Biogeography, evolution and palaeoecology of *Nothofagus* (Nothofagaceae): the contribution of the fossil record

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Abstract. *Nothofagus* is an ancient genus with a distribution that has attracted considerable interest from biogeographers. The lack of consensus among biogeographical reconstructions is probably due to emphasis being placed solely or largely on the living species. *Nothofagus* had a much greater distribution and diversity in the past than it has now; this makes it difficult to reconstruct its history from living species' interrelationships and distribution. Unfortunately, the fossil record is difficult to interpret, and contains many records that convey no useful information or possibly even misinformation. However, the best fossil records of *Nothofagus* provide past distributions that must be explained by biogeographical hypotheses and place minimum times on evolutionary events within the genus. They also provide information on past ecological associations that are best explained by invoking extinct climates.

Introduction

Van Steenis (1971) called *Nothofagus* a 'key genus' in the study of plant biogeography. Like many other researchers since, Van Steenis was drawn to *Nothofagus* as possibly providing a general explanation of Southern Hemisphere biogeography because it is usually a prominent tree, it grows on many of the southern landmasses, it has an excellent fossil record and it is not adapted for wind dispersal of fruits. However, almost 30 years after Van Steenis' conclusion, and following a great deal of research, there is still much debate about the history of *Nothofagus*. There are many reasons why *Nothofagus* is a difficult subject for biogeographic reconstruction, but probably the most important is also part of the reason so many people have been drawn to work on it—*Nothofagus* is an extremely ancient genus. The fossil record clearly demonstrates a Cretaceous origin for *Nothofagus*, and that it is now well past its maximum diversity and distribution. Analysis of a genus that is in decline, predominantly on the basis of information obtained from the living species, is unlikely to provide a convincing reconstruction of its history.

Paramount to biogeographic reconstruction is a comprehensive phylogenetic analysis of the taxon concerned. The fossil record can be important in phylogenetic reconstruction by placing minimum time limits on changes in character states. This can assist in biogeographic analysis as well, since such minimum times can be related to past continental histories. For example, a change in character state that took place before two continents rifted apart may place an important constraint on the history of the ancestral taxon involved.

The fossil record should be considered complementary to the neobotanical data base in a genus like *Nothofagus*, and theoretically it should help overcome the problems that the limited extant distribution and diversity may cause. However, there are complications with the fossil record that make this more difficult than it should be, and my purpose here is to use *Nothofagus* as an example to demonstrate the problems with the fossil record and also some of the possible advantages that it offers.

The data source

Nothofagus fossils, like those of any other taxon, are not uniformly informative. The fossil record of *Nothofagus* can be conveniently split into three—pollen, macrofossils without organic preservation, and macrofossils with organic preservation.

Pollen

Nothofagus pollen offers a particularly useful fossil data source. The pollen contains synapomorphies which allow unambiguous generic identification. Furthermore, *Nothofagus* pollen is wind-dispersed, is produced in vast amounts, and much of it has landed in sedimentary deposits where it fossilises well. Fossil *Nothofagus* pollen is assigned to the genus *Nothofagidites*, which was formalised by Potonié (1960) and seems to have come into general use, in Australia at least, following the revision by Stover and Evans

(1973). The continued use of this name is curious, since Dettmann *et al.* (1990) note that *Nothofagidites* 'has provided an important basis for elucidating the history of its parental source, *Nothofagus*'. Since the 'parental source' is so obvious, why not assign the pollen taxa to *Nothofagus* in order to avoid confusion?

The *Nothofagus* pollen record is important for three reasons.
(1) It is relatively extensive.
(2) It provides a general indication of past diversity.
(3) It provides broad times of arrival on different land masses and distribution patterns for the genus, the subgenera and species.
It is instructive to consider the evidence for each of these statements.

The extent of the Nothofagus *pollen record*

Darwin's (1859) eloquent argument regarding the incompleteness of the fossil record is known to everyone with an interest in evolution. Even today the incompleteness of the fossil record is often used as an argument against its utility. However, the reality is that there are many cases where the fossil record is extensive, and gaps in our knowledge are likely to be smaller than many presume. It is also disingenuous to criticise the fossil record without offering a similar criticism to our understanding of the living biota. Jones (1999), in his 'update' of Darwin's (1859) classic work, notes the following (p. 208): 'The smugness shown by students of living creatures when they decry the gaps in our knowledge of those long gone…skates over our ignorance of the modern world'.

This statement is especially true of *Nothofagus*. It is probable that the number of fossil pollen grains of *Nothofagus* that have been examined and recorded is orders of magnitude greater than the number of pollen grains of living *Nothofagus* species that have been examined (for example, M. K. Macphail (pers. comm.) estimates that between 500 000 and 50 000 000 palynomorphs have been examined from the Gippsland Basin alone, and a significant proportion of these are *Nothofagus*). If this is added to the widespread examination of sediment that has now taken place, the copious pollen production of *Nothofagus*, its wind pollination, and often excellent preservation, then it is possible to conclude that this fossil record is indeed very well known. However, there are still limitations. It is possible that sediments from some crucial locations (e.g. northern Australia and mainland Antarctica) will provide important new information on the history of *Nothofagus*. It is also probable that improved dating resolution will refine our understanding of the patterns observed among fossil *Nothofagus* pollen.

There are some things we will never know about *Nothofagus* from the fossil record, but there is much that we do know. *Nothofagus* pollen is so distinctive and common as a fossil that even its absence is important. For example, the absence of *Nothofagus* pollen from sediments in Africa and India is good evidence that this genus never occurred on those land masses. However, some researchers persist with the view that negative evidence in the fossil record has no value. For example, Linder and Crisp (1995), in discussing the possibility of long-distance dispersal of *Nothofagus* from Australia to New Zealand, note that Hill (1992) and Pole (1993*a*, 1994) 'rely on the absence of *Nothofagus* fossils from the Late Cretaceous and Early Tertiary from New Zealand as being strong evidence for the absence of the genus from the area prior to the postulated Tertiary colonisation'. This statement is inaccurate, since Hill (1992) never mentions this evidence, Pole (1993*a*) states that *Nothofagus* pollen is absent from one mid-Eocene location in New Zealand (Livingstone), but draws no conclusions from that, and Pole (1994) states that '*Nothofagus* pollen is absent in some Early Tertiary localities in New Zealand…The possibility that these absences represent a real, regional loss from New Zealand should be investigated'. Contrary to Linder and Crisp's (1995) statement, this is not a presentation of strong evidence. Linder and Crisp then note that 'We do not think that absence data in the fossil record are informative'. As a blanket statement this is untenable, but even in this example it is shortsighted. Most people accept the value of absence data in the fossil record, otherwise we would have little reason to accept the reality of mass extinctions as recorded by the lack of previously common fossil taxa after these events. The question is one of the degree of confidence we can have in a particular example of absence in the fossil record. If the evidence is strong enough, absence data are important, and at the very least can be a valid means of generating hypotheses that are open to testing, which is all that Pole (1994) was suggesting.

