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Panbiogeography of *Nothofagus* (Nothofagaceae): analysis of the main species massings

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ABSTRACT

Aim The aim of this paper is to analyse the biogeography of *Nothofagus* and its subgenera in the light of molecular phylogenies and revisions of fossil taxa.

Location Cooler parts of the South Pacific: Australia, Tasmania, New Zealand, montane New Guinea and New Caledonia, and southern South America.

Methods Panbiogeographical analysis is used. This involves comparative study of the geographic distributions of the *Nothofagus* taxa and other organisms in the region, and correlation of the main patterns with historical geology.

Results The four subgenera of *Nothofagus* have their main massings of extant species in the same localities as the main massings of all (fossil plus extant) species. These main massings are vicariant, with subgen. *Lophozonia* most diverse in southern South America (north of Chiloé I.), subgen. *Fuscospora* in New Zealand, subgen. *Nothofagus* in southern South America (south of Valdivia), and subgen. *Brassospora* in New Guinea and New Caledonia. The main massings of subgen. *Brassospora* and of the clade subgen. *Brassospora*/subgen. *Nothofagus* (New Guinea–New Caledonia–southern South America) conform to standard biogeographical patterns.

Main conclusions The vicariant main massings of the four subgenera are compatible with largely allopatric differentiation and no substantial dispersal since at least the Upper Cretaceous (Upper Campanian), by which time the fossil record shows that the four subgenera had evolved. The New Guinea–New Caledonia distribution of subgenus *Brassospora* is equivalent to its total main massing through geological time and is explained by different respective relationships of different component terranes of the two countries. Global vicariance at family level suggests that Nothofagaceae/*Nothofagus* evolved largely as the South Pacific/Antarctic vicariant in the breakup of a world-wide Fagales ancestor.

Keywords

Brassospora, dispersal, fossils, main massing, *Nothofagus*, Pacific, panbiogeography, rain forest, terrane, vicariance.

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INTRODUCTION

The 35 extant species of southern beeches (*Nothofagus*, the only genus in Nothofagaceae) are found in cooler rain forests of the South Pacific. They occur in south-east Australia, Tasmania, New Zealand, montane New Guinea and New Caledonia, and southern South America (Fig. 1). They are usually large trees (most New Guinea species are 45–50 m tall; van Steenis, 1972), often dominant or co-dominant, and are well known to foresters and ecologists.

Because of its disjunct distribution, *Nothofagus* is also of special interest to biogeographers. The South Pacific disjunction has intrigued biologists for over a century, and *Nothofagus* is perhaps the best-known example. The nuts appear to have limited powers of movement and have generally been assumed to be incapable of trans-oceanic dispersal. The trees produce abundant pollen that is found as fossil material in many strata. Fossil wood fragments, leaves and cupules identifiable to subgenus are also known but are much less common.

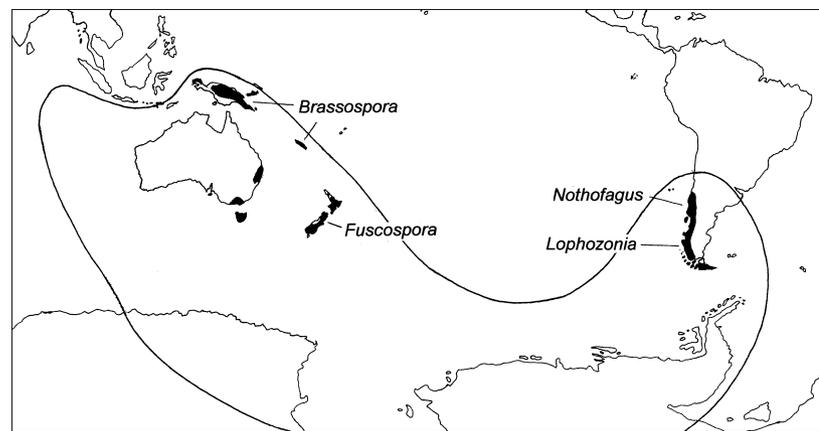


Figure 1 Distribution of *Nothofagus*: fossils (continuous line, including the Ninety East Ridge and Antarctica), extant distribution (solid black), and main massings (extant and fossil plus extant) of the four extant subgenera.

