

The Fossil History of Tasmania's Rainforest Tree Species

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Abstract

Tasmanian rainforests are an important relict of an ancient Gondwanic stock. The available fossil record of the major tree species (Nothofagus cunninghamii, Eucryphia lucida, Atherosperma moschatum, Phyllocladus aspleniifolius, Lagarostrobos franklinii and Athrotaxis selaginoides) is reviewed, and it demonstrates that most of the species can be traced back in Tasmania for over 40 million years, and in some cases substantially more. Evolution has been minor during that time, and has been primarily in response to climatic change.

Introduction

Tasmania's rainforests have long been associated with part of an ancient Gondwanic

vegetation which was first recognised by Hooker (1860) as part of his Antarctic element. However, much of the evidence for the antiquity of the rainforest has been inferential, based on the present distribution (Table 1) and morphological similarity of the nearest living relatives of the component species. Over about the last thirty years the fossil record for southeastern Australia has increased substantially, to the point where it is now possible to determine much of the history of cool temperate rainforest species within that region. This paper traces that history for the major tree species.

The Fossil Record

The plant fossil record comes from two sources - pollen (or microfossils) and large

Table 1. Major tree species in Tasmanian cool temperate rainforest discussed in the text and the present distribution of the genera in which they occur.

Rainforest species	Current distribution of the genus
<i>Atherosperma moschatum</i>	southeastern Australia
<i>Athrotaxis selaginoides</i>	Tasmania
<i>Eucryphia lucida</i>	Chile, Tasmania, southeastern NSW, Mount Bartle Frere (northern Qld)
<i>Lagarostrobos franklinii</i>	Tasmania, New Zealand
<i>Nothofagus cunninghamii</i>	southern South America, southeastern Australia, New Zealand, New Guinea, New Caledonia
<i>Phyllocladus aspleniifolius</i>	Tasmania, New Zealand, New Guinea to Borneo

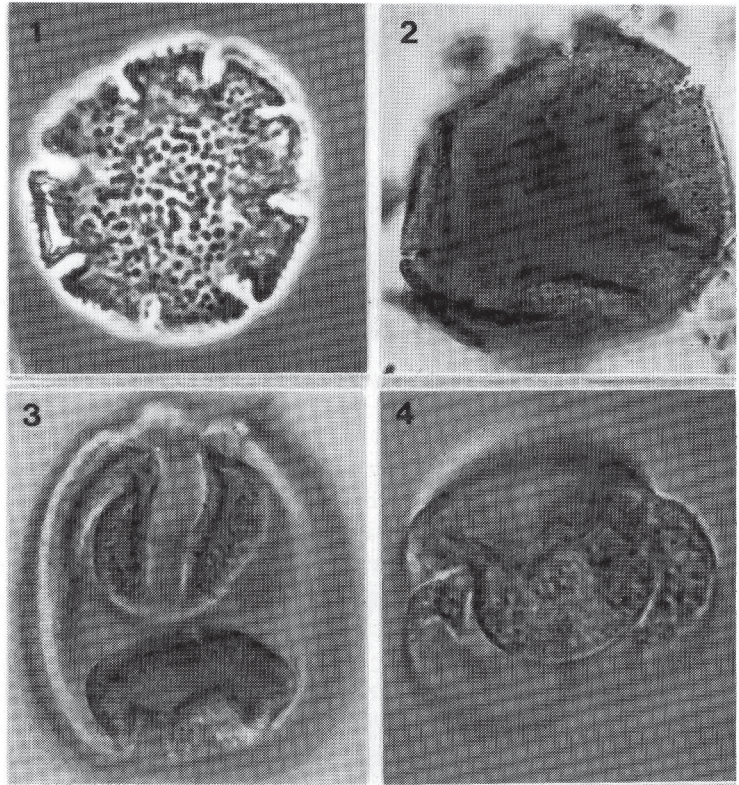
Figures 1-4. Pollen grains from Tasmanian Tertiary sediments (photographs by Dr M.K. Macphail).

Fig. 1. *Nothofagidites vansteenii* from the Late Oligocene-Early Miocene Monpeelyata deposit in central Tasmania. This pollen type is now produced by *Nothofagus* species which grow in the mountains of New Guinea and in New Caledonia. (x1440).

