

# A cladistic scenario of Southern Pacific biogeographical history based on *Nothofagus* dispersal and vicariance analysis

MingLi ZHANG<sup>1,2\*</sup>

<sup>1</sup> Key Laboratory of Biogeography and Bioresources in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China;

<sup>2</sup> Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

**Abstract:** *Nothofagus* is regarded as a key group for interpreting Southern Pacific biogeographical history. Based on a molecular phylogenetic tree, a quantitative dispersal-vicariance analysis (DIVA) of the genus is presented. The results indicate that the ancestral area of *Nothofagus* is a broad realm almost including the total extant distribution pattern of the genus rather than a so-named center of origin. Integrated with the paleogeography, the time of origin and subsequent diversification is inferred to have started in the Late Cretaceous. Most vicariance and dispersal events should be contained in that period. Vicariance events versus dispersal events play a dominant rule in speciation. The dispersal events are hypothesized to happen from the Late Cretaceous to Eocene in terms of the geological history. Rich fossils are collected in the Eocene. South America, comprising three subgenera of *Nothofagus*, should be considered as a diversification region, in which the distribution of the species of subgenus *Fuscospora* and subgenus *Nothofagus* are explained by dispersal events during the Late Cretaceous-Late Eocene.

**Keywords:** *Nothofagus*; Pacific biogeography; distribution; vicariance; dispersal

## 1 Introduction

The genus *Nothofagus* belongs to Nothofagaceae or Fagaceae (Jones, 1986; Nixon, 1989; Hill and Jordan, 1993; APG, 1998, 2009), has about 35 species, and is divided into four subgenera, *Brassospora*, *Fuscospora*, *Lophozonia*, and *Nothofagus*. The genus is distributed mainly in the Southern Pacific region, with most endemic species in southern South America, Southeastern Australia, New Zealand, Tasmania, New Guinea, and New Caledonia (Tanai, 1986; Segutochi *et al.*, 1997; Swenson *et al.*, 2000). The species of the genus form a dominant group in cool temperate forests in the Southern Hemisphere. In general, the southern beech and the kangaroo are regarded as the important groups in Southern Pacific biogeographical history because their distribution patterns related to the fragmentation of Gondwana (Darlington, 1965; van Steenis, 1971, 1972; Hill, 1992).

Using a static geological theory to explain the origin and evolution of *Nothofagus*, Darlington (1965)

considered that the origin of *Nothofagus* was in a subtropical region of the Southern Hemisphere during the Cretaceous. His reasoning was that such subtropical regions were the diversification centers for the genus and taxa occurring in the regions migrated from Malaysia. van Steenis (1962) also considered that Southeast Asia was the center of origin, but the migration was through a land bridge. Raven and Axelrod (1972, 1974) regarded the Northern Hemisphere as the center of origin of *Nothofagus* and that the genus arrived in the Southern Hemisphere via Europe and Africa. Schuster (1976) accepted this point, but suggested that the migration route was via North America to South America and other areas, and the time of origin was Middle Cretaceous. However, Moore (1972) suggested that the center of origin was the Southern Hemisphere. Hanks and Fairbrothers (1976) supported Moore's (1972) point, and further considered the place of origin to be New Zealand, South Antarctic or Australia,

