Endemism in Tasmanian cool temperate rainforest: alternative hypotheses

ROBERT S. HILL AND JENNIFER READ

*Botany Department, University of Tasmania, G.P.O. Box 252C,
Hobart, Tasmania 7001, Australia*

Received May 1985, revised and accepted for publication May 1986

HILL, R. S. & READ, J. **Endemism in Tasmanian cool temperate rainforest: alternative hypotheses.** Evidence is presented which suggests that hypotheses presented by Kirkpatrick & Brown relating to endemic species in Tasmania are either invalid or of limited importance for woody rainforest species.

In their place three hypotheses are presented to account for the presence of endemic species in Tasmanian cool temperate rainforest on the basis of the fossil record and the distribution of species which are closely related to the endemics. The first two hypotheses relate to the presence of the endemic species in the general Tasmanian region. They are:

1. Some species evolved in southeastern Australia during the Tertiary in response to the changing climate. Some of the ancestral species still occur in temperate rainforest at lower latitudes in Australia.

2. Some species have remained essentially unchanged in Tasmania during the Tertiary and Quaternary climatic changes.

The third hypothesis relates to the restriction of these cool temperate rainforest species to Tasmania:

3. Post-glacial climatic changes (especially a decrease in rainfall) and the human influence (especially land clearing and fire) may have combined to eliminate some cool temperate rainforest species from mainland Australia.

ADDITIONAL KEY WORD—Tertiary palaeobotany.

CONTENTS

Introduction	113
Consideration of past hypotheses	114
Material and methods	115
Results and discussion	118
Endemic genera	118
Non-endemic genera absent from mainland Australia	118
Genera in rainforest on mainland Australia	119
Genera in non-rainforest vegetation on mainland Australia	121
Hypotheses to account for endemism in Tasmanian rainforest	122
Acknowledgements	122
References	123

INTRODUCTION

The endemic flora of Tasmania has recently been the subject of a detailed statistical analysis by Kirkpatrick & Brown (1984). They demonstrated strong

correlations between the distribution of endemic species and altitude and precipitation. Endemic species occur in most vegetation types in Tasmania, with a particularly interesting group in cool temperate rainforest. Although only about 17% of the total endemic flora is involved (dicotyledons and gymnosperms only), they appear to have a diverse origin, as evidenced by the distribution of related species outside Tasmania. There is also some evidence available from the fossil record for the past distribution of the endemic rainforest species and their evolutionary relationships (e.g. Hill, 1983, 1984; Hill & Macphail, 1983, 1985). The aim of this study is to consider the origins of endemic Tasmanian cool temperate rainforest species through a consideration of their relationships to other species and the known fossil record of southeastern Australia. This contrasts with the approach adopted by Kirkpatrick & Brown (1984) who formulated their hypotheses to explain the presence of endemic plant species in Tasmania from present day spatial patterns. Their hypotheses are evaluated in light of palaeobotanical and palaeoclimatic evidence.

Consideration of past hypotheses

Kirkpatrick & Brown (1984) proposed two hypotheses to explain the origin of endemic species in Tasmania:

1. "The slow drift of the Australian continental plate northward and the southerly position of Tasmania on that plate logically implies that genetically stable species with high latitude northern limits must become extinct as the dry land on the plate leaves their environmental range. Others must be converted into Tasmanian endemics by the same circumstances."

The rapid climatic oscillations of the Pleistocene have been superimposed on this process such that:

2. "The initial Pleistocene glaciations and deglaciations must have seen a flurry of extinction and speciation in Tasmania associated with rapid changes into cold then warm conditions."

Before considering the evidence for the origins of endemic cool temperate rainforest species in Tasmania, it is necessary to consider the validity of these hypotheses in light of published data.

The first hypothesis should be rejected on the basis of palaeoclimatic evidence. Australia drifted northwards during the Tertiary, and so a knowledge of climatic change at this time is important in considering the first hypothesis. For a species to have a high latitude northern limit which is independent of continental movement, as proposed by Kirkpatrick & Brown (1984), the climate must remain relatively stable with time. However, this was not the case. The Tertiary climate of Australia was influenced by the steady northward drift of Australia through a range of climatic belts, the changing surface temperature of the surrounding seas, the development of the Antarctic ice cap, and the changing continental arrangements (Galloway & Kemp, 1981; Kemp, 1981). The evidence suggests that during the Tertiary the general trend was from a low temperature gradient from equator to pole in the Early Tertiary to a steep gradient by the Late Tertiary. Therefore, as Australia drifted northward during the Tertiary, southeastern Australia experienced a decline in temperature. The evidence for this is summarized by Kemp (1981) and Galloway & Kemp (1981). This means that any species in southeastern Australia with high latitude northern limits in the Early Tertiary would have had their range extended to

lower latitudes as the climate changed during the Tertiary. This would have occurred more quickly than Australia's northward drift and therefore the species would have extended their distribution, and not become extinct as the dry land on the plate left their range as suggested by Kirkpatrick & Brown (1984).

