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NOTHOFAGUS AND PACIFIC BIOGEOGRAPHY

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Abstract — Gondwanan biogeography, particularly the relationships between southern South America, New Zealand, Australia, New Guinea and New Caledonia, has been much studied. *Nothofagus* is often used as the "test taxon", and many papers have been directed at using *Nothofagus* to explain Gondwanan biogeography. Cladistic biogeographers, working on plant material, have generally failed to find congruence among taxa expected from the southern Pacific disjunctions. New morphological and molecular data on the phylogeny of *Nothofagus* have re-opened the issue, and we analysed these data to construct a new hypothesis of the biogeography of the genus. We assembled all plant taxa for which we could find reasonably robust phylogenetic hypotheses, and sought a parsimonious biogeographical pattern common to all. Two analyses, based on different assumptions, produced the same general area-cladogram. We use the general area-cladogram, in conjunction with the fossil record of *Nothofagus* to construct a historical scenario for the evolution of the genus. This scenario indicates extensive extinction, but also suggests that Australia has a more recent relationship to New Zealand than to southern South America. This is not congruent with the current geological theories, nor with the patterns evident from insect biogeography. We suggest that concordant dispersal is an unlikely explanation for this pattern, and propose that the solution might be found in alternative geological hypotheses.

Introduction

Nothofagus' the genus of Southern Beeches, has long been regarded as the key to our understanding of southern hemisphere biogeography, at least for the Pacific region (Darlington, 1965; Van Steenis, 1971, 1972; Melville, 1973; Humphries, 1981, 1983; Hill, 1992). *Nothofagus* dominates cool-temperate forests in the circum-Pacific southern continents, and may be regarded as being a characteristic element of these forests, which are distinct from their surrounding vegetation in almost every possible way (McQuillan, 1993). *Nothofagus* has an excellent fossil record of distinctive pollen (Cranwell, 1963; Hanks and Fairbrothers, 1976; Praglowski, 1982; Dettman et al., 1990) and macrofossils (Carlquist, 1987; Hill, 1987, 1991, 1992; Pole et al., 1993), which is continuous from the Late Cretaceous until the present.

Ever since 1853, when J. D. Hooker drew attention to a widespread antarctic flora in southern South America, Australasia and Africa, separated by vast oceans (Hooker, 1853), several explanations of this disjunction have been proposed: geological or climatic vicariance of a once continuous flora (Hooker, 1853; Croizat, 1952; Humphries, 1981; Craw, 1989; Seberg, 1991; Crisci et al., 1991b; Weston and Crisp, 1994); migration southwards from ancient, continuous distributions around the northern continents (Darwin, 1859; Darlington, 1965);

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migration along land-bridges (Van Steenis, 1963); long-distance dispersal (Darlington, 1965; Pole, 1993, 1994; Hill, 1992); rafting on drifting continents (Brundin, 1965); and short-distance dispersal across much narrower ocean basins (Raven and Axelrod, 1974).

More recently, phylogenetic systematists have provided a method for relating the evolutionary history of biota to that of the earth (Brundin, 1965; Rosen, 1976, 1978; Platnick and Nelson, 1978; Nelson and Rosen, 1981; Humphries and Parenti, 1986). Cladistic biogeographers search for congruent biogeographical patterns from multiple groups of organisms distributed disjunctly over the same areas. If a single pattern is found, it is likely that this is caused by a single series of events, rather than several independent events. Cladistic biogeographical analyses have demonstrated a repeated pattern of vicariance across the Pacific (Brundin, 1966; Edmunds, 1981; Seberg, 1991). Since *Nothofagus* was widely distributed in Eastern Gondwana prior to continental breakup (Dettmann et al., 1990), it appears likely that the relationships of the species between the different Gondwanan fragments should reflect the break-up sequence. Similarly, other taxa with the same disjunct pattern should reflect the same history. Despite expectations, cladistic biogeographical analyses of *Nothofagus*, in conjunction with other plant groups, have failed to produce a single pattern across the southern Pacific common to all taxa (Seberg, 1991; Crisci et al., 1991b). The phylogeny of *Nothofagus* could be fitted onto the Gondwanan fragments only by postulating several long-distance dispersal events (Humphries, 1981, 1983). Recently, the data underlying these earlier phylogenetic hypotheses of *Nothofagus* have been severely criticised (Jones, 1986; Hill, 1991). A new set of morphological characters was used to produce a cladogram (Hill and Jordan, 1993) consistent with a new classification which recognised four subgenera (Hill and Read, 1991). Almost simultaneously, a phylogeny based on nucleotide sequences of the large subunit of the rubisco gene (*rbc*L) was published (Martin and Dowd, 1993). The morphological characters are assumed to be encoded by the nuclear genome, while the *rbc*L gene is located in the chloroplast genome, so the two data sets are logically independent. These new data suggest that a re-analysis of the plant biogeographic patterns across the southern Pacific may be fruitful.

Methods

Phylogeny Reconstruction

The software used for the biogeographical analysis (COMPONENT ver. 2) requires fully resolved trees for its input. If polytomies are input, the programme will resolve these randomly. It was therefore necessary, where biogeographically important nodes were polytomies, to resolve these using the best available information. Consequently, in several of the phylogenies reported below, attempts were made to resolve some of the polytomies.

Nothofagus

Previously published data sets were used: the morphological data set of 26

characters, prepared by Hill and Jordan (1993), and the *rbc*L data set of Martin and Dowd (1993), which has 46 informative characters. For the phylogenetic analyses, PAUP (Phylogenetic Analysis Using Parsimony, Swofford, 1993) and Hennig86 (Farris, 1988) were used. For the PAUP analyses we used heuristic searches, with 500 replicates of random entries to the stepwise addition, and using nchuck=1 and chucklen=1 to restrict the number of trees held at each step during the search. This procedure was found to be more effective than using a single stepwise addition, followed by tree bisection–reconnection branch swapping with the PAUP default of 100 trees held at each step. For Hennig86 the ie* routine was used; this is expected to find all most parsimonious trees. The assumption that the data sets contain a phylogenetic signal (that the characters are cladistically co-variant) was tested by performing a Permutation Tail Probability test. This establishes whether the data set is effectively random or not (Faith, 1991; Faith and Cranson, 1991). Carpenter (1992) suggests that corroboration by itself should be adequate, and that there is no need for statistical tests; however, the possible lack of congruence between parsimonious trees based on different data sets indicates the need for some evaluation of the underlying support for various nodes within data sets. Källersjö et al. (1992) and Hillis (1995) indicate that the permutation approach may indeed provide the best test for the presence of structure within a data set. The relative sensitivity of the nodes on the trees to perturbations in the data set was tested by a bootstrap analysis, in which the frequency occurrence of each node within a set of 500 randomly resampled data sets is established (Felsenstein, 1985; Sanderson, 1989). Hillis and Bull (1993) showed that bootstrapping provides a very conservative test of the accuracy of the cladogram, but that the absolute values may not be very meaningful.

Initially, the two data sets were analysed separately to locate the sets of minimal length trees, to calculate statistics on the robustness of the trees, and to assess the phylogenetic signal in the data sets. The congruence between the data sets was tested by generating the combinable components consensus tree from the two sets of trees (Bremer, 1990), but no further statistics were calculated to establish whether the differences between the trees could be due to chance alone (Rodrigo et al., 1993).

To establish a single phylogenetic hypothesis, the two data sets were combined and analysed as one. There are slight differences in the sampling techniques used to collect the molecular and the morphological data. Molecular data were collected from single specimens, one for each species, and not all species were sampled. The morphological data were collected from several specimens for each species, and all species were represented. Here we assume that the species are correctly delimited, and that the data from single specimens can be combined with data from a set of specimens. Only species for which both molecular and morphological data are available were used and, following Huelsenbeck et al. (1994), the data set was unweighted. The species which lack molecular data all belong to section *Brassospora*, including two of the five New Caledonian species and 10 of the 14 New Guinean species.