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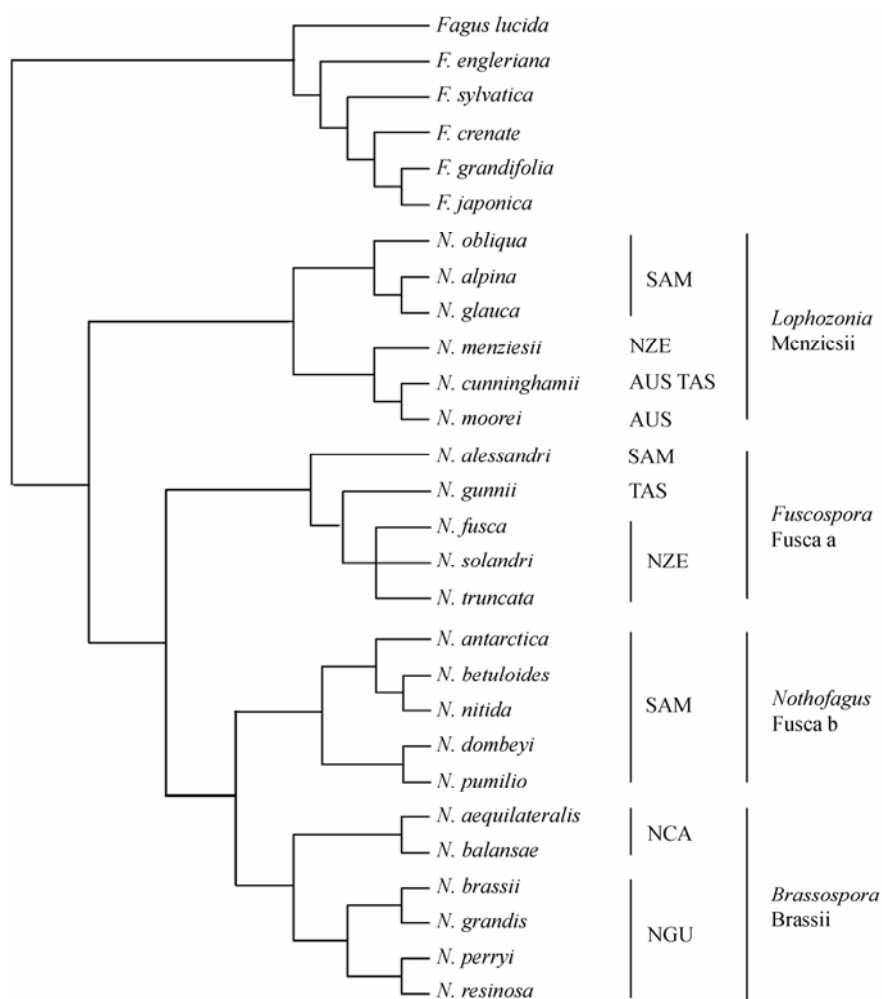
\* Corresponding author: MingLi ZHANG (E-mail: zhangml@ibcas.ac.cn)

and *Nothofagus* migrated to South America via the South Antarctic. Swenson *et al.* (2000) proposed South America as the center of origin and that *Nothofagus* dispersed into Australia. Recently, Knapp *et al.* (2005) presented a molecular phylogenetic dating to demonstrate the long distance dispersal in *Nothofagus*. However, Humphries (1981) considered that the center of origin of *Nothofagus* could not be determined, and to use *Nothofagus* as a key to explain the Southern Hemisphere biogeography was spurious.

After studying *Nothofagus* on the basis of morphology (van Steenis, 1953; Melville, 1973), and pollen morphology (Philipson and Philipson, 1988), several taxonomists established classification systems (van Steenis, 1953; Melville, 1973; Hill and Read, 1991), revisions of the genus (Hill and Read, 1991; Hill and Jordan, 1993), and cladograms (Humphries, 1981). Many results indicate that four subgenera fit

closely to the pollen types (Philipson and Philipson, 1988). There are four pollen types corresponding to extant *Nothofagus* subgenera and species (Hanks and Fairbrothers, 1976; Dettmann *et al.*, 1990; Hill, 2001), namely; Brassii type occurred in subgenus *Brassospora*, Fusca type a in subgenus *Fuscospora*, Fusca type b in subgenus *Nothofagus*, and Menziesii type in subgenus *Lophozonia* (Fig. 1).

During recent years the relationships of *Nothofagus* have been widely researched on the bases of molecular systematics. Similar topologies for the genus have been established based on the morphology and DNA sequence using cladistics (Martin and Dowd, 1993; Linder and Crisp, 1995; Manos, 1997; Segutochi *et al.*, 1997; Jordan and Hill, 1999; Knapp *et al.*, 2005). These cladograms are generally congruent with the classification system (Hill and Read, 1991).



**Fig. 1** A modeltest-based maximum likelihood phylogenetic tree based on nrDNA ITS 5.8S sequence data, the distribution concerning six areas, four subgenera, and four pollen types in *Nothofagus* are labeled. SAM: South America, NZE: New Zealand, AUS: southeastern Australia, TAS: Tasmania, NCA: New Caledonia, NGU: New Guinea