Tertiary climatic change included much more than a change in temperature. There were associated changes in rainfall, humidity, etc. (Kemp, 1981), but it is unlikely that these climatic factors could impose a northern latitudinal limit on a large number of species.

There is abundant evidence that the converse of Kirkpatrick & Brown's hypothesis is true; that is, many species with subtropical affinities have migrated north up the east Australian coast during the course of the Tertiary as temperatures in southeastern Australia declined (Basinger & Christophel, 1985; Christophel, 1980, 1984; Christophel & Blackburn, 1978; Hill, 1982, 1986; Hill & Macphail, 1983; Kemp, 1978; Martin, 1978).

The key feature of the second hypothesis is that with the onset of glaciations there was a "flurry of . . . speciation in Tasmania associated with rapid changes into cold then warm conditions" (Kirkpatrick & Brown, 1984). Negative evidence for this hypothesis would require a demonstration that most extant Tasmanian species were present in Tasmania before glaciation began. Positive evidence would require a convincing demonstration that large numbers of new species were present immediately following the first glaciation. Neither of these options is practical in Tasmania, where the time of the first glaciation is still under debate. However, there is little evidence of rapid speciation in response to glaciation from other parts of the world.

Other forms of evidence can be considered here. Firstly, Tasmania presently has an extremely variable topography and rainfall, and a large number of climatic niches are therefore available for plant species. A similar situation must have occurred for millions of years before the glaciations, since the mountains of Tasmania were formed prior to the Tertiary (Ollier, 1986). Rather than rapid speciation as a result of the onset of glaciations, it is likely that the species growing in cool, dry areas prior to the glaciations expanded their distribution. It is known that there was a diverse microphyllous sub-alpine flora present in Tasmania by the Early Miocene (Hill & Gibson, 1986), which is evidence of species which could take advantage of cooler conditions at lower altitudes when they became available. Secondly, the evidence reviewed in this paper suggests that evolution in rainforest taxa has been very slow, and it is probable that most, if not all rainforest species were in place prior to the onset of glaciations and survived in Tasmania during the glaciations.

Kirkpatrick & Brown (1984) mentioned both extinction and speciation as important factors effecting endemism during the glacial cycles. However, since there were at least three glaciations of major proportions in Tasmania during the Quaternary (Kiernan, 1983), but apparently little ice cover on the Australian mainland (Galloway & Kemp, 1981), it is unlikely that extinction would have been an important factor in restricting species to Tasmania.

MATERIAL AND METHODS

Endemic cool temperate rainforest species in Tasmania were determined from Kirkpatrick & Brown (1984) in conjunction with the Tasmanian rainforest species list compiled by Jarman & Brown (1983). Forty species were recorded in

Table 1. Endemic species in Tasmanian cool temperate rainforest (from Kirkpatrick & Brown (1984) and Jarman & Brown (1983)). The species are divided into four groups depending on the distribution of the genera and the relationship of the endemic species to other species in the genus. Nomenclature follows Curtis (1963, 1967), Curtis & Morris (1975), Philipson (1965), Quinn (1982), Stanley & Ross (1983) and Williams (1982)