Fig. 2. *Nothofagidites asperus* from the Oligocene Pioneer deposit in northwest Tasmania. This pollen type is produced by *Nothofagus cunninghamii* in Tasmania today. (x1280).

Fig. 3. *Lagarostrobos franklinii* from the Late Pliocene-Early Pleistocene Regatta Point deposit near Strahan. (x1360).

Fig. 4. *Podosporites erugatus* from the Monpeelyata deposit. This pollen type is similar to that produced by many living and fossil podocarps. (x1440).



organs (macrofossils). Pollen is produced in vast quantities, especially by wind pollinated species, and much of it does not fulfil its function (pollination) and lands instead away from flowers and sometimes in sedimentary environments. Pollen has an extremely resistant wall, which prevents desiccation of the grain during transport, and this wall aids in fossilisation of the grain. Pollen can vary greatly in morphology among different species (Figs. 1-4), and this aids in the identification of fossil pollen. However, the problem with fossil pollen is that it represents only a very small part of the whole organism, and it is a large act of faith to assume that if the pollen grains of two organisms are alike then the organisms themselves are alike. In some instances evidence from other sources has justified this conclusion, but equally there are examples where this conclusion has been erroneous.

Macrofossils are most commonly leaves, since

this is the organ which plants most often shed, but wood and reproductive structures (including flowers) are often preserved as well (Figs. 5-11). Macrofossils are often more reliable indicators of the identity of the plant which shed them because they are more distinctive morphologically than pollen grains. Therefore it is information from the macrofossil record which gives the most reliable evidence for the past history of rainforest trees in Tasmania, but the pollen record is an important aid, especially given that it is far more extensive. The history of the rainforest tree species will now be considered.

Nothofagus cunninghamii (Fagaceae)

This species dominates much of Tasmania's rainforest and also occurs in some areas of Victoria, where it is usually associated with eucalypts. There is a substantial fossil record for *N.cunninghamii* (and its precursors) and its history is relatively well known (Hill 1983a,b,

manuscript submitted, Hill & Gibson 1986). It has been shown that the earliest species found in southeastern Australia which are closely related to *N.cunninghamii* had much larger leaves, which are very similar to those produced by *N.moorei* which grows today at high altitudes in northern New South Wales and southern Queensland. As time passed in southeastern Australia these plants changed, probably in response to the changing climate (which was becoming cooler, with more seasonal rainfall), and the leaves became smaller, and eventually, by at least 2 million years (m.y.) ago, *N.cunninghamii* was in place in Tasmania (Hill & Macphail 1985).

The oldest fossils which can be related to this complex come from the Late Palaeocene (about 55 m.y. ago), and closely resemble *N.moorei*. They are found in high altitude sediments at Lake Bungarby in southeastern New South Wales. From the mid-late Eocene (38-45 m.y. ago) *Nothofagus* leaves and cupules of this type are common in Tasmania and also occur in some deposits on mainland Australia (Figs. 5, 6; Hill 1988). They were probably common throughout Tasmania, but may have been restricted largely to forest edge communities (e.g. lake or river sides, or interfaces between rainforest and more open vegetation) (Hill in press). Many *Nothofagus* species co-existed during the Oligocene (27-38 m.y. ago), including *N.gunnii* and the complex which evolved into *N.cunninghamii*, but all the others are now extinct in the region. The reasons for this are complex (see Read *et al.*, in press), and include climatic responses and regeneration strategies.

It is clear that plants related to *N.cunninghamii* have a long history in Tasmanian forests, and have been dominant members of forest communities for most of that time. However, it is probable that *N.cunninghamii* itself is a relatively recently evolved species, with *N.moorei* representing a species more closely allied to the ancestral complex. Hill & Read (1987) noted that many of the species which co-occur with *N.moorei* have closely related species in Tasmania, co-existing with *N.cunninghamii*. In all cases the major

difference is that the northern species have substantially larger leaves than the southern species (Table 2). Given the fossil record of the *N.moorei*/*N.cunninghamii* complex in Tasmania, they hypothesised that the northern members of all these species groups were closer to the ancestral form, with the Tasmanian species having evolved in response to the changing climate by reducing their leaf size.

