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Evolution of the Australian Flora in Response to Cenozoic Climate Change

A thesis submitted for the degree of
Doctor of Science

Robert S. Hill

For my parents, Audrey and Clem,
with thanks for letting me go my own way

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(publications listed below have a percentage in parentheses after them. I believe this is a fair estimate of my contribution to each)

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Hill, R.S. & Dettmann, M.E. 1996. Origin and diversification of the genus *Nothofagus*. In: The Ecology and Biogeography of *Nothofagus* Forests (Eds T.T. Veblen, R.S. Hill & J. Read) pp. 11-24. (Yale University Press, Yale). (70%) 1248

Hill, R.S., Jordan, G.J. & Macphail, M.K. 1996. History and Paleoecology of Australian *Nothofagus* forests. In: The Ecology and Biogeography of *Nothofagus* Forests (Eds T.T. Veblen, R.S. Hill & J. Read) pp. 182-199. (Yale University Press, Yale). (70%) 1262

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Read, J., Hope, G.S. & Hill, R.S. 1990. Integrating historical and ecophysiological studies in *Nothofagus* to examine the factors shaping the development of cool rainforest in southeastern Australia. In: J.G. Douglas & D.C. Christophel (eds) *Proceedings 3rd IOP Conference, Melbourne, 1988.* A-Z Publishers, Melbourne. pp. 97-106. (10%) 1316

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Hill, R.S. & Truswell, E.M. 1993. *Nothofagus* fossils in the Sirius Group, Transantarctic Mountains: Leaves and pollen and their climatic implications. In: J. Kennett & D. Warnke (eds) *The Antarctic Paleoenvironment: A Perspective on Global Change (Part 2).* American Geophysical Union, Washington. pp. 67-73. (50%) 1337

*Hill, R.S., Scriven, L.J. and Jordan, G.J. 1995. The fossil record of the Proteaceae. In: A.E. Orchard (ed.) *Flora of Australia. Proteaceae.* Australian Government Publishing Service, Canberra. pp. 21-30. (80%) 1344

(This book chapter was published in 1995 but arrived during 1996 near the completion of this thesis, and thus it is out of order.)

Abstract

The extant Australian flora is the result of a wide range of past factors, most notably climate change and soil nutrients. This thesis contains the results of almost 20 years of publications on the Cenozoic flora, mostly of southeastern Australia, documenting the effects of those factors. Two taxa have formed the focus of detailed research. The genus *Nothofagus* has long been recognised as a key taxon for understanding Southern Hemisphere biogeography. My research has clarified the infrageneric taxonomy of this genus, presented a detailed phylogenetic reconstruction of the extant species, vastly increased our understanding of the macrofossil record (including detailed reconstructions of evolution in response to climate change), and allowed more informed reconstruction of the origin and history of the genus. The southern conifers, and the family Podocarpaceae in particular, have also been an important research focus. I have greatly increased our understanding of the macrofossil record of this group and have reported evolutionary trends that are clearly climatically based. The Podocarpaceae offer great potential for future research into climate change, and that potential has only become clear as a result of my research. More generally, I have undertaken research that demonstrates the temporal fragmentation of complex Early Paleogene rainforests into the patterns exhibited today along the east coast of Australia, and shown that this is a climatically-based phenomenon. I have also undertaken research on the history of the scleromorphic heath flora, and shown that the morphological expression of the effect of low soil nutrients occurred before that of low water availability. In a more restricted way I have been able to show that the alpine flora of Australia was beginning to develop by at least 20 million years ago in Tasmania, and that the ancestors of many of the taxa in the modern alpine flora have a long history *in situ*. My conclusions are broad-based, but always hinge on the strict taxonomic treatment of the fossils concerned. This taxonomic research underpins all my research, and is the most critical part of it.

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution, except as acknowledge in the Table of Contents, and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Robert S. Hill

Acknowledgments

I have been extremely fortunate over the years to have had a group of highly motivated people to work with. They have, in their combined efforts, helped me to retain my enthusiasm and interest, and I am deeply grateful to them and to the Australian University system which has allowed this interaction to flourish. I have supervised many Honours and Postgraduate students over the years, and I thank them collectively for their input. Some people have made a special impact on my research, and I would like to thank them individually. The following have, in many and varied ways, contributed greatly to my research and to my life in general: Drs Ray Carpenter, Greg Jordan, Mike Macphail, Mike Pole, Jennifer Read and Leonie Scriven. Many other researchers around Australia and overseas have been a source of inspiration for a variety of reasons, and I thank them for it.

I hold a special place in my heart for the residents of two towns in South Australia; Renmark and Kingscote, Kangaroo Island. It was in these places that I grew up and saw the Australian biota first hand, and developed an interest that has become a career.

Preface

This thesis contains the results of about 20 years of research on the theme of plant evolution and vegetation dynamics in the Southern Hemisphere, primarily centred on southeastern Australia, but with occasional forays into other regions as material and time has allowed. My research can be separated into a number of distinct but inter-related themes, each of which is considered separately here as a sub-heading. However, they all form part of an integrated whole which is still far from complete. The following summary is not an attempt at a literature review, but rather summarises my contribution. Therefore reference to other people's work is kept to a minimum.

Nothofagus evolution

For many decades *Nothofagus* has been considered one of the key taxa in understanding the biogeography of the Southern Hemisphere. When I first began finding *Nothofagus* macrofossils and examining the literature I was surprised at the lack of detailed understanding of the living species and the poor state of the systematics of the genus. It seemed clear to me that many of the apparently insoluble problems regarding *Nothofagus* mentioned in the literature would probably disappear if a more intensive study was undertaken. I have personally concentrated my research on the morphology of the genus, and have encouraged students (and in particular a doctoral student, Dr Jennifer Read), to undertake field work and physiological research on the extant species.

My own research concentrated firstly on the beautifully preserved Cenozoic leaf and cupule fossils, mainly in Tasmanian sediments, but also in some other localities, and resulted in publications describing new fossil species (Hill 1983a, 1983b, 1984, 1987, 1988a, 1989a, 1991a, 1994a; Kovar *et al.* 1987; Hill & Truswell 1993; Scriven *et al.* 1995) and a first attempt at interpreting evolution within one phylogenetic line in the genus (Hill 1983b). That interpretation has since been refined (Hill & Jordan 1993) and is currently undergoing modification as more fossils are found. This research led to a need to examine the leaf and cupule morphology of the extant species in more detail, and resulted in field work being undertaken in New Zealand and New Guinea. The culmination of this research was the publication of a revised infrageneric classification of the extant species of the genus (Hill & Read 1991; Hill & Jordan 1993).