Group	Species
Group 1. Species in endemic Tasmanian genera	<i>Agastachys odorata</i> R. Br. <i>Anodopetalum biglandulosum</i> A. Cunn. ex Hook. fil. <i>Athrotaxis cupressoides</i> D. Don <i>A. laxifolia</i> Hook. <i>A. selaginoides</i> D. Don <i>Cenarrhenes nitida</i> Labill. <i>Diselma archeri</i> Hook. fil. <i>Prionotes cerinthoides</i> (Labill.) R. Br. <i>Tetracarpaea tasmanica</i> Hook. fil.
Group 2. Endemic species in non-endemic genera absent from mainland Australia*	<i>Archeria eriocarpa</i> Hook. fil. <i>A. hirtella</i> (Hook. fil.) Hook. fil. <i>Lagarostrobos franklinii</i> (Hook. fil.) C. J. Quinn <i>Nothofagus gunnii</i> (Hook. fil.) Oerst. <i>Phyllocladus aspleniifolius</i> (Labill.) Hook. fil. <i>Pseudopanax gunnii</i> (Hook. fil.) Philipson
Group 3. Endemic species in genera which occur in rainforest on mainland Australia (mainland species in brackets)	<i>Acradenia frankliniae</i> Milligan ex Kippist (<i>A. euodiiformis</i> (F. Muell.) T. Hartley) <i>Anopterus glandulosus</i> Labill. (<i>A. macleayanus</i> F. Muell.) <i>Aristotelia peduncularis</i> (Labill.) Hook. fil. (<i>A. australasica</i> F. Muell.) <i>Eucryphia lucida</i> (Labill.) Baill. (<i>E. moorei</i> F. Muell., <i>E. species nova</i>) <i>E. milliganii</i> Hook. fil. <i>Gaultheria hispida</i> R. Br. (<i>G. appressa</i> A. W. Hill) <i>Orites diversifolia</i> R. Br. (<i>O. excelsa</i> R. Br.) <i>Pimelea cinerea</i> R. Br. (<i>P. ligustrina</i> Labill.) <i>Trochocarpa cunninghamii</i> (DC.) W. M. Curtis (<i>T. laurina</i> R. Br.) <i>T. disticha</i> (R. Br.) Spreng. <i>T. gunnii</i> (Hook. fil.) Benth.
Group 4. Endemic species in genera which occur in non-rainforest vegetation on mainland Australia	<i>Acacia riceana</i> Henslow <i>Cyathodes glauca</i> Labill. <i>Epacris mucronulata</i> R. Br. <i>Leptospermum riparium</i> D. I. Morris <i>L. scoparium</i> Forst. var. <i>eximium</i> B. L. Burt <i>Monotoca glauca</i> (Labill.) Druce <i>M. submutica</i> Benth. <i>Olearia persoonioides</i> (DC.) Benth. <i>O. pinifolia</i> (Hook. fil.) Benth. <i>Phebalium squameum</i> ssp. <i>retusum</i> (Labill.) Engler <i>Richea milliganii</i> (Hook. fil.) F. Muell. <i>R. pandanifolia</i> Hook. fil. <i>R. scoparia</i> Hook. fil. <i>Telopea truncata</i> (Labill.) R. Br.

**Nothofagus gunnii* is included here because it belongs to a section (*Nothofagus*) which is absent from mainland Australia. See text for further discussion of this species.

29 genera (Table 1) and the distribution of these genera world wide was determined from a number of sources (Table 2).

Cool temperate rainforest has a disjunct distribution along the east coast of Australia. The Victorian and Tasmanian rainforest is usually dominated by

Table 2. Distribution of species (no. of species) in the genera containing endemic species in Tasmanian cool temperate rainforest.* The number of species in some genera were quite different depending on the source, and therefore the species numbers should not be regarded as exact: from Allen (1961), Curtis (1963, 1967), Curtis & Morris (1975), Dickison (1978), Floyd (1981), Hopper & Maslin (1978), Hou (1960), Johnson & Briggs (1975), Keng (1978), Morley & Toelken (1983), Philipson (1965), Pizarro (1959), Quinn (1982), Sleumer (1964, 1966), Soepadmo (1972) and Viot (1975)

Genus	Tas	Aust	NZ	Chile	NG	NC	Other	Total
<i>Acacia</i>	19	c. 830		1	?	1-2	>200	>1000
<i>Acradenia</i>	1	1						2
<i>Agastachys</i>	1							1
<i>Anodopetalum</i>	1							1
<i>Anopterus</i>	1	1						2
<i>Archeria</i>	4		2					6
<i>Aristotelia</i>	1	4	2	1				8
<i>Athrotaxis</i>	3							3
<i>Cenarrhenes</i>	1							1
<i>Cyathodes</i>	10	1	8				3	c. 20
<i>Diselma</i>	1							1
<i>Epacris</i>	18	c. 25	2		1-2	1		c. 40
<i>Eucryphia</i>	2	2		2				6
<i>Gaultheria</i>	2	2	8	2	24	?	120	>150
<i>Lagarostrobos</i>	1		1					2
<i>Leptospermum</i>	8	c. 70	3			?	?	>70
<i>Monotoca</i>	5	8						11
<i>Nothofagus</i>	2	2	4	9	14	4		34
<i>Olearia</i>	22	c. 60	32					>90
<i>Orites</i>	4	4		1				9
<i>Phebalium</i>	5	41	1					44
<i>Phyllocladus</i>	1		3		1		1	4
<i>Pimelea</i>	19	c. 60	13		2	?	?	>90
<i>Prionotes</i>	1							1
<i>Pseudopanax</i>	1		14	2		1	3	21
<i>Richea</i>	9	1						10
<i>Telochea</i>	1	3						4
<i>Tetracarpaea</i>	1							1
<i>Trochocarpa</i>	4	2			9		2	16

* Tas = Tasmania, Aust = mainland Australia, NZ = New Zealand, NG = New Guinea, NC = New Caledonia.