The large size of the trees and their abundance, the disjunct distribution, the limited means of dispersal, and the extensive fossil record have meant that *Nothofagus* has become a classic biogeographical study group. The diverse Mesozoic fossil record and the lack of any obvious means of trans-oceanic dispersal have led many authors to infer a vicariance explanation for the distribution. However, the extant and fossil species of the four extant subgenera do not group neatly into four geographic regions; instead there is considerable overlap. All four subgenera are recorded, either extant or fossil, in Australia, Tasmania, New Zealand, South America and Antarctica (Table 1). There is also no clear congruence between species cladograms and the breakup sequence of Gondwana, and so a simple vicariance model has been rejected by some workers. Thus discussion on the biogeography of the genus has developed into the usual vicariance vs. dispersal debate, and shows little sign of resolution.

This paper takes a new approach to the distribution and evolution of the group by focusing on the locations of the main massings or geographic concentrations of the species, both extant and fossil, in each subgenus. These data have probably been overlooked because palaeobotanists working on the group have shown little interest in the geographic range of the fossil species (the latest full revision of these, Dettmann *et al.*, 1990, cites localities of types only), and the information is widely scattered in the literature.

The analysis of 'main massings' is a key component of panbiogeographical methodology (Craw *et al.*, 1999, pp. 19–22). However, main massings have little significance in cladistic biogeography since the components of a massing,

while related spatially, do not necessarily form a monophyletic group. The plant family Ericaceae provides a classic example of a group in which the main massings of the main clades are vicariant, with a famous massing of ericoids in South Africa, rhododendroids in Southeast Asia, vaccinioids/gaultherioids in the Pacific and the Americas, and epacrids in the South Pacific (Heads, 2003).

DATING NOTHOFAGUS AND ITS SUBGENERA

The idea that "pollen evidence argues for evolution of *Nothofagus* during the early Campanian" (Upper Cretaceous) (Hill & Dettmann, 1996), simply because the oldest known pollen is early Campanian, is not convincing. In another literal interpretation of the fossil record, Dettmann *et al.* (1990) termed two kinds of fossil pollen "ancestral type (a) and (b)", but Hill (2001) made the important point that, "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 these pollen types are ancestral" (Hill, 2001, p. 323). However, while the details of the fossil record cannot be read literally, broader trends are significant (see Heads, 2005a). For example, the total absence of fossil *Nothofagus* material from India, Madagascar and Africa probably does indicate historical absence from these areas.

Differentiation in *Nothofagus* is often attributed to the breakup of Gondwana, but this was possibly too late to have been involved in the evolution of the extant subgenera. All four extant subgenera have a fossil record in the Upper Cretaceous, which gives a minimum age for them. The Tasman Sea started

Table 1 Extant and fossil distributions of the extant subgenera of *Nothofagus*

Subgenus	Number of extant species and distribution	Extralimital fossil distribution	Main massing of extant species, and fossil plus extant species
<i>Lophozonia</i>	6; Australia, NZ, South America	Tasmania, Antarctica	Southern South America (south of Valdivia)
<i>Fuscospora</i>	5–6; Tasmania, NZ, South America	Australia, Antarctica	New Zealand
<i>Nothofagus</i>	5; South America	Australia, Tasmania, NZ, Antarctica	Southern South America (north of Chiloé I.)
<i>Brassospora</i>	19; New Guinea, New Caledonia	Australia, Tasmania, NZ,	New Guinea, New South America, Antarctica Caledonia

opening about this time, and so may or may not have been involved in the differentiation of the subgenera. The separation of Australia and South America from Antarctica occurred in the Eocene and so was not involved. Swenson *et al.* (2001b) accepted that the four extant subgenera had evolved prior to the breakup of east Gondwana.

Recently, Knapp *et al.* (2005) calibrated a relaxed molecular clock for 12 *Nothofagus* species (none from subgen. *Brassospora*) using fossil ages, i.e. *minimum* ages, but then, based on these calibrations, inferred *maximum* ages for clades and used this “unequivocal molecular clock evidence” to rule out earlier vicariance (Knapp *et al.*, 2005, p. 1). This procedure is currently widely used (cf. Cook & Crisp, 2005) but is obviously logically flawed (Heads, 2005b,c).

DISTRIBUTION OF NOTHOFAGUS SUBGEN. BRASSOSPORA

Subgen. *Brassospora* has 19 species and is by far the largest of the four *Nothofagus* subgenera. It occurs in New Guinea (14 species) and New Caledonia (five species) and is the only subgenus present on these islands. Fossil pollen that can be identified with subgen. *Brassospora* is known from throughout the extant range of the genus, as well as in north-east Australia and Antarctica. This pollen occurs in Australia and Antarctica from the Upper Cretaceous and in New Zealand from the Eocene, but in New Guinea it appears only in the Miocene and in New Caledonia only in the Quaternary. According to Swenson *et al.* (2001a, p. 30) this is a sequence “suggesting... a late colonization” of the last two areas, but Linder & Crisp (1995) did not accept the absence of earlier fossils as meaningful in this case, which seems a safer conclusion, especially for New Caledonia.