Eucryphia lucida (Eucryphiaceae)

One of the perplexing features of the early-mid Tertiary fossil record in southeastern Australia has been the dominance of *Nothofagus* in most deposits and the absence of all other angiosperm rainforest species which currently co-occur with it in Tasmania. This has made reconstruction of the vegetation difficult, since it was not known whether this absence reflected a real event or a quirk of the fossil record. However, *Eucryphia* leaves have recently been recovered from at least one and possibly three early Tertiary floras. The oldest record is from the Late Palaeocene Lake Bungarby deposit, but this must still be regarded as a tentative identification. Similarly, cuticle of a *Eucryphia*-like leaf has been recovered from Early Eocene sediments (about 50-54 m.y. ago) at Regatta Point on Macquarie Harbour, but confirmation is required. However the Late Eocene sediments (about 38-45 m.y. ago) at Loch Aber in northeast Tasmania have yielded many quite well preserved *Eucryphia* leaves (with surfaces similar to that shown in Fig. 10), which unequivocally demonstrates the antiquity of the genus.

These leaves should offer an ideal test of the hypothesis of Hill & Read (1987) regarding the decline in leaf area among Tasmanian rainforest angiosperms during the Tertiary, but unfortunately they do not. This is because *Eucryphia moorei* in New South Wales has a larger leaf area than *E.lucida* because it has compound leaves, but each leaflet is about the same size as a leaf of *E.lucida*. It is impossible to tell whether the 'leaves' recovered from Loch Aber represent whole leaves (which

Fig. 5. Large leaf of *Nothofagus johnstonii* from the Pioneer deposit. (x3).

Fig. 6. Small leaf of *N. johnstonii* from the Pioneer deposit, showing a form much closer to the leaves of *N. cunninghamii*. (x9).

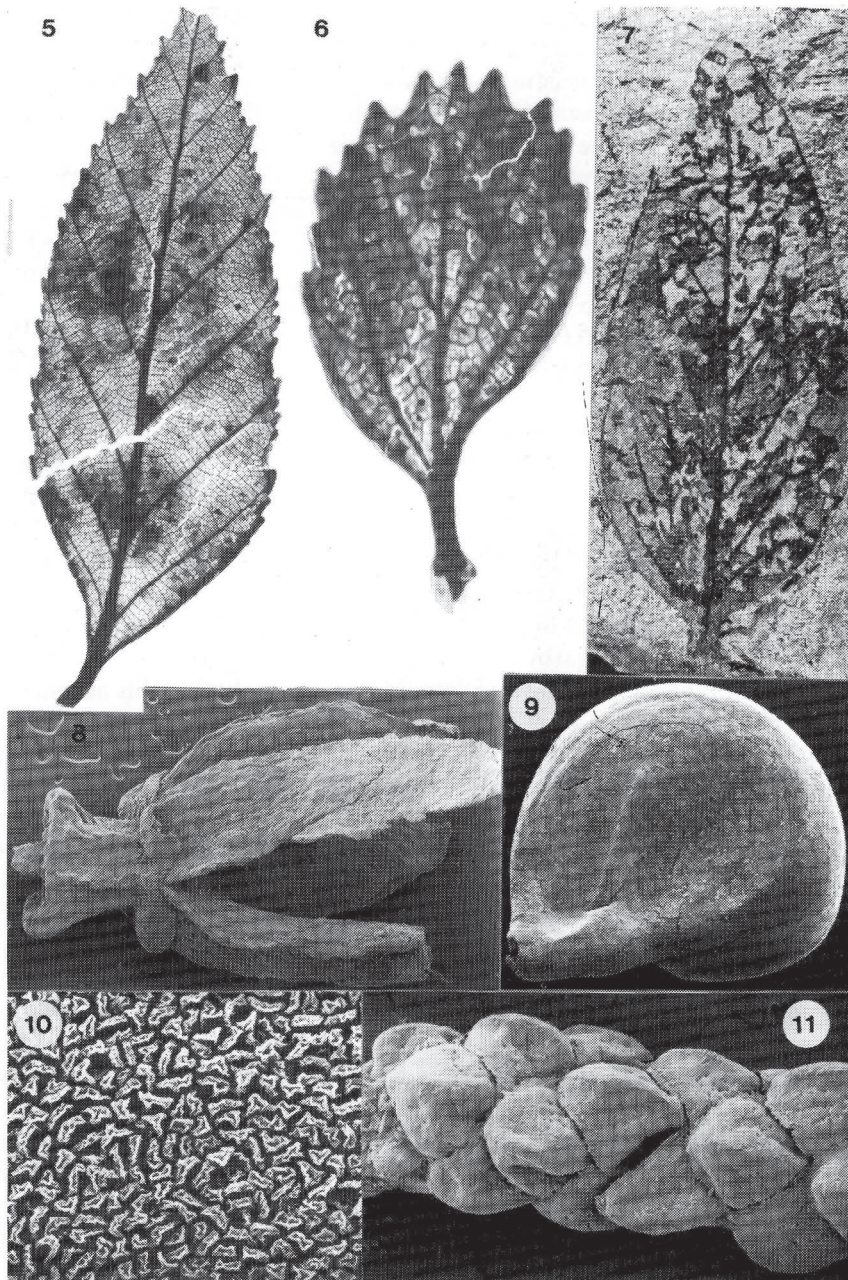
Fig. 7. Leaf of *Atherosperma moschatum* from the Regatta Point deposit. (x3.5).

