Phytotaxa 146 (1): 1–31 (2013)
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.146.1.1

Revised circumscription of *Nothofagus* and recognition of the segregate genera *Fuscospora*, *Lophozonia*, and *Trisyngyne* (Nothofagaceae)

PETER B. HEENAN[1] & ROB D. SMISSEN
Allan Herbarium, Landcare Research, PO Box 69040, Lincoln 7640, New Zealand
[1]*E-mail: heenanp@landcareresearch.co.nz*

Abstract

The generic taxonomy of the Nothofagaceae is revised. We present a new phylogenetic analysis of morphological characters and map these characters onto a recently published phylogenetic tree obtained from DNA sequence data. Results of these and previous analyses strongly support the monophyly of four clades of Nothofagaceae that are currently treated as subgenera of *Nothofagus*. The four clades of Nothofagaceae are robust and well-supported, with deep stem divergences, have evolutionary equivalence with other genera of Fagales, and can be circumscribed with morphological characters. We argue that these morphological and molecular differences are sufficient for the four clades of Nothofagaceae to be recognised at the primary rank of genus, and that this classification will be more informative and efficient than the currently circumscribed *Nothofagus* with four subgenera.

Nothofagus is recircumscribed to include five species from southern South America, *Lophozonia* and *Trisyngyne* are reinstated, and the new genus *Fuscospora* is described. *Fuscospora* and *Lophozonia*, with six and seven species respectively, occur in New Zealand, southern South America and Australia. *Trisyngyne* comprises 25 species from New Caledonia, Papua New Guinea and Indonesia. New combinations are provided where necessary in each of these genera.

Key words: DNA sequence data, Fagales, generic names, genus concept, new combinations

Table of contents

Introduction

The genus *Nothofagus* Blume (1851: 307) as it is currently circumscribed comprises 42 species of deciduous and evergreen forest trees that have a disjunct Southern Hemisphere distribution. Species occur in South America (south-western Argentina and Chile), Australia (south-eastern Australia and Tasmania), New Zealand, New Guinea (Papua New Guinea, Indonesia, and also New Britain and the D'Entrecasteaux

Accepted by Hans-Joachim Esser: 28 Oct. 2013; published: 12 Nov. 2013

Archipelago), and New Caledonia. The genus also has an abundant fossil record (e.g. Hill 1991, 2001) and is well-represented by pollen that first appeared in the early Campanian of the Late Cretaceous (83.5 mya; Dettmann *et al.* 1990). Pollen and macrofossil records both indicate that *Nothofagus* occurred throughout much of southern Gondwana before the breakup of that continent. The widespread distribution and excellent fossil record of *Nothofagus* have resulted in the genus being a key focus of Southern Hemisphere biogeographic research (e.g., Steenis 1971, Humphries 1981, Tanai 1986, Pole 1994, Linder & Crisp 1995, McGlone *et al.* 1996, Ladiges *et al.* 1997, Manos 1997, Sanmartín & Ronquist 2004, Knapp *et al.* 2005).

The current infrageneric taxonomy of *Nothofagus* is now well-established and was erected by Hill & Read (1991). These authors divided the genus into four subgenera: subgenus *Brassospora* Philipson & Philipson (1988: 34), subgenus *Fuscospora* Hill & Read (1991: 69), subgenus *Lophozonia* (Turczaninow 1858: 396) Krasser (1896: 162), and the autonym subgenus *Nothofagus*. This infrageneric classification superseded those of Steenis (1953a) and Philipson & Philipson (1988), classifications that were primarily based on a deciduous or evergreen habit, cupule morphology and leaf vernation and did not incorporate pollen morphology, although an informal taxonomic classification of extant and fossil species based on pollen groupings was being used by palynologists (Cookson 1952, Cookson & Pike 1955, Stover & Evans 1973). Hill & Read (1991) based their subgeneric classification on a thorough synthesis of the morphology of the leaves (including hairs and stomata), pollen and fruiting cupules. There have also been additional studies that have provided detailed analyses of the floral characters of *Nothofagus*, including staminate (Rozefelds 1998, Rozefelds & Drinnan 1998) and pistillate (Rozefelds & Drinnan 2002) flower morphology. Some of these floral characters provide support for the infrageneric taxonomy of Hill & Read (1991), but they need to be integrated with the data used by Manos (1997), Hill & Jordan (1993), and Jordan & Hill (1999) in a new phylogenetic analysis of morphological characters.

DNA sequence data have also played an important role in unravelling the evolutionary history and taxonomy of *Nothofagus*. Martin & Dowd (1993) examined the phylogeny of *Nothofagus* species using the chloroplast *rbc*L gene. They included good sampling of all the *Nothofagus* subgenera of Hill & Read (1991) and recovered clades entirely consistent with their classification, albeit with limited bootstrap support for most clades. Both the monophyly of the *Nothofagus* subgenera and the relationships among them reported by Martin & Dowd (1993) were later confirmed for another chloroplast marker (the *atp*B–*rbc*L intergenic spacer) by Setoguchi *et al.* (1997) using a similar selection of taxa. More significantly, Manos (1997) recovered congruent results using nuclear ribosomal DNA ITS spacer sequences and complementary taxon sampling to Martin & Dowd (1993), and provided a combined analysis of ITS data with the *rbc*L sequences of the earlier authors. Further, consistent DNA phylogenetic analyses have been published by Knapp *et al.* (2005) and Premoli *et al.* (2011), although neither of these studies sampled *Nothofagus* subgenus *Brassospora*. Most recently, Sauquet *et al.* (2012) conducted Maximum Likelihood (ML) phylogenetic analysis of available *atp*B, *rbc*L, *atp*B–*rbc*L intergenic spacer, *trn*L intron, *trn*L–*trn*F intergenic spacer and ITS sequences and recovered a phylogeny in which 11 clades received 95% or greater bootstrap support. These included clades equivalent to each of the *Nothofagus* subgenera and clades consistent with the relationships among them indicated by previous DNA studies: (*Lophozonia* (*Fuscospora* (*Brassospora*, *Nothofagus*))).

While the monophyly of each of the *Nothofagus* subgenera of Hill & Read (1991) and the relationships among them are overwhelmingly supported by DNA sequence data, relationships of species within the subgenera must be considered with caution. There is incongruence among chloroplast and nuclear DNA data sets (Manos 1997), and trans-specific chloroplast DNA polymorphism involving plastid lineages evidently older than the radiation of extant species most probably results from chloroplast capture (Acosta & Premoli 2010, Premoli *et al.* 2011).

Molecular clock dating using DNA sequence data is consistent with the fossil history of *Nothofagus* (Cook & Crisp 2005, Sauquet *et al.* 2012). The *Nothofagus* subgeneric lineages diverged in the Senonian (upper Cretaceous) and Eocene (Tertiary), with stem ages derived from Beast analyses of 72.1 (95% confidence intervals of 53.4–93.2) mya for *Lophozonia*, 52.8 (36.5–70.6) mya for *Fuscospora*, and 42.2 (31.5–56.4) mya for *Nothofagus* and *Brassospora* (Sauquet *et al.* 2012, fig. 2). Crown ages date from the middle Eocene and Oligocene, with *Lophozonia* diversifying at 42.0 (31.5–59.3) mya, *Fuscospora* at 30.0 (10.9–49.5) mya, *Brassospora* at 26.1 (13.9–38.9) mya, and *Nothofagus* at 24.4 (11.1–39.8) mya (Sauquet *et al.* 2012, fig. 2).

Subsequent to the publication of Hill & Read's (1991) subgeneric classification, DNA sequence studies have also clarified the relationship of *Nothofagus* to other genera of Fagales. Importantly, a close relationship with Fagaceae, and in particular a sister group relationship between *Fagus* and *Nothofagus* (Kubitzki 1993), has been rejected and *Nothofagus* has instead been shown to be the sister group of the remaining extant Fagales (Manos & Steele 1997, Li *et al.* 2004, Sauquet *et al.* 2012), and consequently is now placed in the monogeneric Nothofagaceae (Kuprianova 1962, APG 2009). Morphological and anatomical studies (Crepet & Daghlian 1980, Nixon 1982, 1989, Jones 1986, Zheng *et al.* 1999, Li *et al.* 2004) support the recognition of Nothofagaceae. The family Nothofagaceae is therefore used in this paper and a revised family description is presented in the Taxonomy section.

It has now been over 20 years since the widely used *Nothofagus* subgeneric taxonomy was erected by Hill & Read (1991), and given the significant amount of new data from morphology and DNA sequences it is timely to reassess the classification and the appropriateness of the subgeneric rank. An alternative classification of the Nothofagaceae could recognise well-supported clades at generic rank, most obviously by raising the subgenera to generic rank. To evaluate the classification of Nothofagaceae in this paper we provide a synthesis of the heterogeneous body of molecular and morphological evidence and undertake a new phylogenetic analysis of the morphological data. To provide a measure of evolutionary equivalence for interpreting these studies in regard to the generic circumscription of *Nothofagus*, we undertake a comparative study of genetic variation at generic rank in Nothofagaceae and five other families (Betulaceae, Casuarinaceae, Fagaceae, Juglandaceae and Myricaceae) of the order Fagales. Furthermore, to provide consistency in the application of morphological characters to generic circumscription, we also review the characters used in recognising three recently named new genera in the Fagaceae (Nixon & Crepet 1989, Manos *et al.* 2008).

Criteria for recognising genera

Linder *et al.* (2010) identified two categories of criteria for the circumscription of genera. Category 1 consists of criteria that pertain to the delimitation of the clades, and category 2 consists of criteria that pertain to the ranking of the clades. Like Backlund & Bremer (1998) and many other authors, Linder *et al.* (2010) explicitly place category 1 above category 2, preferring that the criterion of monophyly should first be met by any candidate taxon. We concur that monophyly is a desirable characteristic of taxa and that classification systems should seek to maximise the recognition of well-supported monophyletic groups. Because many aspects of the phylogeny of the Nothofagaceae are well-known and straightforward, the criterion of monophyly can be met without unduly sacrificing other criteria. The specific criteria we adopt for category 1 are that: 1—clades received bootstrap support 95% or greater in the analysis of Sauquet *et al.* (2012); 2—clades are able to be defined by morphological synapomorphies.

Considering Linder *et al.* (2010) and also Backlund & Bremer (1998) we adopt the following criteria for the ranking of clades (category 2).

1. Primary taxonomic ranks (e.g. family, genus, species) as defined in the International Code of Nomenclature (ICN; McNeill *et al.* 2012) should be used first in a classification, and secondary ranks (e.g. subgenus) used as required.
2. Classifications should maximise phylogenetic information and minimise redundancy.
3. Taxonomic ranks should reflect evolutionarily-equivalent groups. This encompasses clade age, genetic distance, and morphological diversity. We acknowledge this can be difficult to achieve and needs to consider contemporary use of ranks in related taxa.
4. Ideally, genera will be morphologically homogeneous.
5. For the sake of users and nomenclatural stability name changes should be minimised, but consideration should also be given to the full taxonomic history of a group and not just the last revision.

Material and methods

Morphological phylogeny and character evolution

We present two phylogenetic analyses of morphological data. In Analysis 1, we reanalyse the morphological data of Jordan & Hill (1999), with the addition of characters from other studies (e.g. Hill & Read 1991, Manos 1997, Rozefelds 1998, Rozefelds & Drinnan 1998, 2002, Jordan & Hill 1999). We also add three characters for the presence or absence of three *Cyttaria* (Berkeley 1842: 40) lineages documented in Peterson *et al.* (2010). Character 10 of Jordan & Hill (1999)—pollen equatorial diameter—was omitted because the coding used therein does not agree with the data presented in Praglowski (1982). Character 11 (wood anatomy, tracheids present or absent; Jordan & Hill 1999) was also removed due to criticism by Rozefelds (1998) and Rozefelds & Drinnan (2002). The characters scored are listed in Appendix 1, and the morphological matrix is presented in Appendix 2. Analysis 1 was conducted with the heuristic search option of PAUP* 4.0b10.1 (Swofford 2002), treating all characters as unordered and using default settings. Bootstrap scores were calculated from 100 replicates using full heuristic searches.

The phylogenetic analysis of Sauquet *et al.* (2012) is the most thorough undertaken to date and comprises a maximum likelihood (ML) analysis of combined sequence data from six regions of the chloroplast and nuclear genomes. The tree derived from this ML analysis identified 11 well-supported clades of *Nothofagus* including clades equivalent to the subgenera *Brassospora*, *Fuscospora*, *Lophozonia* and *Nothofagus*. For Analysis 2, we mapped the morphological characters from Analysis 1 onto a tree constrained to match those branches supported by ≥ 95% bootstrap in the Sauquet *et al.* (2012) analysis, with the aim of identifying morphological characters supporting those clades, using MacClade 4.03 (Maddison & Maddison 2001).