The revised infrageneric classification and cladistic analysis was particularly important, since previously the vast palynological record of *Nothofagus* had been treated via an informal classification (see summary in Dettmann *et al.* 1990) that was at odds with the formally recognised treatment. My research resulted in this major problem being solved, and along with a thorough revision of the pollen record carried out at about the same time (Dettmann *et al.* 1990) resulted in most palynologists adopting the subgeneric names proposed in my treatment with Jennifer Read (Hill & Read 1991) for their pollen types. This is a major step forward and makes it possible to examine all morphological data from a firm and common basis.

Some of the fossil finds in Tasmania have been particularly important. I reported the first (and still the only) macrofossil evidence of *Nothofagus* subgenus *Brassospora*, including both cupules and leaves of a minimum of three species from the Early Oligocene sediments at Little Rapid River in northwestern Tasmania (Hill 1987, 1991a, 1994a). This was a particularly critical find, since the pollen of this subgenus is often dominant in Cenozoic assemblages in Australia and New Zealand, and the lack of associated macrofossils had led to several untenable hypotheses regarding the significance of this pollen. Macrofossils of subgenus *Nothofagus* have also been recovered from Little Rapid River (Hill 1991a) and more recently from other Tasmanian sites (Scriven & Hill in press). This subgenus is now restricted to South America, and the Tasmanian fossil records were the first indication of the subgenus outside that landmass, and are therefore of great biogeographic significance. Subgenus *Fuscospora* has been recorded as two species (Hill 1984), one of which, *N. gunnii*, is still present in Tasmania as the only living winter deciduous species of the genus outside South America. A summary of the Cenozoic record of *Nothofagus* in Australia is presented by Hill *et al.* (1996).

Jordan + MacPhail

Recently I have been involved in speculation regarding the origin and early dispersal of *Nothofagus* (Hill 1992, 1994b; Hill & Scriven 1995; Hill & Dettmann 1996). Although this is far from resolved, the options have narrowed to two most plausible centres of origin, and the place of major diversification, the Weddellian Biogeographic Province, seems well established.

Nothofagus fossils also provide important palaeoclimatic information, since a relatively large amount of research has been carried out on the ecophysiology of the living species (Hill *et al.* 1988; Read & Hill 1985a, 1988a, 1989; Read *et al.* 1990a), and this seems to translate well to the fossil relatives. There has also been reasonably extensive field work in *Nothofagus*-dominated ecosystems, concentrating on regeneration strategies and the possible relevance of this to the history of the genus in Australia (Read & Hill 1985b, 1988b; Read *et al.* 1990b).

Conifer evolution

Conifers are extremely diverse as macrofossils in Tasmanian Cenozoic sediments, and also in some sites on mainland Australia (e.g. the Late Paleocene Lake Bungarby site in southern New South Wales). These conifers are important biogeographically, palaeoclimatically and from an evolutionary viewpoint. Three families are represented: Araucariaceae, Cupressaceae (including Taxodiaceae) and Podocarpaceae.

In order to identify conifer macrofossils, most of which were available almost entirely as leaf remains, it proved necessary to first undertake a detailed morphological investigation of the extant species, and especially their cuticular morphology. This has usually been done in tandem with research on fossils, and involved a great deal of scanning electron microscopy, since the robust, three dimensional cuticles of these conifers were difficult to adequately interpret in any other way.

The Araucariaceae are especially diverse in Tasmania, with two of the three extant genera (*Agathis* and *Araucaria*) recorded along with the extinct genus *Araucarioides* (Bigwood & Hill 1985; Hill & Bigwood 1987; Hill 1990a). *Araucarioides* may be ? monophyletic with the newly described extant genus *Wollemia*, although this requires substantial research to test. While this has some palaeoclimatic significance, the Araucariaceae have not yet proven to be particularly informative, since they have a very conservative morphology, and are not common enough to provide substantial temporal data sets.

The Cupressaceae (taken here to include the Taxodiaceae) are represented in Tasmania by many of the extant genera, including *Athrotaxis* (now a Tasmanian endemic, Hill *et al.* 1993), *Austrocedrus* (now restricted to South America, Hill & Carpenter 1989), *Fitzroya* (now restricted to South America, Hill & Whang 1996), *Libocedrus* (now restricted to New Zealand and New Caledonia, Hill & Carpenter 1989) and *Papuacedrus* (now restricted to New Guinea, Hill & Carpenter 1989). There is also an extinct genus, *Austrosequoia*, present in Oligocene sediments at Little Rapid River (Hill *et al.* 1993). Of the extant Australian Cupressaceae, only *Athrotaxis* has been found in pre-Quaternary sediments. Therefore the Cupressaceae fossil record is extremely important biogeographically, and as we learn more about the climatic requirements of the extant species, they will no doubt yield important palaeoclimatic information. However, there is as yet little that can be said about the history of the extant Australian genera, with the exception of *Athrotaxis*, which seems to have been a Tasmanian resident since at least the Early Oligocene.

By far the most abundant conifer family in the macrofossil record of southeastern Australia is the Podocarpaceae. This family is currently the major Southern Hemisphere conifer family, and this appears to have been the case for a very long time. Southeastern Australia currently has five genera (*Lagarostrobos*, *Microcachrys*, *Microstrobos*, *Phyllocladus* and *Podocarpus*), and four of these are present as macrofossils in Tertiary sediments in the region (Hill 1989b; Wells & Hill 1989b). However, many of the other extant genera are also present (e.g. *Acmopyle*, *Dacrycarpus*, *Dacrydium*, *Halocarpus*, *Prumnopitys*, Hill & Carpenter 1991a), as well as some extinct genera that argue for increased diversity in the family in the past (e.g. *Willungia*, *Smithtonia*, Hill & Pole 1992). These macrofossil records have clear biogeographic significance, since many of these genera are now remote from Tasmania, but it is their palaeoclimatic significance that is paramount.