Other Taxa

Phylogenies of *Aristotelia* (Elaeocarpaceae, Coode, 1985), *Cyttaria* (Fungi—

Ascomycotina, Crisci et al., 1988), Restionaceae (Johnson and Briggs, 1981; Linder, 1984, 1987), Iridaceae (Goldblatt, 1990, 1991, 1993; Goldblatt et al., 1990; Rudall, 1994), Haemodoraceae (Simpson, 1990), Danthonieae (Poaceae, Barker et al., 1995, unpublished data), Cunoniaceae (Hufford and Dickison, 1992), Embothrieae (Proteaceae, Weston and Crisp, 1994), *Oreobolus* (Cyperaceae, Seberg, 1988, 1991), Winteraceae (Vink, 1988; Suh et al., 1993), Canellaceae (Wilson, 1964, 1965, 1966) and Strelitziaceae (Kress et al., 1994) were used to construct a general area-cladogram. Most of these were unproblematic, and were used as reported in the literature; in some, however, different data-sources had to be reconciled.

Coode (1985) published a manually constructed cladogram for *Aristotelia*, but did not include a data-table. A data-table was reconstructed from the cladogram and characters and re-analysed.

Iridaceae presented several problems, for although Goldblatt and associates have published extensively on the Iridaceae, they have not compiled a single combined cladogram. We therefore spliced various parts together, using the basal nodes suggested by Goldblatt (1990), and adding the details on the Nivenoideae from Goldblatt (1993) and the Sisyrinchieae from Goldblatt et al. (1990). This is not as satisfactory as compiling a single detailed data set from which a global analysis can be performed, as the support for the topology cannot be assessed. The tree is somewhat at variance with that of Rudall (1994), but this does not affect the biogeographical interpretation.

Oreobolus R. Br. was revised by Seberg (1988), who recognised 14 species and three subspecies. Seberg produced a cladogram which he subsequently modified (Seberg, 1991), due to more efficient parsimony programmes finding more minimal length solutions. We re-analysed the data set, which Ole Seberg kindly made available to us, and repeated his result. In order to find more solution, we applied successive weighting (Carpenter, 1988) to the data set and located a single tree with almost the same topology as originally reported by Seberg.

Winteraceae, like *Nothofagus*, has been analysed in both morphological (Vink, 1970, 1985, 1988) and molecular (Suh et al., 1993) studies. The molecular phylogeny, based on ITS1 and ITS2, could not be rooted, as the sequences of the potential outgroups, *Magnolia, Schisandra* and *Canella*, were too different from the sequences of the Winteraceae to allow alignment. To construct a morphological tree, the data from Vink (1988) were re-analysed. The topology of the morphological tree is congruent with that of the molecular tree, but the molecular tree has more resolution in the *Zygogynum* clade, whereas the morphological tree is rooted, by including the Canellaceae, as suggested by Chase et al. (1993) on the basis of *rbc*L variation. The greater resolution within the *Zygogynum* clade may be due to severe undersampling for the molecular study, as only one of the ca. 28 species of *Bubbia* and none of the numerous New Guinean species of the clade, have been sampled. Thus, the morphological data reflect the variation within the group much more closely than do the molecular data, which results in an inability to distinguish between the genera included by Vink in *Zygogynum*. To obtain a phylogeny with a root provided by the morphological data set and resolution from the molecular data set, the two sets were combined. Of the two cloned paralogous sequences in the molecular data set, only that available for all species was used, taking care that the homologous set was used for the *Zygogynum* clade. Where

Table 1
Data set for Canellaceae, compiled from Wilson (1964, 1965, 1966).

Character list	
0.	Petals: free (0); fused (1).
1.	Flowers: terminal (0); axillary (1).
2.	Petals: numerous (0); 12 four-whorled (1); 10 biwhorled (2); 5 singlewhorled (3) [additive].
3.	Stamens: numerous (0); 12 (1); 10 (2) 5 (3); [additive].
4.	Placentas: 2 (0); 3–4 (1); 5 (2); 6 (3) [additive].
5.	Floral whorls: two (0); one (1).
6.	Vessels in cross-section: round (0); angular (1).
7.	Crystals: absent (0); present (1).
8.	Pollen sulcus margin: distinct (0); indistinct (1).
9.	Vessels: solitary (0); paired or grouped (1).

Distribution of character states	0 5 10
Winteraceae	0000??????
Canella	1132010100
Pleodendron	0011301100
Cinnamodendron	0022201010
Warburgia	0022200111
Cinnamosma	1032111110

there is more than one species sequence per genus, the morphological set was duplicated to fit the sequence data (see Linder and Kellogg, 1995). The analysis was performed using Hennig86, but the result was evaluated using MacClade ver. 3 (Maddison and Maddison, 1992).

Canellaceae are used as outgroup for Winteraceae, following the *rbc*L analyses of Chase et al. (1993). There is no published cladogram for Canellaceae; the data of Wilson (1964, 1965, 1966) were used to compile a data set (Table 1).

The tree of Danthonieae was compiled from unpublished data on variation in the *rpo*C2 grass specific insert variation (Barker et al., in prep.; Cummings et al., 1994).

Biogeographical Analysis

The choice of areas of endemism is critical for a successful biogeographical analysis (Platnick, 1991; Crisci et al., 1991b; Harold and Mooi, 1994). However, the areas of endemism should be appropriate for the hypotheses to be tested, and the organisms should be chosen to fit the areas of endemism. The hypothesis tested in this paper is the areal relationships suggested by the chironomid work of Brundin, that Australia is closer to South America than either is to New Zealand. The appropriate areas for this analysis would be the continental areas around the South Pacific: southern South America, including the Andes (SAm), New Zealand (NZ), Australia (including Tasmania) (Aus) and New Caledonia (NC). New Guinea (NG) was used as a separate area, despite the fact that it is on the same continental block as Australia and Tasmania. As several taxa used have a wider southern Hemisphere distribution, Africa, north-eastern South America and Madagascar were also included in the analyses. The division of South America into separate areas, with separate histories, was suggested by Humphries (1981),

Parenti (1981) and Crisci et al. (1991a), and the division used here separates the southern region, as well as the Andes and the western coastline, into "southern South America", while north-eastern South America includes the Amazon basin and the areas east of the Andes.

To locate biogeographical signal in distributional data and phylogenetic hypotheses, COMPONENT ver. 2 (Page, 1993a) was used. This method maps the area-cladogram of each species onto the postulated general area-cladograms, and measures the fit by a minimum number of items (duplications, deletions, or minimum number of independent losses of leaves) needed to reconcile the cladograms (Page, 1993a). The distributional hypothesis that fitted the data best was chosen by minimising the number of duplications (*ad hoc* hypotheses of sympatric speciation) and deletions (*ad hoc* hypotheses of extinction or dispersal). All analyses were undertaken using two assumptions. Assumption 0 accepts the scored pattern as correct; thus, two areas sharing a widespread taxon are assumed to be sister-areas or monophyletic (Zandee and Roos, 1987). Assumption 1 constrains two areas sharing a widespread taxon to be mono- or paraphyletic (Nelson and Platnick, 1981; Page, 1989). Assumption 2 allows the areas sharing a widespread taxon to be polyphyletic. We did not implement Assumption 2, as it would require the evaluation of nearly 3000 area-cladograms, an impossible task. To get around the COMPONENT limit of ten taxa, we combined Restionaceae, Strelitziaceae and *Aristotelia* in one cladogram, and Canellaceae and Winteraceae into another (Appendix).