The past diversity of Nothofagus

The primary data source for examination of the past diversity of *Nothofagus* is the pollen record. However, this has many complexities and it must be considered carefully. In order to better interpret the fossil pollen record, we must first consider the pollen diversity of the extant *Nothofagus* species. The four extant subgenera of *Nothofagus* produce distinctive pollen. For many years this was recognised in three morphological groupings, informally designated as the *brassii*-, *fusca*- and *menziesii*-type pollen (Cranwell 1939; Cookson 1952; Cookson and Pike 1955). However, Dettmann *et al.* (1990) recognised that the *fusca*-type pollen contained two distinctive morphologies, which they designated *fusca*-type (a) and *fusca*-type (b). The resulting four pollen groups recognised by Dettmann *et al.* (1990) match the extant subgenera recognised by Hill and Read (1991), which have since been demonstrated to represent monophyletic groups (Hill and Jordan 1993; Manos 1997;

Jordan and Hill 1999), so that it is best to call them by their subgeneric names (*brassii*-type = subgenus *Brassospora*, *fusca*-type (a) = subgenus *Fuscospora*, *fusca*-type (b) = subgenus *Nothofagus*, *menziesii*-type = subgenus *Lophozonia*).

Prior to the recognition of the fourth pollen type, Hanks and Fairbrothers (1976) noted that although the pollen of extant *Nothofagus* species can be split into three morphological types, 'Species classified within one of the individual pollen types cannot be distinguished from others in the same pollen type when they are observed with the light microscope'. They included scanning electron microscopy (SEM) of pollen in their study of 30 extant species of *Nothofagus* (24 of which are still recognised). On the basis of their SEM results, they recognised seven groups, four among subgenus *Brassospora*, one in the subgenera *Fuscospora* and *Nothofagus* combined (since split into two by Dettmann *et al.* (1990)), and two in subgenus *Lophozonia*. Walker and Wittmann (1965) used light microscopy to examine 25 collections of subgenus *Brassospora* pollen, including 12 currently recognised species. They concluded that the species examined 'form a series, the quantifiable characteristics of individual members of which overlap with those of their neighbours.' They did recognise some morphological differences, but further concluded that 'a population of sub-fossil pollen grains could only tentatively be ascribed to a group of species or, better, excluded from identification with those species with which its characteristics did not overlap'. M. K. Macphail (pers. comm.) concludes that pollen of the extant species of subgenus *Brassospora* can be split into the following subclasses:

(1) Types resembling *Nothofagidites falcatus* (e.g. *Nothofagus aequilateralis*, some forms of *N. brassii*, *N. codonandra*, *N. discoidea*, *N. perryi* and *N. pullei*).
(2) Types loosely falling within the *Nothofagidites emarcidus–N. astrus–N. mataurensis* morphological range (most other extant species).
(3) Types which seem to display thickening around the colpi that is not dissimilar to that found in all *Fuscospora* species (e.g. *Nothofagus grandis*, *N. rubra*).
(4) *Nothofagus balansae* pollen has very long spinules that are similar in size to those of *Nothofagidites longispinosa*.

These data suggest that a maximum of six *Nothofagidites* species would be recorded among the extant *Brassospora* species, and that value will be used here. It is therefore possible to conclude that the extant *Nothofagus* species produce the equivalent of about nine fossil pollen species (one in each of *Fuscospora*, *Lophozonia* and *Nothofagus*, six in *Brassospora*).

This information can be placed into context with the fossil pollen record. McGlone *et al.* (1996) conclude that differentiation among pollen taxa within the four extant subgenera is marked in the fossil record. However, there is evidence that the pollen record contains even more diversity than this suggests. Dettmann *et al.* (1990) recognised the four extant subgenera among the fossil pollen taxa they examined, but they recognised other groupings as well. One of these is easy to recognise, since it was given a name that separates it from the extant subgenera—the 'ancestral' pollen type. Dettmann *et al.* (1990) recognised three fossil species in two different morphologies that they called ancestral. In retrospect, this is an unfortunate choice of name, since apart from the fact that they appear first in the fossil record there is no reason to assume that these pollen types are ancestral. However, two other pollen types are effectively hidden in the literature because of the names they were given—*brassii*-type (b) and *brassii*-type (c). Dettmann *et al.* (1990) recognised three different pollen morphologies that they called *brassii*-types. *Brassii*-type (a) contains 10 fossil species according to Dettmann *et al.* (1990). Furthermore, they state that this is also the type that is produced by all the living species in subgenus *Brassospora*, although the conclusions listed above for the morphology of the extant species in New Guinea suggest that this may need revision. That is, subgenus *Brassospora* as we know it today can only be linked to *brassii*-type (a) of Dettmann *et al.* (1990). The taxonomic relationships of *brassii*-type (b), with as many as seven fossil species, and *brassii*-type (c), with four fossil species, are, according to Dettmann *et al.* (1990), 'unknown, but there is little doubt that they are of *Nothofagus* affiliation'. Therefore, despite their names, and the fact that most palynologists tend to consider them as members of subgenus *Brassospora*, they may represent extinct subgenera. These pollen types occurred at very high palaeolatitudes, and there are many probable *Nothofagus* leaves in the fossil record that were winter deciduous (see later discussion of these impression fossils). Thus, there are strong ecological reasons to suspect that major *Nothofagus* lineages from this time and place may now be extinct.