The New Guinea species of subgen. *Brassospora* mass on the eastern half of the island, Papua New Guinea (PNG) (Heads, 2001a), which is a typical pattern for Australasian–Pacific groups (Heads, 2003). Two species are also present on nearby New Britain, and two on the D’Entrecasteaux Archipelago. In New Caledonia, all five species occur on the southern ultramafic massifs; two are endemic there and three extend two-thirds of the way to the northern end of the island (maps in Read & Hope, 1996). The genus is not known from the Solomon Islands or Vanuatu.

Although a New Guinea–New Caledonia distribution pattern is seen in many groups (Appendix 1), Swenson *et al.* (2001a) referred to the extant range of *Brassospora* as ‘curious’, ‘enigmatic’, and a ‘riddle’. The distribution has generally been left unexplained in studies of the genus, and the reason why it is both enigmatic and neglected is clear (Heads, 1985): while the New Caledonia–New Guinea connection is highly significant for the biogeography of the southwest Pacific, it is incongruent with the concept of New Caledonia as a simple fragment of Gondwana. Most geological models have the Norfolk Ridge and its emergent northern section, New Caledonia, separating from the Lord Howe Rise and eastern Australia in the Upper Cretaceous, without there ever having

been direct contact with New Guinea. Thus Swenson *et al.* proposed that *Brassospora* is in New Caledonia as a result of dispersal via New Zealand, and in New Guinea as a result of dispersal from northeastern Australia.

They conceded, however, that “A surprisingly strong biogeographic signal in extant *Nothofagus* is concordant with the geological hypothesis... that New Caledonia, in one way or another, is closely related to New Guinea” (Swenson *et al.*, 2001a, p. 45). Despite this, they were “reluctant to regard the conventional view of Earth history as erroneous... geologically... these two areas have completely different origins...” (Swenson *et al.*, 2001a, p. 45). Nevertheless, the geology of this region is not yet well established and there are obvious parallels between New Caledonia and New Guinea (and New Zealand) in their biogeography and terrane tectonics.

In fact, Swenson *et al.* (2001a, p. 38) noted that both New Zealand and New Caledonia “have complex geological histories and may in fact represent the coalescence of numerous distinct Late Palaeozoic and Early Mesozoic terranes...” This is a crucial observation. Furthermore, terrane amalgamation in New Caledonia extended into the Tertiary, and the accretion history of New Guinea is similar to that of New Caledonia and New Zealand. As Swenson *et al.* (2001a, p. 45) concluded (cf. Craw, 1982): “New Caledonia has a complicated geological origin, which probably confounds a simple understanding of its biogeography”.

Swenson *et al.* (2001a) asked whether the New Caledonia–New Guinea affinity indicates an alternative geological hypothesis, biotic interchange, or large-scale extinctions. The second option involves “biotic interchange between New Caledonia and New Guinea via an island-arc system over the past 8–10 Myr” (Swenson *et al.*, 2001a, p. 40), but this dating relies on the oldest known fossils and is thus a minimum age that does not preclude much older connections. With respect to the first option – alternative geological ideas – “The position of New Caledonia on Tasmantis and its close geological relationship with New Zealand need not be refuted. Rather, New Caledonia could be perceived as a composite area, a product of reticulate geology... It could arguably support biotas derived both from New Zealand (ancient) and New Guinea (recent) via past land connections” (Swenson *et al.*, 2001a, p. 40). Again, the basic idea seems correct although the chronology is probably not, and ‘New Caledonia’ did not receive imports from ‘New Guinea’ or ‘New Zealand’ as none of these entities existed at the time of the dispersal. Instead, it is a question of evolution on different terranes before these amalgamated to form the current islands.

GEOLOGY OF NEW GUINEA AND NEW CALEDONIA AND THE RIDDLE OF SUBGEN. BRASSOSPORA

The sector New Zealand–New Caledonia–New Guinea, skirting eastern Australia, has long featured in geological discussion, either as one of three Southern Hemisphere Mesozoic geosynclines (Haug, 1900), the inner part of a First

Australasian Arc (Suess, 1913, p. 1024), an Inner Melanesian Zone (Glaessner, 1950), or a Neo-Australian fold belt (Arkell, 1956). Biogeographers have often referred to it as the 'inner Melanesian arc', although geologically it is a belt of ophiolite complexes and not simply a volcanic island arc. Describing the northern part of the belt, Carey (1996) wrote that "all geologists who have visited [the Papuan Peninsula of eastern PNG and New Caledonia] have been struck by the identity of facies, sequence, petrology and tectonics".