Nothofagus cunninghamii, while that in New South Wales and southern Queensland is dominated by *N. moorei* or *Eucryphia moorei*. Hartley (1977) noted that the cool temperate rainforests of Tasmania and New South Wales contain a number of genera with closely related species (Table 1, group 3). Specimens and seedlings of these species were collected throughout their range. The areas of 5–10 leaves of herbarium specimens and glasshouse-grown plants were measured photometrically. Specimens housed in the Tasmanian Herbarium (HO) were also included in the analysis. The non-endemic *Nothofagus cunninghamii* and the Australian mainland species *N. moorei* were included for comparison, because their fossil history is relatively well documented. The aim was to determine whether the pattern of leaf size reduction in Tasmanian rainforest species is consistent, and whether it is genetically fixed. In conjunction with the fossil history of *Nothofagus* in

southeastern Australia, this adds evidence of the past history of these rainforest species.

RESULTS AND DISCUSSION

The endemic species of Tasmanian cool temperate rainforest can be split into four groups on the basis of their present distribution and relationships to other species (Table 1). These groups will be discussed in turn, with fossil evidence being considered where available. Macrofossil evidence is preferred to palynological data in most cases, since the taxonomy of fossil pollen is often not precise at the specific or generic level.

Endemic genera

Seven genera of woody plants are endemic to Tasmanian rainforest. *Athrotaxis* belongs to the extremely disjunct family Taxodiaceae. *Athrotaxis* has been present in Tasmania since at least the Early Tertiary (Hill & Macphail, 1983; Townrow, 1965) with fossil species resembling *A. selaginoides* and *A. cupressoides* being recorded. Townrow discussed fossils from mainland Australia and New Zealand, but in the absence of cuticular preservation he considered that they should be regarded with caution. *Athrotaxis* has also been described from the Cretaceous of Patagonia, but again cuticular preservation is lacking (Townrow, 1965). Therefore, as Townrow suggested, the present restriction of *Athrotaxis* to Tasmania probably represents a contraction of its earlier range, not a spread into a new area.

The other endemic genera have no macrofossil record in Australia. *Cenarrhenes* and *Agastachys* belong to the subtribe *Cenarrheninae* of the Proteaceae (Johnson & Briggs, 1975). Johnson & Briggs considered this subtribe to be an assemblage of relict genera whose ancestors must have evolved by the early Upper Cretaceous. *Diselma* is one of several genera of the Cupressaceae with a restricted southern hemisphere distribution. Florin (1963) considered these genera to be relicts now occupying restricted areas. *Prionotes* is a monospecific genus which most authors (e.g. Arroyo, 1975) consider is most closely related to the monospecific Chilean genus *Lebetanthus*. It is therefore likely that *Prionotes* belongs to a group of the Epacridaceae with a long history in Gondwanaland. *Tetracarpaea* and *Anodopetalum* are monospecific and have no close relatives.

Non-endemic genera absent from mainland Australia

Four Tasmanian rainforest genera are absent from mainland Australia, but occur in other parts of the world (Table 2). *Nothofagus gunnii* has been included in this group because it is the only Australian representative of the section *Calusparassus*, and is clearly distinct from the other two Australian *Nothofagus* species.

Nothofagus gunnii is closely related to the Chilean endemic *N. pumilio* (Hill, 1984; Hill & Gibson, 1986), and has a Tasmanian macrofossil record which extends back at least to the Oligocene (Hill, 1984). The fossil *N. gunnii* leaves are indistinguishable from the extant species, which suggests that *N. gunnii* has been extant since at least the Early Tertiary. There is no macrofossil evidence

for *N. gunnii* on mainland Australia. Pollen possibly produced by *N. gunnii* (*N. fusca* type) is present in Tertiary sediments from mainland Australia, but the type was produced by several species, and cannot be regarded as conclusive evidence for the presence of *N. gunnii*.

Playford & Dettmann (1979) considered that the fossil pollen species *Phyllocladites mawsonii* was produced by podocarpaceous plants identical with, or very closely related to, *Lagarostrobus franklinii*. This pollen type is known from the fossil record of southern Australia, New Zealand, southern South America, Antarctica and the Kerguelen Islands from the Early Cretaceous onwards. It was particularly abundant in latest Cretaceous to Eocene forest vegetation of cool to cold temperate latitudes, but appears to have become more restricted in the Miocene (Playford & Dettmann, 1979). While this is strong evidence for the antiquity of *L. franklinii*, the identification of a modern species in the Tertiary or Cretaceous on the basis of pollen morphology alone should be regarded with caution.