One of the major advantages of the podocarp fossils is that they are so common that it has been possible to trace some phylogenetic lines temporally. This has so far been achieved for *Acmopyle* and *Dacrycarpus* (Hill & Carpenter 1991a). In both genera there is strong evidence for modification of the foliage in response to climate change, notably declining temperature (although the exact form of this decline is unclear), and decreasing water availability (Hill & Carpenter 1991a; Hill 1994b, 1995). Since both genera are still extant, this has led to some very obvious physiological research, which has been the subject of a Ph.D. thesis by a student under my supervision, Tim Brodribb. His research has clearly demonstrated some important interactions between morphology and physiological response. While this work has only recently been submitted for publication (Brodribb & Hill manuscript submitted a, b, c), and is thus not included in this thesis, it shows the way to a more sophisticated approach to palaeoclimatic reconstruction in the future.

Temperate rainforest history

Rainforest in Australia today occurs in fragmented patches along the entire east coast, from sea level on Cape York Peninsula in the north to the tree line on the mountains of Tasmania in the south. Along this latitudinal gradient the rainforest goes through a transition from true tropical (megathermal) forest to extreme dwarf montane forms in the temperate zone. However, the macrofossil record of this rainforest clearly demonstrates that this has not always been the case, and the history of this complex vegetation type offers some important lessons on community evolution and stability through time.

Rainforest is well represented in Tertiary sediments in southeastern Australia both because the climate during much of the Tertiary was conducive to rainforest formation and because fossils are biased towards wet environments where rainforest naturally occurs. Although the macrofossil record for the region is sporadic, the data base has increased substantially over the last 20 years, primarily as a result of my research, and we can now reconstruct vegetation changes relatively precisely.

For my Ph.D. research, I described a Middle Eocene macroflora from Nerriga, in southern New South Wales (Hill 1978, 1980, 1982, 1986, 1989c). The vegetation represented was clearly rainforest of a type that is now found much further north along the Australian east coast. Similar results have been reported for other Middle Eocene macrofloras in southeastern Australia (e.g. Christophel & Blackburn 1978; Christophel *et al.* 1987; Scriven 1993). This sparked my interest in the evolution of the temperate rainforests of southeastern Australia and that has remained an important research focus for me. There are few macrofossil sites on mainland Australia that offer major insights into the segregation of the complex rainforests of the early Paleogene into the simpler array seen over much of the latitudinal range today, but the Tasmanian macrofossil record stands in stark contrast to this.

In Tasmania, there are a large number of macrofossil sites covering the age range from Early Eocene to Early Miocene, where preservation varies from good to excellent. There is currently a gap between the Early Miocene and Early Pleistocene, but there is an increasing number of extremely valuable Quaternary macrofossil locations becoming available.

The oldest Tasmanian macrofossil location (Early Eocene, Regatta Point) contains plant species with their nearest living relatives mostly at low latitudes, and clearly demonstrates vegetation growing under relatively warm, wet conditions, or more probably a climate where there was little annual temperature variation (Bigwood & Hill 1985; Hill 1990b; Pole & Macphail 1996). There is at least one temperate element present at Regatta Point (*Eucryphia*, Hill 1991b), but most of the other identified macrofossils suggest complex closed forest with a large conifer element and reasonably diverse angiosperms. There are other probable Eocene sites in Tasmania (Loch Aber and Hasties) but the macrofloras of these sites still require some work before we understand their full importance. Mike Pole, a postdoctoral fellow with me in the early 1990s, described the Hasties macroflora in some detail (Pole 1992), and it is interesting that at least some temperate elements are present among generally mesothermal taxa.

However, the critical fossil sites in unravelling the history of rainforest segregation in eastern Australia occur in northern Tasmania and span the Early Oligocene to Early Miocene. Several Early Oligocene sites have been collected, and the best understood are Little Rapid River, Cethana and Lea River. Little Rapid River in particular has been the subject of a great deal of taxonomic research. The Early Oligocene was a critical time in Tasmania, since Australia had recently separated from Antarctica to the point where a major seaway had developed between the two landmasses, and the Circum-Antarctic current had begun to form. This represented a major change in ocean circulation patterns, ultimately leading to an increased temperature gradient between the equator and the pole, increasing seasonality in both temperature and rainfall, and a decrease in rainfall across most of Australia. The terminal Eocene cooling event may have been a result of this change in ocean currents, and certainly by the Early Oligocene temperate elements are much more in evidence in lowland fossil floras like Little Rapid River than they were at any time during the Eocene (Hill 1990b; Carpenter *et al.* 1994).

Little Rapid River contains a remarkable mix of macrofossil taxa that have nearest living relatives growing everywhere from alpine Tasmania (Microthermal) to lowland tropical regions (Meso-Megathermal). Such an extraordinary mix of taxa in the Early Oligocene is clearly of major climatic significance, but in order to deal with the range of forms found, it was necessary to categorise them according to their nearest living relatives. I did this by separating them into the following groups (Hill 1990b, 1990c, 1990d, 1991c; Hill & Carpenter 1991b):

1. Those taxa that still occur in Tasmania, more or less unchanged.
2. Those taxa that have migrated (or been restricted in range) northward, but have left descendants in place in Tasmania.
3. Those taxa that have migrated (or been restricted in range) northward and are now extinct in Tasmania.
4. Those taxa that are globally extinct.

In categorising the fossil taxa in this way, it is important to note that these groupings represent artificial breaks in a continuum, with the possible exception of the distinction between groups 2 and 3. The taxa in groups 1 and 2 are today genuinely microthermal, and occur either in Tasmanian cool temperate rainforest or in the isolated patches of cool temperate rainforest at high altitudes in northern New South Wales and southern Queensland. The taxa in group 3 seem to have a genuinely different temperature requirement and can be categorised as mesothermal at least. More research is required to refine this tentative hypothesis, but there does seem to be a real distinction here.

The Late Oligocene-Early Miocene Pioneer locality in northeastern Tasmania offers an insight into lowland rainforest some time after the major climatic change in the Late Eocene. Unfortunately this site is no longer accessible, as cessation of tin mining operations has meant that the pit has filled with water, creating an artificial lake. However, the site is reasonably well known (Hill 1983a, Hill & Macphail 1983; Macphail & Hill 1983) and clearly represents a simplification of the Early Oligocene rainforest in the northwest.