We tested for significant congruence of area-patterns among the input taxa. Our method derives from Page (1988, 1989), and is further explained by Weston and Crisp (1994) and Crisp et al. (1995). We compared the real data set with many randomised data sets, each including the same number of input cladograms (ten) as the real data set. The randomised data sets included the real distributions of the taxa. Twenty randomisations were made (a larger number would have been computationally impractical), and each analysis was done under both assumptions for widespread species. The optimized value (number of leaves added) was compared in the results from real and randomised data sets: if no randomised data set achieved a value as low as (or lower than) the real data, then congruence could be considered significant at a probability level of less than 5%.

To test the fit of the cladogram for *Nothofagus* to the general area-cladogram, the *Nothofagus* cladogram was reconciled to the general area-cladogram, using COMPONENT ver. 2.

Results

Phylogenetic Hypotheses

The morphological data for all taxa of *Nothofagus* supported 12 equally parsimonious trees (L=59, CI=0.644, RI=0.9, Fig. 1), and the *rbc*L sequence data supported 54 trees (L=160, CI=0.637, RI=0.801, Fig. 2). The combinable components consensus of the *rbc*L and the morphological trees produced very poorly resolved results (Fig. 3), with only four clades retrieved: *Nothofagus* and subgenera *Nothofagus, Lophozonia* and *Fuscospora,* as well as some structure in subgenus *Fuscospora.*

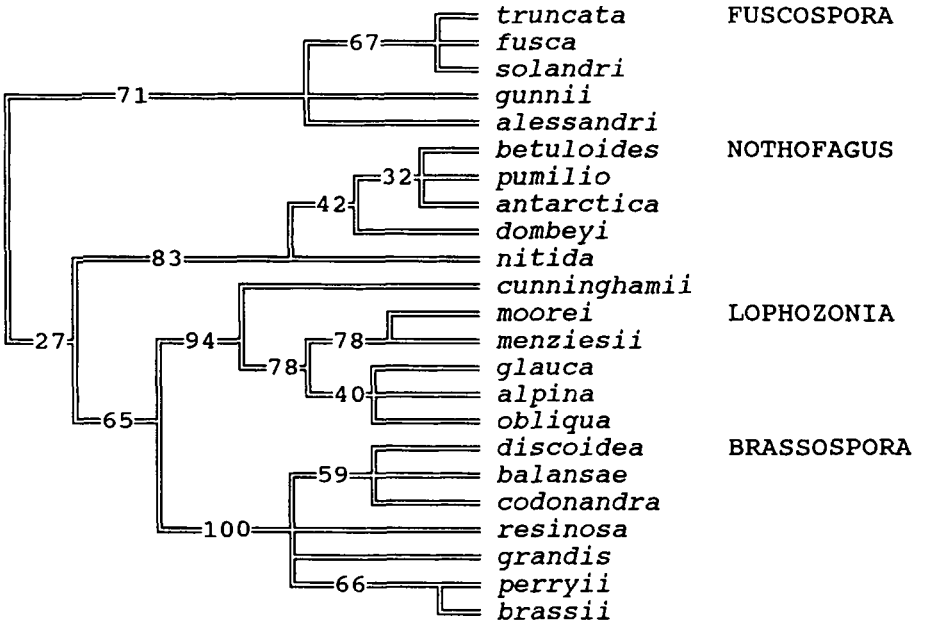

Fig. 1. Strict consensus tree based on the morphological data for taxa for which molecular data are available: L=57, CI=0.632, RI=0.9. The figures on the internodes indicate the bootstrap values for 100 replicates. Note that subgenera *Fuscospora* and *Nothofagus* were linked by 55% of the replicates.

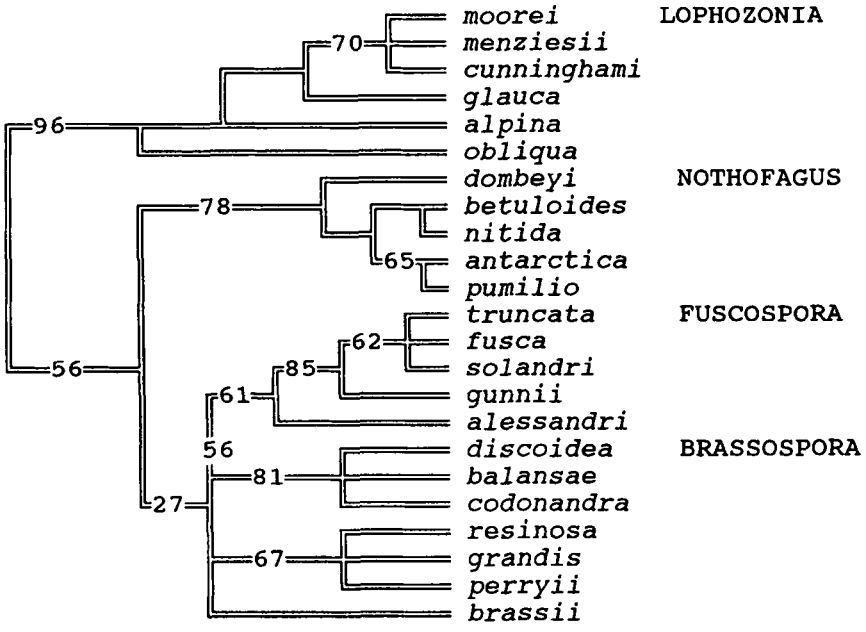

Fig. 2. Strict consensus tree based on the *rbc*L data, with 200 bootstrap replicates values added. The bootstrap value for subgen. *Brassospora* is added, as this exceeds 55%.