Phyllocladus is represented by both pollen and macrofossils in the Australian Tertiary. The most recent mainland Australian record of *P. asplenifolius* is from 1100 BP at Lake Keilambete in Victoria (Churchill & Dodson, 1980), although Head (1985) refutes this claim and offers evidence that the pollen probably had its source in Tasmania and/or New Zealand.

The best preserved *Phyllocladus* macrofossils, from the Miocene Yallourn valley coals, could not be confidently separated from any living species by Cookson & Pike (1954). It is possible that this species was *P. asplenifolius*, or that *P. asplenifolius* has evolved from it. One of the species of *Phyllocladus* in New Zealand is considered by Keng (1978) to be a variety of *P. asplenifolius*, and while this could be the result of long distance seed dispersal (Kirkpatrick (1977) considered that seed of *P. asplenifolius* could be successfully bird-dispersed) it could also be considered as strong evidence for the antiquity of the species, since Australia and New Zealand have not had a land connection since the Cretaceous. A *Phyllocladus* macrofossil has been retrieved from the Pioneer Oligocene locality in Tasmania (Hill & Macphail, 1983), but the specific affinities of this fossil are uncertain at present.

Pseudopanax is found mainly in the southern hemisphere, with a centre of diversity in New Zealand (Table 2; Philipson, 1965). *Pseudopanax gunnii* is an uncommon species on the west coast of Tasmania, and probably represents the extant evidence of a long record of the genus in Australia. *Archeria* contains four species in Tasmania and two in New Zealand. It is unlikely that *Archeria* has been dispersed from Tasmania to New Zealand or vice versa via long distance dispersal in relatively recent times, since there is no adaptation of the fruit or seeds for animal or wind dispersal. Therefore the extant species of this genus may represent the remnants of a geographically more widespread Cretaceous or Tertiary ancestral group. There is no evidence for *Pseudopanax* or *Archeria* in the macrofossil record in Australia.

Genera in rainforest on mainland Australia

Eight genera have endemic Tasmanian species and species in mainland Australian rainforest (Table 1, group 3). *Nothofagus cunninghamii* is not included in Table 1, but it is relevant to the discussion. It dominates rainforest in

Tasmania from sea-level to the subalpine zone, and occurs in restricted areas in Victoria. It is endemic to southeastern Australia.

In Tasmania, the ancestor of *N. cunninghamii* first appears in the Late Eocene or Early Oligocene (Hill, 1983, and unpublished data). Its leaves are indistinguishable in size and morphology from extant *N. moorei*, which occurs in isolated pockets of high altitude rainforest in northern New South Wales and southern Queensland. During the Tertiary in southeastern Australia these *Nothofagus* leaves decreased in size and changed in morphology. The *N. cunninghamii* leaf type first appeared in the Early Miocene (Hill & Gibson, 1986) and was the only type present by the end of the Tertiary (Hill, 1983). Therefore in this line there was a decrease in leaf size during the Tertiary which may have been caused by declining temperatures and/or changing rainfall patterns millions of years before the onset of glaciations, giving rise to a new species in southeastern Australia. The ancestral type (*N. moorei*) has survived at lower latitudes. It is notable that extant *N. cunninghamii* has a larger leaf area in

Figure 1. Leaf area of species collected in the field. For each genus the endemic Tasmanian species are shown first, followed by closely related species from cool temperate rainforest on mainland Australia (see Table 1, group 3). The leaf area is the mean of several populations from throughout the range of the species. Ninety-five per cent confidence limits are drawn in, and the comparative leaf areas within a genus are given as a percentage. *Pimelea* species were not considered due to extreme variation in leaf size within individual plants.

Victoria than Tasmania, although both are much smaller than *N. moorei* (Fig. 1). In the Early Eocene–uppermost Oligocene Cethana deposit, the ancestor of *Nothofagus cunninghamii* occurs with leaves which are indistinguishable from *N. gunnii* (Hill, 1983, 1984). This suggests that *N. gunnii* was extant for many millions of years before *N. cunninghamii*.

The other genera in this group show a similar trend in leaf size to *Nothofagus cunninghamii* and *N. moorei*. That is, the low latitude species has a greater leaf area than the high latitude species (Fig. 1). One exception is a still undescribed species of *Eucryphia*, from Mt Bartle Frere in north Queensland (B. P. M. Hyland, personal communication) which has a small leaf area (Fig. 1). However, the general trend exhibited is compelling evidence that these genera may have responded to Tertiary climatic change in southeastern Australia in a similar way to *Nothofagus*, with the Tasmanian species being derived from those at lower latitudes through a reduction in leaf size.