For both analyses we used two outgroups—Betulaceae and *Fagus* Linnaeus (1753: 997–998)—both representatives of the sister group to Nothofagaceae (being the clade encompassing the other families of Fagales) and each having been used in previous cladistic analyses of the family using morphological characters (Hill & Jordan 1993, Manos 1997, Jordan & Hill 1999). Character coding for outgroups was based on these previous studies and information from Praglowski (1982), Dengler & MacKay (1975) and Denk (2003).

Evolutionary equivalence

Comparison of rbc*L variation in families of Fagales*

In order to provide a measure of evolutionary equivalence and taxonomic diversity and to be consistent in the application of generic circumscription in Nothofagaceae in comparison with genera in other families of the Fagales, we undertook an analysis of DNA sequence variation among genera of the Betulaceae, Casuarinaceae, Fagaceae, Juglandaceae and Myricaceae. Nothofagaceae are represented in this analysis by (a) the genus *Nothofagus* and (b) the four *Nothofagus* subgenera. The chloroplast gene *rbc*L is well-sampled across these families and so we used this locus to estimate genetic distances within and among genera. We used MEGA 5.05 (Tamura *et al.* 2011) to align all the *rbc*L sequences available at the time in GenBank (totalling 445) and generated a Neighbour-Joining tree using Jukes-Cantor distances. Using this tree as a guide we selected 161 representative sequences covering the phylogenetic diversity of each genus and reducing the level of redundancy in taxon coverage. Sequences were then grouped according to family and genera and genetic distances computed using the p-distance model. The data were subjected to the ML molecular clock test implemented in MEGA. The GenBank accession numbers of the sequences used are provided in Appendix 3.

Morphology of new genera in Fagaceae

Three new genera in Fagaceae have recently been described. *Formanodendron* Nixon & Crepet (1989: 840) and *Colombobalanus* Nixon & Crepet (1989: 840–841) are monotypic genera segregated from the now monotypic *Trigonobalanus* Forman (1962: 140). The monotypic *Notholithocarpus* Manos, Cannon & Oh (2008: 188) was segregated from *Lithocarpus* Blume (1826: 526). We review the morphological characters used to circumscribe these genera, and compare these characters and their variation to similar characters in Nothofagaceae.

Results

Category 1 criteria—circumscribing clades

A heuristic search of the morphological character matrix in PAUP 3.1 (Analysis 1) found 12 most parsimonious trees with a length of 84 steps, consistency index 0.679, rescaled consistency index 0.599, and retention index of 0.883. These trees featured four main clades (Fig. 1) corresponding to the four *Nothofagus* subgenera and indicating that each of these is monophyletic. *Nothofagus* subgenus *Lophozonia* appears as sister group to the remainder of the family and *Nothofagus* subgenus *Nothofagus* is sister group to a clade composed of *Nothofagus* subgenus *Fuscospora* and *Nothofagus* subgenus *Brassospora*. The strict consensus tree along with bootstrap support values is shown in Figure 1.

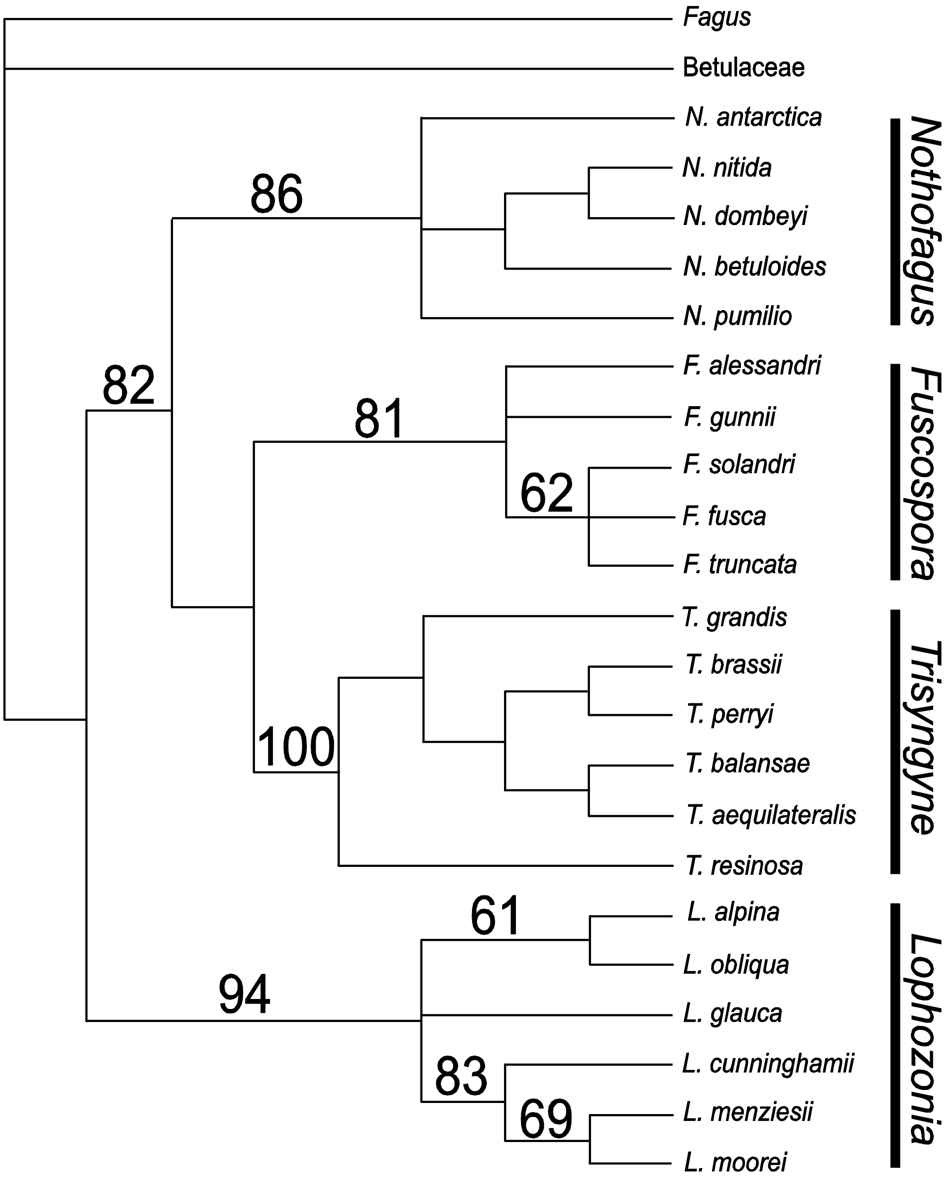

FIGURE 1. Strict consensus of most-parsimonious trees from heuristic search of morphological character data (Analysis 1) for *Fuscospora* (*Nothofagus* subgenus *Fuscospora*), *Lophozonia* (*Nothofagus* subgenus *Lophozonia*), *Nothofagus* (*Nothofagus* subgenus *Nothofagus*), and *Trisyngyne* (*Nothofagus* subgenus *Brassospora*). Numbers above branches are bootstrap values from 100 replicates where these are > 50.

We traced morphological character evolution onto a tree constrained by a 95% bootstrap consensus tree based on the DNA phylogeny of Sauquet *et al.* (2012) (Analysis 2; Fig. 2). This identified unique morphological synapomorphies for eight of the 11 clades supported by 95% bootstrap or greater as detailed below. Our analysis did not identify unique morphological synapomorphies for three clades that were well-supported in the DNA sequence analysis of Sauquet *et al.* (2012). These clades were the one combining the South American species of *Nothofagus* subgenus *Lophozonia*, one combining *N. menziesii* and *N. moorei*, and a clade comprising the Australian and New Zealand members of *Nothofagus* subgenus *Fuscospora*.

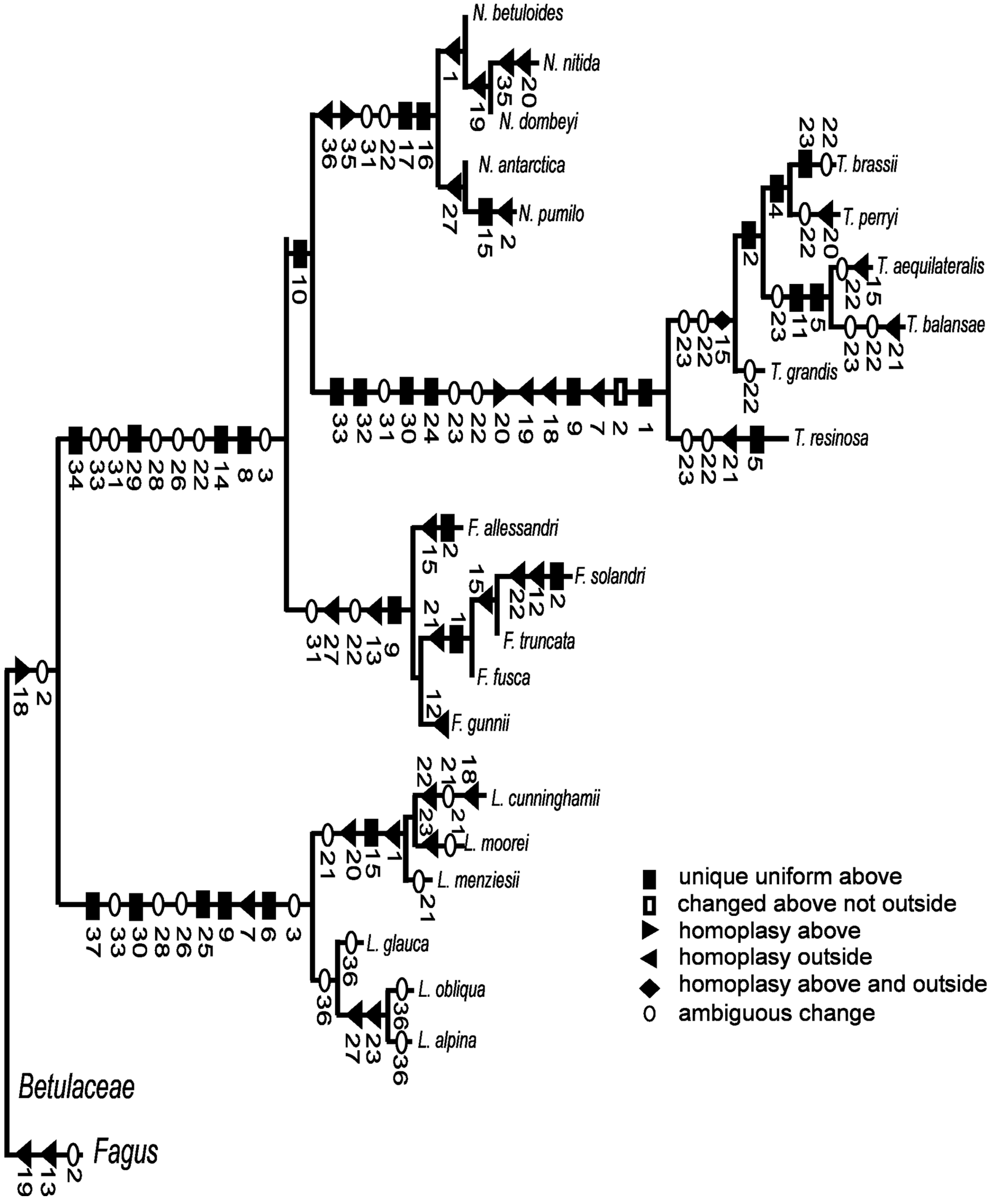

FIGURE 2. Morphological characters mapped onto a 95% bootstrap consensus tree, derived from Sauquet *et al.* (2012) (Analysis 2) for *Fuscospora* (*Nothofagus* subgenus *Fuscospora*), *Lophozonia* (*Nothofagus* subgenus *Lophozonia*), *Nothofagus* (*Nothofagus* subgenus *Nothofagus*), and *Trisyngyne* (*Nothofagus* subgenus *Brassospora*).

Nothofagus subgenus *Brassospora*

Analysis 2 suggested six unique synapomorphies for subgenus *Brassospora* (Fig. 2). These are character 1, state 3: leaf vernation conduplicate; character 9, state 2: pollen aperture rimmed; character 24, state 1: filaments connate; character 30, state 2: staminate perianth tubular; character 32, state 2: anther distal connective protrusion strongly developed; and character 33, state 2: cupule glabrous.