Fig. 8. Scanning electron micrograph (SEM) of a cupule of an extinct *Nothofagus* species from the Oligocene Little Rapid River deposit in northwest Tasmania. The closest living relative of this species grows in Chile. (x16).

Fig. 9. SEM of a seed of *Drimys lanceolata* from the Regatta Point deposit. (x36).

Fig. 10. SEM of the leaf surface of *Eucryphia lucida* showing the unusual hairs which characterise the evergreen species of the genus. (x185).

Fig. 11. SEM of a leafy twig of *Lagarostrobos franklinii* from the Regatta Point deposit. (x30).



would refute the hypothesis) or leaflets from a compound leaf (which would support the hypothesis).

It appears that *Eucryphia* was relatively uncommon during the Tertiary compared with *Nothofagus*, but from the end of the Tertiary (in sediments at Regatta Point) and into the Quaternary leaves and reproductive

structures of *Eucryphia* are commonly found as fossils (e.g. Hill & Macphail 1985, Colhoun *et al.*, 1989).

Atherosperma moschatum (Monimiaceae)

There is only one macrofossil record of this species, a single leaf from Late Pliocene-Early Pleistocene sediments (2-3 m.y. ago) at

Table 2. Mean leaf area (mm^2) of species in common genera which occur in temperate rainforest in Tasmania or northern New South Wales (standard deviation in brackets). *Nothofagus cunninghamii* is separated into Victorian and Tasmanian populations. Adapted from Hill & Read (1987).

Species (location)	Leaf area (standard deviation)
<i>Acradenia euodiiformis</i> (NSW)	9817 (3424)
<i>A. frankliniae</i> (Tas)	756 (338)
<i>Anopterus macleayanus</i> (NSW)	13846 (3326)
<i>A. glandulosus</i> (Tas)	3420 (1664)
<i>Eucryphia moorei</i> (NSW)	2278 (1024)
<i>E. lucida</i> (Tas)	405 (140)
<i>E. milliganii</i> (Tas)	75 (33)
<i>Nothofagus moorei</i> (NSW)	1649 (692)
<i>N. cunninghamii</i> (Vic)	130 (59)
<i>N. cunninghamii</i> (Tas)	83 (36)
<i>Trochocarpa laurina</i> (NSW)	566 (310)
<i>T. disticha</i> (Tas)	62 (20)
<i>T. gunnii</i> (Tas)	31 (10)
<i>T. cunninghamii</i> (Tas)	24 (12)

Regatta Point (Fig. 7; Hill & Macphail 1985). While it is probable that *A. moschatum* has a considerably longer history than this, it will be difficult to demonstrate, because leaves of this species decay very quickly following their loss from the tree (Howard 1973) and its pollen is very nondescript. It is also probable that a species like this, which is usually part of the subcanopy, will not have large organs such as leaves reaching sedimentary environments as often as some of the canopy species.