Thus, on the basis of the fossil pollen data, 14 of the 38 fossil species (36 listed by Dettmann *et al.* (1990), plus two new *Nothofagidites* species in subgenus *Lophozonia* subsequently described by Zamaloa (1992) and Zamaloa and Barreda (1992)), or approximately 37%, may belong to extinct groupings at the level of subgenus. If we add to this the fact that the extant species, if considered only from the viewpoint of light microscopy of their pollen grains, are equivalent to nine 'species' (*c.* 24%), it is easy to see that most of the diversity of *Nothofagus* is in the past.

However, there are still two outstanding questions to consider:
(1) We know that there are about 35 extant species, even if they do provide only nine pollen morphologies recognised by light microscopy. Is it possible that recent

speciation has led to larger species numbers per pollen morphology now than in the past?

(2) There may have been a lot more *Nothofagus* species in the past than at present, but this represents about 80 million years of history. Was there ever a single time when there were more *Nothofagus* species than at present?

For three of the subgenera the first question can clearly be answered in the negative. Subgenus *Fuscospora* has five extant species—one in South America, one in Tasmania and three in New Zealand. While it is possible that the species number in New Zealand might have increased relatively recently, this could involve no more than two new species. The Tasmanian and South American species are phylogenetically and geographically remote and are likely to be ancient (there is macrofossil evidence of this for the Tasmanian species, *N. gunnii* (Hill 1991)). Subgenus *Lophozonia* has six extant species, three in South America, two in Australia and one in New Zealand. The three South American species are all winter deciduous, but not particularly morphologically similar (see Hill and Read 1991). The two Australian species have been linked through the macrofossil record (see Hill 1991), but there is a large gap between them both spatially and morphologically, and the fossil record suggests they have been separate entities for millions of years. Therefore, there is no evidence for unusually high species numbers in this subgenus today. Subgenus *Nothofagus* has five species in South America, two of which are winter deciduous. These deciduous species are very distinct morphologically and are highly unlikely to represent recent speciation. The three evergreen species are more similar morphologically, and it is possible that they represent recent speciation. However, the most likely place where recent speciation may be important is in subgenus *Brassospora*. The five species in New Caledonia have many similarities and could share a relatively recent common ancestor. There is currently no evidence regarding when that shared ancestry may have occurred. However, in New Guinea there are at least 14 species and obviously the possibility of recent speciation on a larger scale should be considered here. In a later section the argument is presented that much of the variation exhibited by the extant New Guinea species was in place by the Early Oligocene in Tasmania, which suggests that the species in New Guinea may not represent an unusual amount of recent speciation, but some doubt must remain. It should also be noted that these 14 extant species have been considered here to produce the equivalent of five fossil pollen species (the sixth is produced by the New Caledonian endemic *N. balansae*), so their diversity was not hidden in the earlier discussion.

The second question is best answered by two means—how many fossil species overlap stratigraphically, and how many are found within single fossil localities. On the basis of the pollen record, the most diverse time for *Nothofagus*

globally was the Oligocene–Early Miocene, and especially the Late Oligocene–Early Miocene. This was also the time of maximum spatial distribution of *Nothofagus*. According to the data presented by Dettmann *et al.* (1990), Zamaloa (1992) and Zamaloa and Barreda (1992), 17 fossil *Nothofagus* pollen species were present during the Late Oligocene. Given that the extant species can be represented by nine fossil species, this suggests that the Late Oligocene was a time of much greater diversity than today. A hidden aspect of diversity is the morphological range of pollen species. Palynology has several uses, and one of the most important of these is stratigraphy. When palynologists use pollen species to date sediments, they tend to develop a very broad interpretation of 'species', unless the morphotype is of stratigraphic value, since pollen stratigraphers are not often inclined to name new species. According to M. K. Macphail (pers. comm.) this is exactly what has happened with *Nothofagus*, and many of the fossil pollen species contain a very broad diversity of forms, and probably several biological species. Even if the fossil pollen species do not exceed the extant species in this regard, it is probable that the number of *Nothofagus* species present in the Late Oligocene was significantly in excess of extant species numbers. This is supported by McGlone *et al.* (1996), who estimate that during the Early Miocene New Zealand 'is likely to have contained tens of species, mainly in *Brassospora*'.

Individual sites in south-eastern Australia can also play a role in estimating species numbers. Three sites from the Late Oligocene–Early Miocene provide examples. Pioneer in north-eastern Tasmania has at least nine *Nothofagus* pollen species, Monpeelyata in central Tasmania has at least seven, and Kiandra in south-eastern New South Wales has at least nine (Table 1). Between them these sites provide a minimum of 10 fossil pollen species in all four extant subgenera, plus the *brassii*-types (b) and (c). This argues for a regional species diversity in the same order as that suggested for New Zealand in the Early Miocene. Only six of the 10 fossil pollen species found in south-eastern Australia are also found among the 11 Early Miocene species recorded from New Zealand (McGlone *et al.* 1996; Table 1), suggesting significant regional differences.

Therefore, although there are some aspects of the fossil pollen record that are still imperfectly understood, there is abundant evidence to suggest that *Nothofagus* was extremely diverse at times in the past, and that the number of species remaining today is small compared to the peak of diversity, possibly during Late Oligocene–Early Miocene time.

Times of arrival and distribution on different land masses

Although the four extant subgenera appear early and apparently unequivocally in the fossil record there are potential problems with this interpretation. Although some pollen taxa are placed in extinct 'ancestral' groups

Table 1. **Fossil *Nothofagus* pollen species identified from three Late Oligocene–Early Miocene sites in south-eastern Australia, and for the whole of New Zealand**
Data from Hill and Macphail (1983), Owen (1988), Macphail *et al.* (1991) and McGlone *et al.* (1996)

Nothofagidites species	Subgenus or pollen group	Kiandra[A]	Monpeelyata[A]	Pioneer	New Zealand
N. asperus	*Lophozonia*	+	+	+	+
N. brachyspinulosus	*Fuscospora*	+	+	+	
N. cranwelliae	*Brassospora*				+
N. deminutus	*brassii*-type (c)	+	+	+	+
N. emarcidus	*Brassospora*	+	+	+	+
N. falcatus	*Brassospora*	+	+	+	+
N. flemingii	*Nothofagus*	+	+	+	+
N. goniatus[B]	*Brassospora*	+		+	
N. heterus	*brassii*-type (b)	+	+	+	
N. incrassatus	*Fuscospora*	+			
N. lachlaniae[C]	*Nothofagus*				+
N. longispinosus	*brassii*-type (c)			+	
N. matauraensis	*Brassospora*				+
N. spinosus	*brassii*-type (c)				+
N. suggatei	*brassii*-type (b)				+
N. vansteenisii	*brassii*-type (c)	+	+		+

[A]*Nothofagites emarcidus* and *N. heterus* are grouped together as a single morphotype in these sites.
[B]Some researchers consider *N. goniatus* to be an unusual form of *Lophozonia* pollen (M. K. Macphail, pers. comm.).
[C]Hill and Truswell (1993) consider *N. lachlaniae* to be in subgenus *Fuscospora*.