For character 2, subgenus *Brassospora* is unique in presenting character states 1 (valves 2, fruit 3 dimerous) and 2 (valves 2, fruit 1 dimerous). Manos (1997) interpreted the dimerous flowers as a bicarpellate synapomorphy for subgenus *Brassospora*. Character 18, state 0 (giant stomata present) is also optimised as a synapomorphy for subgenus *Brassospora*, but giant stomata also occur in *N. cunninghamii* (Hooker 1840: 152, t. 7) Ørsted (1871: 355) of subgenus *Lophozonia* and in the outgroups. Character 19, state 0 (stomatal size more or less even excluding giant stomata) is also optimised as a synapomorphy for subgenus *Brassospora,* but this condition occurs in *N. dombeyi* (Mirbel 1827: 467, t. 24) Ørsted (1871: 354) and *N. nitida* (Philippi 1858: 44) Krasser (1896: 163) of subgenus *Nothofagus* and in *Fagus*. Character 20, state 2 (upper epidermal cells over veins thinner than areolar cells) is unique to subgenus *Brassospora* but in *N. perryi* Steenis (1952a: 146) is reversed to state 1 (upper epidermal cells over veins not distinguishable from areolar cells). Within *Nothofagus* subgenus *Brassospora*, the New Caledonian species (*N. aequilateralis* and *N. balansae*) share the unique synapomorphies of character 5, state 0: cupule valves woody, and character 11, state 1: phyllotaxy spiral.

Nothofagus subgenus *Fuscospora*

Only one unambiguous and unique synapomorphy for subgenus *Fuscospora* was suggested by Analysis 2 (Fig. 2). This is character 9, state 1 (pollen aperture with heavy thickening).

One additional character is a potential syapomorphy. Character 13, state 1 (unicellular trichome type A absent) was optimised as synapomorphic for *Fuscospora* in Analysis 2 and is unique in Nothofagaceae, but also occurs in *Fagus*.

Nothofagus subgenus *Lophozonia*

Unambiguous and unique synapomorphies supporting the monophyly of subgenus *Lophozonia* are (Fig. 2): character 6, state 1: staminate flowers pseudanthium present; character 9, state 3: pollen aperture unthickened; character 25, state 1: usually > 20 stamens (sometimes with < 20 stamens in *N. cunninghamii*); character 30, state 1: perianth open and broadly campanulate; and character 37, state 1: *Cyttaria* lineage C present.

Four further characters are potentially synapomorphies of subgenus *Lophozonia* but because they were not scored or are polymorphic in the outgroups they can be optimised equally parsimoniously as synapomorphies for the other three subgenera combined. These potential synapomorphies are character 3, state 1: cupule with glandular lamellae; character 26, state 1: pollen aperture ends V-shaped; character 28, state 1: stamen development pseudocentrifugal; and character 33, state 1: outer surface of valves densely covered with simple trichomes.

Within this clade the evergreen species [*N. cunninghamii*, *N. menziesii* (Hooker 1844: t. 652) Ørsted (1871: 355), and *N. moorei* (Mueller 1866: 109) Krasser (1896: 161)] are characterised by the unique synapomorphy of broad-based conical trichomes; character 15, state 2.

Nothofagus subgenus *Nothofagus*

Analysis 2 suggested two unambiguous and unique synapomorphies for subgenus *Nothofagus* (Fig. 2). These are character 16, state 1 (stomates with thickened T-pieces of cuticle at the poles) and character 17, state 1 (stomatal orientation mostly parallel with the midrib).

One additional character is a potential synapomorphy. Character 35 state 1 (*Cyttaria* lineage A present) was optimised as a unique synapomorphy for subgenus *Nothofagus*, but has been lost in *N. nitida*.

Nothofagus subgenus *Fuscospora* + subgenus *Brassospora* + subgenus *Nothofagus*

Unambiguous and unique synapomorphies supporting the monophyly of this clade are character 34, state 0: pollen aperture length 4–11 µm; character 29, state 0: staminate perianth lobe number 4; character 14, state 1: solitary unicellular trichome type C absent; and character 8, state 1: pollen equatorial diameter l/E < 0.3. In addition, there are the four ambiguously optimised character state changes described above as possible synapomorphies for subgenus *Lophozonia* that could be synapomorphies for this clade with equal parsimony.

Nothofagus subgenus *Brassospora* + subgenus *Nothofagus*

A single synapomorphy was identified by Analysis 2 for this clade. This was character 10, state 1: stipule attachment peltate.

Category 2 criteria—ranking the clades

Comparison of rbcL *variation in families of Fagales*

DNA-sequence-based genetic distances can provide a useful guide to the range of phylogenetic diversity represented by taxa. Although we do not suggest that in isolation genetic distances are an appropriate measure for determining taxonomic rank, they can be used to assess evolutionary equivalence and can be considered along with other data in the decision-making process. We used genetic distances at the chloroplast *rbc*L locus to compare the level of genetic diversity within *Nothofagus* and its subgenera with genetic diversity within and among genera in other families of the Fagales. While a strict molecular clock can be confidently rejected for the Fagales *rbc*L data we have analysed ($P < 0.0001$), examination of phylograms suggests that the level of variation in substitution rate is not so great as to entirely invalidate such a comparison.

By far the greatest phylogenetic diversity (as estimated from *rbc*L sequences) of any family in the order Fagales is found in Fagaceae (Table 1). Most of this diversity is captured by the division of the family into two clades corresponding with *Fagus* on the one hand and the remaining genera on the other. Net p-distance between *Fagus* and the other genera ranges from 0.029 to 0.035. Within the non-*Fagus* clade, *Chrysolepis* Hjelmquist (1948: 117) *rbc*L sequences differ by p-distances between 0.011 and 0.014 from the other genera. P-distances among the sequences of *Castanopsis* (Don 1825: 56) Spach (1841: 185), *Castanea* Miller (1754: 278), *Lithocarpus*, *Quercus* Linnaeus (1753: 993–997), and *Trigonobalanus* are all 0.005 or less. The greatest *rbc*L sequence diversity within a genus in the Fagales (excluding *Nothofagus*) is found in *Fagus* (Fagaceae) with *rbc*L p-distances of up to 0.017 between species.

Sequence diversity of *rbc*L within Nothofagaceae (with *Nothofagus* as the sole genus) is nearly twice as great as for *Fagus* at 0.030 (Table 1). Even with the four *Nothofagus* subgenera treated as four genera as proposed in this paper, *rbc*L p-distances within them would range from 0.015 to 0.018 (ie, from slighly less to slightly more than within *Fagus*). The net *rbc*L p-distances among the four proposed genera of *Nothofagus* range from 0.006 to 0.011, well above the minimum distances observed among genera in all the other Fagales families.

TABLE 1. Variation in *rbc*L sequence data for families of the Fagales. Nothofagaceae is included twice to compare the single genus concept (*Nothofagus* sens. lat.) with the four genus concept advocated in this paper.

Family	# genera	Mean net p-distance between genera (range)	Max p-distance within genus
Fagaceae	7 genera	0.013 (0–0.035)	0.017
Casuarinaceae	4 genera	0.011 (0.002–0.015)	0.009
Myricaceae	4 genera	0.010 (0.002–0.017)	0.007
Juglandaceae	8 genera	0.007 (0–0.018)	0.003
Betulaceae	6 genera	0.007 (0.003–0.015)	0.011
Nothofagaceae	1 genus, 4 subgenera	N/A	0.030
Nothofagaceae	4 genera	0.008 (0.006–0.011)	0.018

Morphology of new genera in Fagaceae

Three new genera have recently been described in the Fagaceae (Nixon & Crepet 1989, Manos *et al.* 2008), and analysis of these provides a useful comparative framework in which to evaluate generic circumscription in Nothofagaceae. *Formanodendron* and *Colombobalanus* are monotypic genera segregated from the now monotypic *Trigonobalanus*, and these collectively form a monophyletic clade (Nixon & Crepet 1989). When placed in *Trigonobalanus*, the three species are united by characters such as valved cupules, flowers and fruits more than one per cupule, fruit triangular and often winged, and epigeal germination. However, the three species were each placed in monotypic genera as they have characters unique in the Fagaceae. These unique characters include whorled or alternate leaves; stipules connate in pairs or free, naked or scale-covered buds; erect or lax and axillary or terminal inflorescences; variation in pollen morphology; and cupules opposite/whorled or alternate.

The monotypic *Notholithocarpus* was segregated from *Lithocarpus* and distinguished on the basis of pollen morphology and multiradiate leaf trichomes (Manos *et al.* 2008). Indeed, as Manos *et al.* (2008) commented, 'we consider the pollen and multiradiate leaf trichomes and its phylogenetic placement to be strong evidence to recognise *L. densiflorus* as a separate genus'.

The characters used by Nixon & Crepet (1989) and Manos *et al.* (2008) for the recognition of *Colombobalanus*, *Formanodendron* and *Notholithocarpus* are directly comparable with the range of characters that have been used to distinguish the four subgeneric groups in *Nothofagus* (Hill & Read 1991, Manos 1997, Rozefelds 1998, Rozefelds & Drinnan 1998, 2002, Jordan & Hill 1999). Characters used to define the subgenera in *Nothofagus* include those of leaf trichomes, leaf vernation, stomata, inflorescences, flowers, pollen, and cupules.

Discussion

Our new phylogenetic analyses of morphological data support the monophyly of the four subgenera recognised by Hill & Read (1991). This is consistent with the results of previous phylogenetic studies of morphological and DNA sequence data (e.g. Hill & Jordan 1993, Martin & Dowd 1993, Manos 1997, Jordan & Hill 1999, Cook & Crisp 2005, Sauquet *et al.* 2012). In addition to the four subgenera, four further clades meet the criteria we have adopted for delimiting clades for taxonomic recognition in Nothofagaceae (category 1, see introduction). That is, they received 95% or greater bootstrap support in the analysis of Sauquet *et al.* (2012) and are diagnosable by morphological synapomorphies. These additional clades are: firstly, a clade including the *Nothofagus* subgenera *Fuscospora*, *Brassospora* and *Nothofagus*; secondly, a clade comprising *Nothofagus* subgenera *Brassospora* and *Nothofagus*; thirdly, an evergreen clade within subgenus *Lophozonia* (*N. cunninghamii*, *N. menziesii* and *N. moorei*); and fourthly, the New Caledonian species of *Nothofagus* subgenus *Brassospora*. However, the second of these additional clades does not appear in the shortest trees from parsimony analysis of morphological characters alone (Fig. 1). Our morphological phylogeny has *Nothofagus* subgenus *Fuscospora* as sister to *Nothofagus* subgenus *Brassospora*. However, the morphological phylogenies of Manos (1997) and Jordan & Hill (1999) have *Nothofagus* subgenus *Nothofagus* as sister to *Nothofagus* subgenus *Brassospora*; but we note that the species assigned to *Nothofagus* subgenus *Fuscospora* do not form a clade in the strict consensus tree for morphological data in the study of Manos (1997). In our morphological analysis an increase in tree length from 84 steps to 85 is required to make *Nothofagus* subgenus *Brassospora* sister to *Nothofagus* subgenus *Nothofagus*. In our bootstrap analysis of the morphological data, the monophyly of all the subgenera, and the sister group relationship between *Nothofagus* subgenus *Lophozonia* and the other three subgenera, together are supported by moderate to high bootstrap values (between 81% and 100%), but there is no support for relationships among the *Nothofagus* subgenera *Brassospora*, *Fuscospora* and *Nothofagus.* The third additional clade, containing the evergreen *Lophozonia* species, is unambiguously supported by our morphological analysis and robustly supported in the analysis of Sauquet *et al.* (2012), but its sister group relationships to the deciduous genera were not robustly resolved in either analysis. Likewise, the fourth clade (New Caledonian species of *Nothofagus* subgenus *Brassospora*) is unambiguously supported but its sister group relationships to New Guinean taxa were not robustly resolved in either analysis.

Since 1991 support has also accumulated for the recognition of Nothofagaceae (Kuprianova 1962) as a family distinct from Fagaceae. A close affinity of these two families within the order Fagales has been strongly rejected by phylogenetic analysis of DNA sequences. As a result the family Nothofagaceae and the genus *Nothofagus* currently name the same clade and the rank of subgenus is introduced to name its subclades—thereby using three taxonomic ranks (family, genus, and subgenus). The use of the secondary rank of subgenus is not necessary and does not conform to our preference (category 2, criterion 1, see Introduction) that primary ranks should be first used in a classification and secondary ranks only introduced if required. Our preference is to raise the four *Nothofagus* subgenera of Hill & Read (1991) to generic rank. This maintains the phylogenetic information encapsulated in the current taxonomy, but minimises the redundancy inherent in names at two ranks referring to identical clades. Moreover, because generic names form part of the binomial names of species, the groups they refer to are far more apparent to non-taxonomists than are subgenera. The elevation of Hill and Read's groups to genus rank will have the effect of promoting this important advance in the understanding of relationships among species of Nothofagaceae outside taxonomic circles (category2, criterion 2).