Geologically, New Guinea and New Caledonia are complex, composite entities and their biotas are probably the result of ancient juxtaposition of terranes, rather than of recent radiation (Heads, 2001b, 2003). New Guinea comprises the northern margin of the Australian craton plus 32 allochthonous accreted terranes, while New Caledonia comprises the three basement terranes plus three to five allochthonous accreted terranes (Cluzel *et al.*, 1994).

The three or four basement terranes of New Caledonia formed from island-arc-derived material in the south-west Pacific. They amalgamated and were accreted to east Gondwana (east Australia) in the Late Jurassic/Early Cretaceous Rangitata orogeny (Aitchison *et al.*, 1998). The New Caledonia basement then separated from Australia with the Late Cretaceous opening of the Tasman Sea (during the breakup of Gondwana).

By the beginning of the Eocene, spreading had ended in the Tasman Basin, and subduction was occurring along a Norfolk Ridge–New Caledonia–Rennell I. (SW Solomons)–Papua trench system. The progressive development of a collision zone can be traced from New Zealand through New Caledonia to PNG (Aitchison *et al.*, 1995).

The Poya terrane is a mafic allochthon mainly comprising pillow basalts formed during the Upper Cretaceous–Palaeocene opening of the South Loyalty basin east of the Norfolk Ridge. It was originally located to the north-east of Grande Terre (the mainland of New Caledonia). Local alkali basalts accompanied by Palaeocene pelagic foraminifera in carbonate sediments may represent the remnants of intraplate seamounts. The terrane crops out beneath the ophiolitic nappe (see below) but is not genetically related: it was overthrust by the ophiolitic nappe. The Diahot-Pouébo terrane is in part a metamorphosed equivalent of the Poya terrane, but includes a diversity of rocks (metamorphosed arc-related basalts, associated terrigenous sediments, and remnants of cliff conglomerates) that indicate a mixed origin from both 'oceanic' and 'continental' terranes.

Mid-Eocene collision of the rifted continental basement terranes with intra-oceanic island-arc systems led to the obduction of ophiolite terranes in New Caledonia and New Guinea. The location of the volcanic island arc that collided with New Caledonia is important biogeographically but remains uncertain. It probably lay to the north or north-east of New Caledonia, and andesitic remnants of the arc proper may be preserved as the basement of the Loyalty Islands (Aitchison *et al.*, 1995). Rawling *et al.* (1996) and Rawling & Lister (1997, 1999) proposed the existence of a major Eocene

mountain belt stretching from New Zealand through New Caledonia to New Guinea and beyond.

Swenson *et al.* (2001a, p. 45) concluded that "The presence of the subgenus *Brassospora* on [New Caledonia] is a riddle that is beginning to be answered". However, despite their hint that the composite geology of New Caledonia is important, their answer to the riddle still involved a centre of origin and dispersal (from New Zealand), and the question remains: why is subgen. *Brassospora*, once widespread throughout the range of the genus, now restricted to New Guinea and New Caledonia? Swenson *et al.* (2001a, p. 45) wrote, "We suggest that the migration route to New Caledonia included some form of ancient land link to New Zealand", but a centre of origin/dispersal model seems unlikely and unnecessary, and in any case does not answer the riddle of why *Brassospora* became extinct in Australia, New Zealand, and Antarctica, but not New Guinea or New Caledonia. These are not lowland plants, growing in hot conditions absent from New Zealand and southern Australia: they are abundant and sometimes dominant trees in the mountains (up to 3000 m – they do not tolerate frost), areas that share many biogeographical connections with New Zealand and Australia. Why, exactly, subgen. *Brassospora* is absent from the rain forests of northern New Zealand, northern New South Wales, Queensland and the Andes is indeed a riddle.

There is another component to the riddle: why are the three other *Nothofagus* subgenera absent from New Guinea and New Caledonia? In the New Guinea fossil record of *Nothofagus* (there is none in New Caledonia from before the Quaternary), all pollen belongs to *Brassospora*, apart from Upper Cretaceous records of *Nothofagus senectus* (not referable to any extant subgenus and supposedly an 'ancestral type') and some records of *Fuscospora* pollen that Swenson & Hill (2001) felt could have easily been confused with *Brassospora*. It is usually implied that *Brassospora* is in Melanesia because it managed to disperse there, while the other three subgenera did not. But why did they not? New Guinea is easily accessible from Australia, and, in the Upper Cretaceous, when the subgenera already existed, so were the basement terranes of New Caledonia.