The area relationships have been discussed (Melville, 1973; Humphries, 1981) using different historical biogeographical analyses, such as the subtree analysis (Ladiges *et al.*, 1997; Nelson and Ladiges, 2001), component analysis (Swenson and Hill, 2001; Swenson *et al.*, 2001a, b), and ancestral area analysis (Swenson *et al.*, 2000). The events in Pacific biogeography have been studied (Linder and Crisp, 1995) and the biota and geological history have been inferred (Swenson *et al.*, 2001b) through combining the area cladogram of this genus and related groups. By employing a molecular clock approach, Knapp *et al.* (2005) and Cook and Crisp (2005) investigated the origin of genus, diversification, dispersal and vicariance of infrageneric groups. These results give some understanding of the biogeographical history of the Southern Hemisphere, however, they could not perfectly support a key to the biogeographical history of the regions. Two further approaches have been devised to analyze the distribution pattern. These are LAGRANGE (maximum likelihood based) (Ree and Smith, 2008) and dispersal-vicariance analysis (DIVA) (maximum parsimony based) (Ronquist, 1997; Kodandaramaiah, 2010; Xie *et al.*, 2010), and S-DIVA (Yu *et al.*, 2010). In general, both approaches produce similar results (Xie *et al.*, 2010), and in most cases only DIVA has been used. This paper analyzed the distribution patterns of *Nothofagus* by means of DIVA based on the cladogram, and discussed the origin and evolution of the genus, and Southern Hemisphere biogeographical history.

## 2 Material and methods

### 2.1 Phylogenetic analysis

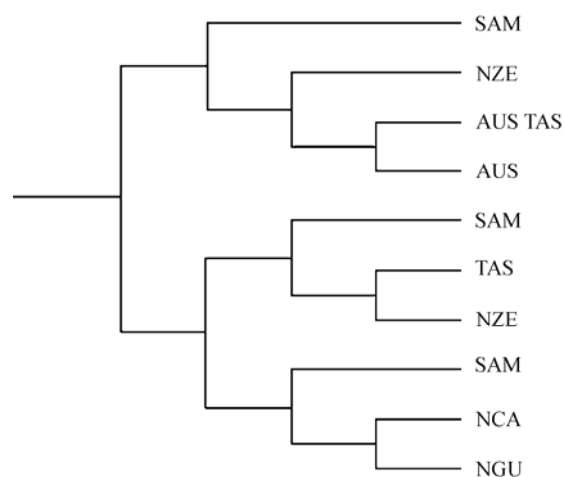
There are many cladograms based on morphology or DNA sequences, or both (Martin and Dowd, 1993; Manos, 1997; Segutochi *et al.*, 1997; Knapp *et al.*, 2005). Here nuclear ribosomal DNA internal transcribed spacers (ITS) 5.8S sequence data was downloaded from GenBank and was used to construct a phylogenetic tree (see Appendix). The 'outgroup' was selected as *Fagus*, of the six species sequence data used to constitute an original dataset. In total 28 species were sampled (see Appendix).

Modeltest version 3.5 (Posada and Crandall, 1998) was used to find the most appropriate DNA substitute model for phylogenetic analysis. The parameters of the

AIC (Akaike Information Criterion) from the Modeltest program were inputted into the maximum likelihood (ML) analysis. ML phylogenetic analysis was implemented in PAUP PAUP version 4.0 (Swofford, 2002).

### 2.2 Area

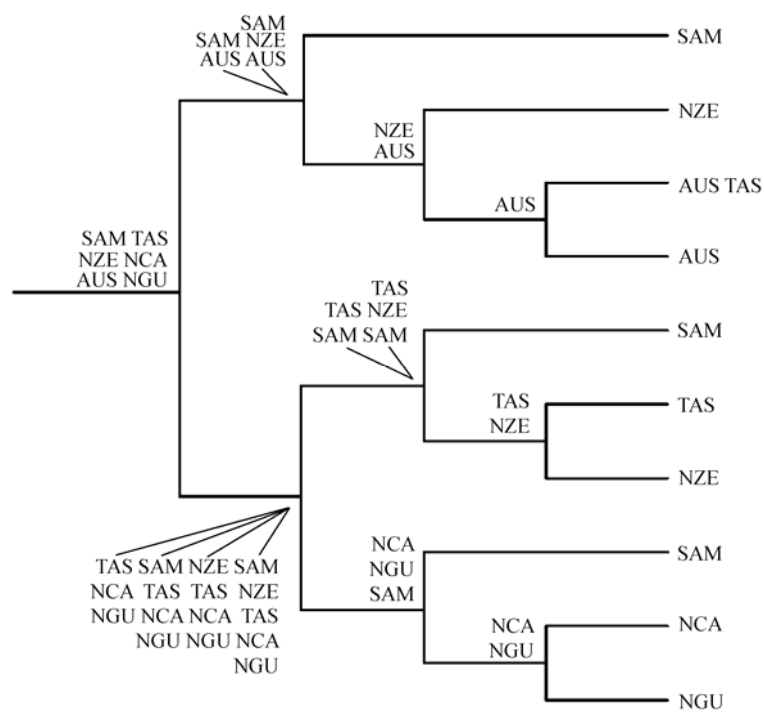
There are country-wide endemic distribution patterns in *Nothofagus*. Six isolated areas were selected in previous studies (Humphries, 1981; Tanai, 1986; Linder and Crisp, 1995; Ladiges *et al.*, 1997; Manos, 1997; Jordan and Hill, 1999; Swenson *et al.*, 2000; Swenson and Hill, 2001; Swenson *et al.*, 2001a), namely, southern South America (SAM), southeastern Australia (AUS), New Zealand (NZE), Tasmania (TAS), New Caledonia (NCA) and New Guinea (NGU) (Fig. 1). Based on Fig. 1, a reduced area cladogram (Manos, 1997) was obtained (Fig. 2).