(Dettmann *et al.* 1990), there is, as noted earlier, no compelling case to suggest that they are indeed ancestral to other *Nothofagus* taxa. It is possible that one of the extant subgenera bears the pollen type of the ancestor to all *Nothofagus* subgenera, and thus the appearance of this pollen type in the fossil record would not necessarily signal the appearance of the subgenus. Because of this, care is required in interpreting the pollen record. Nevertheless, it should not be ignored that the 'ancestral' pollen types appear significantly earlier in the pollen record (by several million years) than any of the extant subgeneric pollen types, and this fact adds weight to the argument that this may indeed be the pollen morphology of the ancestral *Nothofagus* complex.

The fossil pollen record does demonstrate conclusively that *Nothofagus* has been more widely distributed in the past than it is today. *Nothofagus* now occurs in spatially widespread localities, but even if we assume that there was once continuous distribution between these extant localities we fall well short of the past distribution of the genus. This is particularly apparent in Australia, where *Nothofagus* is now restricted in the south-east of the continent, and yet pollen (and macrofossil) evidence suggests it was widespread across the southern half at times during the Cainozoic. The other large land mass where *Nothofagus* was clearly widespread is Antarctica. Pollen and macrofossil

evidence suggest that the Antarctic Peninsula and at least parts of coastal East Antarctica supported complex *Nothofagus* forests during the Cainozoic. At the subgeneric level the evidence for a restricted extant distribution is compelling, particularly for subgenera *Brassospora* and *Nothofagus*, which are relatively restricted today, but were widespread across South America, Antarctica, Australia and New Zealand during the mid–Late Eocene (Dettmann *et al.* 1990).

At a higher taxonomic resolution, *Nothofagus* pollen data compiled by M. K. Macphail (see Hill *et al.* 1996*b*) show the time of first appearance of several fossil species across all extant subgenera in Australia and New Zealand (Table 2). The only common pattern in the list is that all species appear first in Australia, and later in New Zealand, in all cases well after New Zealand was an isolated land mass. Such data have been used to support the hypothesis that several species of *Nothofagus* arrived in New Zealand from Australia by long-distance dispersal, along with many other taxa (Hill *et al.* 1996*b*; Macphail 1997). However, some caution is required with this conslusion, since, as noted earlier, each of these fossil pollen species probably represents more than one biological species, and more convincing evidence is required to support the hypothesis that these fossil occurrences are of the same biological species.

Table 2. A comparison of first appearances of fossil *Nothofagus* pollen species common to south-eastern Australia and New Zealand
Adapted from Macphail *et al.* (1994)

Subgenus or pollen group	*Nothofagidites* species	First appearance in Australia	First appearance in New Zealand
Lophozonia	N. asperus	Palaeocene	Late Eocene
Fuscospora	N. brachyspinulosus	Maastrichtian	Palaeocene
brassii-type (c)	N. deminutus-vansteenisii	Early Eocene	Middle Eocene
Brassospora	N. falcatus	Middle Eocene	Oligocene
Nothofagus	N. flemingii	Campanian	Middle Eocene
brassii-type (c)	N. longispinosus	Middle Eocene	Pliocene

Macrofossils without organic preservation

The majority of described *Nothofagus* macrofossils are leaves without organic preservation (impression fossils). The major problem with such fossils is that it is very difficult to justify that they are *Nothofagus* at all. In some instances, comparison is made at the species level, and effectively identification is made by use of autapomorphies (Table 3). In such cases the identification process is first made at the species level and then at the generic level by default. While this is an unusual process, it is probably effective and such records can be considered to have validity as long as the process is properly justified.

However, when the leaves are not particularly similar to any one extant species but simply have a broad resemblance to *Nothofagus*, the identification of the leaves to genus has

little validity. This problem has been handled in a variety of ways. For example, Campbell (1985) erected the genus *Nothofagaphyllites* for fossil leaves in New Zealand. He noted that 'the use of the generic name *Nothofagus* for the fossils carries the implication that a separation from *Fagus* has been made. This has not been satisfactorily done…'. Other form genera have also been erected to deal with this problem, but in effect it does little more than provide a name for the fossil taxon and no clear idea of its affinities. Pole (1993*b*) approached this problem by the use of 'if-then' production rules to place fossil taxa within *Nothofagus*. However, there is no evidence that any of the characters used in his 'if' combinations represent synapomorphies for *Nothofagus*, and given that the last is 'leaves are associated with *Nothofagus* pollen' then any identification based on these criteria must be considered to involve circularity and must always be discussed exclusive of the pollen data.

Essentially, from the point of view of biogeography and evolution, impression fossils of *Nothofagus* are not a reliable data source unless they are identified through autapomorphies with extant species. Thus, at present the majority of the published *Nothofagus* macrofossil record can be disregarded.