THE FOSSIL RECORD OF SUBGEN. *BRASSOSPORA*

Fossils of 'brassii-type' pollen are widespread and abundant. The type was named for the similarity with pollen of *Nothofagus brassii*, an extant member of *Brassospora*. Some New Zealand palynologists (e.g. McGlone *et al.*, 1996; Pole & Douglas, 1998; McGlone, 2001) have identified all *brassii*-type pollen as *Brassospora*. However, in the last revision of fossil pollen of *Nothofagus* (*Nothofagidites*), Dettmann *et al.* (1990) concluded that there were in fact three *brassii*-types, which they termed (a), (b) and (c), and that while type (a) can be attributed to *Brassospora*, the taxonomic relationships of types (b) and (c) are 'unknown'. Hill (2001), in an important review, agreed that only *brassii*-type (a) could be identified with *Brassospora*. As for *brassii*-type (b) and (c) pollen, Hill (2001,

p. 323) wrote that, “Despite their names, and the fact that most palynologists tend to consider them as members of subgenus *Brassospora*, they may represent extinct subgenera”.

Macphail & Truswell (2004) emphasized the difficulties of identifying samples of *Nothofagidites* (putative fossil pollen of *Nothofagus*) to species level, and preferred to use broader ‘species complexes’. They also suggested that unreliable characters have been used to elevate closely related morphotypes into separate species, and, in particular, that what may prove to be conspecific types have been assigned to different species on different land masses.

The fossil record of *Brassospora* consists of five cupule species, three (possibly four) leaf species (Hill, 2001; Paull & Hill, 2003), and four pollen species of *brassii*-type (a) (Dettmann *et al.*, 1990 accepted six, of which *N. emarcidus* is usually now treated under *N. heterus* of *brassii*-type (b), and *N. goniatus* is a form of subgen. *Lophozonia*; M. Macphail, pers. comm.; Hill, 2001). (In their table 2, Dettmann *et al.*, 1990 rather confusingly listed four species that were synonymized in the text, and this has misled several authors.) Leaves, cupules and pollen have not been found attached, and so some of the 12 organ species very probably belong to the same biological species. In the Australian and Tasmanian fossil record there is one pollen species of *brassii*-type (a), and three leaf species and five cupule species of *Brassospora*. New Zealand has three pollen species, but no leaves or cupules. Fossil leaves and what are possibly *Nothofagus* seeds from New Zealand show similarities with *Brassospora* (Campbell, 1985), but in their thoughtful discussions Campbell (1985) and Hill (2001) refrained from actually identifying these with the modern subgenus. Hill (2001) criticized Pole’s (1993) more sanguine but perhaps less realistic approach. South America and Antarctica each have one species of *brassii*-type (a) pollen (Dettmann *et al.*, 1990; Raine, 1998). Poole (2002, p. 269) noted that “Interestingly, there are no documented macrofossils of [*Brassospora*] in Antarctica or South America”.

Thus the extant New Guinea–New Caledonia distribution of *Brassospora* represents by far the greatest known centre of diversity in its history, involving more species than in all of its fossil records put together. This does not mean that the group was not more diverse in the past – it probably was – but it does have significant implications. The podocarp genus *Falcatifolium* is a similar case. It has five extant species in New Caledonia, New Guinea and Malesia (de Laubenfels, 1984), and one fossil species in Victoria, Australia (Hill & Scriven, 1999).

SUBGENERA NOTHOFAGUS, FUSCOSPORA AND LOPHOZONIA

The sister group of *Brassospora* is subgen. *Nothofagus* (Martin & Dowd, 1993; Linder & Crisp, 1995; Manos, 1997), which comprises five extant species of southernmost South America. It has a fossil record comprising six pollen species (although one of these, *N. lachlaniae*, has been placed in *Fuscospora*) (possibly four in Antarctica, three in each of South America

and New Zealand, and two in Australia), one cupule species (Tasmania), one or possibly two leaf species (Tasmania; Hill, 2001), and one fossil wood species (Antarctica and South America; Poole, 2002). (Macphail & Truswell, 2004 treated Antarctic pollen morphotypes in species complexes, and all members of the complexes are accepted here as being present in Antarctica. Thus numbers of fossil pollen species of *Nothofagus* given for Antarctica are probably overestimates.) Hill (1991, p. 109) wrote that “it is not clear why this subgenus is extinct outside South America”, but this may simply be a function of its always having had greater diversity there and perhaps in Antarctica. Scriven & Hill (1996) argued that its need for large-scale disturbance by landslides, earthquakes, windstorms, avalanches, and volcanism may have eliminated it from Australia and Tasmania, but the subgenus has also disappeared from New Zealand, where these kinds of disturbances are frequent (Ogden *et al.*, 1996).

