealand is probably tied to the effects of the Quaternary glaciations.

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