Obviously the co-occurrence of fossil taxa in the Early Oligocene that have nearest living relatives (NLRs) with quite distinct climatic requirements led us to undertake physiological research on the NLRs to try to determine why the fossil taxa could co-occur while today their NLRs do not. The results are not always simple to interpret, but the current working hypothesis is that the climate in the Early Oligocene in Tasmania was extremely wet, and usually humid and cloudy, and this had the effect of reducing temperature extremes (i.e. little or no frost stress). Few such places exist on earth today, but where they do a phenomenon called ecological compression has been noted, and many species are able to co-exist that otherwise are separated (e.g. along an altitudinal gradient, Hyndman & Menzies 1990). Thus it is probable that at this time, even though temperatures had declined since the Eocene, the extremely wet and humid climate allowed many taxa to co-exist that cannot do so today (Hill 1990b; Carpenter *et al.* 1994).

As time progressed, the climate continued to cool at high southern latitudes with the increase in the effect of the Circum-Antarctic current, so that even though Australia was moving into lower latitudes the increase in the equator to pole temperature gradient meant that southern Australia, and Tasmania in particular, continued to cool. As this occurred rainfall patterns also changed, leading to seasonality in rainfall and development of a dry atmosphere for at least part of the year. This in turn meant that temperature fluctuations increased and plants began to encounter problems with temperature extremes (e.g. frost). This change probably led to the eventual demise of the mesothermal taxa, although in some cases at least they lingered into the Early Pleistocene, a phenomenon demonstrated by one of my postgraduate students, Greg Jordan (Jordan 1992), and so the process of regional extinction was very slow. Similarly, climatic changes like this probably led to evolution of new species in Tasmania, the descendant taxa mentioned in point 2 above (Hill & Read 1987). A Late Oligocene site at Berwick Quarry in Victoria seems to show the effects of a drying climate on rainforest at this time, since the site, although dominated by rainforest elements, also contains some taxa that today are associated with drier environments, most notably *Eucalyptus* (Pole *et al.* 1993).

By the Early Pleistocene many of the extant Tasmanian rainforest species were in place (Hill & Macphail 1985; Macphail *et al.* 1993), and there was also a diversity of other species present that have since become extinct (Jordan 1992; Jordan & Hill 1991). The final climatic filter that further simplified the structure and composition of Tasmanian rainforest was the Quaternary glaciations. Although the detailed history of this is not yet understood, we know that the Early Pleistocene rainforests were much more species rich than any extant forests on the island, and that the major intervening climatic events have been glaciations (Colhoun *et al.* 1989, 1993; Fitzsimons *et al.* 1990; Jordan *et al.* 1991, 1995; Jordan & Hill 1994). Furthermore, the species that have become extinct include several that have mesomorphic NLRs and thus extreme low temperature is likely to have played a key role in their extinction.

Alpine vegetation history

The origin of the Australian alpine flora has been the subject of conflicting ideas for some time. While there is a general recognition that there are many taxa in the extant alpine flora that have a long history in the Southern Hemisphere, there has been debate over how recently they have reached Australia, with the extreme view being that they are essentially a Quaternary phenomenon here, having migrated up from the Subantarctic islands during the glaciations (e.g. Smith 1986). The main justification proposed for this hypothesis is that none of Australia occurred below the tree-line prior to the Quaternary. This has still not been adequately tested, but macrofossil evidence suggests it is not necessarily relevant anyway.

Several of Tasmania's Cenozoic deposits occur well above sea level, but one in particular represents a good test for the time of origin of the alpine flora. The Monpeelyata sediments occur in central Tasmania at 920 m above sea level in a geologically very stable area, on what is now an extremely cold and windswept plain. The sediments are a localised lake infill, with a basalt cap (Macphail *et al.* 1991). Within these sediments, the most common fossils are leaf fragments and megaspores of *Isoetes*, a freshwater hydrophyte that was almost certainly growing *in situ* (Hill 1988b). Today *Isoetes* is common at high altitudes, but not restricted there, and so offers only weak support for a cool climate flora. However, other macrofossils within the sediment offer greater support for the interpretation of a cool climate. For example, leaves of *Nothofagus gunnii* are relatively common (Hill & Gibson 1986a), and this species is now restricted to high altitudes in Tasmania, *Microstrobos microfolius* is common (Wells & Hill 1989b), and this species is very similar in leaf morphology to the extant *M. niphophilus*, a sub-alpine or alpine shrub (Wells & Hill 1989a). Other conifers that have been identified include three species of *Araucaria* (section *Eutacta*, Hill 1990a), *Austrocedrus* (Hill & Carpenter

1989) and three species of *Dacrycarpus* (Wells & Hill 1989b). As mentioned earlier, these *Dacrycarpus* species are outside the range of morphology exhibited by the extant species and clearly suggest that they were cool climate variants (Hill & Carpenter 1991a; Hill 1994b, 1995; Hill & Scriven in press). There are a number of taxa of Epacridaceae among the large number of extremely small leaves that make up the relatively diverse angiosperm flora, and this extremely small leaf size is also a cool climate indicator (Hill & Gibson 1986a, 1986b; Hill 1990b).

Despite the evidence for a cool climate from a variety of botanical sources, it is clear that this site occurred below the climatic tree-line. Among the many macrofossils recovered is a section of wood about a metre long and 20cm in diameter (Hill & Gibson 1986a). At the very least this was the trunk of a small tree, and thus we are not dealing with a true alpine vegetation. However, it is likely that this vegetation represents the precursor to true alpine vegetation, since it shares many taxonomic similarities with this flora and it is likely that this similarity will increase as further taxonomic research is completed. Thus evidence to date strongly supports the view that the alpine flora, at least in part, has a long history in Australia, developing slowly at marginal cold-climate sites and eventually forming a true alpine vegetation when the tree-line became depressed enough to ensure stable landscape for colonisation above it.

The evolution of scleromorphy

One of the key events in the history of the Australian vegetation was the evolution of the very distinctive and highly endemic scleromorphic heath flora. There has been a great deal of extremely high quality research on the living species that constitute this flora, and on the basis of this several hypotheses have been formulated to explain its origin and subsequent evolution. These hypotheses are at least in part amenable to testing via the macrofossil record. This is so because the vast majority of macrofossils are leaves, and these are the organs most obviously affected by scleromorphy.