The affinity of *Brassospora* with South American plants (subgen. *Nothofagus*), rather than with Australian or New Zealand taxa, indicates that the group is part of a standard, but seldom recognized, New Caledonia–South America track (Appendix 2). The podocarp genus *Retrophyllum* Page (= *Decussocarpus* de Laub. sect. *Decussocarpus*) has a distribution pattern very similar to that of *Brassospora/Nothofagus*, with extant species in New Guinea/the Moluccas, New Caledonia, Fiji, and tropical South America (Peru to Colombia and Venezuela), and fossil species in Australia, New Zealand and Chile (Herbert *et al.*, 2002).

Nothofagus subgen. *Fuscospora* is sister to the *Brassospora/Nothofagus* clade (Martin & Dowd, 1993). Extant *Fuscospora* comprises three or four species in New Zealand, one in south-west Tasmania, and one local endemic (*N. alessandri*) in Chile (Rio Maule, between Concepción and Santiago). There are three fossil pollen species (one in each of New Zealand and Australia, two in South America, and possibly three in Antarctica), one fossil leaf species (Tasmania), and one fossil wood species (Antarctica). This gives a main massing of fossil plus extant species in New Zealand, where most of the living species occur. The three subgenera in this clade thus have main massings that are vicariant: *Brassospora* in New Guinea–New Caledonia, *Nothofagus* in South America, and *Fuscospora* in New Zealand.

The last subgenus, *Lophozonia*, is ‘basal’, i.e. sister, to the others and has three extant species in South America, two in Australia, and one in New Zealand. In the fossil record there are possibly three fossil pollen species in Antarctica, two in each of Australia and South America, and one in New Zealand, four fossil leaf species in Australia and one in New Zealand, one cupule species in Tasmania (Hill, 2001), and five fossil wood species in Antarctica and four in South America (Poole, 2002). Like subgen. *Nothofagus*, *Lophozonia* has an extant centre of massing in South America (there are more fossil leaf and cupule species in Australia, giving an equal number of species overall (nine), but no fossil leaves or cupules have yet been described from South America). However, the five species of subgen. *Nothofagus* are all found together only south of

41° (near Valdivia), while all three *Lophozonia* species are only north of 42° (near Chilóe I.) (Hoffmann, 1978; Veblen *et al.*, 1996). This part of Chile is an important node of differentiation in many groups (Heads, 1999).

The vicariant main massings of the four subgenera are compatible with largely allopatric differentiation and no substantial dispersal since at least the Upper Cretaceous (Upper Campanian), by which time the fossil record shows that the four subgenera had evolved.

After the initial period of vicariance, the fossil record shows that rates of evolution in *Nothofagus* through the Tertiary are likely to have been extremely slow. Fossil members of subgen. *Nothofagus* from Tasmania are “so similar to the extant [South American] species that they tell us little about evolution within the group, except that it may have been very slow during the last thirty-five million years” (Hill *et al.*, 1996). Likewise, Hill (1991) regarded the close similarity of three *Brassospora* cupule species from the Tasmanian Oligocene with extant New Guinea species as ‘remarkable’. *Nothofagus smithtonensis*, described later from the Tasmanian Oligocene, is “difficult to separate from extant species” (Hill *et al.*, 1996, p. 193). The tie between these eastern Australian species and those of New Guinea recalls the high diversity of *Nothofagus* species on the Australian craton portion of New Guinea (Heads, 2001a), as well as on the accreted terrane part of the country, where there are biogeographical connections with New Caledonia (e.g. in *Hunga*, *Amyema* and *Phyllanthus*; Appendix 1).

DISTRIBUTION OF THE FAMILY NOTHOFAGACEAE IN THE ORDER FAGALES

Nothofagaceae are sister to the rest of the Fagales (Savolainen *et al.*, 2000), which have the following extant records:

- Fagaceae – North America, Eurasia to New Guinea;
- Ticodendraceae – Central America (Mexico to Panama);
- Betulaceae – North America, northern South America, Eurasia to S China;
- Casuarinaceae – Malesia, Australia, and the Pacific islands;
- Myricaceae – North America, South America (not the far south), Eurasia to New Caledonia (not Australia);
- Juglandaceae – North and South America (not southern South America), Mediterranean to New Guinea;
- Rhoipteleaceae – South China and Indochina.