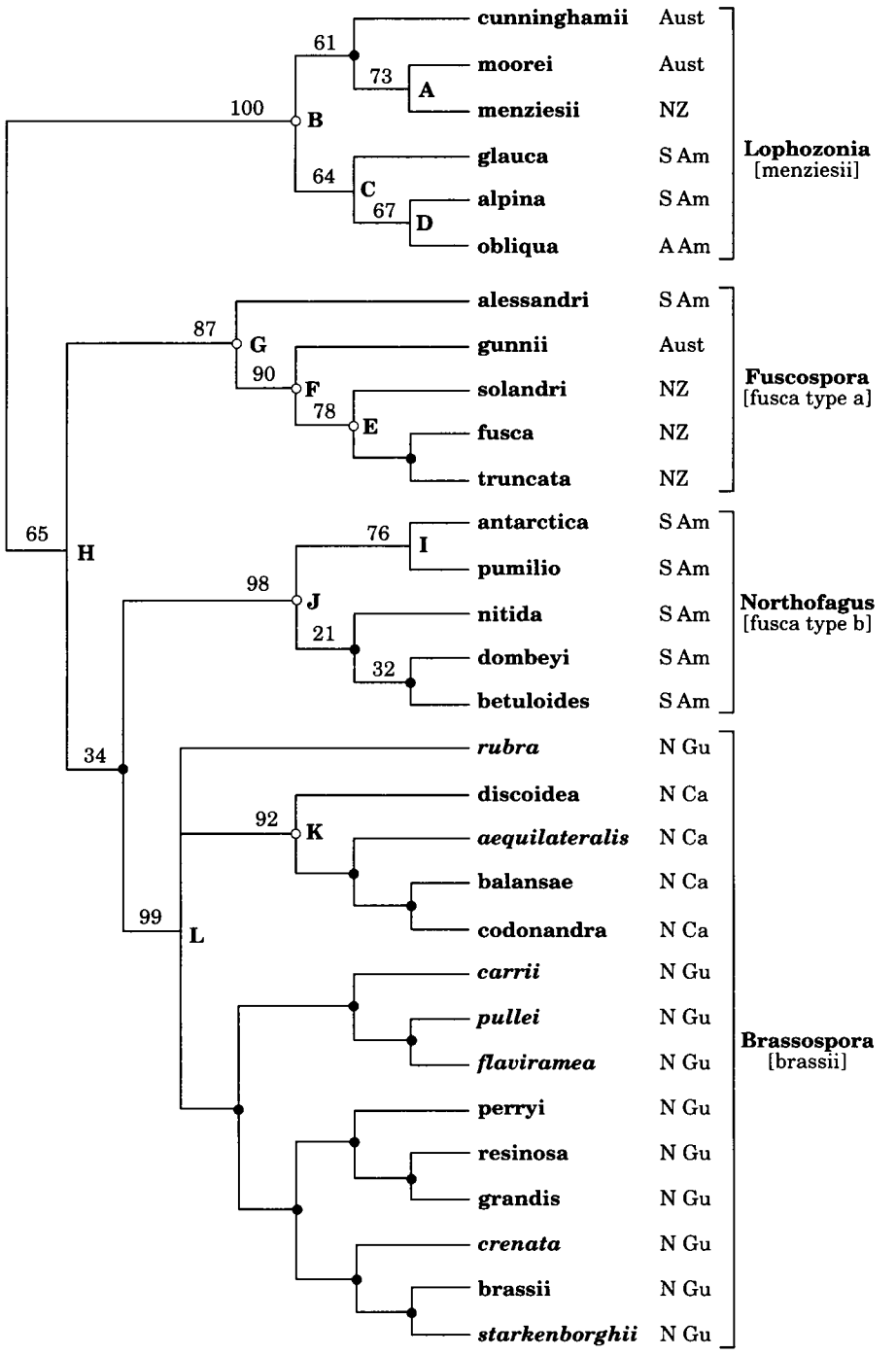

Fig. 3. Hypothesized phylogenetic tree for *Nothofagus*, using morphological and molecular (*rbcL* sequence) data. Taxa for which molecular data are not available are inserted on the evidence of the morphological data. Open circles indicate nodes found in a consensus analysis of separate morphological and molecular trees; closed circles indicate nodes not common to all minimal length trees from the total evidence analysis. Pollen types are shown in square brackets below the subgeneric classification. Bootstrap values are indicated below the nodes.

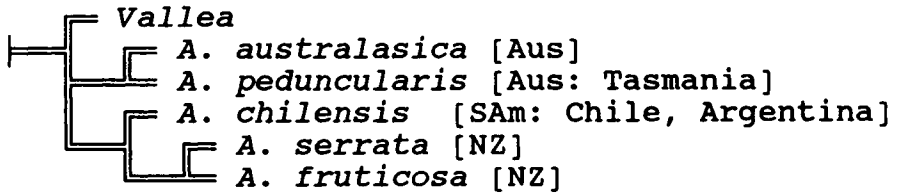

Fig. 4. Cladogram for *Aristotelia* with areas plotted on the tree.

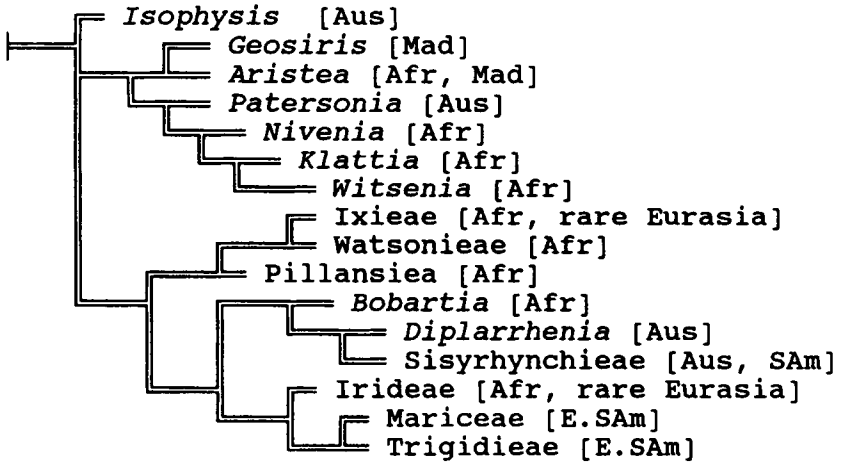

Fig. 5. Phylogeny for Iridaceae, with the areas plotted on the trees.

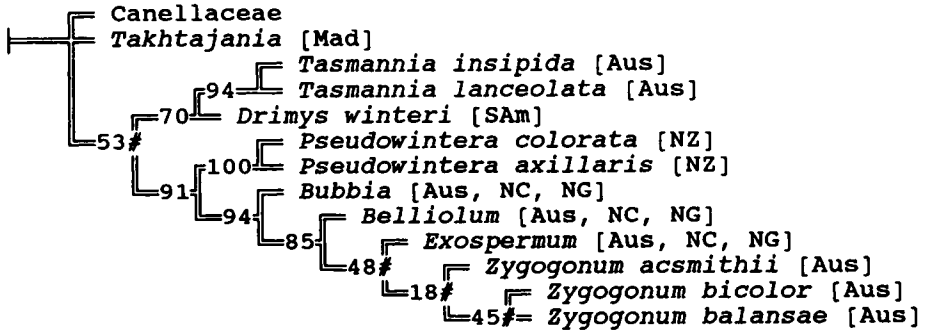

Fig. 6. One of the eight minimal length trees located for combined molecular and morphological data sets of Winteraceae. The length is 105 steps, the retention index 90. Nodes which collapse in the strict consensus tree are indicated by hashes; bootstrap percentiles from 500 resampled replicate data sets are indicated on the branches. The distribution areas for each species are plotted onto the cladogram.

An analysis of the combined data sets, but excluding the 12 taxa for which only morphological data are available, resulted in 18 trees (L=301, CI=0.714, RI=0.828). The strict consensus tree (Fig. 3) is better resolved than the *rbc*L tree. An analysis of the combined data sets, including taxa for which only morphological data are

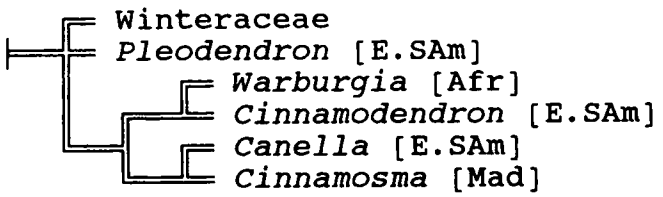

Fig. 7. One of three cladograms for Canellaceae, based on Table 1, with L=17, CI=88, RI=75. The distribution areas for each species are plotted onto the cladogram.