This trend in leaf size was also exhibited by plants grown under glasshouse conditions (Fig. 2). This shows that the trend is genetically fixed, with little environmental influence. There is no evidence for these genera in the fossil record, except that *Eucryphia* leaves occur in the Late Pliocene–Early Pleistocene macroflora at Regatta Point on the west coast of Tasmania (Hill & Macphail, 1985). These leaves are intermediate in area between the Tasmanian endemics *E. lucida* and *E. milliganii*.

Genera in non-rainforest vegetation on mainland Australia

Most of these genera have the majority of their species in sclerophyllous vegetation on mainland Australia. There are some exceptions, e.g. *Richea*, with most species in Tasmania and *Cyathodes*, with several species in Tasmania and New Zealand. However, in general, it is probable that these genera evolved in sclerophyll vegetation and some species have recently invaded rainforest. Many of the species in this group (Table 1, group 4) also occur in sclerophyllous vegetation, and their status as rainforest species may be in some doubt.

Figure 2. Leaf area of species from specimens grown in a glasshouse. For each genus the endemic Tasmanian species are shown first, followed by closely related species from cool temperate rainforest on mainland Australia (see Table 1, group 3). The leaf area is the mean of leaves from one or more populations. Ninety-five per cent confidence limits are drawn in, and the comparative leaf areas within a genus are given as a percentage.

HYPOTHESES TO ACCOUNT FOR ENDEMISM IN TASMANIAN RAINFOREST

Past hypotheses dealing with the cool temperate rainforest species of Tasmania have concentrated on their antiquity (e.g. Barlow, 1981). Evidence summarized here suggests that many endemic and non-endemic Tasmanian rainforest species evolved relatively recently *in situ*, in response to the Tertiary climatic change. The fossil evidence for *Nothofagus cunninghamii* (Hill, 1983) indicates that this species evolved slowly during the Tertiary from a large-leaved ancestor, which was identical in leaf form to extant *N. moorei* of northern New South Wales and southern Queensland. While the fossil evidence is limited for other species, several Tasmanian rainforest species have relatives with a similar distribution to *N. moorei*, and a leaf area gradation similar to that exhibited by *N. moorei* and *N. cunninghamii* (Figs 1, 2; Table 1, group 3). Therefore it is possible that these species evolved in a similar way to *N. cunninghamii*.

Other endemic rainforest species have no close relatives in the temperate rainforests of New South Wales and southern Queensland (Table 1, groups 1, 2 and 4), but they could still have evolved in a similar way to *N. cunninghamii*. If this was the case, the ancestral species have become extinct either during or since the Tertiary. However, there is at least one other hypothesis to account for the origin of these species. That is, that these species were extant before the Tertiary climatic change began and have been more or less unaffected by it. These species may have once had a wider distribution, or they may have always been restricted to Tasmania. The fossil evidence for *Nothofagus gunnii*, *Lagarostrobos franklinii*, *Athrotaxis selaginoides* and *A. cupressoides* suggests that these species at least fall into this category.

Both of these hypotheses would result in species which occurred in Tasmania but which were not necessarily endemic there. In order for species which once occurred outside Tasmania (i.e. on mainland Australia) to become endemic to Tasmania, a third hypothesis is required. Climatic changes (especially a decrease in rainfall) and the human influence (especially land clearing and fire) may have caused the extinction of species on mainland Australia. There is likely to have been an interaction between a decrease in rainfall and the incidence of fire.

While these hypotheses may account for many of the endemic species in rainforests (and other vegetation types) in Tasmania, it is unlikely that they account for all endemic species. New evidence may require the formulation of alternative hypotheses to account for endemism. The third hypothesis does not necessarily predict that all species in that category would be restricted to Tasmania at the same time. Sluiter & Kershaw (1982) presented evidence for the restriction of evergreen rainforest in southeastern Australia in the Late Miocene and Pliocene in response to drier conditions. It is possible that some species were restricted to Tasmania at that time. However, some species may have only recently become endemics, for example *Phyllocladus aspleniifolius*, which has only become extinct on King Island in western Bass Strait since the arrival of European settlers (Kirkpatrick & Brown, 1984). It is also possible that some species which still occur on mainland Australia could be restricted to Tasmania in the future by similar processes (e.g. *Nothofagus cunninghamii*).