Macrofossils with organic preservation

Described macrofossils with organic preservation include leaves, cupules and wood. In many cases preservation is good enough to provide synapomorphies for *Nothofagus* and so identification at the generic level can be confirmed. However, organic preservation does not ensure this, since the quality varies, and each fossil record must be assessed on its

Table 3. Fossil *Nothofagus* species based on organically preserved leaves or leaves that share autapomorphies with extant *Nothofagus* species
The species listed here can be placed in extant subgenera with relative confidence, except for *N. microphylla*. Quaternary records of extant species are excluded. *Nothofagus beardmorensis* is not included because of doubts about its subgeneric placement and *N. ninnisiana* from New Zealand is not included because Pole (1993*b*) expressed doubts about whether the illustrated cuticle in Kovar *et al.* (1987) came from the same species as the lectotype

Nothofagus species	Subgenus	Age	Location	Source
N. cethanica[A]	*Fuscospora*	Early Oligocene	Tasmania	Hill (1984)
N. gunnii[A]	*Fuscospora*	Oligocene	Tasmania, Antarctica	Hill (1984, 1991)
N. lobata	*Nothofagus*	Early Oligocene	Tasmania	Hill (1991)
N. maidenii	*Lophozonia*	Late Oligocene – Early Miocene	Tasmania, Victoria	Pole *et al.* (1993)
N. microphylla	*Nothofagus?*	Late Oligocene – Early Miocene	Tasmania	Scriven and Hill (1996)
N. mucronata	*Brassospora*	Early Oligocene	Tasmania	Hill (1991)
N. muelleri	*Lophozonia*	Late Eocene	New South Wales	Hill (1988)
N. novaezealandiae	*Lophozonia*	mid–Late Miocene	New Zealand	Pole (1993*b*)
N. pachyphylla	*Lophozonia*	Early Pleistocene	Tasmania	Jordan (1999)
N. serrata	*Brassospora*	Early Oligocene	Tasmania	Hill (1991)
N. tasmanica	*Lophozonia*	Eocene–Early Oligocene	Tasmania, south-western Australia	Hill (1991), Hill and Merrifield 1993, Carpenter and Pole (1995)

[A]Leaves share autpomorphies with extant *Nothofagus* species.

Table 4. Fossil *Nothofagus* species from Tasmania based on organically preserved cupules

Nothofagus species	Subgenus	Age	Source
N. balfourensis	*Brassospora*	Late Oligocene–Early Miocene	Hill (2001)
N. bulbosa	*Nothofagus*	Early Oligocene–Early Miocene	Hill (1991, 2001)
N. cooksoniae	*Brassospora*	Early Oligocene	Hill (1991)
N. glandularis	*Lophozonia*	Early Oligocene–Early Pleistocene	Hill (1991, 2001), Jordan (1999)
N. peduncularis	*Brassospora*	Early Oligocene–Early Miocene	Hill (1991, 2001)
N. robustus	*Brassospora*	Late Oligocene–Early Miocene	Hill (2001)
N. smithtonensis	*Brassospora*	Early Oligocene	Hill (1994)

merits. There are isolated records of *Nothofagus* wood, but these fossils are in need of revision and it is difficult to assess their value at present. They do not constitute a major data source. One example of fossil *Nothofagus* wood will be mentioned later, where it occurs in conjunction with other *Nothofagus* macrofossils in Antarctica.

Leaf macrofossils with organic preservation are relatively rare outside of Tasmania, with none reported from South America, only one species from Antarctica, one from New Zealand that can be considered reliable, two from mainland south-eastern Australia, and one from south-western Australia. In contrast, the Tasmanian fossil leaf record is diverse and very well preserved, often allowing identification to the subgeneric level at least (Table 3). Fossil cupules are much less common than leaves, and only the Tasmanian fossil record contains described species of organically preserved cupules (Table 4).

Many of the organically preserved leaves and cupules can be identified to subgenera relatively easily, but there are two interesting exceptions that demonstrate the difficulties involved in making these identifications with fossils. The first is *Nothofagus microphylla*, based on leaves from Late Oligocene–Early Miocene sediments in Tasmania. This species was placed in subgenus *Nothofagus* by Scriven and Hill (1996), but a cladistic analysis by Jordan and Hill (1999) placed the species as basal to the evergreen members of subgenus *Lophozonia*. However, this placement is only weakly supported, and alternatives are in more basal positions or in subgenus *Nothofagus*. Because the support for the subgeneric placement of *N. microphylla* in Jordan and Hill's (1999) analysis is relatively weak, it is probably best treated as ambiguous.

The second exception consists of not only leaves, but also wood and pollen from the probable late Pliocene Sirius Group at Oliver Bluffs in the Dominion Range, Transantarctic Mountains. The woody material, consisting of krummholz-like stems and branching twigs, was identified as *Nothofagus* by Carlquist (1987). Francis and Hill (1996) noted highly asymmetrical growth, abrasion scars on the stems and small stem diameters that all suggest a prostrate growth habit, with no main vertical stem. They suggested that the modern Arctic dwarf willow (*Salix arctica*) offered a good analogue to the growth habit of the fossil *Nothofagus*. Carlquist (1987) considered the anatomy of this wood to closely match that of the present day Chilean-Argentinean-Fuegian *Nothofagus betuloides* (subgenus *Nothofagus*) and the Tasmanian alpine *Nothofagus gunnii* (subgenus *Fuscospora*).

Nothofagus pollen was first reported from these sediments by Askin and Markgraf (1986), and they assigned them to the *fusca*-type, which encompasses the two extant subgenera *Fuscospora* and *Nothofagus*. They concluded that these *Nothofagus* pollen grains were probably recycled from older Tertiary deposits where such forms are abundant. The later discovery of *Nothofagus* wood and leaves in the sediments refocused attention on the origin of the pollen grains and particularly the question of reworking. Hill and Truswell (1993) noted the dominance of *Nothofagus* pollen (assigned to *Nothofagidites*), and concluded that this was consistent with an *in situ* *Nothofagus*-dominated vegetation. All the *Nothofagidites* grains they observed represented a single morphotype, which conformed to that illustrated by Askin and Markgraf (1986). Most of the grains are thin-walled, and while Askin and Markgraf (1986) had interpreted this as being the result of corrosion, Hill and Truswell (1993) offered the countersuggestion that this was at least in part the primary condition. They further concluded that the grains most closely resemble *N. lachlaniae*, which was originally described from an Early Pleistocene sample from New Zealand. This species has been widely reported from Antarctica, extending back possibly to the middle Eocene (Mohr 1990). Dettmann *et al.* (1990) assigned *Nothofagidites lachlaniae* to subgenus *Nothofagus* (their *fusca*-type (b)), but Hill and Truswell (1993) noted that for this species the distinction between the *fusca*-type (a) and type (b) pollen groups is not clear-cut, because of ambiguity in the nature of the pollen grain wall and also because of deterioration of the holotype. This led Dettmann *et al.* (1990) to select a topotype. According to Hill and Truswell (1993), this topotype appears to possess colpi that are more distinctly collared and generally more robustly thickened than the holotype, and may represent a move away from the original morphological concept. They concluded that the

Oliver Bluffs specimens were more consistent with pollen produced by extant species in subgenus *Fuscospora* (*fusca*-type (a) of Dettmann *et al.* (1990)). They compared the fossil pollen most directly with the extant *N. gunnii*, a Tasmanian winter-deciduous endemic, but noted some morphological differences.