In essence, there is debate in Australia as to whether low soil nutrient levels were the primary factor behind the evolution of the scleromorphic heath flora, or whether it was the onset of aridity and consequently xeromorphy that was of primary significance.

My research has concentrated on the problem of separating the effects of scleromorphy from those of xeromorphy. The morphological expression of these two phenomena can be quite similar, but there are logical differences. Scleromorphy is regarded as a response to low nutrients, and especially low phosphorus, whereas xeromorphy is a response to low water availability. Many scleromorphic responses pre-adapt a plant to xeromorphy, but there are some xeromorphic characteristics that are inherently unlikely as a scleromorphic response. Most obvious of these is stomatal protection. In an environment where water is limiting, plants with evergreen leaves that have a long life span will often have major morphological adaptations to protect the stomatal openings, so that water loss is restricted because of increased boundary layer resistance. The trade-off is that carbon dioxide uptake will also be restricted, which means that photosynthetic rates will be slowed. A plant growing in a low nutrient environment that has a scleromorphic response has no obvious need for morphological protection of stomata. Therefore, in examining fossils it is possible to look for the time of appearance of generalised scleromorphic/xeromorphic characters in comparison with specialised xeromorphic characters (stomatal protection) in order to determine whether the morphological expression of low nutrients or low water availability was in evidence first in Australia.

My main approach to this has been via two main phylogenetic lines - the tribe Banksieae of the Proteaceae and the Casuarinaceae. We have recently begun research on the macrofossil Epacridaceae as well (Jordan & Hill 1995, 1996), but it is too soon to draw any conclusions from that source. The tribe Banksieae of the Proteaceae contains four extant genera, the rainforest members *Austromuellera* and *Musgravea*, which have very few species, and the highly species diverse *Banksia* and *Dryandra*, which are restricted to scleromorphic heath and do not occur in rainforest. This tribe is common in the macrofossil record (Cookson & Duigan 1950; Hill & Christophel 1988; Hill 1990e; Hill & Merrifield 1993; Carpenter *et al.* 1994; Hill *et al.* 1995) and most fossil leaves are assigned to the genus *Banksieaephyllum* (if organic preservation occurs and cuticular characters can be assessed) or *Banksieaeformis* (for leaf impressions). These generic names denote membership of the tribe, but since there is as yet no reliable method for separating extant *Banksia* leaves from extant *Dryandra* leaves the identification can go no further. We know that *Banksia* has been present in Australia since the Eocene, since the extremely distinctive mature seed-bearing structures (the "cones") are known from that time (McNamara & Scott 1983). Within *Banksieaephyllum* there is little evidence of stomatal protection prior to some Miocene species from the Latrobe Valley coal (Hill & Christophel 1988; Hill 1994b), although the oldest species recorded to date, *Banksieaephyllum taylorii*, from the Late Paleocene sediments at Lake Bungarby in southern New South Wales, does have stomata sunken into pits (Carpenter *et al.* 1994).

The Casuarinaceae contains four extant genera, *Allocasuarina, Casuarina, Ceuthostoma* and *Gymnostoma*. All have highly scleromorphic photosynthetic units (cladodes), and in *Gymnostoma* the stomata are unprotected on the surface of these units. In contrast, the stomata on the other two common genera, *Casuarina* and *Allocasuarina*, are sunken deep within grooves on the cladodes and these grooves are often filled with trichomes to further reduce water loss. Thus extant *Gymnostoma* is best characterised as scleromorphic but not xeromorphic, whereas *Casuarina* and *Allocasuarina* are both scleromorphic and xeromorphic. *Gymnostoma* has an extensive Cenozoic macrofossil record (Hill 1994b; Scriven & Hill 1995), but other genera do not appear until very late in the Cenozoic (Hill 1994b). However, no transitional forms have yet been discovered and thus it is not clear whether *Gymnostoma* is genuinely ancestral or whether it simply occurred in wet habitats where fossilisation was likely and the other genera are absent in the Australian Cenozoic fossil record because they were restricted to drier habitats.

A different approach to the problem of the origin of scleromorphy and xeromorphy has been to examine whole floras where at least one of these responses was in evidence. The best example of this that I have worked on is the West Dale macroflora from southwestern Western Australia (Hill & Merrifield 1993). The time control on this flora is poor, being constrained within the Eocene - Early Oligocene, but good palaeobotanical information from the Cenozoic of Western Australia is so rare that it is still a very important record.

The West Dale flora is very species diverse, dominated by the angiosperm families Myrtaceae and Proteaceae, but with others represented, along with conifers and ferns. The majority of taxa present are clearly scleromorphic, but there is little evidence of stomatal protection (although this is certainly not completely absent). Many of the families and even some of the genera and species present at West Dale still occur in the region, and presumably have made the transition into more xeric conditions very well. However, many have become at least regionally extinct, and it is interesting to note which these are. Among the angiosperms, *Nothofagus* subgenus *Lophozonia* is no longer found in Western Australia, and clearly would not survive such dry conditions. Similarly, among the Casuarinaceae, *Gymnostoma* has been replaced by the more xeromorphic genera. All of the conifers found at West Dale are also now extinct, and in all cases they are quite scleromorphic but have little or no adaptation to restrict water loss except for stomatal pugs, which recent physiological work has suggested have an important function, but not in a very dry climate (Brodribb & Hill manuscript submitted c).

Conclusion

In conclusion, my research has concentrated on some of the major themes regarding the evolution of the Australian flora that can be answered via the macrofossil record. This work has been largely summarised in three books that I have either edited or co-edited in the last few years (Hill 1994c; Enright & Hill 1995; Veblen *et al.* 1996). My research is far from complete, but these books represent an obvious milestone, and seemed a good point to conclude a significant part of my research career with this submission.

References

Bigwood, A.J. & Hill, R.S. 1985. Tertiary araucarian macrofossils from Tasmania. *Australian Journal of Botany* **33,** 645-656.

Brodribb, T.J. & Hill, R.S manuscript submitted a. The drought physiology of a diverse group of Southern Hemisphere conifer species is correlated with minimum seasonal rainfall. Functional Ecology.