The recognition of four genera in Nothofagaceae would greatly increase the consistency of application of genus rank across the Fagales in line with our view that genera should reflect evolutionarily-equivalent groups (category 2, criterion 3, see Introduction). Specifically: 1—variation in genetic diversity of *rbc*L within and among genera of other families of the Fagales is comparable with that found within and among the four clades of Nothofagaceae. 2—morphological characters of recently described genera of the Fagaceae are comparable with the characters that diagnose the four clades of the Nothofagaceae. 3—the four clades of the Nothofagaceae have deep divergences older than or comparable with genera in other families of the Fagales (Sauquet *et al.* 2012).

Alternative generic taxonomies for the Nothofagaceae could also recognise two or three genera. Two genera could be the *Lophozonia* clade and another genus comprised of the remaining three *Nothofagus* subgenera. Three genera could be the *Lophozonia* clade, the *Fuscospora* clade, and the *Nothofagus* and *Brassospora* clades together. Either of these options would provide genera that are phylogenetically equivalent to each other, but in each case the larger grouping would be morphologically heterogeneous and still more diverse than genera in other families of Fagales. The three-genus option would recognise a genus composed of the current *Nothofagus* subgenera *Brassospora* and *Nothofagus*. Although this clade is supported by 95% or greater bootstrap value in the analysis of Sauquet *et al.* (2012), and is morphologically diagnosable, therefore meeting our category 1 criterion—this clade is not supported by phylogenetic analysis of morphological characters alone. This reflects the morphological heterogeneity of a clade combining the current *Nothofagus* subgenera *Brassospora* and *Nothofagus*; this would be even more the case if *Nothofagus* subgenus *Fuscospora* were also included with these latter two subgenera in a two-genus system.

Our final criterion for ranking clades—that of stability (category 2, criterion 5)—would clearly be best achieved by maintaining the status quo; that is, one genus *Nothofagus* with four subgenera as recognised by Hill & Read (1991). The two-, three-, and four-genus options would require successively more name changes. However, we note that the genus *Trisyngyne* Baillon (1874: 136), originally placed by Baillon in Euphorbiaceae, has been previously segregated from *Nothofagus* by Baumann-Bodenheim (1953, 1992) to accommodate the members of *Nothofagus* subgenus *Brassospora*, although the majority of species require new combinations in *Trisyngyne*. Steenis (1954, 1955, 1971, 1972, 1986) rejected this move, based on his view that *Nothofagus* was certainly allied with Fagaceae—a position no longer tenable. The name *Lophozonia* Turczaninow (1858: 396) is available at genus rank, although new combinations are required for all species. In balance, we consider it appropriate in this case to sacrifice nomenclatural stability in the short term, given that contemporary knowledge, as discussed above, means that the other category 1 and 2 criteria are best met by four genera. Accordingly, in the Taxonomy section that follows we propose a new classification recognising four genera in the Nothofagaceae.

Additional evidence for the recognition of four genera in Nothofagaceae comes from three other sources. Firstly, naturally occurring wild and cultivated *Nothofagus* hybrids have been recorded only between species that belong to the same subgenus. These hybrids occur between species assigned to subgenus *Fuscospora* [e.g., *N.* ×*eugenananus* Gillanders (2008: 56), *N.* ×*apiculata* (Colenso 1885: 335) Krasser (1896: 163), and *N.* ×*blairii* (Kirk 1885: 297, t. 16) Cockayne (1911: 172)], subgenus *Lophozonia* [e.g., *N.* ×*dodecaphleps* Grant & Clement (2004: 448) and *N.* ×*leonii* Espinosa (1928: 187)], and subgenus *Nothofagus* (Cockayne & Atkinson 1926, Wigston 1979, Donoso *et al.* 1990, Grant & Clement 2004, Stecconi *et al.* 2004, Gillanders 2008). This suggests a strong degree of intrinsic reproductive isolation among the different subgenera. This is an important observation since species from the subgenera *Fuscospora*, *Lophozonia* and *Nothofagus* often have sympatric distributions, and therefore have the opportunity to hybridise but apparently don't. Subgenus *Brassospora* has an isolated distribution in Papua New Guinea, Indonesia and New Caledonia, and so has no opportunity to hybridise with species from other subgenera.

Secondly, flavonoids provide diagnostic characters in *Nothofagus* subgenera *Fuscospora*, *Lophozonia* and *Nothofagus* (Russell *et al.* 2000, Wollenweber *et al.* 2003). In subgenus *Fuscospora* most species are characterized by the presence of pinosylvin, galangin flavonols and methyl ethers; in subgenus *Lophozonia* there are abundant kaempferol-type flavonols and apigenin flavones, but galangin and pinosylvin are absent; and in subgenus *Nothofagus* (*N. antarctica* only) galangin is present and pinosylvin is absent.

Thirdly, felt scales of the genera *Madarococcus* Hoy, *Chilecoccus* Miller & González, *Chilechiton* Hodgson & Miller, and *Intecticoccus* Kondo (Eriococcidae) are almost exclusively *Nothofagus* feeding (Hardy *et al.* 2008), with different lineages corresponding to *Nothofagus* subgenera. Only one species, *Madarococcus podocarpi* (Miller & Gimpel) Hoy has been collected from a host other than *Nothofagus*, being collected once from the New Zealand *Dacrycarpus dacrydioides* (Richard 1832: 358) Laubenfels (1969: 337) (Hardy *et al.* 2008). There are three clades of South American Eriococcidae that occur on *Nothofagus*. One clade of *Chilechiton* and *Intecticoccus* and another of *Chilecoccus* are endemic to South America and occur only on *Nothofagus* subgenus *Nothofagus*. The third South American clade comprises species of *Madarococcus* that occur on subgenera *Nothofagus* and *Lophozonia*. The New Zealand and Australian species of *Madarococcus* form a clade that predominantly occurs on subgenus *Lophozonia*, but also subgenus *Fuscospora*.

Furthermore, a recent New Zealand study has shown greater similarity of the endophytic fungal communities between species of subgenus *Fuscospora* (*N. fusca* and *N. solandri*) than between them and *N. menziesii* (subgenus *Lophozonia*) (Johnston *et al.* 2012). While this study is restricted to New Zealand species, further analyses of endophytic fungi on Nothofagaceae in other geographic regions are warranted.

Taxonomy

In the classification proposed here, we provide a family description for Nothofagaceae, descriptions for each of its four genera, and where needed new combinations at species rank in *Fuscospora*, *Lophozonia* and *Trisyngyne*. In addition to the application of subgeneric rank in *Nothofagus* several authors have proposed additional taxonomic ranks utilising section, subsection and/or series (e.g. Steenis 1952a, 1953a, Philipson & Philipson 1988, Hill & Read 1991). Here we do not recognise any taxa at infrageneric ranks, instead treating the infrageneric taxa of other authors as synonyms or invalid names. We present available information on holotype and lectotype specimens, and have undertaken lectotypifications when necessary. A full synonymy of homotypic names is presented for the accepted species. We do not present a synonymy of heterotypic names, and regional floras and other taxonomic treatments should be consulted for this.

There are well-preserved and identified fossil species of Nothofagaceae that have confidently been identified with a *Nothofagus* subgenus, and these too should be transferred to the appropriate genus. However, a considerable number of the fossil species of Nothofagaceae cannot be confidently placed in the genera accepted in this treatment. Therefore, we envisage further nomenclatural papers that deal with the generic placement of fossil names.

Nothofagaceae Kuprianova (1962: 21) ≡ Fagaceae tribe *Nothofageae* Baumann-Bodenheim (1992: 104) ≡ Fagaceae subfamily *Nothofagoideae* Wang & Pu (2004: 116). Type:—*Nothofagus* Blume.

When designating the type for the family, Kuprianova (1962) gave the authority for *Nothofagus* incorrectly as Oerst., and incorrectly indicated the type of *Nothofagus* as *N. obliqua* Oerst.

Trees or shrubs. Leaves evergreen or deciduous, distichous or spiral; lamina simple, pinnately veined, entire or serrate, sometimes doubly serrate; minor leaf veins without phloem transfer cells; cuticle usually with large globular glandular trichomes. Stipules attached basally or peltate, point of attachment associated with elongate colleters. Inflorescences a dichasium, monoecious; flowers usually trimerous, central flower of the female dichasium dimerous or absent. Male flowers sessile to shortly pedunculate 1- to 3-flowered dichasia; perianth splitting irregularly; stamens 4–90 per flower, filaments long and flexible; anthers basifixed, elongate, with distal connective protrusion, proximal lobes lie above the point of connection. Pollen oblate to peroblate; exine thin, with granular bacules, and small, widely spaced projections; regular foot layer and tectum; colpi 3–10, short, usually with raised margins. Female flowers (1–)3–7(–15), sessile or shortly stalked, involucre persistent; ovary inferior, ovules unitegemic; styles short, erect to reflexed; stigmas decurrent. Cupule 1- to 4-valved or valves absent, valves free throughout development; with lamellar appendages. Nuts lenticular or triangular, usually winged; endocarp glabrous; cotyledons plicate, with fat reserve; endosperm absent; germination epigeal. Chromosome number $n = 13$.

Four genera, in New Zealand, Australia, Tasmania, New Caledonia, New Guinea and southern South America.

Key to genera

1. Leaves with solitary unicellular trichome type C present; perianth open and broadly campanulate; staminate perianth with 6–14 lobes; stamen development pseudocentrifugal, usually > 20 stamens; pollen aperture length >15 µm, aperture unthickened and ends V-shaped; cupule appendages glandular .... *Lophozonia*

\- Leaves with solitary unicellular trichome type C absent; perianth narrowly campanulate or tubular; staminate perianth with 0–4 lobes; stamen development centripetal, usually < 20 stamens; pollen aperture length 4–11 µm, aperture annulate, rimmed or with heavy thickening and ends U-shaped; cupule appendages lamellate 2

2. Leaf vernation conduplicate; leaf veins with giant stomata; filaments connate; staminate perianth tubular; anther distal connective protrusion weakly or strongly developed; pollen aperture rimmed; cupule glabrous; cupule with 2 valves .... *Trisyngyne*

\- Leaf vernation planar or revolute when evergreen and plicate when deciduous; leaf veins without giant stomata; filaments free; staminate perianth narrowly campanulate; anther distal connective protrusion absent; pollen aperture annulate or with heavy thickening; cupule with simple trichomes; cupule with 2 or 4 valves 3

3. Leaf vernation planar when evergreen or plicate when deciduous; leaves with unicellular trichome type A absent; stomata orientation mostly parallel with the midrib and with thickened T-pieces of cuticle at the poles; pollen aperture annulate ....*Nothofagus*

\- Leaf vernation revolute when evergreen or plicate when deciduous; leaves with unicellular trichome type A present; stomata orientation random and without thickened T-pieces of cuticle at the poles; pollen aperture with heavy thickening .... *Fuscospora*

Fuscospora (R.S.Hill & J.Read) Heenan & Smissen, *comb. et stat. nov.* ≡ *Nothofagus* subgenus *Fuscospora* Hill & Read (1991: 69) (as *Fuscaspora*; orthography corrected by Hill & Jordan 1993). = *Nothofagus* section *Sempervirentes* Steenis (1952a: 146) ≡ *Nothofagus* section *Planae* Steenis (1952b: 306), *nom. illeg. superfl.* = *Nothofagus* section *Sempervirentes* subsection *Quadripartitae* Steenis (1952a: 146) ≡ *Nothofagus* section *Calusparassus* subsection *Quadripartitae* (Steenis) Steenis (1953a: 337). Type:—*Nothofagus fusca* (Hook.f.) Oerst. [≡ *Fuscospora fusca* (Hook.f.) Heenan & Smissen].

Steenis (1952b) provided the superfluous name of sect. *Planae* for the previously published *Nothofagus* section *Sempervirentes* (Steenis 1952a) in an erratum. Steenis (1953a) gives the type of *Nothofagus* section *Calusparassus* subsection *Quadripartitae* as *N. betuloides*, but clearly cites Steenis (1952a) for the basionym where *N. fusca* is given as the type.

= *Nothofagus* section *Calusparassus* subsection *Tripartitae* Steenis (1953a: 338). Type:—*Nothofagus solandri* (Hook.f.) Oerst. [≡ *Fuscospora solandri* (Hook.f.) Heenan & Smissen].