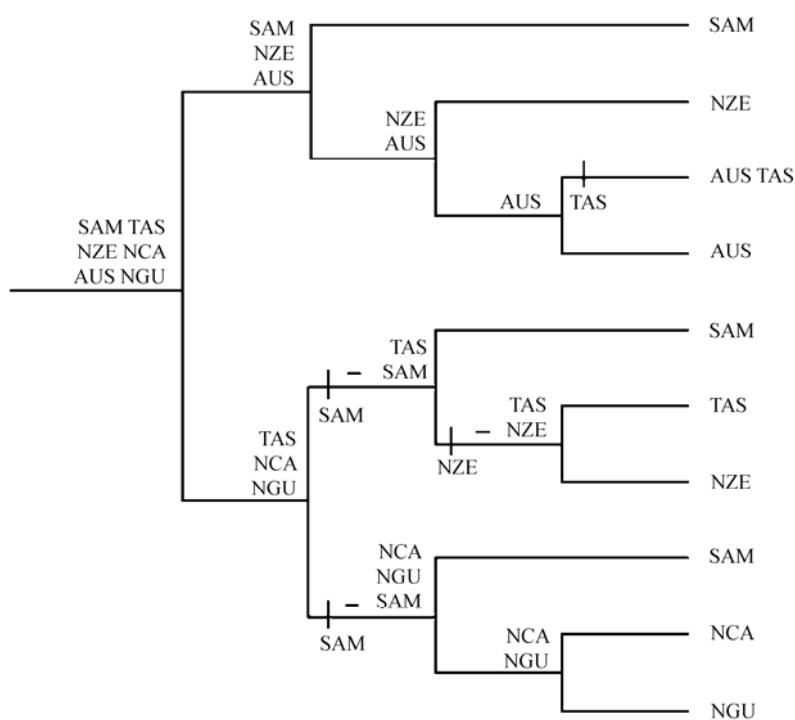
**Fig. 2** A resolved area cladogram based on Fig. 1. The taxa in Fig. 1 are replaced by areas which hold the taxa

### 2.3 Dispersal-vicariance analysis

DIVA program (Ronquist, 1997) was applied (Fig. 2). The different ancestral area combinations at the node of the tree were obtained and labeled on the area cladogram (Fig. 3). The vicariance and dispersal events were obtained through employing optimization criteria for minimizing dispersal and extinction events (Enghoff, 1993; Nordlander *et al.*, 1996; Ronquist, 1996, 1997; Fritsch *et al.*, 2001; Xiang *et al.*, 2001; Davis *et al.*, 2002). Then it should be possible to determine the ancestors at the nodes and the dispersal events on the tree. Thus, finally the particular scenario for the history of *Nothofagus* was obtained through the vicariance and dispersal analysis (Fig. 4).



**Fig. 3** A reconstruction of ancestral distribution of *Nothofagus* using DIVA. At each node, the optimal distribution prior to vicariance is given, four dispersals are required



**Fig. 4** Suggested biogeographical history of *Nothofagus*; ancestral areas and vicariances events are indicated near the nodes, and four dispersal events with four vertical lines are indicated on the branches

3 Results

An aligned original dataset included 651 bps (base pairs), of which 436 bps were constant, and 27

variable bps were parsimony-uninformative, and 188 bps were parsimony-informative. The best sequence substitute model was selected to be GTR+G from AIC of Modeltest, with the Log

Likelihood score  $-\ln L=2,513.2729$ , nucleotide frequencies  $A=0.2128$ ,  $C=0.2976$ ,  $G=0.2832$ ,  $T=0.2064$ , gamma shape parameter 0.4183, and assumed proportion of invariable sites 0.