Lagarostrobos franklinii (Podocarpaceae)

There are at least three reasons to expect that *L. franklinii* will have an extensive macrofossil record:

1. The species today frequently occurs alongside water courses and is ideally placed to input litter into sedimentary environments.
2. The species belongs to an ancient family, which extends back about 200 m.y. (Miller 1977), and therefore would be expected to

be relatively little changed (and therefore easily recognisable as a fossil) over the last 50-60 million years when modern forests have been evolving.

3. Pollen attributed to *L. franklinii* (*Phyllocladidites mawsonii*, Playford & Dettmann 1978) is common and sometimes dominant in Tertiary sediments throughout southeastern Australia and even further afield.

Despite this, the oldest certain record of *L. franklinii* is from the Late Pliocene-Early Pleistocene sediments at Regatta Point (Fig. 11; Hill & Macphail 1985, Wells & Hill 1989). A closely related species, *L. marginatus*, has been described from Oligocene sediments (27-38 m.y. ago) at Little Rapid River in northwest Tasmania, but only a single specimen of this species is known (Wells & Hill 1989). *L. marginatus* is somewhat intermediate in form between *L. franklinii* and the other living *Lagarostrobos* species, *L. colensoi* from New Zealand. Given the large amount of fossil material examined, this

strongly suggests that *L. franklinii* was uncommon in the past, and may even be a relatively recently evolved species.

The lack of a substantial macrofossil record is difficult to reconcile with the abundant fossil pollen record. However, there is at least one possible reason for this apparent discrepancy. *Lagarostrobos franklinii* belongs to the large conifer family Podocarpaceae. The conifers were much more prominent in the vegetation before the rise to dominance of the flowering plants, but since that time they, unlike the flowering plants, have been declining in diversity. Therefore, when a pollen type is recognised in fossil sediments as belonging to only one living conifer species there is a good chance that much larger groups of species produced this pollen type in the past with most having since become extinct. This is one of the inherent dangers of working with a group that is reducing in diversity through time. Thus the pollen record may greatly over-estimate the amount of *L. franklinii* or even its close relatives present in the past.

Phyllocladus aspleniifolius (Podocarpaceae)

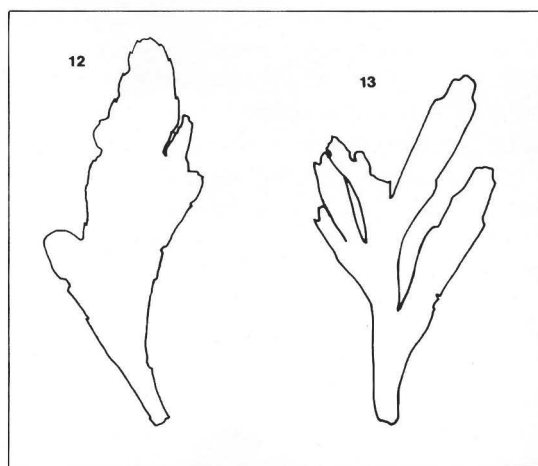
Phyllocladus is quite common as a macrofossil in southeastern Australia (Hill 1989), but only some of the specimens can be directly related to *P. aspleniifolius*. The oldest record is *P. arberensis* from the Late Eocene Loch Aber sediments, and this species also occurs in the Oligocene Little Rapid River sediments (Fig. 12). There are no other recordings of the *P. aspleniifolius* type until the Late Pliocene-Early Pleistocene Regatta Point sediments, but it is reasonable to assume that the species complex was present in southeastern Australia throughout the Tertiary.

The other *Phyllocladus* species which occur in southeastern Australia during the Tertiary fall into two groups; those which are related to living species in New Zealand or Malesia, and those which belong to extinct lines within the genus. The extinct line is of interest since it demonstrates how *Phyllocladus* may have evolved into its present form. *Phyllocladus* is unique among the living podocarps in that

the adult photosynthetic organs are not leaves but flattened branch systems. According to current botanical theory such a photosynthetic system would most likely evolve firstly by a three dimensional branch system becoming flattened, and then by photosynthetic tissue filling in the gaps between the branches ('webbing'). Therefore in a primitive *Phyllocladus* you might expect to see a photosynthetic system where the webbing is incomplete, and this is precisely what is found. In *P. lobatus* from the Oligocene Little Rapid River sediments webbing is very incomplete (Fig. 13; Hill 1989). However, it would be premature to consider *P. lobatus* to be an ancestor to any of the extant *Phyllocladus* species, since *P. arberensis*, which is very much like *P. aspleniifolius*, is also present at Little Rapid River, suggesting that evolution in *Phyllocladus* was already well advanced at that time. Nonetheless it can be said that *P. lobatus* illustrates the ancestral form of the photosynthetic organ in this genus.