ACKNOWLEDGEMENTS

Our thanks to Yvonne Menadue for assistance with the data collection; to Dr A. E. Orchard for permission to include specimens from the Tasmanian

Herbarium (HO) in the analysis; and to the N.S.W. National Parks and Wildlife Service, the N.S.W. Forestry Commission, and the Tasmanian National Parks and Wildlife Service for permission to collect seed, seedling and herbarium specimens from areas under their control. We especially thank Mr A. G. Floyd for his assistance in locating rainforest sites in N.S.W. This study was supported by the Australian Research Grants Scheme and a Commonwealth Forestry Postgraduate Research Award to J. R.

REFERENCES

- ALLEN, H. H., 1961. *Flora of New Zealand, 1*. Wellington: Government Printer.
- ARROYO, S., 1975. *Lebetanthus*, genero austroamericano de *Epacridaceae* y sus diferencias con el genero *Prionotes* de Tasmania. *De Darwiniana*, 19: 312-330.
- BARLOW, B. A., 1981. The Australian flora: its origin and evolution. In A. S. George (ed.), *Flora of Australia, 1*. Canberra: Australian Government Publication Service.
- BASINGER, J. F. & CHRISTOPHEL, D. C., 1985. Fossil flowers and leaves of the Ebenaceae of southern Australia. *Canadian Journal of Botany*, 63: 1825-1843.
- CHRISTOPHEL, D. C., 1980. Occurrence of *Casuarina* megafossils in the Tertiary of south-eastern Australia. *Australian Journal of Botany*, 28: 249-259.
- CHRISTOPHEL, D. C., 1984. Early Tertiary Proteaceae: the first floral evidence for the Musgraveaceae. *Australian Journal of Botany*, 32: 177-186.
- CHRISTOPHEL, D. C. & BLACKBURN, D. T., 1978. The Tertiary megafossil flora of Maslin Bay, South Australia—a preliminary report. *Alcheringa*, 2: 311-319.
- CHURCHILL, D. M. & DODSON, J. R., 1980. The occurrence of *Phyllocladus aspleniifolius* (Labill.) Hook. f. in Victoria, prior to 1100 B.P. *Muelleria*, 4: 277-284.
- COOKSON, I. C. & PIKE, K. M., 1954. The fossil occurrence of *Phyllocladus* and two other podocarpaceous types in Australia. *Australian Journal of Botany*, 2: 60-67.
- CURTIS, W. M., 1963. *The Student's Flora of Tasmania. Part 2*. Tasmania: Government Printer.
- CURTIS, W. M., 1967. *The Student's Flora of Tasmania. Part 3*. Tasmania: Government Printer.
- CURTIS, W. M. & MORRIS, D. I., 1975. *The Student's Flora of Tasmania. Part 1*. Tasmania: Government Printer.
- DICKISON, W. C., 1978. Comparative anatomy of Eucryphiaceae. *American Journal of Botany*, 65: 722-735.
- FLORIN, R., 1963. The distribution of conifer and taxad genera in time and space. *Acta Horti Bergiani*, 20: 121-312.
- FLOYD, A. G., 1981. *N.S.W. Rainforest Trees. Part II*, 2nd edition. Sydney: Forestry Commission of N.S.W.
- GALLOWAY, R. W. & KEMP, E. M., 1981. Late Cainozoic environments in Australia. In A. Keast (Ed.), *Ecological Biogeography of Australia*. The Hague: W. Junk.
- HARTLEY, T. G., 1977. A revision of the genus *Acradenia* (Rutaceae). *Journal of the Arnold Arboretum*, 58: 171-181.
- HEAD, L., 1985. Further discussion of *Phyllocladus* and its pollen in Victoria during the Holocene. *Australian Journal of Ecology*, 10: 73-76.
- HILL, R. S., 1982. The Eocene megafossil flora of Nerriga, New South Wales, Australia. *Palaeontographica Abt. B*, 181: 44-77.
- HILL, R. S., 1983. Evolution of *Nothofagus cunninghamii* and its relationship to *N. moorei* as inferred from Tasmanian macrofossils. *Australian Journal of Botany*, 31: 453-465.
- HILL, R. S., 1984. Tertiary *Nothofagus* macrofossils from Cethana, Tasmania. *Alcheringa*, 8: 81-86.
- HILL, R. S., 1986. Lauraceous leaves from the Eocene of Nerriga, New South Wales. *Alcheringa*, 10: 327-351.
- HILL, R. S. & GIBSON, N., 1986. Macrofossil evidence for the evolution of the alpine and sub-alpine vegetation of Tasmania. In B. A. Barlow (Ed.), *Flora and Fauna of Alpine Australasia: Ages and Origins*. Melbourne: CSIRO.
- HILL, R. S. & MACPHAIL, M. K., 1983. Reconstruction of the Oligocene vegetation at Pioneer, north-east Tasmania. *Alcheringa*, 7: 281-299.
- HILL, R. S. & MACPHAIL, M. K., 1985. A fossil flora from rafted Plio-Pleistocene mudstones at Regatta Point, western Tasmania. *Australian Journal of Botany*, 33: 497-517.
- HOPPER, S. D. & MASLIN, B. R., 1978. Phytogeography of *Acacia* in Western Australia. *Australian Journal of Botany*, 26: 63-78.
- HOU, D., 1960. Thymelaeaceae. *Flora Malesiana*, 6: 1-48.
- JARMAN, S. J. & BROWN, M. J., 1983. A definition of cool temperate rainforest in Tasmania. *Search*, 14: 81-87.
- JOHNSON, L. A. S. & BRIGGS, B. A., 1975. On the Proteaceae—the evolution and classification of a southern family. *Botanical Journal of the Linnean Society*, 77: 83-182.