The most striking plant material consists of dense leaf litter mats of *Nothofagus* in the fluvial sandstones. The best-preserved material is found where leaf litter mats are compressed against the undersides of boulders (usually Jurassic intrusive dolerite), although single leaves also survive on the bedding planes of fluvial sandstones and siltstones. The leaves also represent a single morphotype, and it is thus reasonable to assume that the wood, pollen and leaves of *Nothofagus* recovered from these sediments all belong to the same species. The leaves were assigned to the new species *Nothofagus beardmorensis* by Hill *et al.* (1996*a*). The plicate vernation of the fossil leaves and the presence of dense leaf mats led them to conclude that *N. beardmorensis* was winter deciduous.

Despite the organic preservation of the leaves, the quality of preservation does not allow synapomorphies for *Nothofagus* to be observed (Hill *et al.* 1996*a*). However, all the characters available for the leaves are consistent with *Nothofagus*, and these are much more detailed than have been used in many other cases to justify an affinity with the genus. That, in conjunction with the strong circumstantial evidence provided by the close association with *Nothofagus* wood and pollen, was used to justify assignment of the fossils to that genus.

At least two species of extant deciduous *Nothofagus*, *N. alessandri* and *N. obliqua*, have a leaf size, shape, margin and venation pattern that is similar to the fossils. The fossil leaves are clearly distinct from both of these extant species in the form and number of serrations, and can thus be recognised as a distinct species. *Nothofagus alessandri* and *N. obliqua* are in different subgenera (*Fuscospora* and *Lophozonia*, respectively), and thus doubt remains about the subgeneric identity of *N. beardmorensis*. As noted earlier, the fossil wood and pollen also have uncertain subgeneric affinities, with both *Nothofagus* and *Fuscospora* being options.

The presence of this species in Antarctica in the Pliocene suggests a much different climate than at present. No extant *Nothofagus* species can survive temperatures below about –22°C in winter, and temperatures must have been substantially above 0°C for a relatively long period during the growing period for the growth and reproductive effort observed. This would require a shift of at least +13°C from present conditions (Francis and Hill 1996). It is likely that *N. beardmorensis* was growing under conditions at one extreme of the limits of *Nothofagus* survival, and consequently it may have had some unusual morphological responses that also make subgeneric classification difficult.

Past distribution of Nothofagus *macrofossils*

A very positive feature of the *Nothofagus* fossil record is that its pollen can be used to give a precise indication of the past distribution of the genus and, with less certainty, the subgenera (see Hill and Dettmann 1996 for a summary). The pollen record was discussed earlier, and the intention here is to demonstrate how the macrofossil record also provides evidence of past distributions.

The Tasmanian macrofossil record provides unequivocal evidence of two subgenera that no longer occur there— *Brassospora* and *Nothofagus*. Subgenus *Brassospora* has been recorded as leaves and cupules from three Early Oligocene localities (Little Rapid River, Cethana and Lea River) and one Oligocene–Early Miocene locality (Balfour, Hill 2001) (Tables 3, 4). The best data are from Little Rapid River, where two species have been described from leaves and three species from cupules (Hill 1991, 1994), and Balfour, where three species have been described on the basis of cupules, one of which is shared with Little Rapid River (Hill 2001). These fossils are closely related to extant species in New Guinea (see later). Subgenus *Nothofagus* is represented by leaves and cupules at two Early Oligocene localities, Little Rapid River (Hill 1991) and Lea River (Scriven and Hill 1996) and by cupules at the Late Oligocene–Early Miocene Balfour site (Hill 2001). It is also possible that leaves assigned to *N. microphylla* from the Late Oligocene–Early Miocene Monpeelyata sediments belong to this subgenus, but that is open to some doubt (see earlier discussion). The leaves and cupules that co-occur at Little Rapid River and Lea River probably belong to the same species, but have been described as two different species because they are not organically connected (Hill 1991).

Such fossil data provide records in time and space that must be accounted for in any biogeographic reconstructions of the genus. This is particularly critical, since both subgenera are now restricted to only a small part of the range of the whole genus (*Brassospora* to New Caledonia and New Guinea, *Nothofagus* to South America).

Evolution within *Nothofagus*

The four extant subgenera of *Nothofagus* are distinct morphologically, to the extent that a strong case could be made to elevate them to generic level. Furthermore, the available fossil evidence suggests that these subgenera have been distinct entities for many tens of millions of years (Hill and Dettmann 1996). Therefore, at some early stage in the evolutionary history of *Nothofagus* there must have been major radiations to produce these differences. However, all the fossil evidence suggests that since the subgenera appeared, evolutionary change within *Nothofagus* has been slow. Some ancient fossil remains have been assigned to extant species, for example leaves of *N. gunnii* from Early

Oligocene sediments in Tasmania (Hill 1984), and many others have been closely compared to extant species (e.g. Hill 1991).

However, this does not mean that evolutionary change in *Nothofagus* has not been detected in the fossil record. The best documented example is the reduction in leaf size during the Cainozoic in subgenus *Lophozonia* in Tasmania (Hill 1983, 1991; Scriven and Hill 1996). There is also evidence for a decline in leaf size in Tasmania in subgenus *Nothofagus* prior to its extinction there (Scriven and Hill 1996).

The fossil record not only has the capacity to demonstrate evolution, but perhaps more critically it can offer evidence of the minimum time in the past for evolutionary events to have taken place. A good example of this occurs within subgenus *Brassospora*. The macrofossil record of this subgenus is so far restricted to Tasmania, whereas the extant species are restricted to New Caledonia (five species) and New Guinea (14 species). The macrofossils provide evidence of both leaf and cupule morphology. Two fossil species have been described from fossil leaves, both from the Early Oligocene sediments at Little Rapid River. Both species are serrate margined, a condition that also occurs among the extant species, but is relatively uncommon. More critically, one species has a very waxy leaf surface and the other has a moderately waxy surface (Hill 1991). This is only observed in two extant *Nothofagus* species, *N. resinosa* and *N. pseudoresinosa* (both subgenus *Brassospora* in New Guinea). In fact Hill (1991) notes that one of the fossil species, *N. mucronata*, is 'very similar to some leaves of *N. pseudoresinosa* in most aspects'. Not only are these fossil leaves clearly members of subgenus *Brassospora*, but they share at least one synapomorphy (waxy leaves) with two of the 14 extant species in New Guinea.