Athrotaxis selaginoides (Taxodiaceae)

Athrotaxis is a very important genus in the major conifer family Taxodiaceae, which



Figures 12, 13. Outlines of phylloclades of *Phyllocladus* species from the Little Rapid River deposit.

Fig. 12. *P. arberensis*, which is closely related to *P. aspleniifolius*. (x1.5).

Fig. 13. *P. lobatus*, which has no close living relatives. (x3).

includes some of the most interesting living conifers (e.g. the Californian Redwood of North America and the Dawn Redwood of China). Although there are records of fossils similar to *Athrotaxis* from other parts of the world, none have stood up to close scrutiny, and at the present time the only definite *Athrotaxis* fossils are from Tasmania. Townrow (1965) described Eocene shoots of *Athrotaxis* from sediments at Buckland, but they were closest to *A.cupressoides*. These specimens may be a doubtful record of *Athrotaxis* and are currently being re-examined. There are leafy shoots which are very similar to *A.selaginoides* in Oligocene sediments at Pioneer in northeast Tasmania (Hill & Macphail 1983) and Little Rapid River, although neither of these have been thoroughly examined. It has recently become clear that there are extinct taxodiaceous fossils in Tasmania which are superficially similar to *Athrotaxis*, and this makes it more difficult to determine the affinities of some of the fossils. There are good specimens of *A. selaginoides* in the Late Pliocene-Early Pleistocene sediments at Regatta Point (Hill & Macphail 1985).

Other species

There are only scattered and insubstantial records of other rainforest species, but some are worth noting. Seeds of *Drimys* (ex *Tasmannia*) *lanceolata* are very distinctive, and have been recovered from the Late Pliocene-Early Pleistocene Regatta Point deposit (Fig. 9). Similar seeds are found in the Oligocene Little Rapid River deposits, but they may reflect the presence of the genus or even the family (Winteraceae) rather than a particular species or evolutionary line.

Microstrobos niphophilus, which is usually regarded as a subalpine-alpine shrub, can occur in rainforest associations (Jarman & Brown 1983). Fossil leafy shoots which are very similar to this species have been recovered from the Oligocene Little Rapid River and Late Oligocene-Early Miocene Monpeelyata sediments (Wells & Hill 1989). The occurrence of the fossil species,

M.microfolius, at Little Rapid River is particularly interesting, since it not only represents the earliest record of the genus, but also places it in lowland vegetation which contained true rainforest trees, some with subtropical affinities. Thus it would appear that *Microstrobos* occurred over a much broader climatic range in the past, and has only recently become restricted to the cooler end of the climatic spectrum.

Many of the common rainforest understorey species, for example *Anopterus glandulosus*, *Cenarrhenes nitida*, *Anodopetalum biglandulosum*, have no fossil record at all prior to the Quaternary, and so their history is based entirely on inference.

Conclusion

In most cases Tasmanian rainforest tree species can clearly be demonstrated to be of great antiquity, and for *Nothofagus cunninghamii*, *Eucryphia lucida*, *Phyllocladus aspleniifolius* and *Athrotaxis selaginoides* the fossil record exceeds 40 million years. In some cases (most notably *N.cunninghamii*) evolution has taken place during that time, but it is relatively minor. Tasmania's rainforests therefore represent a living example of one of the most primitive vegetation formations on Earth, and those species which remain have demonstrated an extraordinary survival. Work is continuing on Tasmanian Tertiary fossil-bearing sediments, and new species are frequently encountered. It is likely that the next few years will see our understanding of the history of all Tasmania's rainforest species increase greatly.

Acknowledgements

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