Brodribb, T.J. & Hill, R.S. manuscript submitted b. Light response characteristics of a morphologically diverse group of Southern Hemisphere conifers as measured by chlorophyll fluorescence. Oecologia.

Brodribb, T.J. & Hill, R.S. manuscript submitted c. The effects of imbricacy and stomatal wax plugs on maximum leaf conductance in a group of Southern Hemisphere conifers. Australian Journal of Botany.

Carpenter, R.J., Hill, R.S. & Jordan, G.J. 1994. Cenozoic vegetation in Tasmania: Macrofossil evidence. *In:* R.S. Hill (ed.) *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge, pp. 276-98.

Carpenter, R.J., Jordan, G.J. & Hill, R.S. 1994. *Banksieaephyllum taylorii* (Proteaceae) from the Late Paleocene of New South Wales and its relevance to the origin of Australia's scleromorphic flora. *Australian Systematic Botany* **7,** 385-392.

Christophel, D.C. & Blackburn, D.T. 1978. Tertiary megafossil flora of Maslin Bay, South Australia: A preliminary report. *Alcheringa* **2,** 311-319.

Christophel, D.C., Harris, W.K. & Syber, A.K. 1987. The Eocene flora of the Anglesea locality, Victoria. *Alcheringa* **11,** 303-323.

Colhoun, E.A., Benger, S.N., Fitzsimons, S.J., van de Geer, G. & Hill, R.S. 1993. Quaternary organic deposit from Newton Creek Valley, western Tasmania. *Australian Geographic Studies* **31,** 26-38.

Colhoun, E.A., van de Geer, G., Hill, R.S. & Bird, T. 1989. Interglacial pollen and plant macrofossils from Langdon River, western Tasmania. *New Phytologist* **111,** 531-548.

Cookson, I.C. & Duigan, S.L. 1950. Fossil Banksieae from Yallourn, Victoria, with notes on the morphology and anatomy of living species. *Australian Journal of Scientific Research series B* **3,** 133-165.

Dettmann, M.E., Pocknall, D.T., Romero, E.J. & Zamaloa, M. del C. 1990. *Nothofagidites* Erdtman ex Potonie, 1960; a catalogue of species with notes on the paleogeographic distribution of *Nothofagus* Bl. (southern beech). *New Zealand Geological Survey Paleontological Bulletin* **60,** 1-79.

Enright, N.J. & Hill, R.S. (eds) 1995. *Ecology of the Southern Conifers*. Melbourne University Press, Melbourne. 342pp.

Fitzsimons, S.J., Colhoun, E.A., van de Geer, G. & Hill, R.S. 1990. Definition and character of the Regency Interglacial and Early-Middle Pleistocene stratigraphy in the King Valley, western Tasmania, Australia. *Boreas* **19,** 1-15.

Hill, R.S. 1978. Two new species of *Bowenia* Hook. ex Hook.f. from the Eocene of eastern Australia. *Australian Journal of Botany* **26,** 837-846.

Hill, R.S. 1980. Three new Eocene cycads from eastern Australia. *Australian Journal of Botany* **28,** 105-122.

Hill, R.S. 1982. The Eocene megafossil flora of Nerriga, New South Wales, Australia. *Palaeontographica Abt. B* **181,** 44-77.

Hill, R.S. 1983a. *Nothofagus* macrofossils from the Tertiary of Tasmania. *Alcheringa* **7,** 169-183.

Hill, R.S. 1983b. 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. 1987. Discovery of *Nothofagus* fruits corresponding to an important Tertiary pollen type. *Nature* **327,** 56-58.

Hill, R.S. 1988a. A re-investigation of *Nothofagus muelleri* (Ett.) Paterson and*Cinnamomum nuytsii* Ett. from the Late Eocene of Vegetable Creek. *Alcheringa* **12,** 221-231.

Hill, R.S. 1988b. Tertiary *Isoetes* from Tasmania. *Alcheringa* **12,** 157-162.

Hill, R.S. 1989a. Fossil leaf. *In* P.J. Barrett (ed.) *Antarctic Cenozoic History from the CIROS-1 Drillhole, McMurdo Sound. DSIR Bulletin* **245,** 143-144.

Hill, R.S. 1989b. New species of *Phyllocladus* (Podocarpaceae) macrofossils from southeastern Australia. *Alcheringa* **13,** 193-208.

Hill, R.S. 1989c. Early Tertiary leaves of the Menispermaceae from Nerriga, New South Wales. *Alcheringa* **13,** 37-44.

Hill, R.S. 1990a. *Araucaria* (Araucariaceae) species from Australian Tertiary sediments - a micromorphological study. *Australian Systematic Botany* **3,** 203-220.

Hill, R.S. 1990b. Evolution of the modern high latitude southern hemisphere flora: evidence from the Australian macrofossil record. In: J.G. Douglas & D.C. Christophel (eds) *Proceedings 3rd IOP Conference, Melbourne, 1988.* A-Z Publishers, Melbourne. pp. 31-42.

Hill, R.S. 1990c. The fossil history of Tasmania's rainforest tree species. *Tasforests* **2,** 5-12.

Hill, R.S. 1990d. Sixty million years of change in Tasmania's climate and vegetation. *Tasforests* **2,** 89-98.

Hill, R.S. 1990e. Tertiary Proteaceae in Australia: A re-investigation of *Banksia adunca* and *Dryandra urniformis*. *Proceedings of the Royal Society of Victoria* **102,** 23-28.

Hill, R.S. 1991a. Tertiary *Nothofagus* (Fagaceae) macrofossils from Tasmania and Antarctica and their bearing on the evolution of the genus. *Botanical Journal of the Linnean Society* **105,** 73-112.

Hill, R.S. 1991b. Leaves of *Eucryphia* (Eucryphiaceae) from Tertiary sediments in south-eastern Australia. *Australian Systematic Botany* **4,** 481-497.

Hill, R.S. 1991c. History of rainforest - evidence from plant macrofossils. *In:* G. Werren & P. Kershaw (eds) *The Rainforest Legacy.* Australian National Rainforest Study. Volume 3. *Special Australian Heritage Publication Series Number* 7(3), 17-29.