Of the seven families, only one, Casuarinaceae, appears to show major overlap with Nothofagaceae, having sizeable contingents in New Caledonia and New South Wales, Australia. However, the two families are largely vicariant with respect to their main massings. None of the subgenera of *Nothofagus* has a main massing in Australia, while the main concentrations of extant Casuarinaceae species are in eastern and south-western Australia (Wilson & Johnson, 1989). Of the four genera in Casuarinaceae, only one is present (fossil) in South America (Johnson & Wilson, 1989).

This vicariance at family level suggests that Nothofagaceae/*Nothofagus* evolved largely as the South Pacific/Antarctic vicariant in the breakup of a world-wide Fagales ancestor. A

reversible parsimony analysis (Swenson *et al.*, 2000) gave a similar result, finding that the ancestral area of the genus included Australia, New Caledonia, New Guinea and South America. Likewise, the subgenera of *Nothofagus* evolved largely as South American, New Zealand, and New Caledonia/New Guinea vicariants in the breakup of a South Pacific/Antarctic ancestor. This is in contrast with the view that the family and the subgenera evolved in restricted centres of origin from which they have spread.

CONCLUSIONS

In biogeographical analysis, it is often assumed that a single extralimital fossil – for example a single Northern Hemisphere fossil of a Southern Hemisphere group – renders the extant distribution meaningless. However, the *Nothofagus* data show that, while extralimital fossils occur in all four subgenera, the extant main massings of the subgenera are the same as the main massings based on all species, both fossil and extant. Since fossil material of *Nothofagus* is so abundant, this correlation seems especially significant. In other words, the location of the extant main massings is a reliable guide to the location of the main massings through geological time. They have remained more or less *in situ* since their origin, and so it is of considerable interest that they are vicariant.

Of course, fossils do show that many groups formerly ranged more widely than they do now. However, the location of the extant members is not simply random and will often reflect prior patterns of regional diversity. For example, a group of conifers may have been widespread globally in the Mesozoic, but have had most diversity in the south-west Pacific on terranes that eventually contributed to New Caledonia and New Zealand. After extinction through the Tertiary the group may be represented today by only two or three species, and these are likely to range in New Zealand–New Caledonia. As another example, consider the spider *Migas* (Migidae), which is represented in New Zealand (30 species), Tasmania (two species), Queensland (one species) and New Caledonia (one species) (<http://www.research.amnh.org/entomology/spiders/catalog/>). On average, groups such as this may, in twenty million years, be extant only in the New Zealand region, reflecting the earlier main massing.

Several points concerning subgen. *Brassospora* have not been adequately addressed in previous studies. It is by far the largest extant subgenus in *Nothofagus*, larger than the other subgenera put together. Despite an excellent fossil record, however, only a handful of fossil *Brassospora* species are known in areas outside the present range. These seem to have distracted attention from the striking main massing. The fact that the New Guinea–New Caledonia biogeographical track of *Brassospora* is so standard provides an important clue to the riddle of its distribution, which can be answered simply. *Brassospora* and its ancestors were always most diverse in New Guinea–New Caledonia (or, rather, on their component terranes), where the group currently maintains considerable diversity. Furthermore,

Brassospora vicariates here neatly with the other subgenera. The absence of the latter from the mountains (and probably the fossil record) of New Caledonia and New Guinea is just as difficult to explain ecologically as the presence of *Brassospora*, but both phenomena can be explained by a basically vicariant evolution of the subgenera. *Brassospora* became extinct in what were essentially secondary outlier areas, as these were never major centres of its genetic diversity.

It is not a question of ignoring fossils and their distribution – these must be integrated into analysis. But, equally, the extant distributions of taxa cannot be written off as meaningless, since they represent a sequential development of past distributions and often constitute the greatest known massing of diversity, frequently involving more species than all the fossil species combined. The evidence from the extant species and from the fossil record indicates that the region New Caledonia–New Guinea does not represent a secondary outlier for *Nothofagus*, but rather an important centre of evolution in its own right.

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APPENDIX 1 THE NEW CALEDONIA–NEW GUINEA TRACK

In fungi, *Mycena irritans* is known from New Caledonia and New Guinea (Horak, 1983), as is the moss *Bescherellia elegantissima* (Sastre-De Jesús, 1987). In ferns, *Ctenopteris subsecundo-dissecta* is in southern New Caledonia and New Guinea (Brownlie, 1969), and *Coryphopteris fasciculata* (Thelypteridaceae) is in New Caledonia, New Guinea, and Sulawesi (Holttum, 1977).