Fossil cupules of subgenus *Brassospora* are more common and diverse in Tasmania than leaves. Three species have been described from Little Rapid River, and three from the Oligocene–Early Miocene Balfour sediments (one of which is among the Little Rapid River species) (Hill 2001). Among the extant species of subgenus *Brassospora*, cupules vary from massive and woody (all New Caledonian and some New Guinea species, Figs 1, 2), through to membranous, and in many species they are reduced in size (Figs 3, 4), and in some they are absent altogether. This variability in cupule size and woodiness occurs only in New Guinea, and in the absence of a fossil record it would be easy to hypothesise that this variability evolved after the subgenus reached New Guinea. However, the five fossil species based on cupules from the Oligocene–Early Miocene in Tasmania also vary considerably in their size and woodiness. *Nothofagus peduncularis* (Fig. 5) has the largest cupules, but the valves are very thin and almost membranous, and are usually preserved closely appressed to one another. *Nothofagus cooksoniae* cupules are very small compared with most extant species, but the valves are woody and

usually preserved in a gaping position (Fig. 6). The cupules from Balfour include *N. peduncularis*, and also *N. balfourensis*, which has gaping cupule valves that are free to the base, and *N. robustus*, which has woody cupule valves that are fused for most of their length. None of these species has been preserved with fruits present. However, *Nothofagus smithtonensis* (Hill 1994, Fig. 7) from Little Rapid River is quite distinct. The two valves of the cupule are small and membranous, and the enclosed fruit, which is well preserved, clearly exserts beyond the cupule valves. No fossil cupules have been found that are more reduced than *N. smithtonensis*, but they would be difficult to recognise, especially if the fruit was not present. It is possible that *N. smithtonensis* represents an immature specimen, although the chances of preservation of such a specimen are remote. The other feature that *N. smithtonensis* demonstrates unequivocally is the reduction in fruit number from three to one. A few of the extant New Guinea species and all of the New Caledonian species have three fruits per cupule, whereas most of the New Guinea species have only one fruit per cupule (these were recognised as series *Triflorae* and *Uniflorae* by Van Steenis (1953)). Given that three fruits per cupule is common throughout the rest of the genus, it is likely that one fruit per cupule represents a synapomorphy among those species of subgenus *Brassospora* in New Guinea that possess this character. The presence of one fruit per cupule in the Tasmanian fossil species *N. smithtonensis* also suggests monophyly with these New Guinea species and another aspect of morphological reduction that had occurred in the subgenus a long way from New Guinea.

The fossil cupules discovered in Tasmania cover a reasonable proportion of the variability exhibited by the extant New Guinea species, and are much more morphologically variable than the extant New Caledonian species. In fact, they are more similar to the derived forms of cupules found in New Guinea, providing evidence that a great deal of the variability in cupule morphology that today is unique to the New Guinea species was in place when the subgenus occurred at much higher latitudes in the Early Oligocene. From an evolutionary perspective, the fossil record demonstrates that there is no reason to expect that this variability evolved after the subgenus arrived in New Guinea, and the high species diversity there today may have an ancient and distant origin. This is supported by the relatively high diversity exhibited by fossil pollen of subgenus *Brassospora*.