A phylogenetic tree can be obtained through ML phylogenetic analysis based on Modeltest (Fig. 1), which has an agreement with previous tree topology, especially those based on molecular form (Martin and Dowd, 1993; Manos, 1997; Segutochi *et al.*, 1997; Knapp *et al.*, 2005).

There are nine vicariance and four dispersal events evident from DIVA (Fig. 4), especially, the ancestral area at the deepest position, which is a combination of six areas. This implies that the ancestral area of *Nothofagus* was a broad realm covering almost the entire distribution area of extant taxa. In other words, the differentiation of *Nothofagus* started from a combination of ancestral areas with all six ancestral areas in the vicariance framework.

## 4 Discussion

### 4.1 Ancestral area

The ancestral area as seen in this paper is not equivalent to the general center of origin. In general, the center of origin is frequently regarded as a small place from where dispersal expanded the distribution range. Because the ancestral area of *Nothofagus* is a broad, continuous tract over the trans-Antarctica region, and dispersal ability of the species is limited (Manos, 1997), 'the dispersal versus vicariance pattern' is of secondary status in the speciation pattern and process.

The ancestral area of *Nothofagus* is clearly the entire distribution realm of extant species, which was Gondwanaland encircling the Pacific region (Fig. 4). Consequently, the result is not consistent with there being a point that can be designated as a center of origin and diversification center of the genus, such as South America (Hill, 1991, 1996; Hill and Dettmann, 1996; Swenson *et al.*, 2000), Australia (Truswell *et al.*, 1987), Southeast Asia, and the Northern Hemisphere in which *Fagus* occurs and *Fagus* was treated as the ancestor of *Nothofagus* (Raven and Axelrod, 1972, 1974; Schuster, 1976). Vicariance started as a broad ancestral area and was the dominant mode of the speciation process confirmed by fossil evidence.

The primary differentiation time of the genus can be

identified as the Late Cretaceous in terms of the fossil records from Australia, New Zealand and southern South America (Hanks and Fairbrothers, 1976; Dettmann *et al.*, 1990; Hill, 2001; Swenson and Hill, 2001), and macrofossils (Hill, 1991, 2001). Differentiation of the four sub-genera occurred quite early, in the explosive radiation time about 83–70 Ma (Manos, 1997) at least in the Oligocene. This evidence and the inference from *Nothofagus* are consistent with the earth history (Briggs, 1995; McLoughin, 2001), or, put another way, the biogeography of *Nothofagus* and the earth history are reciprocal illuminators (Humphries and Parenti, 1999). In the Late Cretaceous, Gondwana and Pacific as the ancestral area of *Nothofagus* was connected or at least in close proximity, which justifies the ancestral area being a large area. However, the time of origin could not be earlier than Late Cretaceous because prior to that both South America and South Africa were joined (Briggs, 1995; McLoughin, 2001), and there is no temporal distribution nor fossil of the genus in South Africa. Therefore, the time of origin for *Nothofagus* is inferred to be Late Cretaceous.

### 4.2 Speciation

According to the results of the present analysis as well as the fossil record and earth history, three modes of speciation could have occurred in *Nothofagus* since the Late Cretaceous, namely, vicariance, dispersal and extinction.

#### 4.2.1 Vicariance

The vicariance events in *Nothofagus* are shown in Figs. 3 and 4. There are a total of nine vicariance events on area cladograms (Figs. 3 and 4) based on DIVA. At first, the entire area resulted in a vicariance (SAM, NZE, AUS) V (TAS, NCA, NGU). Then, obvious vicariance events are: SAM V (NZE, AUS); SAM V AUS; SAM V (NCA, NGU). Subsequently, the vicariances occur between NZE and AUS, NCA and NGU. The larger vicariances related to South America (SAM), or vicariance occurs between South America and other areas (Fig. 4). A typical vicariance is between New Caledonia (NCA) and New Guinea (NGU), which related to the subgenus *Brassospora*.

The main cause of vicariance events should be explained as considerable endemism in the genus, namely, each species has its endemic distribution area

except the species, *C. cunninghamii* which appears in southeastern Australia and Tasmania. Furthermore, the extant species have been conserved since the formation of the four subgenera by their exploded radiation (Hill, 1991, 2001; Manos, 1997; Swenson and Hill, 2001; Swenson *et al.*, 2001a, b) during the period 55–44 Ma (Cook and Crisp, 2005), and they are the traces of Gondwana history and geology. Therefore, the vicariance mode holds a long history and should be the dominant mode of speciation and distribution pattern in *Nothofagus*. Subsequently the vicariations could be easily obtained from the disruption of Gondwana and land movement in geological history (Hooker, 1853; Engler, 1879; Croizat, 1952; Brundin, 1965; Humphries, 1981; Craw, 1989; Crisci *et al.*, 1991a, b; Seberg, 1991; Weston and Crisp, 1994; Ladiges *et al.*, 1997; Nelson and Ladiges, 2001; Swenson *et al.*, 2001a, b).