In monocots, *Freycinetia* sect. *Solmsiella* (Pandanaceae) (Stone, 1981) is in New Caledonia and New Guinea, as is *Liparis indifferens* (Orchidaceae) (Hallé, 1977). *Bulbophyllum lophoglossis* (Orchidaceae) of the southern ultramafic massif in New Caledonia is very closely related to *B. plumula* of the PNG mountains ((Hallé, 1977; André Schuiteman, pers. comm.). In dicots, *Phyllanthus* subgen. *Gomphidium* sect. *Adenoglochidion* (Euphorbiaceae: Phyllanthoideae) is in New Caledonia and western New Guinea (Jayapura and Biak I.) (Holm-Nielsen, 1979). *Phyllanthus bourgeoisii* (sect. *Gomphidium*) is in New Caledonia, New Britain, and the Vogelkop Peninsula (western New Guinea) (Webster & Airy Shaw, 1971). *Sloanea* sect. *Antholoma* (Elaeocarpaceae) (van Balgooy, 1971) is only found in New Caledonia and New Guinea. *Hunga* (Chrysobalanaceae) is restricted to New Caledonia and PNG, where it occurs in the Papuan Peninsula on and east of a line: Bakaia/Sogeri, and also in the Milne Bay islands (Prance, 1979). *Amyema scandens* (Loranthaceae) is only known from New Guinea and

New Caledonia, and an 'extreme variant' of *A. artensis* occurs on Rossel I. (Milne Bay, PNG) and New Caledonia (Barlow, 1992). *Meiogyne glabra* (Annon.) of central New Britain is keyed out next to *M.* 'spec. 1' of New Caledonia by van Heusden (1994). *Nepenthes* (Nepenthaceae) has closely related forms in New Caledonia (*N. vieillardii*) and western New Guinea (*N. lamii*; Cheek & Jebb, 2001). A clade in *Dubouzetia* (*D. kairoi*, *D. dentata*, *D. elegans*) (Elaeocarpaceae) is restricted to New Guinea/Moluccas and New Caledonia, as is *D. elegans* (Coode, 1987).

In invertebrates, the spider *Desis maxillosa* (Desidae) is in New Caledonia and New Guinea, as is the fly *Elephantomyia* subgen. *Elephantomyia* (Tipulidae). *Phrynovelia* (Hemiptera) is restricted to New Caledonia and north-east New Guinea (Andersen & Polhemus, 2003). In beetles, the eucnemid *Mesogenus austrocaledonicus* of New Caledonia is sister to *M. cavifrons* of New Guinea (Muona, 1991). In butterflies, *Papilio montrouzieri* (Papilionidae) and *Polyura clitarchus* (Nymphalidae) have their closest relatives in the Papuan region (Holloway & Peters, 1976). In moths, Holloway (1979) cited six New Caledonian endemics that have their closest relatives in New Guinea: *Epilema lateritica* (Uraniidae), *Anisozyga caledonica*, *Chloroclystis macroaedeagus* (both Geometridae), *Agrius fasciatus* (Sphingidae), *Nycteola canoides* and *Veia pectinata* (both Noctuidae).

APPENDIX 2 THE NEW CALEDONIA/ MELANESIA-AMERICA TRACK

In fungi, *Amparoina spinosissima* is known from New Caledonia, Argentina, and Colombia (Horak, 1983). In monocots, *Heliconia* (Heliconiaceae) occurs in the south-west Pacific (New Guinea/Moluccas, Bismarcks, Solomons, Vanuatu, New Caledonia, Fiji and Samoa) and in tropical America (Mexico, West Indies to south Brazil) (Kress, 1990). The New Caledonian endemic orchid genera *Clematepistephium* and *Eriaxis* are sister taxa, and the pair is sister to *Epistephium*, widespread in tropical South America (Cameron, 2003). In dicots, Polygalaceae tribe Moutabeeae comprises *Balgoya* of New Caledonia, *Eriandra* of New Guinea and the Solomons, and three other genera of northern South America (van Balgooy & van der Meijden, 1993; Eriksen, 1993). In invertebrates, the flatworm *Pimea* of New Caledonia is related to the Neotropical *Choeradoplana* (Winsor, 1991), and in spiders, *Aucana* (Pholcidae) is in New Caledonia and Chile (<http://www.research.amnh.org/entomology/spiders/catalog/>).