- KEMP, E. M., 1978. Tertiary climatic evolution and vegetation history in the southeast Indian Ocean region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 24: 169–208.
- KEMP, E. M., 1981. Tertiary palaeogeography and the evolution of Australian climate. In A. Keast (Ed.), *Ecological Biogeography of Australia*. The Hague: W. Junk.
- KENG, H., 1978. The genus *Phyllocladus* (Phyllocladaceae). *Journal of the Arnold Arboretum*, 59: 249–273.
- KIERNAN, K. A., 1983. Weathering evidence for an additional glacial stage in Tasmania. *Australian Geographical Studies*, 21: 197–220.
- KIRKPATRICK, J. B., 1977. Native vegetation of the west coast region of Tasmania. In M. R. Banks & J. B. Kirkpatrick (Eds), *Landscape and Man*. Hobart: Royal Society of Tasmania.
- KIRKPATRICK, J. B. & BROWN, M. J., 1984. A numerical analysis of Tasmanian higher plant endemism. *Botanical Journal of the Linnean Society*, 88: 165–183.
- MARTIN, H. A., 1978. Evolution of the Australian flora and vegetation through the Tertiary: evidence from pollen. *Alcheringa*, 2: 181–202.
- MORLEY, B. D. & TOELKEN, H. R., 1983. *Flowering Plants in Australia*. Adelaide: Rigby.
- OLLIER, C. D., 1986. Origin of landforms. In B. A. Barlow (Ed.), *Flora and Fauna of Alpine Australasia: Ages and Origins*. Melbourne: CSIRO.
- PHILIPSON, W. R., 1965. The New Zealand genera of the Araliaceae. *New Zealand Journal of Botany*, 3: 333–341.
- PIZARRO, C. M., 1959. *Sinopsis de la flora chilena*. Ediciones de la Universidad de Chile.
- PLAYFORD, G. & DETTMANN, M. E., 1979. Pollen of *Dacrydium franklinii* Hook. f. and comparable Early Tertiary microfossils. *Pollen et Spores*, 20: 513–534.
- QUINN, C. J., 1982. Taxonomy of *Dacrydium* Sol. ex Lamb. emend. de Laub. (Podocarpaceae). *Australian Journal of Botany*, 30: 311–320.
- SLEUMER, H., 1964. Ericaceae. *Flora Malesiana*, 6: 469–668.
- SLEUMER, H., 1966. Epacridaceae. *Flora Malesiana*, 6: 422–444.
- SLUITER, I. R. & KERSHAW, A. P., 1982. The nature of Late Tertiary vegetation in Australia. *Alcheringa*, 6: 211–222.
- SOEPADMO, E., 1972. Fagaceae. *Flora Malesiana*, 7: 265–403.
- STANLEY, T. D. & ROSS, E. M., 1983. *Flora of south-eastern Queensland, 1*. Brisbane: Queensland Department of Primary Industries.
- TOWNROW, J. A., 1965. Notes on Tasmanian pines II. *Athrotaxis* from the Lower Tertiary. *The Papers and Proceedings of the Royal Society of Tasmania*, 99: 109–113.
- VIROT, R., 1975. Epacridacées. In A. Aubreville & J.-F. Leroy (Eds), *Flora de la Nouvelle Calédonie et dépendances*. Paris: Muséum National d'Histoire Naturelle.
- WILLIAMS, J. B., 1982. *Checklist of the Rainforest Flora of New South Wales*, 2nd edition. Armidale: University of New England.