#### 4.2.2 Dispersal

There are four dispersal events in *Nothofagus* (Fig. 4). One of them is illustrated by Tasmania in which *N. cunninghamii* appears, and it is postulated that the species dispersed from southeastern Australia. The dispersal time from Australia to Tasmania should be at least in the Oligocene because of the fossil records for this period from Tasmania (Hill, 1991, 2001; Swenson *et al.*, 2001a, b), which justifies the statement that the species was widespread once. Another dispersal was New Zealand (NZE) and the process is between node TAS-SAM and node TAS-NZE (Fig. 4). One of the possibilities is that species in New Zealand (NZE), *N. solandri*, *N. fusca*, and *N. truncata* have been dispersed from ancestors in Tasmania and South America (TAS-SAM, Fig. 4). Knapp *et al.* (2005) interpreted the absence of *Lophozonia* and *Fuscospora* pollen types in New Zealand and the Cretaceous as evidence for Tertiary dispersals of *Nothofagus* to New Zealand. According to the geological history (Briggs, 1995; McLoughin, 2001), a dispersal event from an ancestor in Tasmania and South America to New Zealand (TAS-SAM→NZE (TAS-NZE)) would be available and considered as a Late Cretaceous event because these areas were connected in this period. After dispersal NZE from node TAS-SAM to TAS-NZE, then a vicariance event occurred from node TAS-NZE (Figs. 1 and 4), and was represented by those species (*N. solandri*, *N. fusca*, and *N. truncata*) of New Zealand

and *N. gunnii* of Tasmania.

Other two dispersal events are illustrated by southwestern South America (SAM) (Fig. 4, SAM and vertical lines). The ancestor node of both dispersals is hypothesized to be node TAS NCA NGU (Fig. 4). These two dispersal processes occur in node TAS NCA NGU→node TAS-SAM, and node TAS NCA NGU→node NCA NGU-SAM, respectively.

If dispersal is supposed to happen through areas that are connected or nearly connected, the dispersal period should be inferred during the Late Cretaceous in light of the geological history (Briggs, 1995; McLoughin, 2001). The ancestral area of Tasmania and South America (TAS-SAM) probably includes not only TAS NCA NGU (Fig. 4, node TAS NCA NGU→node TAS-SAM) but also the South Antarctica and Australia because all of them were nearly combined as one land mass in the Late Cretaceous. Why are the South Antarctic and Australia absent from the ancestor node TAS NCA NGU? The extinctions and the pollen fossil evidence found from Australia (Swenson and Hill, 2001; Swenson *et al.*, 2001a, b) offers a confirmation.

By analogy, the TAS NCA NGU node is similar to NCA NGU-SAM, and the ancestral area of New Caledonia, New Guinea and South America should be properly included because South America was nearly joined to them from the Late Cretaceous to the Paleocene according to geological and fossil data (Briggs, 1995; McLoughin, 2001). New Guinea and New Caledonia were also connected to Australia during this period.

Consequently, how does one explain the dispersal possibilities of South America from the ancestor mentioned above in Tasmania, New Guinea and New Caledonia (node TAS NCA NGU→node TAS-SAM; node TAS NCA NGU→node NCA NGU-SAM)? At first, node TAS NCA NGU in fact should be postulated as a big land mass. Secondly, South America, South Antarctica, Australia, New Zealand, Tasmania, New Guinea and New Caledonia were continuous land mass, or near each other, even though sometimes the continuity was interrupted during the period of the Late Cretaceous to the Paleocene (Briggs, 1995; McLoughin, 2001). Therefore, the dispersal explained here should be conceivable. In addition, the evidence in pollen fossil records for some aforementioned spe-

cies are found in the Eocene and that fact indicates the extinction and distribution traces except for Tasmania, New Caledonia and New Guinea. For instance, the fossil pollen type of *N. fusca*, which is distributed in New Zealand, is even recorded in the Cretaceous from New Zealand (Humphries, 1981).