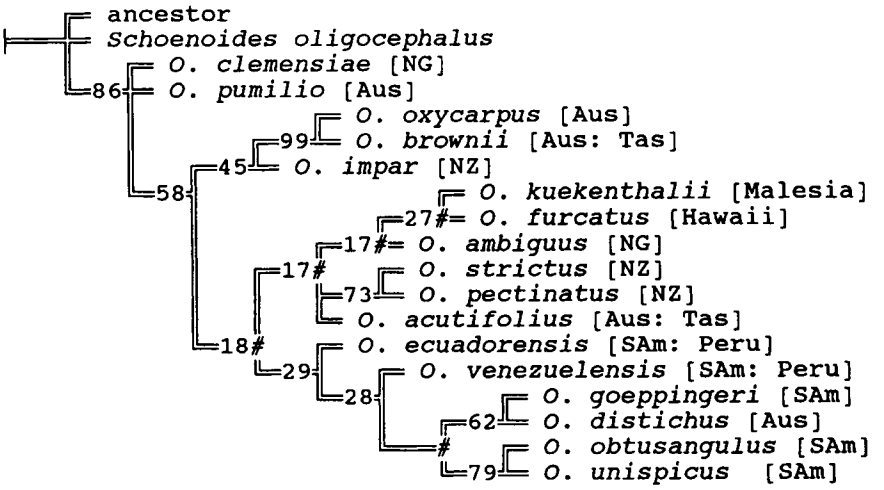

Fig. 8. Tree for *Oreobolus* (Cyperaceae) located by successive weighting from the set of 10 most parsimonious trees. Nodes which collapse in the strict consensus tree are indicated with hashes; bootstrap percentiles from 500 resampled replicate data sets are indicated on the branches. The distribution areas for each species are plotted onto the cladogram.

available (i.e. including all species of *Nothofagus*), resulted in 900 trees before the memory ran out (L=303, CI=0.710 and RI=0.845). The strict consensus tree is identical to the tree with the excluded taxa, and the added taxa are all included in the subgen. *Brassospora*, where they form an unresolved polytomy at the basal node of the subgenus.

The cladogram for *Aristotelia* is given in Fig. 4, Iridaceae in Fig. 5, Winteraceae in Fig. 6, Canellaceae in Fig. 7, and *Oreobolus* in Fig. 8. Bootstrap values and tree statistics, where appropriate, are given in the figures.

Biographical Hypotheses

The analysis located a single tree for both assumptions (Fig. 9). Both assumptions 0 and 1 were significant at the 5% level. For assumption 0, the real data gave 249 minimum leaves added, while the randomised data gave between 298 and 300 leaves added. For assumption 1, the real data gave 243 leaves added, and the randomised data gave between 280 and 331 leaves added.

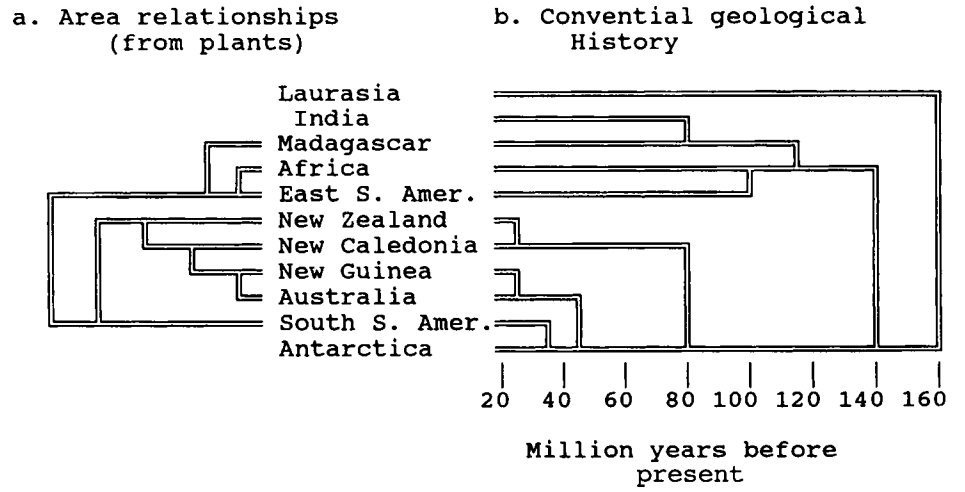

Fig. 9. General area-cladogram, constructed using Page's (1994) modification of component analysis, and matched against a reconstruction of geological vicariance events, based on Scotese et al. (1988). An approximate time-scale is indicated below the diagram.

The reconciled tree for *Nothofagus* is given in Fig. 10, and indicates the postulated extinction and sympatric speciation events.

Discussion

Phylogenetic Hypotheses: The Use of All Evidence

The strict consensus tree from our re-analysis of the morphological data set is congruent with that found by Hill and Jordan (1993), but we could not retrieve the trees and statistics reported by Martin and Dowd (1993) for the *rbc*L data, perhaps due to differing analytical procedures. Specifically, we failed to find support for a monophyletic subgen *Brassospora*. The combined analysis retrieved a more resolved set of most parsimonious trees than the combinable components consensus from the separate morphological and molecular trees.

There has been some debate on whether to combine different data sets that are informative on the phylogeny of a group of taxa, or whether to partition the data sets (Miyamoto, 1985; Kluge, 1989; Barrett et al., 1991; Swofford, 1991; Vane-Wright et al., 1992; Bull et al., 1993; De Queiroz, 1993; Chippindale and Wiens, 1994; Olmstead and Sweere, 1994; Miyamoto and Fitch, 1995). Combining all data into one "total evidence" analysis is logically sound and analytically advantageous (Kluge, 1989; Olmstead and Sweere, 1994); but if different data sets do not track the same phylogeny the results will be misleading (Swofford, 1991; Doyle, 1992). For *Nothofagus* and the Winteraceae, both morphological and molecular data are available. In the Winteraceae the molecular tree is based on a nuclear gene, and returns substantially the same phylogeny as the morphological data. For this family it makes no difference whether the two data sets are analysed separately and the