Hill, R.S. 1992. *Nothofagus* : Evolution from a southern perspective. *Trends in Ecology and Evolution* **7,** 190-194.

Hill, R.S. 1994a. *Nothofagus smithtonensis* (Nothofagaceae), a new macrofossil species from Early Oligocene sediments in northwest Tasmania, Australia, and its phylogenetic significance. *Review of Palaeobotany and Palynology* **80,** 115-121.

Hill, R.S. 1994b. The history of selected Australian taxa. *In:* R.S. Hill (ed.) *History of the Australian Vegetation: Cretaceous to Recent.* Cambridge University Press, Cambridge, pp. 390-419.

Hill, R.S. (ed.) 1994c. *History of the Australian Vegetation: Cretaceous to Recent.* Cambridge University Press, Cambridge, 433pp.

Hill, R.S. 1995. Conifer origin, evolution and diversification in the Southern Hemisphere. *In:* N.J. Enright & R.S. Hill (eds) *Ecology of the Southern Conifers.* Melbourne University Press, Melbourne. pp. 10-29.

Hill, R.S. & Bigwood, A.J. 1987. Tertiary gymnosperms from Tasmania: Araucariaceae. *Alcheringa* **11,** 325-335.

Hill, R.S. & Carpenter, R.J. 1989. Tertiary gymnosperms from Tasmania: Cupressaceae. *Alcheringa* **13,** 89-102.

Hill, R.S. & Carpenter, R.J. 1991a. Evolution of *Acmopyle* and *Dacrycarpus* (Podocarpaceae) foliage as inferred from macrofossils in south-eastern Australia. *Australian Systematic Botany* **4,** 449-479.

Hill, R.S. & Carpenter, R.J. 1991b. Extensive past distributions for major Gondwanic floral elements: macrofossil evidence. *Papers and Proceedings of the Royal Society of Tasmania* **124,** 239-247.

Hill, R.S. & Christophel, D.C. 1988. Tertiary leaves of the tribe Banksieae (Proteaceae) from south-eastern Australia. *Botanical Journal of the Linnean Society* **97,** 205-227.

Hill, R.S. & Dettmann, M.E. 1996. Origin and diversification of the genus *Nothofagus*. In: The Ecology and Biogeography of *Nothofagus* Forests (Eds T.T. Veblen, R.S. Hill & J. Read) pp. 11-24. (Yale University Press, Yale).

Hill, R.S. & Gibson, N. 1986a. 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. C.S.I.R.O., Melbourne. pp. 205-17.

Hill, R.S. & Gibson, N. 1986b. Distribution of potential macrofossils in Lake Dobson, Tasmania. *Journal of Ecology* **74,** 373-384.

Hill, R.S. & Jordan, G.J. 1993. The evolutionary history of *Nothofagus* (Nothofagaceae). *Australian Systematic Botany* **6,** 111-126.

Hill, R.S., Jordan, G.J. & Carpenter, R.J. 1993. Taxodiaceous macrofossils from Tertiary and Quaternary sediments in Tasmania. *Australian Systematic Botany* **6,** 237-249.

Hill, R.S., Jordan, G.J. & Macphail, M.K. 1996. History and Paleoecology of Australian *Nothofagus* forests. In: The Ecology and Biogeography of *Nothofagus* Forests (Eds T.T. Veblen, R.S. Hill & J. Read) pp. 182-199. (Yale University Press, Yale).

Hill, R.S. & Macphail, M.K. 1983. Reconstruction of the Oligocene vegetation at Pioneer, northeast Tasmania. *Alcheringa* **7,** 281-299.

Hill, R.S. & Macphail, M.K. 1985. A fossil flora from rafted Plio-Pleistocene mudstones at Regatta Point, Tasmania. *Australian Journal of Botany* **33,** 497-517.

Hill, R.S. & Merrifield, H.E. 1993. An Early Tertiary macroflora from West Dale, southwestern Australia. *Alcheringa* **17,** 285-326.

Hill, R.S. & Pole, M.S. 1992. Leaf and shoot morphology of extant *Afrocarpus, Nageia* and *Retrophyllum* (Podocarpaceae) species, and species with similar leaf arrangement from Tertiary sediments in Australasia. *Australian Systematic Botany* **5,** 337-358.

Hill, R.S. & Read, J. 1987. Endemism in Tasmanian cool temperate rainforest: alternative hypotheses. *Botanical Journal of the Linnean Society* **95,** 113-124.

Hill, R.S. & Read, J. 1991. A revised infrageneric classification of *Nothofagus* (Fagaceae). *Botanical Journal of the Linnean Society* **105**, 37-72.

Hill, R.S., Read, J. & Busby, J.R. 1988. The temperature-dependence of photosynthesis of some Australian temperate rainforest trees and its biogeographical significance. *Journal of Biogeography* **15,** 431-449.

Hill, R.S. & Scriven, L.J. 1995. The angiosperm-dominated woody vegetation of Antarctica: a review. *Review of Palaeobotany and Palynology* **86,** 175-198.

Hill, R.S. & Scriven, L.J. in press. Palaeoclimate across an altitudinal gradient in the Oligo-Miocene of northern Tasmania: an investigation of nearest living relative analysis. *Australian Journal of Botany*.

Hill, R.S., Scriven, L.J. and Jordan, G.J. 1995. The fossil record of the Proteaceae. In: A.E. Orchard (ed.) *Flora of Australia. Proteaceae.* Australian Government Publishing Service, Canberra. pp. 21-30.

Hill, R.S. & Truswell, E.M. 1993. *Nothofagus* fossils in the Sirius Group, Transantarctic Mountains: Leaves and pollen and their climatic implications. In: J. Kennett & D. Warnke (eds) *The Antarctic Paleoenvironment: A Perspective on Global Change (Part 2).* American Geophysical Union, Washington. pp. 67-73.

Hill, R.S. and Whang, S.S. 1996. A new species of *Fitzroya* (Cupressaceae) from Oligocene sediments in north-western Tasmania. *Australian Systematic Botany* in press.

Hyndman, D.C. & Menzies, J.I. 1990. Rain forests of the Ok Tedi headwaters, New Guinea: an ecological analysis. *Journal of Biogeography* **17,** 241-273.