= *Nothofagus* section *Calucechinus* subsection *Saccofagus* Baumann-Bodenheim (1992: 93).
Type:—*Nothofagus gunnii* (Hook.f.) Oerst. [≡ *Fuscospora gunnii* (Hook.f.) Heenan & Smissen].

= *Pleiosyngyne* Baumann-Bodenheim (1992: 86), *nom. inval.*

Pleiosyngyne is invalid as it was published without a Latin description (McNeill *et al.* 2012, ICN Art. 39.1).

Trees up to 30 m high. Leaves distichous, revolute when evergreen or plicate when deciduous, entire or teeth with 1–2 serrations, fimbrial veins incomplete or absent; with or without large globular glandular trichomes on cuticle; with solitary unicellular trichome type A with a very small, unthickened base and with a large, unicellular, thin-walled trichome emerging; without solitary unicellular trichome type C with a large base equal to or greater than the diameter of the trichome and with a large, unicellular, thin-walled trichome emerging; with or without conical unicellular trichomes with a heavily thickened foot cell. Stomata randomly oriented; without thickened T-pieces of cuticle at the poles separating the two guard cells; without giant stomata over the major veins; stomata size within the areoles variable. Upper epidermal cells over veins more elongate than areolar cells, with granular cell walls. Stipules not peltate. Dichasia with 1 central dimerous flower and 2 lateral trimerous flowers, or 1 or 0 dimerous flower and 1 trimerous flower. Male floral meristem round. Staminate flowers with narrowly campanulate, often bell-shaped perianth; lobes 4, rarely 3 or 5, prominent, symmetric and regular; stamens <20, centripetal development; anthers 2.5–4.5 mm long, slightly curved, distal connective protrusion weakly developed, filament connective free, without epidermal papillae. Pollen peritreme, mesocolpia straight to convex; colpi short, spatulate or parallel-sided, with U-shaped ends, margins inwardly conspicuously heavily thickened, aperture 4–11 μm long, polar to equatorial lengths ratio ≤ 0.3. Cupule valves 2–4; outer surface of valves with simple trichomes; lamellae membranous, glabrous; fruits 0–1 dimerous, 1–2 trimerous, or 4–7.

Six species in New Zealand, southern South America, and Tasmania.

Fuscospora alessandri (Espinosa) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus alessandri* Espinosa (1926: 268). Lectotype (designated here):—CHILE. Tapar prope Empedrado, 27 February 1921, *M. Espinosa s.n.* (SGO47510, image!).

F. M. Vásquez (in sched., 20 September 1995) annotated SGO47510 as lectotype. We are unaware of any other published lectotypification and as we concur with this assessment we formally designate this specimen as lectotype.

= *Pleiosyngyne alessandri* (Espinosa) Baumann-Bodenheim (1992: 86), *nom. inval.* This name is not validly published as it lacks a full and direct reference to the basionym (McNeill *et al.* 2012, ICN Art. 41.5).

Fuscospora cliffortioides (Hook.f.) Heenan & Smissen, *comb. nov.* ≡ *Fagus cliffortioides* Hooker (1844: 673) ≡ *Nothofagus cliffortioides* (Hook.f.) Ørsted (1871: 355) ≡ *Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole (1958: 563). Type:—NEW ZEALAND. Dusky Bay, no date, '*Mr. Menzies'* (holotype K, image!).

This taxon was treated as *N. solandri* var. *cliffortioides* (Poole 1958; Allan 1961), having been accepted at species rank as *Fagus cliffortioides* (Hooker 1844, 1864, Cheeseman 1906) and *Nothofagus cliffortioides* (Cheeseman 1925, Cockayne 1926, Cockayne & Atkinson 1926, Poole 1950). Placement at the taxonomic rank of variety has not been universally accepted in New Zealand (e.g., Molloy *et al.* 1999, Meurk & Hall 2006, McGlone *et al.* 2011), and as we concur with these latter authors that this taxon is morphologically and ecologically distinct from *Fuscospora solandri* it is here accepted at species rank.

Fuscospora fusca (Hook.f.) Heenan & Smissen, *comb. nov.* ≡ *Fagus fusca* Hooker (1844: t. 630, 631) ≡ *Nothofagus fusca* (Hook.f.) Ørsted (1871: 355). Lectotype (designated by Allan 1961):—NEW ZEALAND. Without locality, no date, *W. Colenso 1767* (K, image!).

Fuscospora gunnii (Hook.f.) Heenan & Smissen, *comb. nov.* ≡ *Fagus gunnii* Hooker (1851: t. 881) ≡ *Nothofagus gunnii* (Hook.f.) Ørsted (1871: 354). Lectotype (designated here):—AUSTRALIA. Near summit of Mt. Olympus, 5 January 1847, *R. C. Gunn 2034* (K, image!).

Fuscospora solandri (Hook.f.) Heenan & Smissen, *comb. nov.* ≡ *Fagus solandri* Hooker (1844: t. 639) ≡ *Nothofagus solandri* (Hook.f.) Ørsted (1871: 355). Lectotype (designated by Allan 1961):—NEW ZEALAND. Without locality, no date, *W. Colenso 36* (K, image!).

Fuscospora truncata (Colenso) Heenan & Smissen, *comb. nov.* ≡ *Fagus truncata* Colenso (1898: 280) ≡ *Nothofagus truncata* (Colenso) Cockayne (1926: 21). Lectotype (designated by Allan 1961):—NEW ZEALAND. Ruahine Mountain-range, October 1898, *H. Hill s.n.* (WELT SP035538!).

Govaerts & Frodin (1999) placed *N. truncata* in synonymy of *Nothofagus fusca* var. *colensoi* (Hooker 1853: 229) Cheeseman (1906: 641). This treatment is incomprehensible and contradicts the available ecological, morphological and genetic evidence on the distinctiveness of *F. fusca* and *F. truncata* and is therefore not accepted here or elsewhere (e.g., Allan 1961, Wardle 1984, Mark & Lee 1985, Haase 1990, 1992, Dawson & Lucas 2011).

Fuscospora ×apiculata (Colenso) Heenan & Smissen, *comb. nov.* ≡ *Fagus apiculata* Colenso (1885: 335–336) ≡ *Nothofagus ×apiculata* (Colenso) Krasser (1896: 163). Lectotype (designated here):—NEW ZEALAND. Matamau and Dannevirke, County of Waipawa, 1883, *W. Colenso s.n.* (WELT SP036833a!).

Hybrid parentage:—*Fuscospora solandri* (Hook.f.) Heenan & Smissen × *F. truncata* (Colenso) Heenan & Smissen (Cockayne & Allan 1934).

Fuscospora ×blairii (Kirk) Heenan & Smissen, *comb. nov.* ≡ *Fagus ×blairii* Kirk (1885: 297, *t.* 16) ≡ *Nothofagus ×blairii* (Kirk) Cockayne (1911: 172) ≡ *Nothofagus apiculata* nothovar. *blairii* (Kirk) Govaerts (in Govaerts & Frodin 1999: 193). Lectotype (designated here):—NEW ZEALAND. Valley of the Dart, January 1877, *T. Kirk s.n.* (WELT SPO36861!).

Hybrid parentage:—*Fuscospora fusca* (Hook.f.) Heenan & Smissen × *F. cliffortioides* (Hook.f.) Heenan & Smissen (Cockayne & Allan 1934).

Fuscospora ×dubia (Kirk) Heenan & Smissen, *comb. nov.* ≡ *Fagus fusca* var. *dubia* Kirk (1889: 182, t. 91 figs. 1–3) ≡ *Fagus ×apiculata* var. *dubia* (Kirk) Cheeseman (1906: 642) ≡ *Nothofagus ×apiculata* var. *dubia* (Kirk) Cheeseman (1925: 375) ≡ *Nothofagus apiculata* nothovar. *dubia* (Kirk) Govaerts (in Govaerts & Frodin 1999: 193), *nom. superfl.* Lectotype (designated here):—NEW ZEALAND. Hutt Valley, no date, *T. Kirk s.n.* (WELT SP036893!).

= *Fagus fusca* var. *obsoleta* Kirk (1889: 182, t. 91 fig. 4). Lectotype (designated here):—NEW ZEALAND. Illustration (t. 91 fig. 4!) in Kirk (1889).

Hybrid parentage:—*Fuscospora solandri* (Hook.f.) Heenan & Smissen × *F. fusca* (Hook.f.) Heenan & Smissen. This interspecific hybrid often occurs when the two parent species are sympatric (Cockayne & Atkinson 1926; Allan 1929). *Nothofagus ×solfusca* was proposed by Allan (1929) for this interspecific hybrid, but this was not validly published and was preceeded by the combination *Fagus fusca* var. *dubia* (Kirk 1889: 182).

Fuscospora ×eugenananus (Gilland.) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus ×eugenananus* Gillanders (2008: 56). Type:—AUSTRALIA. Woodbank gardens, Longley, Tasmania, May 2007, *K. D. Gillanders s.n.* (holotype HO544640).

Hybrid parentage:—*Fuscospora fusca* (Hook.f.) Heenan & Smissen × *F. alessandri* (Espinosa) Heenan & Smissen (Gillanders 2008).

Lophozonia Turczaninow (1858: 396) ≡ *Nothofagus* subgenus *Lophozonia* (Turcz.) Krasser (1896: 162). Type:—*Lophozonia heterocarpa* Turczaninow (1858: 396) [= *Lophozonia obliqua* (Mirb.) Heenan & Smissen subsp. *obliqua*].

= *Nothofagus* subgenus *Nothofagus* section *Calusparassus* subsection *Menziesiae* Philipson & Philipson (1988: 34). = *Nothofagus* subgenus *Menziesospora* Hill & Read (1991: 69). Type:—*Nothofagus menziesii* (Hook.f.) Oerst. [≡ *Lophozonia menziesii* (Hook.f.) Heenan & Smissen].

= *Nothofagus* subgenus *Nothofagus* section *Adenofagus* Baumann-Bodenheim (1992: 94, 114), *nom. nud.*

Trees up to 40 m high. Leaves distichous, planar when evergreen or plicate when deciduous, teeth with 1–2 or 2-or-more serrations, fimbrial veins incomplete or absent; with large globular glandular trichomes on cuticle; without solitary unicellular trichome type A with a very small, unthickened base and with a large, unicellular, thin-walled trichome emerging; with solitary unicellular trichome type C with a large base equal to or greater than the diameter of the trichome and with a large, unicellular, thin-walled trichome emerging; with conical unicellular trichomes with a heavily thickened foot cell and broad base. Stomata randomly oriented; without thickened T-pieces of cuticle at the poles separating the two guard cells; usually without or one species with giant stomata over the major veins; stomata size within the areoles variable. Upper epidermal cells over veins more elongate than areolar cells or not distinguishable from areolar cells, with or without granular cell walls. Stipules not peltate. Dichasia with 1 central dimerous flower and 2 lateral trimerous flowers. Male floral meristem broadly oval, relatively flat topped. Staminate flowers with an open and broadly campanulate pseudanthium; lobes 6–14, prominent, asymmetric and irregular; stamens usually >20, centrifugal development; anthers 1.5–3.0 mm long, often curved, distal connective protrusion weakly developed, filament connective free, without epidermal papillae or with isomorphic rounded papillae. Pollen peritreme or goniotreme, mesocolpia straight to convex; colpi long, tenuimarginate, with V-shaped ends, margins not thickened, aperture > 15.0 µm long, polar to equatorial lengths ratio 0.35–0.4. Cupule valves 4; outer surface of valves with densely pubescent simple trichomes; lamellae glandular; fruits 1 dimerous or 2 trimerous.

Seven species in New Zealand, southern South America, and Australia.

Lophozonia alpina (Poepp. & Endl.) Heenan & Smissen, *comb. nov.* ≡ *Fagus alpina* Poeppig & Endlicher (1838: 69) ≡ *Nothofagus alpina* (Poepp. & Endl.) Ørsted (1871: 354). Lectotype (designated here):—CHILE. Illustration (tab. 198, A, 1–10) in Poeppig & Endlicher (1838).

Vázquez & Rodríguez (1999) selected as lectotype two illustrations (tab. 196 and tab. 198, A, 1–10) in Poeppig & Endlicher (1838). The lectotypification proposed here is a second step lectotypification (McNeill *et al.* 2012, ICN Art. 9.17), whereby we have designated a single figure (tab. 198, A, 1–10) as the lectotype.

Lophozonia cunninghamii (Hook.f.) Heenan & Smissen, *comb. nov.* ≡ *Fagus cunninghamii* Hooker (1840: 152, t. 7) ≡ *Nothofagus cunninghamii* (Hook.f.) Ørsted (1871: 355). Lectotype (designated here):—AUSTRALIA. Without locality, 1833, *R. C. Gunn 178 ex J. B. L.* (K000741836, image!).