#### 4.2.3 Extinction

After the variation of the four sub-genera in the ancestral area during the Late Cretaceous, the extinction event was probably another important speciation mode along with vicariance and dispersal. The extinction process happened together with the break-up of Gondwana and as a result of climate change (Hill, 2001; McLoughin, 2001). The fossil record provided direct evidence of extinction (Dettmann *et al.*, 1990; Hill, 1991, 2001; Swenson and Hill, 2001). Because of extinction, the vicariance and dispersal events become rather blurry, making it necessary to uncover the distribution pattern.

The most remarkable extinction event occurred in the differentiation process among the species of the sub-genus *Brassospora* and sub-genus *Nothofagus* (Humphries, 1981; Dettmann *et al.*, 1990; Hill, 1991, 2001; Swenson and Hill, 2001). The species of sub-genus *Brassospora* is endemic to New Guinea and New Caledonia, but the fossils are found in almost all trans-Antarctic areas, i.e. South America, South Antarctica, Tasmania, New Zealand and Australia. Therefore, the extinction had certainly occurred in these areas. The species of sub-genus *Nothofagus* is endemic to South America, but its fossil records can be found in South Antarctica, New Zealand and Tasmania. Therefore, the extinction events in those areas are also affirmative. *N. gunnii* of sub-genus *Fuscospora* is restricted to Tasmania, but the fossils were found in South Antarctica. *N. fusca* occurs in New Zealand but its fossil record is in Tasmania; *N. moorei* of sub-genus *Lophozonia* is distributed in southeastern Australia but a lot of fossils are found in Tasmania, New Zealand, and Southeastern Australia during the Eocene-Oligocene of the Tertiary. Consequently, the extinction events of the genus can be frequently found in their distribution areas.

#### 4.3 New Guinea and New Caledonia

The species of sub-genus *Brassospora* is endemic to New Guinea and New Caledonia and is the only

sub-genus in these areas. This sub-genus consists of the special *Brassii* pollen type. So, New Guinea and New Caledonia are distinguished from other sub-genera in *Nothofagus*. However, the *Brassii* pollen fossils are also recorded in South America, Australia and New Zealand during Late Cretaceous (Humphries, 1981). So far, the earliest fossils are found in New Guinea from the Upper Miocene, while in New Caledonia the earliest fossils came from the Quaternary period and Pleistocene (Humphries, 1981; Dettmann *et al.*, 1990; Hill, 2001; Swenson and Hill, 2001).

Based on the endemic distribution and special pollen types in New Guinea and New Caledonia, van Steenis (1962) and Darlington (1965) suggested Southeastern Asia as the place of origin for *Nothofagus* and from where the taxa dispersed into Australia and South America via New Guinea and New Caledonia. Because of the endemism, the species in New Guinea and New Caledonia could be suitably explained as a vicariance instead of a migration or dispersal. According to Fig. 4, as a part of the ancestral area from the deepest ancestral node, both New Guinea and New Caledonia remained united after three vicariance events with other areas from the deepest node ancestor, SAM, TAS, NZE, NCA, AUS, and NGU.

#### 4.4 New Zealand

New Zealand was the first area to break away from Gondwana during the period of 80–70 Ma (Wilford and Brown, 1994). During the Cretaceous, New Zealand was joined to western South Antarctica, and Australia was joined to eastern South Antarctica. Moreover, the relationships of the three areas were provided by Linder and Crisp (1995) from the earth history (NZ, (SA, Aust)), plants (SA, (Aust, NZ)), and insects ((SA, NZ), Aust). It is fairly clear that there is a close floristic relationship between New Zealand and Australia.

How does one explain the area relationships between New Zealand and Australia? One approach is by dispersal (Mildenhall, 1980; Truswell *et al.*, 1987; Hill, 1994; Macphail *et al.*, 1994), and another by vicariance (Linder and Crisp, 1995). The latter suggested that the temporal distribution patterns came from a continuous land mass and subsequent differences have been caused by plate tectonics and extinctions.

The results revealed that the taxa in New Zealand

results from vicariance and dispersal. *N. menziesii* of the sub-genus *Lophozonia* remains an isolated group originating from vicariance. The vicariance events and area relationships revealed that the sub-genus *Lophozonia* is in accordance to the general area relationship in the Southern Hemisphere (SA, (Aust, NZ)) (Linder and Crisp, 1995; Ladiges *et al.*, 1997; Nelson and Ladiges, 2001; Swenson and Hill, 2001; Swenson *et al.*, 2001a). However, the distribution of three species of *N. solandri*, *N. fusca* and *N. truncata*, belonging to sub-genus *Fuscospora*, is considered to be due to dispersal events. Because the seed dispersal capability of *Nothofagus* is hypothesized to be limited (only 15 km) in the air (Manos, 1997), the dispersal of these three species would only happen at the Late Cretaceous when New Zealand and Tasmania were connected (Briggs, 1995; McLoughin, 2001). In the Late Cretaceous, New Zealand, South Antarctica, Tasmania, and Australia were close to each other so that dispersal was possible.