Palaeoecology

Because *Nothofagus* pollen is so widely wind-dispersed, it is difficult to use this data source to reconstruct possible species co-occurrences within local vegetation. However, the macrofossil record does not suffer from this problem, since it is likely that most *Nothofagus* macrofossils are deposited very close to their source plants. In Tasmania in particular,
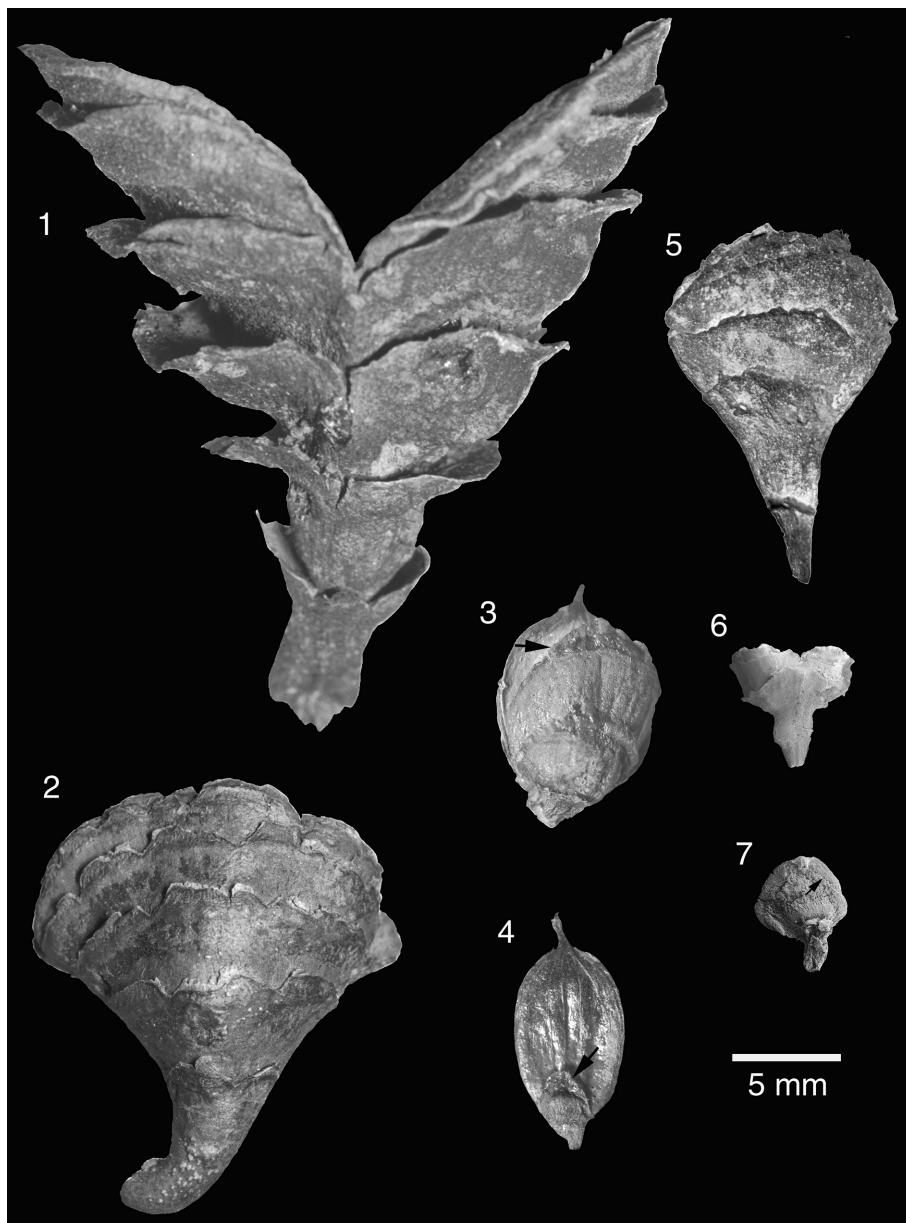
Figs 1–7. *Nothofagus* cupules. **Fig. 1.** Light micrograph of a cupule of *N. codonandra* from New Caledonia. Note the massive, woody and gaping cupule valves. The fruits are absent. **Fig. 2.** Light micrograph of a cupule of *N. brassii* from New Guinea. Only one of the valves is shown. The fruits are absent. **Fig. 3.** Light micrograph of a cupule of *N. rubra* from New Guinea. One valve is shown and the fruit is present, with part of the fruit and the style clearly visible above the cupule valve (margin arrowed). **Fig. 4.** Light micrograph of a cupule of *N. pullei* from New Guinea. The single cupule valve visible is a small, membranous scale (margin arrowed) and the fruit is much larger and emergent from it. **Fig. 5.** Light micrograph of a cupule of *N. peduncularis* from the Early Oligocene of Tasmania. Only one cupule valve is shown. The fruits are absent. **Fig. 6.** Scanning electron micrograph of a cupule of *N. cooksoniae* from the Early Oligocene of Tasmania. Note the gaping cupule valves. The fruits are absent. **Fig. 7.** Scanning electron micrograph of a cupule of *N. smithtonensis* from the Early Oligocene of Tasmania. The single cupule valve visible (margin arrowed) is membranous and smaller than the fruit, which can be seen with the style partially present but folded over.

this demonstrates species associations in the palaeovegetation that are remarkably different from anything that occurs today in *Nothofagus*. The exceptional preservation of many of the macrofossils in Tasmania has made it possible to demonstrate that at least six species of *Nothofagus* co-existed within small patches of forest in the Oligocene–Early Miocene, and all four extant subgenera were present. While subgenera *Fuscospora* and *Lophozonia*

both occur in Australia, New Zealand and South America today, the restriction of *Brassospora* to New Caledonia and New Guinea and *Nothofagus* to South America makes such a close co-occurrence in the past unexpected. Some of the fossil species of *Nothofagus* involved are similar enough in morphology to some extant species to suggest that they are likely to have had a similar physiology. This is a reasonable hypothesis, given that fossil leaves are well preserved and have been compared in detail with extant species. Leaves are likely to be very sensitive to climate and the similarity of the fossil leaves to some extant species has been used to justify physiological experiments on extant species with the aim of providing data to test hypotheses concerning these past subgeneric co-occurrences (Read *et al.* 1990).

Read *et al.* (1990) concluded that increasing seasonal and daily variability of temperature and rainfall, together with a shift towards a winter-dominated rainfall in south-eastern Australia during the Cainozoic, were major influences on distributional change during this period. The extremely wet and mild climate of the Oligocene–Early Miocene allowed ecological associations that are no longer possible, since the prevailing Tasmanian climate of that time no longer exists. There is still much to learn about past vegetation associations, but it is clear that the climates we now experience do not cover all the possibilities, and extinct climates may have allowed quite different ecological associations.

Discussion

Nothofagus remains a key genus to our understanding of the history of the biota of Gondwana, but a note of caution must be added. The fossil record clearly demonstrates that *Nothofagus* is an ancient genus that is well past its peak of diversity and distribution. These fossil data have been available for a long time, but they have been difficult to interpret correctly for the following reasons.

(1) Too many macrofossil species have been described on the basis of inadequate material. For researchers wishing to access the useful fossil record this makes the task very difficult. The Tasmanian macrofossil record is usually an exception to this because, for reasons that are unknown, the macrofossils there have particularly good organic preservation, allowing detailed descriptions, and usually confident assignment to subgenera and species.

(2) The fossil pollen record has developed unfortunate terminology that makes it difficult to determine how many major groupings are present. It is likely that as well as the four extant subgenera, up to four other major groups (possibly equivalent to subgenera) were present but are now extinct. Two of these are listed as 'ancestral' and the other two as *brassii*-type (b) and *brassii*-type (c) (Dettmann *et al.* 1990).

(3) Because the emphasis in the fossil pollen record has been on stratigraphy, many fossil pollen species remain undescribed, and are grouped within large morphological groups that are given species names. Therefore much of the diversity in the fossil pollen record is hidden in the literature.

However, the pollen record of *Nothofagus* is so well documented that even its absence can be informative. For example the lack of a fossil record of *Nothofagus* in Africa and India continues to provide strong support for the hypothesis that the genus never was in those places. Less clear-cut absence data, such as a possible Palaeogene gap in New Zealand, must be treated with more care, but can still be the basis of legitimate hypothesis generation.

The *Nothofagus* fossil record continues to expand, but it is important that identifications be made with much greater scientific rigour. Recent findings have provided supporting evidence for hypotheses generated from previous fossil finds, but no doubt we still have much to learn from the fossil record. While macrofossil finds are relatively rare, the pollen record is extensive. It should be a matter of priority to refine the pollen record, so that much of the information that is currently only known to specialists is made available to the general scientific community so that it can be properly incorporated in our study of this important Southern Hemisphere genus.

Acknowledgments

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