Lophozonia glauca (Phil.) Heenan & Smissen, *comb. nov.* ≡ *Fagus glauca* Philippi (1858: 43) ≡ *Nothofagus glauca* (Phil.) Krasser (1896: 163). Lectotype (designated here):—CHILE. Without locality, January 1856, *P. Germain s.n.* (SGO63396, image!).

F. M. Vásquez (in sched., 20 September 1995) annotated SGO63396 as lectotype. We are unaware of any other published lectotypification and as we concur with this assessment we formally designate this specimen as lectotype.

Lophozonia macrocarpa (A.DC.) Heenan & Smissen, *comb. nov.* ≡ *Fagus obliqua* var. *macrocarpa* Candolle (1864: 120) ≡ *Nothofagus macrocarpa* (A.DC.) Vazquez & Rodríguez (1999: 81). Lectotype (designated by Vásquez & Rodíguez 1999):—CHILE. Aculeo, 1861, *F. Philippi s.n.* (G-DC, image!).

Lophozonia menziesii (Hook.f.) Heenan & Smissen, *comb. nov.* ≡ *Fagus menziesii* Hooker (1844: t. 652) ≡ *Nothofagus menziesii* (Hook.f.) Ørsted (1871: 355). Lectotype (designated by Allan 1961):—NEW ZEALAND. Dusky Bay, 1781, *A. Menzies s.n.* (K, image!).

Lophozonia moorei (F.Muell.) Heenan & Smissen, *comb. nov.* ≡ *Fagus moorei* Mueller (1866: 109–110) ≡ *Nothofagus moorei* (F.Muell.) Krasser (1896: 161). Lectotype (designated here):—AUSTRALIA. Bellinger River, no date, *C. Moore s.n.* (K000741834, image!).

Lophozonia obliqua (Mirb.) Heenan & Smissen, *comb. nov.* ≡ *Fagus obliqua* Mirbel (1827: 465. t. 23) ≡ *Nothofagus obliqua* (Mirb.) Ørsted (1871: 354). Lectotype (designated by Vásquez & Rodíguez 1999):—CHILE. Without locality, no date, *J. Dombey s.n.* (P, image!).

Autonym:—*Lophozonia obliqua* (Mirb.) Heenan & Smissen subsp. *obliqua.*

= *Lophozonia heterocarpa* Turczaninow (1858: 396). Lectotype (designated here):—CHILE, Valdivia, 1844, *T. C. Bridges s.n.* (LE, image!).

Vazquez & Rodriguez (1999) treated *Lophozonia heterocarpa* Turcz. as a synonym of *N. obliqua* subsp. *obliqua*, although they did not see the type specimen. Having seen a digital image of the type specimen at LE we concur with this taxonomic assessment.

Lophozonia obliqua **subsp.** ***andina*** (F.M.Vazquez & R.A.Rodr.) Heenan & Smissen, *comb. nov.*

≡ *Nothofagus obliqua* subsp. *andina* Vázquez & Rodríguez (1999: 80). Type:—CHILE. Arauco, Puente Quelén-Quelén, 6 January 1977, *C. Marticorena, M. Quezada & R. Rodriquez s.n.* (holotype CONC 45625, image!).

Lophozonia obliqua **subsp.** ***valdiviana*** (Phil.) Heenan & Smissen, *comb. nov.* ≡ *Fagus valdiviana* Philippi (1864: 236) ≡ *Nothofagus obliqua* subsp. *valdiviana* (Phil.) Vazquez & Rodríguez (1999: 79). Lectotype (designated by Vásquez & Rodíguez 1999):—CHILE. Valdivia, 1864, *F. Philippi s.n.* (SGO 47528, image!).

Lophozonia* ×*dodecaphleps (Mike L.Grant & E.J.Clement) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus ×dodecaphleps* Grant & Clement (2004: 448). Type:—ENGLAND. Surrey, Alice Holt Lodge, Wrecclesham, Farnham, 11 October 1999, *Jinks s.n.* (holotype WSY).

Hybrid parentage:—*Lophozonia obliqua* (Mirb.) Heenan & Smissen × *L. alpina* (Poepp. & Endl.) Heenan & Smissen (Grant & Clement 2004: 448).

Nothofagus Blume (1851: 307), *nom. cons*. (see Steenis 1953b: 329, Lanjouw *et al.* 1961: 251) ≡ *Fagus* section *Nothofagus* (Blume) Candolle (1864: 121). = *Nothofagus* section *Calucechinus* subsection *Antarcticae* Steenis (1953a: 334), *nom. inval.* = *Nothofagus* subgenus *Molischia* Krasser (1896: 162), *nom. inval.* Conserved type (designated by Lanjouw *et al.* 1961: 251):—*Nothofagus antarctica* (G.Forst.) Oerst.

In proposing the conservation of *Nothofagus*, Steenis (1953b) did not nominate a type, but the proposal was nonetheless recommended by the Committee for Spermatophyta with the provision that this deficiency was remedied (Rickett 1958). When the conservation of the name was published, *N. antarctica* was given as the type (Lanjouw *et al.* 1961, Appendix 3). This was an unfortunate choice as Blume (1851) did not include *N. antarctica* among the species he placed in *Nothofagus*. *Nothofagus* subgenus *Molischia* and *Nothofagus* section *Calucechinus* subsection *Antarcticae* each include the type of *Nothofagus* (*N. antarctica*) and are therefore invalid (McNeill *et al.* 2012, ICN Art. 22.2).

= *Fagaster* Spach (1841: 142), *nom. rejic.* (see Steenis 1953b: 329, Lanjouw *et al.* 1961: 251). Type:—*Fagus dombeyi* Mirb. [≡ *Nothofagus dombeyi* (Mirb.) Oerst.].

= *Calucechinus* Hombr. & Jacquinot (in Dumont d'Urville 1843: t. 6), *nom. rejic.* (see Steenis 1953b: 329, Lanjouw *et al.* 1961: 251) ≡ *Nothofagus* subgenus *Molischia* section *Calucechinus* (Hombr. & Jacquinot) Krasser (1896: 162), *nom. inval*. Type:—*Calucechinus antarctica* (G.Forst.) Hombr. & Jacquinot [≡ *Nothofagus antarctica* (G.Forst.) Oerst.].

= *Calusparassus* Hombr. & Jacquinot (in Dumont d'Urville 1843: t. 6), *nom. rejic.* (see Steenis 1953b: 329, Lanjouw *et al.* 1961: 251) ≡ *Nothofagus* subgenus *Molischia* section *Calusparassus* (Hombr. & Jacquinot) Krasser (1896: 163). Type:—*Calusparassus forsteri* Hombr. & Jacquinot [=*Nothofagus betuloides* (Mirb.) Oerst.].

= *Fagus* section *Eufagus* Candolle (1864: 118) *pro parte, nom. inval.*

Candolle divided *Fagus* into a section for evergreen species (section *Nothofagus*, see above) and a section for deciduous species (section *Eufagus*). *Fagus* section *Eufagus* is treated here as invalid (McNeil *et al.* 2012, ICN Art. 21.3).

= *Nothofagus* section *Deciduae* Steenis (1952a: 146) ≡ *Nothofagus* section *Plicatae* Steenis (1952b: 306), *nom. illeg. superfl*. Type:—*Nothofagus betuloides* (Mirb.) Blume.

= *Nothofagus* section *Calucechinus* subsection *Pumiliae* Steenis (1953a: 336) ≡ *Nothofagus* subgenus *Nothofagus* section *Pumiliae* (Steenis) Hill & Read (1991: 69). Type:—*Nothofagus pumilio* (Poepp. & Endl.) Krasser.

= *Nothofagus* subgenus *Pumiliae* (Steenis) Baumann-Bodenheim (1992: 93), *nom. inval.*

This name does not include a full and direct reference to the basionym (McNeill *et al.* 2012, ICN Art. 41.5).

Autonyms:—*Nothofagus* Blume subgenus *Nothofagus*, in Philipson & Philipson (1988: 33); *Nothofagus* Blume subgenus *Nothofagus* section *Nothofagus*, in Philipson & Philipson (1988: 33).

Trees up to 45 m high. Leaves distichous, planar when evergreen or plicate when deciduous, teeth with 1–2 or 2-or-more serrations, fimbrial veins incomplete or absent; with large globular glandular trichomes on cuticle; without solitary unicellular trichome type A with a very small, unthickened base and with a large, unicellular, thin-walled trichome emerging; without solitary unicellular trichome type C with a large base equal to or greater than the diameter of the trichome and with a large, unicellular, thin-walled trichome emerging; with or without conical unicellular trichomes with a heavily thickened foot cell. Stomata parallel to long axis of leaf; with thickened T-pieces of cuticle at the poles separating the two guard cells; without giant stomata over the major veins; stomata size within the areoles variable or more-or-less even. Upper epidermal cells over veins more elongate than areolar cells or not distinguishable from areolar cells, with or without granular cell walls. Stipules peltate. Dichasia with 1 central dimerous flower and 2 lateral trimerous flowers, or 1 trimerous flower. Male floral meristem round. Staminate flowers with narrowly campanulate, often bell-shaped perianth; lobes 4, rarely 3 or 5, prominent, symmetric and regular; stamens <20, centripetal development; anthers 2.5–4.0 mm long, slightly curved, distal connective protrusion weakly developed, filament connective free, without epidermal papillae. Pollen peritreme, mesocolpia straight to convex; colpi short, spatulate or parallel-sided, with U-shaped ends, margins conspicuously thickened, annulate, aperture 4–11 µm long, polar to equatorial lengths ratio ≤ 0.3. Cupule valves (2–)4(–8), or 2 asymmetrical; outer surface of valves with simple trichomes; lamellae membranous, usually glabrous, or sometimes glandular; fruits 1 dimerous or 1–2 trimerous.

Five species in southern South America.

Nothofagus antarctica (G.Forst.) Ørsted (1871: 354) ≡ *Fagus antarctica* Forster (1789: 42, as 24). Lectotype (designated here):—CHILE. Terra del Fuego, Christmas Harbour, 1774, *W. Anderson* (BM000949987, image!).

The description provided by Forster (1789) includes male and female flowers, and we have designated a specimen with male flowers as the lectotype.

Nothofagus betuloides (Mirb.) Ørsted (1871: 354) ≡ *Fagus betuloides* Mirbel (1827: 469, t. 25). Lectoype (designated here):—CHILE. Magellan, October 1767, *P. Commerson s.n.* (P744727, image!).

Nothofagus dombeyi (Mirb.) Ørsted (1871: 354) ≡ *Fagus dombeyi* Mirbel (1827: 467, t. 24). Lectotype (designated here):—CHILE. Without locality, no date, *J. Dombey 931* (P744730, image!).

Nothofagus nitida (Phil.) Krasser (1896: 163) ≡ *Fagus nitida* Philippi (1858: 44). Lectotype (designated here):—CHILE. Huaitecas y Chonos, January 1857, *F. Fonck 159* (SGO63009, image!).

C. Muñoz (in sched., February 1960) annotated SGO63009 as type specimen. We are unaware of any other published lectotypification and as we concur with this assessment we formally designate this specimen as lectotype.

Nothofagus pumilio (Poepp. & Endl.) Krasser (1896: 161) ≡ *Fagus pumilio* Poeppig & Endlicher (1838: 68, t. 195). Type:—CHILE. (none cited).

A lectotypification is not undertaken as we have been unable to locate original material.

Trisyngyne Baillon (1874: 136). Lectotype (designated by Baumann-Bodenheim 1953):—*Trisyngyne codonandra* Baill.

= *Nothofagus* section *Sempervirentes* subsection *Bipartitae* Steenis (1952a: 146) ≡ *Nothofagus* section *Calusparassus* subsection *Bipartitae* (Steenis) Steenis (1953a: 338). = *Nothofagus* section *Sempervirentes* subsection *Bipartitae* series *Triflorae* Steenis (1952a: 146) ≡ *Nothofagus* section *Calusparassus* subsection *Bipartitae* series *Triflorae* (Steenis) Steenis (1953a: 338). = *Nothofagus* subgenus *Brassospora* Philipson & Philipson (1988: 34). Type:—*Nothofagus brassii* Steenis [≡ *Trisyngyne brassii* (Steenis) Heenan & Smissen].

= *Nothofagus* section *Sempervirentes* subsection *Bipartitae* series *Uniflorae* Steenis (1952a: 146) ≡ *Nothofagus* section *Calusparassus* subsection *Bipartitae* series *Uniflorae* (Steenis) Steenis (1953a: 338). Type:—*N. pullei* Steenis [≡ *Trisyngyne pullei* (Steenis) Heenan & Smissen].