Jordan, G.J. 1992. *Macrofossil Evidence for Quaternary Plant Extinction and Vegetation in Western Tasmania*. Ph.D. Thesis, University of Tasmania

Jordan, J.G., Carpenter, R.J. & Hill, R.S. 1991. Late Pleistocene vegetation and climate near Melaleuca Inlet, south-western Tasmania. *Australian Journal of Botany* **39,** 315-333.

Jordan, G.J. & Hill, R.S. 1991. Two new *Banksia* species from Pleistocene sediments in western Tasmania. *Australian Systematic Botany* **4,** 499-511.

Jordan, G.J. & Hill, R.S. 1994. Past and present variability in leaf length of evergreen members of *Nothofagus* subgenus *Lophozonia* related to ecology and population dynamics. *New Phytologist* **127,** 377-390.

Jordan, G.J. & Hill, R.S. 1995. Oligocene leaves of Epacridaceae from Little Rapid River, Tasmania, and the identification of fossil Epacridaceae leaves. *Australian Systematic Botany* **8,** 71-83.

Jordan, G.J. & Hill, R.S. 1996. The fossil record of the Epacridaceae. *Annals of Botany* **77,** 341-346.

Jordan, G.J., Macphail, M.K., Barnes, R. & Hill, R.S. 1995. An Early to Middle Pleistocene flora of subalpine affinities in lowland western Tasmania. *Australian Journal of Botany* **43,** 231-242.

Kovar, J.B., Campbell, J.D. & Hill, R.S. 1987. *Nothofagus ninnisiana* (Unger) Oliver from Waikato Coal Measures (Eocene-Oligocene) at Drury, Auckland, New Zealand. *New Zealand Journal of Botany* **25,** 79-85.

Macphail, M.K. & Hill, R.S. 1983. Cool temperate rainforest in Tasmania: a reply. *Search* **14,** 186-187.

Macphail, M.K., Hill, R.S., Forsyth, S.M. & Wells, P.M. 1991. A Late Oligocene-Early Miocene cool climate flora in Tasmania. *Alcheringa* **15,** 87-106.

Macphail, M.K., Jordan, G.J. & Hill, R.S. 1993. Key periods in the evolution of the flora and vegetation in western Tasmania I. the Early-Middle Pleistocene. *Australian Journal of Botany* **41,** 673-707.

McNamara, K.J. & Scott, J.K. 1983. A new species of *Banksia* (Proteaceae) from the Eocene Merlinleigh Sandstone of the Kennedy Range, Western Australia. *Alcheringa* **7,** 185-193.

Pole, M.S. 1992. Eocene vegetation from Hasties, north-eastern Tasmania. *Australian Systematic Botany* **5,** 431-475.

Pole, M.S., Hill, R.S., Green, N. & Macphail, M.K. 1993. The Late Oligocene Berwick Quarry flora - rainforest in a drying environment. *Australian Systematic Botany* **6,** 399-428.

Pole, M.S. & Macphail, M.K. 1996. Eocene *Nypa* from Regatta Point, Tasmania. *Review of Palaeobotany and Palynology* **92,** 55-68.

Read, J. & Hill, R.S. 1985a. Photosynthetic responses to light of Australian and Chilean species of *Nothofagus* and their relevance to the rainforest dynamics. *New Phytologist* **101,** 731-742.

Read, J. & Hill, R.S. 1985b. Dynamics of *Nothofagus*-dominated rainforest on mainland Australia and lowland Tasmania. *Vegetatio* **63,** 67-78.

Read, J. & Hill, R.S. 1988a. Comparative responses to temperature of the major canopy species of Tasmanian cool temperate rainforest and their ecological significance. I. Foliar frost resistance. *Australian Journal of Botany* **36,** 131-143.

Read, J. & Hill, R.S. 1988b. The dynamics of some rainforest associations in Tasmania. *Journal of Ecology* **76,** 558-584.

Read, J. & Hill, R.S. 1989. The response of some Australian temperate rain forest tree species to freezing temperatures and its biogeographical significance. *Journal of Biogeography* **16,** 21-27.

Read, J., Hope, G.S. & Hill, R.S. 1990a. Integrating historical and ecophysiological studies in *Nothofagus* to examine the factors shaping the development of cool rainforest in southeastern Australia. In: J.G. Douglas & D.C. Christophel (eds) *Proceedings 3rd IOP Conference, Melbourne, 1988.* A-Z Publishers, Melbourne. pp. 97-106.

Read, J., Hope, G.S. & Hill, R.S. 1990b. The dynamics of some *Nothofagus*-dominated rain forests in Papua New Guinea. *Journal of Biogeography* **17,** 185-204.

Scriven, L.J. 1993. *Diversity of the Mid-Eocene Maslin Bay Flora, South Australia.* Ph.D. Thesis, University of Adelaide.

Scriven, L.J. & Hill, R.S. 1995. Macrofossil Casuarinaceae: their identification and the oldest macrofossil record, *Gymnostoma antiquum* sp. nov., from the Late Paleocene of New South Wales, Australia. *Australian Systematic Botany* **8,** 1035-1053.

Scriven, L.J. & Hill, R.S. in press. Relationships among Tasmanian Tertiary *Nothofagus* (Nothofagaceae) populations. *Botanical Journal of the Linnean Society*.

Scriven, L.J., McLoughlin, S. & Hill, R.S. 1995. *Nothofagus plicata* (Nothofagaceae), a new deciduous Eocene macrofossil species, from southern continental Australia. *Review of Palaeobotany and Palynology* **86,** 199-209.

Smith, J.M.B. 1986. Origins of Australasian tropicalpine and alpine floras. *In:* B.A. Barlow (ed.) Flora and Fauna of Alpine Australasia: Ages and Origins. C.S.I.R.O., Melbourne. pp. 109-128.

Veblen, T.T., Hill, R.S. & Read, J. (eds) 1996. *The Ecology and Biogeography of* Nothofagus *Forests*. Yale University Press, Yale. 403pp.

Wells, P.M. & Hill, R.S. 1989a. Leaf morphology of the imbricate-leaved Podocarpaceae. *Australian Systematic Botany* **2,** 369-386.

Wells, P.M. & Hill, R.S. 1989b. Fossil imbricate-leaved Podocarpaceae from Tertiary sediments in Tasmania. *Australian Systematic Botany* **2,** 387-423.

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