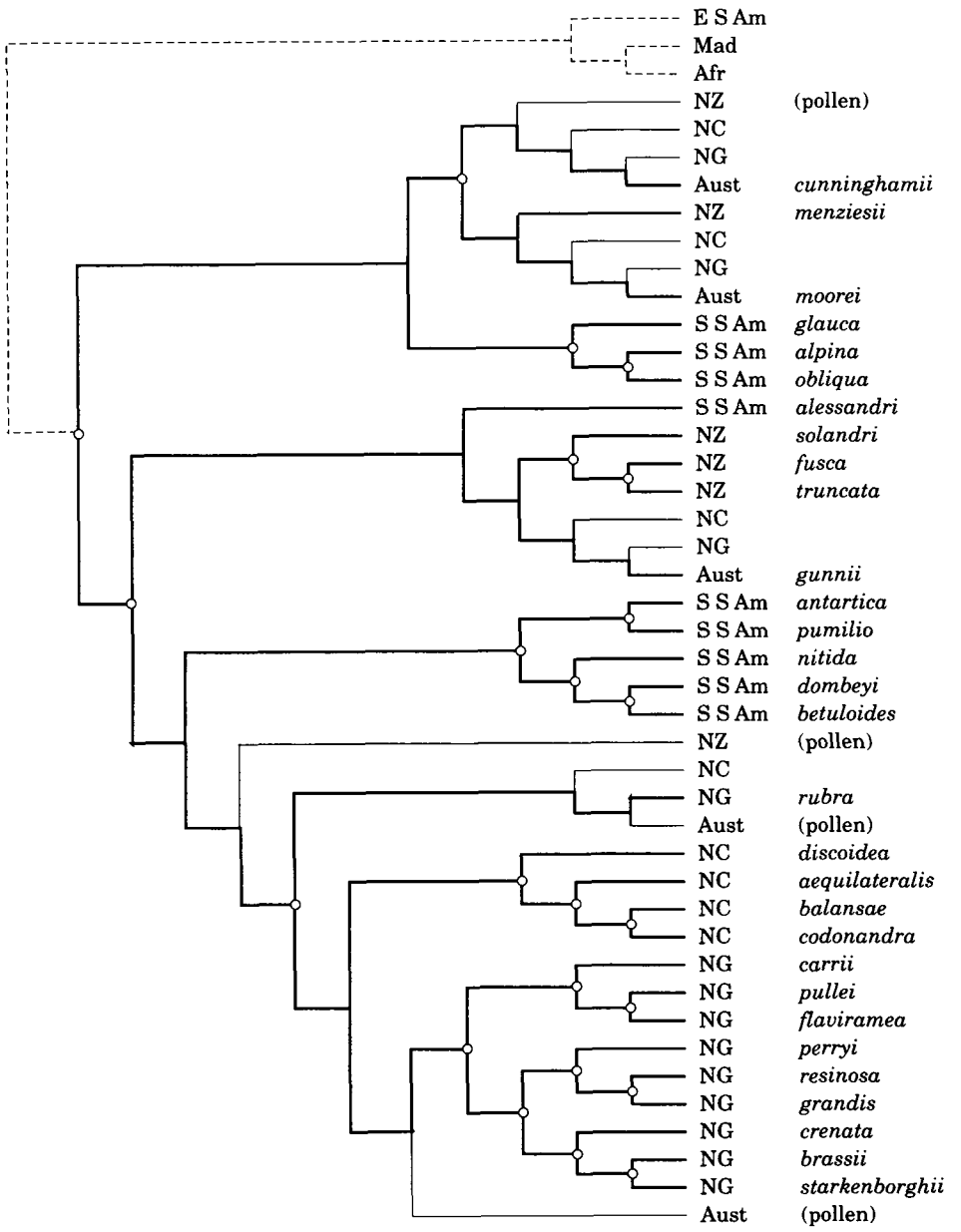

Fig. 10. Reconciliation between the general area-cladogram and the cladogram for *Nothofagus*. Circles indicate duplication of components (equivalent to sympatric speciation events). Thick lines indicate those components of the general area-cladogram that are represented by extant taxa; thin lines indicate missing components (no extant taxon); dashed lines indicate components for which *Nothofagus* is uninformative.

consensus of the two analyses is obtained, or whether the data sets are combined for a "total evidence" analysis.

This is not the situation in *Nothofagus*. The molecular data set is chloroplast-

Table 2

Evaluation of the support in the morphological and molecular trees for the nodes located in the combined analysis. The node codes are given in Fig. 3, the figures refer to bootstrap values, unresolved nodes are indicated by (+), while conflicting nodes are shown by (−). The average values are calculated for all nodes retrieved in the strict consensus trees for each data set.

Node	*rbc*L	Morphology	Total
A	+	78	73
B	96	94	100
C	−	40	64
D	−	+	67
E	62	67	78
F	85	+	90
G	61	71	87
H	56	−	65
I	65	+	76
J	78	83	98
K	81	59	92
L	+	100	99
Average	63	64.4	81

encoded, while the morphological data set is assumed to be nuclear-encoded. A consensus analysis of cladograms from the two sources of data supports delimitation of three subgenera, and cladistic structure within subgenus *Fuscospora*, but does not resolve groupings at other levels (Fig. 3). The basal branching within the genus is incongruent between the two data sets, and the detailed structure within three of the four subgenera is not identical. Incongruence between the two sets of phylogenetic hypotheses may result from the nuclear and plastic genes which, respectively, code for the morphology and the large subunit of rubisco, tracking different phylogenies (Doyle, 1992). Alternatively, it may be that the data samples are inadequate to establish accurate phylogenetic hypotheses (Rodrigo et al., 1993). The congruence in the delimitation of the subgenera suggests that the incongruence at higher levels may be due to the latter problem. This is further supported by the relatively low bootstrap values at these nodes for the separate data sets (27–65%). Furthermore, the solution for the combined data set (*Lophozonia*, (*Fuscospora*, *Nothofagus*, *Brassospora*)) differs from that of the morphological data set (*Fuscospora*, *Nothofagus*, (*Lophozonia*, *Brassospora*)) but is consistent, though less resolved, than that of the *rbc*L (*Lophozonia*, (*Nothofagus*, (*Brassospora*, *Fuscospora*)). In this instance, the molecular data set appears to track deeper history better than the morphological data set.

At species level, the situation is reversed, and the results of the combined analysis differ from the morphological analysis only in providing additional resolution (e.g. nodes D, F and I, Table 2), while being incongruent with two nodes on the *rbc*L tree (nodes C and D, Table 2). This suggests that the morphological data may be more informative than the molecular data for more recent events.

Olmstead and Sweere (1994) report that bootstrap values appear to be related to the number of characters used. This is partially corroborated here: the 26 morphological and 46 molecular characters both returned averaged bootstrap values of 60–65%, while the 72 combined characters returned 81%. Note that these were only calculated for nodes retained in the strict consensus trees.

However, this may simply indicate that in *Nothofagus* the combined analysis combines the strengths of the two data sets (*rbc*L for the basal nodes, morphological for the terminal nodes) rather than the weaknesses, thus resulting in a generally better result (cf. Donoghue and Sanderson, 1992). Thus, despite the incongruence between the *rbc*L and morphological results, a combined analysis may return more informative results.

Biogeography: the Pattern

Many of the taxa used in the analysis are not restricted to the southern Pacific; consequently, we used a set of areas that encompasses the whole Southern Hemisphere. However, here we do not wish to extend our interpretation to the Atlantic patterns. Nonetheless, an intriguing pattern emerges, which links Madagascar as sister area to Africa plus north-eastern South America. These three areas form a sister-area relationship to the southern Pacific areas.

The general pattern for the relationship around the southern Pacific from our plants is (SAm, (NZ, (Aus, NG))) (Fig. 9). Although numerous extant taxa have distributions that span the Pacific (Hooker, 1853; Croizat, 1952; Takhtajan, 1986; Crisci et al., 1991b), until now it has been difficult to locate a single congruent pattern, largely due to the different phylogeny estimates for *Nothofagus*. This pattern is consistent with most taxa examined, suggesting that it is robust. We note, though, that many taxa do not show unambiguous three-area statements and are therefore not informative on this pattern, and the degree of corroboration of the pattern may therefore not be as high as it seems.

This pattern is incongruent with that found for chironomid midges (Brundin, 1966) and mayflies (Edmunds, 1981; Cranston and Naumann, 1991): (Aus, (NZ, SAm)). Craw (1989), combining the available plant and animal distributions and analysing them under Assumption 0, also retrieved the (Aus, (NZ, SAm)) pattern, which is also consistent with the conventional hypothesis of the breakup sequence of Gondwana (Fig. 9). According to this convention, New Zealand has been isolated for 80 Myr (Stevens, 1989), while both Australia and South America have been in contact via Antarctica until ca. 40–30 Myr (Barker and Burrell, 1977; Coleman, 1980; Crook, 1981; Veevers, 1991).

Consequently, there are now two patterns reported for the southern Pacific: (SAm, (NZ, Aus)), supported by the plant data reported here, and (Aus, (SAm, NZ)), supported by insect data and geology.

Biogeography: Evolution of *Nothofagus*

The biogeographical history of a taxon can be interpreted from a variety of sources. "Narrative biogeography" (Ball, 1975) constructs a hypothesis for a taxon in isolation from other histories (see also modern attempts at this, e.g. Bremer, 1992; Enghoff, 1993; Ronquist, 1994). Cladistic biogeography may interpret the extent to which the biogeography of a taxon matches a general explanation, using the "items of error" criterion developed by Nelson and Platnick (1981) and implemented by Page (1993a, 1993b).