#### 4.5 Southwestern South America

Southwestern South America consists of the cool temperate region of Chile and Argentina. Based on the classification system (Hill and Read, 1991), three of the four sub-genera in *Nothofagus* occurred in this region, of them sub-genus *Nothofagus* is endemic. These three genera correspond to three pollen types. In terms of molecular cladograms (Linder and Crisp, 1995; Manos, 1997; Segutochi *et al.*, 1997; Knapp *et al.*, 2005), there were not only some primitive species of sub-genus *Lophozonia* (positionally plesiomorphic on the cladograms), but also some advanced species of sub-genus *Nothofagus* (positionally apomorphic) that occurred in this region. Therefore, this region can be regarded as the center of diversification of the genus. But it could not be regarded as the center of origin because there are no traces of dispersal from this region to other regions from the present analysis.

Because of the geographical isolation between southwestern South America and southeastern Australia and New Zealand in the Late Cretaceous, the differentiation and vicariance (SAM NZE AUS→SAM and NZE AUS, Fig. 4) in sub-genus *Lophozonia* should appear from the Late Cretaceous to Paleocene. In the other two sub-genera, southwestern South America has respectively two dispersal events (Fig. 4,

SAM and vertical lines) from Tasmania, New Guinea and New Caledonia (node TAS NCA NGU, Fig. 4). Later, South America and other areas, such as Tasmania, New Caledonia and New Guinea, could constitute ancestor nodes, consequently resulting in the vicariations in sub-genera *Nothofagus* and *Brassopora* respectively (Fig. 4).

## 5 Conclusion

In short, the DIVA results for *Nothofagus* revealed some events of vicariance, dispersal and extinct, which could be explained and confirmed by the fossil of *Nothofagus* and Gondwana geological history. The ancestral area of *Nothofagus* most likely broad realms which are today covered almost entirely by the distribution of extant taxa, in other words, the vicariance occurred in the broad realm. Certain parts of this cladistic scenario for the Southern Pacific biogeographical history are stressed. The time of origin and subsequent divergence in *Nothofagus* is inferred to be the Late Cretaceous. The geological record supports the possibility of vicariance and origin. Southwestern South America is really the diversification center of three sub-genera, however, most taxa in this area are postulated to be dispersed. The rich fossil records for *Nothofagus* confirmed various extinction and vicariance events, as well as the possibility of several dispersal events.

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- Appendix:** Twenty-eight sampled species of *Nothofagus* and *Fagus*, with Gene Bank accession numbers
- Nothofagus*: *N. aequilateralis* (Baum.-Bodenh.) Steenis, U96864; *N. alessandri* Espinosa, U96854; *N. alpina* (Poepp. & Endl.) Oerst., U96865; *N. antarctica* Oerst., U96849; *N. balansae* (Baill.) Steenis, U96863; *N. betuloides* Blume, U96852; *N. brassii* Steenis, U96860; *N. cunninghamii* (Hook.) Oerst., U96868; *N. dombeyi* Blume, U96853; *N. fusca* (Hook.f.) Oerst., U96857; *N. glauca* Krasser, U96866; *N. grandis* Steenis, U96859; *N. gunnii* Oerst., U96855; *N. menziesii* (Hook.f.) Oerst., U96896; *N. moorei* (F.Muell.) Krasser, U96870; *N. nitida* Reiche, U96850; *N. obliqua* (Mirb.) Oerst., U96867
- N. perryi* Steenis, U96861; *N. pumilio* (Poepp. & Endl.) Krasser, U96851; *N. resinosa* Steenis, U96862; *N. solandri* (Hook.f.) Oerst., U96856; *N. truncata* Cockayne, U96858.
- Fagus*: *F. crenata* Blume, AF456969; *F. engleriana* Seemen ex Diels, AY220148; *F. grandifolia* Ehrh., AY220144; *F. japonica* Maxim., AY040503; *F. lucida* Red. & E. H. Wilson, AY040507; *F. sylvatica* L., AY040502.