The optimisation of *Nothofagus* onto the generalised area-cladogram (Fig. 10) makes a set of predictions of sympatric speciation and extinctions. If there are no

predicted sympatric speciations or extinctions, then each vicariance event is assumed to be accompanied by a speciation event. In addition, it implies that there are no speciation events without vicariance, and there are no extinctions. In fact, Fig. 10 indicates substantial sympatric speciation and extinction. Virtually every subgenus has undergone some sympatric speciation and, considering the size of the areas used here, this is not surprising. These speciation events need not be sympatric at a smaller scale; this would be tested only by splitting the continents into several smaller areas for further biogeographical analysis. Of interest are the extinctions suggested by the optimisation—these are suggested by "missing" sister-lineages. For example, subgen. *Brassospora* is currently known from New Guinea and New Caledonia, with fossil records indicating extinction in Australia, New Zealand and South America. The optimisation predicts the extinctions from Australia and New Zealand, and would also have been predicted as extinct from South America but subgen. *Nothofagus*, the sister-lineage of subgen. *Brassospora*, is known from there. Conversely, if subgen. *Brassospora* were not the sister-lineage of subgen. *Nothofagus*, then subgen. *Nothofagus* would be recorded as extinct from all other areas. Considering the weak support for these nodes on the cladogram, the alternatives, of even more extensive extinction, should also be entertained. Thus, the predictions from this analysis are consistent with what is known from the fossil record. Where extinction and sympatric speciation have not occurred, the optimised tree accounts for speciation by vicariance, and this is shown in subgen. *Fuscospora* and *Lophozonia*, in which the vicariance pattern is (SAm, (Aus, NZ)).

On this basis several evolutionary scenarios can be built. The dispersalist scenario suggests that *Nothofagus* has a centre of origin, whence it dispersed to its present areas (e.g. Truswell et al., 1987; Hill, 1994). This scenario requires no hypotheses of extinction, only of sympatric speciation. It requires at least two trans-Tasman dispersal events, in a genus said to be a poor disperser (Preest, 1963). The vicariance scenario requires as a starting hypothesis that the genus was widespread in its current distribution area, and that the modern distribution of the species was established by vicariance and extinction, as well as by sympatric speciation (Croizat et al., 1974). This latter scenario is consistent with the fossil record of *Nothofagus*.

Nothofagus was a significant component of the "*Nothofagidites*" floristic province of south-eastern Gondwana in the late Cretaceous. Floristic descriptions have been published for different areas for the Late Cretaceous and Early Tertiary, e.g. Australia, Tasmania (Hill, 1987, 1992), New Zealand (Pole, 1993) and Antarctica (Dettmann, 1989; Askin, 1990; Truswell, 1990). These all indicate a remarkably homogeneous flora and vegetation over southern South America, portions of Antarctica, New Zealand and southern Australia. Unfortunately, there appear to be no fossil records from New Guinea and New Caledonia for this period. Palaeopollen data indicate that the subgenera of *Nothofagus* were widespread on the Gondwanan continents in the Tertiary (Dettmann et al., 1990), suggesting that diversification to the level of subgenera occurred in the genus before the relevant continents became separated. If this were the case, then the relationships between species, rather than between the subgenera, should reflect post-break-up differentiation, as suggested by Fig. 10. We have found this for all trans-Pacific taxa except the Winteraceae and Embothriinae, which have different genera on the different sides of the Pacific. The fossil data therefore corroborate the extensive extinctions predicted from the cladistic biogeographical analysis, showing that the

current restriction of subgen. *Nothofagus* and subgen. *Brassospora* to single continents is the result of extensive extinction.

Two subgenera (*Lophozonia* and *Fuscospora*) of the four are potentially informative about the biogeography of the Gondwanan fragments, because they have living representatives in South America, New Zealand and Australia (including Tasmania). The other two subgenera have living representatives in only one or two areas. Subgenus *Nothofagus* is restricted to southern South America, while subgenus *Brassospora* is found in New Guinea and New Caledonia. Both biogeographically informative subgenera suggest that Australia is more closely related to New Zealand than to South America.

Some interpret this pattern as the result of long-distance dispersal from Australia to New Zealand during the Tertiary, citing also the presence of *Acacia, Eucalyptus* and *Casuarina* in New Zealand during the Tertiary (Hill, 1992; Pole, 1993, 1994). They further 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. We do not think that absence data in the fossil record are informative, and support three well-known arguments for the vicariance hypothesis against the dispersal hypothesis (Nelson and Platnick, 1981). First, if dispersal is stochastic, then each disjunction is established as a separate event and, given that many taxa share the Australia–New Zealand–southern South America disjunction, it would take many dispersal events, but only two vicariance events, to explain this (Patterson, 1981). Second, the details of the relationship between the three areas are remarkably constant among the data sets, with Australia consistently more closely related to New Zealand than to South America. Such congruence is expected under a vicariance model (Croizat et al., 1974; Platnick and Nelson, 1978; Patterson, 1981). Third, the predicted ancestral presence of certain subgenera of *Nothofagus* in New Zealand, Australia and South America (Fig. 6) is substantiated by the fossil record (Dettmann et al., 1990), with current absence presumably resulting from extinction.

A close phytogeographic relationship between Australia and New Zealand suggests that the conventional chronology of continental breakup may not accurately reflect the establishment of disjunctions in the biota. This may be due to several factors. First, there may have been land connections between New Zealand and Australia during the Tertiary. The Lord Howe Rise, a continental fragment running north-west from New Zealand, remained very close to the exposed Queensland Plateau until the mid-Tertiary (Walley and Ross, 1991). The notion of a "composite New Zealand", as suggested by Humphries and Parenti (1986), may reflect a similar situation, where some terranes may show a closer relationship to Australia, while others have more affinity to South America. Second, an unknown vicariance may have occurred between South America and the land areas now comprising Australia and New Zealand while they were still part of this contiguous East Gondwana. This even would be older than 80 Myr, and might involve West Antarctica (Storey et al., 1988). It might also be linked to climatic deterioration along the Antarctic Peninsula, which would have closed off this connection between South America and Australia–New Zealand (Askin, 1990). Third, concordant dispersal (Page and Lydeard, 1994) of plants, perhaps mediated by the westerly circulation which was established around 30 Myr, may have established a

close Australia–New Zealand relationship (e.g. Pole, 1994). Concordance dispersal models will predict that different taxa should have dispersed independently over a long period and should therefore not be congruent when timing is taken into account. New Zealand should then have a complex history, linking closely but at different times to both South America and Australia.

A molecular clock might provide a test for vicariance versus dispersalist explanations of the observed pattern (Martin and Dowd, 1988, 1991; Hedges et al., 1994). However, such tests must be constructed carefully to avoid the numerous problems with molecular clocks (Page and Lydeard, 1994); currently available data are not sufficiently replicated to be used.

Conclusions

We have demonstrated general biogeographic congruence among the plants of Eastern Gondwana, linking southern South America to New Zealand, Australia, New Caledonia and New Guinea. This generality would suggest a single historical explanation, which is vicariance across a disintegrating Gondwana. With a reliable phylogeny, we have found *Nothofagus* to be completely congruent with the general pattern. The excellent fossil record of *Nothofagus* allows this general pattern, with its associated hypotheses of ancestral presence (and subsequent extinction), to be tested, thus corroborating the relationship between geological and biological evolution.

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Appendix: Datafile from COMPONENT

```
  NEXUS
BEGIN TAXA;
  DIMENSIONS NTAX=9;
  TAXLABELS
    Mad
    Aust
    NZ
    SAm
    NC
    NG
    Afr
    NAm
    EAm

  ;

ENDBLOCK;

BEGIN DISTRIBUTION;
    TITLE='Nothofagus';
    NTAX=30;
    RANGE
```

```
    alessandrii      : 4,
    alpina           : 4,
    antarctica       : 4,
    balansae         : [2 3 4 6] 5,
    betuloides       : 4,
    brassii          : [2 3 4 5] 6,
    codonandra       : [2 3 4 6] 5,
    cunninghamii     : 2,
    discoidea        : [2 3 4 6] 5,
    dombeyi          : 4,
    fusca            : 3,
    glauca           : 4,
    grandis          : [2 3 4 5] 6,
    gunii            : 2,
    menziesii        : 3,
    moorei           : 2,
    nitida           : 4,
    obliqua          : 4,
    perryii          : [2 3 4 5] 6,
    pumilio          : 4,
    resinosa         : [2 3 4 5] 6,
    solandri         : 3,
    truncata         : 3,
    aequilateralis   : [2 3 4 6] 5,
    carrii           : [2 3 4 5] 6,
    crenata          : [2 3 4 5] 6,
    flaviramea       : [2 3 4 5] 6,
    pullei           : [2 3 4 5] 6,
    rubra            : [2 3 4 5] 6,
    starkenborghii   : [2 3 4 5] 6;

TREE
T1=(((1,(14,(22,(11,23)))),(((3,20),(17,(5,10))),(29,(9,(24,(4,7))),
(((26,(6,30)),(19,(13,21))),(25,(27,28))))))),((12,(2,18)),(8,(15,16))));

ENDBLOCK;


BEGIN DISTRIBUTION;
  TITLE='Winteracea';
  NTAX=10;
  RANGE
     Takhtaja      : 1,
     Tasmanni      : 2, 6,
     Zygogynu      : 2 5 6,
     Pseudowi      : 3,
     Drimys        : 4,
     Pleodendron   : 9,
```

```
    Warburgia       : 7,
    Cinnamodendron  : 9,
    Canella         : 9,
    Cinnamosma      : 1;

TREE T1=((1,((2,5),(3,4))),(6,((7,8),(9,10))));

ENDBLOCK;


BEGIN DISTRIBUTION;
  TITLE='Restionaceae';
  NTAX=5;
  RANGE
    Hopkinsia       : 2,
    Restio          : 1 7,
    Centrolepis     : 2 3 4 6,
    Alexgeorgia     : 2,
    Leptocarpus     : 2 3 4 6;

TREE T1=(1,(2,(3,(4,5))));

ENDBLOCK;


BEGIN DISTRIBUTION;
  TITLE='Haemodoraceae';
  NTAX=13;
  RANGE
    Barberetta      : 7,
    Blancoa         : 2,
    Conostylis      : 2,
    Dilatris        : 7,
    Haemodorum      : 2,
    Lachnanthes     : 8,
    Anigozanthos    : 2,
    Phlebocarya     : 2,
    Pyrrohiza       : 9,
    Schieckia       : 9,
    Tribonanthes    : 2,
    Wachendorffia   : 7,
    Xiphidium       : 9;

TREE
T1=((((13,(1,12)),(9,10)),(4,6)),(5,(8,(11,(7,(2,3))))));

ENDBLOCK;
```

```
BEGIN DISTRIBUTION;
  TITLE='Danthonioid';
NTAX=16;
RANGE
      Merxmuellera      :  7,
      Prionanthium      :  7,
      Pentaschistis     :  7,
      Pentameris        :  7,
      Chionochloa       :  3,
      Lamprothyrsis     :  3, 4,
      Pseudopentameris  :  7,
      Chaetobromus      :  7,
      Danthonia         :  4 8,
      Plinthanthesis: 2,
      Notochloe         :  2,
      Schismus          :  7,
      Karoochloa        :  7,
      Tribolium         :  7,
      Pyrranthera       :  3,
      Rytidosperma      :  2 3 4 6;

TREE
T1=(1,((4,(2,3)),(5,(6,((7,8),((9,(10,11)),(14,(12,13),(15,16)))))));

ENDBLOCK;



BEGIN DISTRIBUTION;
  TITLE='Embothriinae';
  NTAX=12;
RANGE
      E—coccineum       :  2 4,
      O—grandiflora     :  4,
      O—mucronata       :  4,
      A—pinnatum        :  2,
      A—wickhamii       :  2,
      A—flammeum        :  2,
      A—brachycarpum    :  6,
      T—speciossisim    :  2,
      T—sp              :  2,
      T—truncata        :  2,
      T—oreades         :  2,
      T—mongaensis      :  2;

  TREE T1=(1,((2,3),(4,(5,(6,7))),((8,9),(10,(11,12)))));

ENDBLOCK;
```

```
BEGIN DISTRIBUTION;
  TITLE='Iridaceae';
  NTAX=16;
  RANGE
     Geosiris        : 1,
     Aristea         : 1 7,
     Patersonia      : 2,
     Nivenia         : 7,
     Klattia         : 7,
     Witsenia        : 7,
     Ixieae          : 7,
     Watsonieae      : 7,
     Pillansieae     : 7,
     Trigideae       : [4] 9,
     Mariceae        : [4] 9,
     Irideae         : 7,
     Sisyrinchium    : 2 4,
     Diplarrhena     : 2,
     Bobartia        : 7,
     Isophysis       : 2;

  TREE
T1=(16,(((1,2),(3,(4,(5,6)))),((9,(7,8)),((12,(10,11)),(15,(13,14))))));

ENDBLOCK;



BEGIN DISTRIBUTION;
  TITLE='Oreobolus';
  NTAX=15;
  RANGE
     clemens         : 6,
     pumilio         : 2,
     oxycarpus       : 2,
     brownii         : 2,
     impar           : 3,
     ambiguus        : 6,
     strictus        : 3,
     pectinatus      : 3,
     acutifolius     : 2,
     ecuadorensis    : 4,
     venezuelensis   : 4,
     goepping        : 4,
     distichus       : 2,
     obtusang        : 4,
     unispicatus     : 4;
```

```
  TREE
T1=(1,2,((5,(3,4)),((6,9,(7,8)),(10,(11,((12,13),(14,15)))))));

ENDBLOCK


BEGIN DISTRIBUTION
  TITLE='Cyttaria';
  NTAX=11;
  RANGE
     darwinii          : 4,
     bertonii          : 4,
     hookeri           : 4,
     gunnii            : 2 3,
     hariotii          : 4,
     espinosa          : 4,
     septentrionalis   : 2,
     johowii           : 4,
     nigra             : 3,
     pallida           : 3,
     exigua            : 4;

  TREE T1=((5,((1,11),(6,(2,((4,10),(7,9)))))),(3,8));

ENDBLOCK;


BEGIN DISTRIBUTION;
  TITLE='Aristotelia';
  NTAX=5;
  RANGE
     australasica      : 2,
     peduncularis      : 2,
     chilensis         : 4,
     serrata           : 3,
     fruticosa         : 3:

  TREE T1+((1,2),(3,(4,5)));

ENDBLOCK;



BEGIN DISTRIBUTION;
  TITLE='Strelitziaceae';
  NTAX=3;
  RANGE
     Ravenala          : 1,
```

```
    Phenakospermum :  9,
    Strelitzia     :  7;

  TREE T1=(1,(7,9));

ENDBLOCK;


BEGIN DISTRIBUTION;
  TITLE='Cunoniaceae';
  NTAX=24;
  RANGE
    ackama         :  3,
    acrophyllu     :  2,
    aistopetal     :  6,
    anodopetal     :  2,
    aphanopeta     :  2,
    bauera         :  2,
    brunellia      :  4,
    caldcluvia     :  2 3 4,
    callicoma      :  2,
    ceratopeta     :  2 6,
    codia          :  2 5 6,
    cunonia        :  5 7,
    eucryphia      :  2 4,
    geissois       :  2 5,
    gillbeea       :  2 6,
    opocunonia     :  6,
    pancheria      :  5,
    platylophu     :  7,
    pseudowein     :  2,
    schizomeri     :  2,
    spiraeanth     :  2 5 6,
    spiraeopsi     :  6,
    vesseleowsk    :  2,
    weinmannia     :  1 3 4;

  TREE
T1=(15,(22,(((16,(1,(8,9,(2,5,6)))),(23,(12,17,24))),((4,(10,20),(14,19)),
(11,18)))),(13,(3,(7,21))));

ENDBLOCK;
```