= *Trisyngyne* subgenus *Papuofagus* Baumann-Bodenheim (1992: 111–112), *nom. inval.*

This name is invalid as Baumann-Bodenheim (1992) included six species in this subgenus but he did not indicate a type (McNeill *et al.* 2012, ICN Art. 40.1).

= *Trisyngyne* subgenus *Papuofagus* section *Papuofagus* Baumann-Bodenheim (1992: 112), *nom. inval.*

Baumann-Bodenheim (1992) indicated the type of this taxon as *T. pullei*, itself not a validly published name because it lacked a full and direct reference to the basionym (McNeill *et al.* 2012, ICN Art. 41.5).

= *Trisyngyne* subgenus *Papuofagus* section *Papuofagus* subsection *Papuofagus* Baumann-Bodenheim (1992: 112), *nom. inval.*

Baumann-Bodenheim (1992) indicated the type of this taxon as *T. pullei*, itself not validly published at the time because it lacked a full and direct reference to the basionym (McNeill *et al.* 2012, ICN Art. 41.5).

= *Trisyngyne* subgenus *Papuofagus* section *Papuofagus* subsection *carri* Baumann-Bodenheim (1992: 112), *nom. inval.*

Baumann-Bodenheim (1992) indicated the type of this taxon as *T. carri*, itself not validly published at the time because it lacked a full and direct reference to the basionym (McNeill *et al.* 2012, ICN Art. 41.5).

= *Trisyngyne* subgenus *Papuofagus* section *Trysyngynopsis* Baumann-Bodenheim (1992: 113), *nom. inval.*

Baumann-Bodenheim (1992) indicated the type of this taxon as *T. brassi*, itself not validly published at the time because it lacked a full and direct reference to the basionym (McNeill *et al.* 2012, ICN Art. 41.5).

= *Trisyngyne* subgenus *Trisyngyne* section *Trisyngyne* series *Balansae* Baumann-Bodenheim (1992: 110–111), *nom. inval.*

This name is invalid as Baumann-Bodenheim (1992) included three species in this taxon but did not indicate a type (McNeill *et al.* 2012, ICN Art. 40.1).

= *Trisyngyne* subgenus *Trisyngyne* section *Trisyngyne* series *Baumanniae* Baumann-Bodenheim (1992: 110).

Type:—*Trisyngyne baumanniae* Baum.-Bod.

Baumann-Bodenheim (1992) did not explicitly indicate a type for this taxon but included only *T. baumanniae* which is acceptable as an indication of the type (McNeill *et al.* 2012, ICN Art. 40.3).

Trees up to 40 m high, or sometime shrubs. Leaves distichous or spiralled, conduplicate, evergreen, entire or teeth with 1–2 serrations, fimbrial veins incomplete or absent; with large globular glandular trichomes on cuticle; without solitary unicellular trichome type A with a very small, unthickened base and with a large, unicellular, thin-walled trichome emerging; without solitary unicellular trichome type C with a large base equal to or greater than the diameter of the trichome and with a large, unicellular, thin-walled trichome emerging; with or without conical unicellular trichomes with a heavily thickened foot cell. Stomata randomly oriented; without thickened T-pieces of cuticle at the poles separating the two guard cells; with giant stomata over the major veins; stomata size within the areoles more-or-less even. Upper epidermal cells over veins thinner than areolar cells or not distinguishable from areolar cells, without granular cell walls. Stipules peltate. Dichasia 1- or 3-dimerous. Male floral meristem round. Staminate flowers with a tubular strongly connate perianth; lobes 4, rarely 2, 3 or 5, reduced, symmetric and regular; stamens <20, centripetal development; anthers 2.0–8.0 mm long, straight with only the apex slightly curved, distal connective protrusion pronounced and strongly developed, filament connective connate, with epidermal cells consisting of longitudinal ridges of striated papillae, often with papillose ornamentation on the distal connective protrusion and weakly ornamented cells on the lateral, dorsal and ventral sides. Pollen goniotreme, mesocolpia straight to concave; colpi parallel-sided with U-shaped ends, margins inwardly thickened and/or inflexed; aperture 4–11 µm long, polar to equatorial lengths ratio > 0.3. Cupule valves 2 or absent; outer surface of valves glabrous; lamellae membranous or woody, glabrous, entire; fruits 1 or 3 dimerous.

Twenty-five species from Papua New Guinea, Indonesian Papua and New Caledonia.

Notes:—Baumann-Bodenheim (1992) proposed the transfer of a number of names in *Nothofagus* to *Trisyngyne*. However, he did not provide a full and direct reference to the basionym and place of publication and therefore his combinations are not validly published (McNeill *et al.* 2012, ICN Art. 41.5). It is therefore necessary to make new combinations in *Trisyngyne* for names published in *Nothofagus*, and this action is taken below.

Trisyngyne aequilateralis Baumann-Bodenheim (1953: 421) ≡ *Nothofagus aequilateralis* (Baum.-Bod.) Steenis (1954: 266). Type:—NEW CALEDONIA. Grande Terre, zwischen Vallée Riv. Blanche und Riv. Bleu, 16 August 1951, *M. Baumann-Bodenheim 15273* (holotype Z, image!).

Trisyngyne balansae Baillon (1874: 137) ≡ *Nothofagus balansae* (Baill.) Steenis (1954: 266). Type:—NEW CALEDONIA. Forêts au dessus de Téné près Bourail, 19 March 1869, *B. Balansa 1377* (holotype P, image!).

Trisyngyne baumanniae Baumann-Bodenheim (1953: 420) ≡ *Nothofagus baumanniae* (Baum.-Bod.) Steenis (1954: 266). Type:—NEW CALEDONIA. Grande Terre, Mt. Mou Gipfel am Übergang zum Nebelwald, 13 March 1951, *M. Baumann-Bodenheim 11277* (holotype Z, image!).

Trisyngyne bernhardii (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus bernhardii* Steenis (1952a: 147). Type:—INDONESIA. Papua, 18 km SW of Bernhard Camp, Idenburg River, February 1939, *L. J. Brass 12453* (holotype L, image!).

Trisyngyne brassii (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus brassii* Steenis (1952a: 146). Type:—INDONESIA. Papua, Bele River camp, 18 km NE of Lake Habbema, November 1938, *L. J. Brass & C. Versteegh 11115* (holotype L, image!).

Trisyngyne carrii (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus carrii* Steenis (1952a: 147). Type:—PAPUA NEW GUINEA. Below The Gap, 8 January 1936, *C. E. Carr 15028* (holotype L, image!).

Trisyngyne codonandra Baillon (1874: 136–137) ≡ *Nothofagus codonandra* (Baill.) Steenis (1954: 266). Lectotype (designated by Baumann-Bodenheim 1953):—NEW CALEDONIA. Mt. Mou, 14 April 1870, *B. Balansa 2749* (P, image!).

Trisyngyne cornuta (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus cornuta* Steenis (1952a: 147). Type:—INDONESIA. Papua, Wissel Lake region, base of Bubeiro and Enarotali, August 1939, *P. J. Eyma 5122* (holotype L, image!).

Trisyngyne crenata (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus crenata* Steenis (1952a: 147). Type:—INDONESIA. Papua, Bele River camp, 18 km NE of Lake Habbema, November 1938, *L. J. Brass 11335* (holotype L, image!).

Trisyngyne decipiens (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus decipiens* Steenis (1952a: 147). Type:—INDONESIA. Papua, 18 km SW of Bernhard Camp, Idenburg, February 1939, *L. J. Brass 12675* (holotype L, image!).

Trisyngyne discoidea Baumann-Bodenheim (1953: 420) ≡ *Nothofagus discoidea* (Baum.-Bod.) Steenis (1954: 266). Type:—NEW CALEDONIA. Grande Terre, Mois de Mai, Vallée de la River Blance, 4 August 1951, *M. Baumann-Bodenheim 15000* (holotype Z, image!).

Trisyngyne dura (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus dura* Steenis (1952a: 147). Type:—INDONESIA. Papua, 9 km NE of Lake Habbema, October 1938, *L. J. Brass & C. Versteegh 10443* (holotype L, image!).

Trisyngyne eymae (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus eymae* Steenis (1952a: 147). Type:—INDONESIA. Papua, Wissel Lake, 29 March 1939, *P. J. Eyma 4800* (holotype L, image!).

Trisyngyne flaviramea (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus flaviramea* Steenis (1955: 281). Type:—PAPUA NEW GUINEA. Finschaffen [Finschhafen], Ngadua–Yunzain, 25 April 1953, *J. S. Womersley NGF 5139* (holotype L, image!).

Trisyngyne grandis (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus grandis* Steenis (1952a: 147). Type:—PAPUA NEW GUINEA. Aiyura, near Kuminankira, October 1944, *L. S. Smith NGF 1098* (holotype A, image!).

Trisyngyne nuda (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus nuda* Steenis (1972: 285). Type:—PAPUA NEW GUINEA. Upper Wenna Creek branch of the Tauri River near Paina Village, Gulf District, 15 March 1966, *R. Pullen 6582* (holotype CANB 162512, image!).

Trisyngyne perryi (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus perryi* Steenis (1952a: 146). Type:—PAPUA NEW GUINEA. East Mt. Taffa, near Nemodi, July 1935, *L. J. Brass 5057a* (holotype A, image!).

Trisyngyne pseudoresinosa (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus pseudoresinosa* Steenis (1952a: 147). Type:—PAPUA NEW GUINEA. Sattelberg, Mt. Sarawaket, 24 March 1937, *M. S. Clemens 5849* (holotype A, image!).

Trisyngyne pullei (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus pullei* Steenis (1952a: 146–147). Type:—PAPUA NEW GUINEA. Mt. Hellwig, 4 January 1913, *A. A. Pulle 909* (holotype L, image!).

Trisyngyne recurva (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus recurva* Steenis (1952a: 146). Type:—INDONESIA. Papua, Mt. Arfak, Angi Gita Lake, 9–22 October 1948, *A. J. G. H. Kostermans 2384* (holotype L, image!).

Trisyngyne resinosa (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus resinosa* Steenis (1952a: 147). Type:—INDONESIA. Papua, 9 km NE of Lake Habbema, 22 October 1938, *L. J. Brass 10479* (holotype L, image!).

Trisyngyne rubra (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus rubra* Steenis (1952a: 147). Type:—INDONESIA. Papua, 18 km SW of Bernhard Camp, Idenburg River, 03 February 1939, *L. J. Brass & C. Versteegh 11997* (holotype A, image!).

Trisyngyne starkenborghii (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus starkenborghii* Steenis (1952a: 146). Type:—INDONESIA. Papua, Camp at Bele River, 18 km NE of Lake Habbema, November 1938, *L. J. Brass 11369* (holotype L, image!).

Trisyngyne stylosa (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus stylosa* Steenis (1986: 732). Type:—INDONESIA. Papua, Mt. Trikora, September 1982, *J. M. Mangen 229* (holotype L, image!).

Trisyngyne womersleyi (Steenis) Heenan & Smissen, *comb. nov.* ≡ *Nothofagus womersleyi* Steenis (1972: 294). Type:—INDONESIA. Papua, Watjetoni Mt., Kebar valley, *BW (C. Versteegh) 10320* (holotype L, image!).

Acknowledgements

We thank Edward Doonerwind of the Landcare Research Library, Lincoln, for assistance with literature; Ilse Breitwieser, Phil Novis and Christine Bezar for reviewing the draft manuscript; Matt McGlone for discussion; Hans-Joachim Esser for his editorial expertise and assistance; Kanchi Gandi for nomenclatural advice; and Ivan Tatanov (LE), Leon Perrie (WELT) and Ines Schoenberger (CHR) for assistance with type material. This research was supported by Core funding for Crown Research Institutes from the New Zealand Ministry of Business, Innovation and Employment's Science and Innovation Group.

References

Acosta, M.C. & Premoli, A.C. (2010) Evidence of chloroplast capture in South American *Nothofagus* (subgenus *Nothofagus*, Nothofagaceae). *Molecular Phylogenetics and Evolution* 54: 235–242.
http://dx.doi.org/10.1016/j.ympev.2009.08.008

Allan, H.H. (1929) Illustrations of wild hybrids in the New Zealand flora. VI. *Genetica* 11: 491–508.
http://dx.doi.org/10.1007/bf01718904

Allan, H.H. (1961) *Flora of New Zealand*. Government Printer, Wellington, 1085 pp.

APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105–121.
http://dx.doi.org/10.1111/j.1095-8339.2009.00996.x

Backlund, A. & Bremer, K. (1998) To be or not to be—principles of classification and monotypic plant families. *Taxon* 47: 391–400.
http://dx.doi.org/10.2307/1223768

Baillon, H.E. (1874) Nouvelles observations sur les Euphorbiacées. *Adansonia* 11: 72–138.

Baumann-Bodenheim, M.G. (1953) Fagacées de la Nouvelle Caledonie. *Bulletin du Muséum National d'Histoire Naturelle, series 2*, 25: 419–421.

Baumann-Bodenheim, M.G. (1992) *Trisyngyne*. *Systematik der Flora von Neu-Caledonien (Melanesien-Südpazifik)*. Mrs A. L. Baumann, Herrliberg, 153 pp.

Berkeley, M.J. (1842) On an edible fungus from Tierra del Fuego and allied Chilean species. *Transactions of the Linnean Society of London* 19: 37–43.
http://dx.doi.org/10.1111/j.1096-3642.1842.tb00073.x

Blume, C.L. von (1826) *Bijdragen tot de flora van Nederlandsch Indie* 10. Ter Lands Drukkerij, Batavia, pp. 485–526.

Blume, C.L. von (1851) Ord. Cupulifereae. *Museum Botanicum Lugduno-Batavum* 1: 305–320.

Candolle, A.L.P.P. de (1864) *Prodromus Systematis Naturalis Regni Vegetabilis* 16(2). Victoris Masson et fillii, Paris, 691 pp.

Cheeseman, T.F. (1906) *Manual of the New Zealand flora. 1st edition*. Government Printer, Wellington, 1198 pp.

Cheeseman, T.F. (1925) *Manual of the New Zealand flora. 2nd edition*. Government Printer, Wellington, 1163 pp.

Cockayne, L. (1911) Some hitherto-unrecorded plant-habitats (VI). *Transactions and Proceedings of the New Zealand Institute* 43: 169–174.

Cockayne, L. (1926) Monograph on the New Zealand beech forests. Part 1. The ecology of the forests and taxonomy of the beeches. *New Zealand State Forest Bulletin No. 4.* Government Printer, Wellington, 71 pp.

Cockayne, L. & Allan, H.H. (1934) An annotated list of groups of wild hybrids in the New Zealand flora. *Annals of Botany* 48: 1–55.

Cockayne, L. & Atkinson, E. (1926) On the New Zealand wild hybrids of *Nothofagus*. *Genetica* 8: 1–43.
http://dx.doi.org/10.1007/bf01481819

Colenso, W. (1885) A description of some newly-discovered and rare indigenous plants; being a further contribution towards the making known the botany of New Zealand. *Transactions and Proceedings of the New Zealand Institute* 17: 237–265.

Colenso, W. (1898) Phaenogams [sic]: a description of a few more newly discovered indigenous plants; being a further contribution towards the making known the botany of New Zealand. *Transactions and Proceedings of the New Zealand Institute* 31: 266–281.

Cook, L. & Crisp, M. (2005) Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwanan radiation. *Proceedings of the Royal Society London, series B, Biological Sciences* 272: 2535–2544.
http://dx.doi.org/10.1098/rspb.2005.3219

Cookson, I.C. (1952) Identification of Tertiary pollen grains with those of New Guinea and New Caledonian beeches. *Nature* 170: 127.
http://dx.doi.org/10.1038/170127a0

Cookson, I.C. & Pike, K.M. (1955) The pollen morphology of *Nothofagus* Bl. sub-section *Bipartitae* Steen. *Australian Journal of Botany* 3: 197–206.
http://dx.doi.org/10.1071/bt9550197

Crepet, W.L. & Daghlian, C.P. (1980) Castaneoid inflorescences from the Middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. *American Journal of Botany* 67: 739–757.
http://dx.doi.org/10.2307/2442667

Dawson, J & Lucas, R. (2011) *New Zealand's native trees*. Craig Potton Publishing, Nelson, 576 pp.

Dengler, N.G. & MacKay, L.B. (1975) The leaf anatomy of beech, *Fagus grandifolia*. *Canadian Journal of Botany* 53: 2202–2211.
http://dx.doi.org/10.1139/b75-244

Denk, T. (2003) Phylogeny of *Fagus* L. (Fagaceae) based on morphological data. *Plant Systematics and Evolution* 240: 55–81.
http://dx.doi.org/10.1007/s00606-003-0018-x

Dettmann, M.E., Pocknall, D.T., Romero, E.J. & Zamaloa, M.C. (1990) *Nothofagidites* Erdtman ex Potonie, 1960; a catalogue of species with notes on the palaeogeographic distribution of *Nothofagus* Bl. (Southern Beech). *New Zealand Geological Survey Paleontology Bulletin* 60: 1–79.

Don, D. (1825) *Prodromus Florae Nepalensi*s. J. Gale, London, 256 pp.

Donoso, C., Morales, J. & Romero, M. (1990) Natural hybridisation between *Nothofagus obliqua* (Mirb.) Oerst. and *N. alpina* (Poepp. & Endl.) Oerst. in forests of southern Chile. *Revista Chilena Historia de Natural* 63: 49–60. http://dx.doi.org/10.1079/9781780640266.0119

Dumont d'Urville, J.S.C. (1843) *Voyage au Pôole sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée. Botanique, Atlas* part 6. Gide, Paris, t. 6.

Espinosa, M.R. (1926) Nota preliminar sobre dos especies nuevas chilenas del género *Nothofagus* Blume. *Revista Chilena Historia de Natural* 30: 268.

Espinosa, M.R. (1928) Dos especies nuevas de *Nothofagus*. *Revista Chilena Historia de Natural* 32: 171–197.

Forman, L.L. (1962) A new genus in the Fagaceae. *Taxon* 11: 139–140.

Forster, G. (1789) Fasciculus Plantarum Magellanicum. *Commentationes Societatis Regiae Scientiarum Gottingensis* 9: 13–45.

Gillanders, K. (2008) A new hybrid *Nothofagus*. *The Plantsman* 7: 55–57.

Govaerts, R. & Frodin, D.G. (1999) *World Checklist and Bibliography of Fagales*. Royal Botanic Gardens, Kew, 408 pp.

Grant, M.L. & Clement, E.J. (2004) Clarification of the name *Nothofagus alpina* and a new epithet for a *Nothofagus* hybrid. *Botanical Journal of the Linnean Society* 146: 447–451. http://dx.doi.org/10.1111/j.1095-8339.2004.00346.x

Haase, P. (1990) *Nothofagus truncata* (hard beech) in the upper Taramakau catchment, South Island, New Zealand. *New Zealand Journal of Ecology* 14: 31–35.

Haase, P. (1992) Isozyme variability and biogeography of *Nothofagus truncata* (Fagaceae). *New Zealand Journal of Botany* 30: 315–328. http://dx.doi.org/10.1080/0028825x.1992.10412910

Hardy, N.B., Penny, A.E., Gullan, J., Henderson, R.C. & Cook, L.G. (2008) Relationships among felt scale insects (Hemiptera: Coccoidea: Eriococcidae) of southern beech, *Nothofagus* (Nothofagaceae), with the first descriptions of Australian species of the *Nothofagus*-feeding genus *Madarococcus* Hoy. *Invertebrate Systematics* 22: 365–405. http://dx.doi.org/10.1071/is07032

Hill, R.S. (1991) Tertiary *Nothofagus* (Fagaceae) macrofossils from Tasmania and Antarctica and their bearing on the evolution of the genus. *Botanical Journal of the Linnean Society* 105: 73–112. http://dx.doi.org/10.1111/j.1095-8339.1991.tb00200.x

Hill, R.S. (2001) Biogeography, evolution and palaeoecology of *Nothofagus* (Nothofagaceae): The contribution of the fossil record. *Australian Journal of Botany* 49: 321–332.

Hill, R.S. & Jordan, G.J. (1993) The evolutionary history of *Nothofagus* (Nothofagaceae). *Australian Systematic Botany* 6: 111–126. http://dx.doi.org/10.1071/sb9930111

Hill, R.S. & Read, J. (1991) A revised infrageneric classification of *Nothofagus* (Fagaceae). *Botanical Journal of the Linnean Society* 105: 37–72. http://dx.doi.org/10.1111/j.1095-8339.1991.tb00199.x

Hjelmquist, H. (1948) Studies on the floral morphology and phylogeny of the Amentiferae. *Botaniska Notiser Supplement* 2: 1–171.

Hooker, W.J. (1840) On the *Fagus antarctica* of Forster, and some other species of beech of the Southern Hemisphere. *Journal of Botany: being a second series of the botanical miscellany* 2: 147–157.

Hooker, J.D. (1844) *Fagus fusca*, Hook. fil. *Icones plantarum*; *or figures, with brief descriptive characters and remarks, of new or rare plants, selected from the authors herbarium* 7: t. 630–631.

Hooker, J.D. (1851) *Fagus gunnii*, Hook. fil. *Icones plantarum*; *or figures, with brief descriptive characters and remarks, of new or rare plants, selected from the authors herbarium* 9: t. 881.

Hooker, J.D. (1853) *The Botany of the Antarctic Voyage of H.M. Discovery Ships Erebus and Terror in the Years 1839-1843. Vol. 2. Flora Novae-Zelandiae Part I. Flowering Plants*. Lovell Reeve & Co., London, 312 pp.

Hooker, J.D. (1964) *Handbook of the New Zealand flora*. Lovell Reeve & Co., London, 392 pp.

Humphries, C.J. (1981) Biogeographical methods and the southern beeches (Fagaceae: *Nothofagus*). *In*: Forey, P.L. (ed.) *The evolving biosphere: chance, change and challenge*. Cambridge University Press, London, pp. 283–297.

Johnston, P.R., Johansen, R.B., Williams, A.F.R., Wikie, J.P. & Park, D. (2012) Patterns of fungal diversity in New Zealand *Nothofagus* forests. *Fungal Biology* 116: 401–412. http://dx.doi.org/10.1016/j.funbio.2011.12.010

Jones, J.H. (1986) Evolution of the Fagaceae: the implications of foliar features. *Annals of the Missouri Botanical Garden* 73: 228–275. http://dx.doi.org/10.2307/2399112

Jordan, G.J. & Hill, R.S. (1999) The phylogenetic affinities of *Nothofagus* (Nothofagaceae) leaf fossils based on combined molecular and morphological data. *International Journal of Plant Science* 160: 1177–1188. http://dx.doi.org/10.1086/314207

Kirk, T. (1885) Description of a new species of *Fagus*. *Transactions and Proceedings of the New Zealand Institute* 17: 297–298.

Kirk, T. (1889) *The forest flora of New Zealand.* Government Printer, Wellington, 345 pp.

Knapp, M., Stockler, K., Havell, D., Delsuc, F., Sebastiani, F. & Lockhart, P.J. (2005) Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beech). *PLoS Biology* 3: 38–43. http://dx.doi.org/10.1371/journal.pbio.0030014

Krasser, F. (1896) Bemerkungen zur Systematik der Buchen. *Annalen des Naturhistorischen Hofmuseums Wien* 11: 155–163.

Kubitzki, K. (1993) Fagaceae. *In*: Kubitzki, K., Rohwer, J.G. & Bittrich, V. (eds.) *The Families and Genera of Vascular Plants 2: Flowering Plants, Dicotyledons, Magnoliid, Hamamelid and Caryophyllid Families.* Springer-Verlag, Berlin, pp. 301–309.

Kuprianova, A.L. (1962) Palinological data and the systematics of the Fagales and Urticales. *In*: Sladkov, A.N. (ed.) *For the first international conference on Palinology: Reports of Soviet Palinologists (extended theses)*. U.S.S.R. Academy of Sciences, Moscow, pp. 17–25.

Ladiges, P.Y., Nelson, G. & Grimes, J. (1997) Subtree analysis, *Nothofagus*, and Pacific biogeography. *Cladistics* 13: 125–129. http://dx.doi.org/10.1111/j.1096-0031.1997.tb00246.x

Lanjouw, J., Baehni, C., Robyns, W., Ross, R., Rousseau, J.M., Schopf, J.M., Schulze, G.M., Smith, A.C., de Vilmorin, R. & Stafleu, F.A. (1961) *International Code of Botanical Nomenclature (Montreal)*. *Regnum Vegetabile* 23. International Bureau for Plant Taxonomy and Nomenclature of the International Association for Plant Taxonomy, Utrecht, 372 pp.

Laubenfels, D.J. de (1969) A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. *Journal of the Arnold Arboretum* 50: 315–369.

Li, R.Q., Chen, Z.D., Lu, A.M., Soltis, D.E., Soltis, P.S. & Manos, P.S. (2004) Phylogenetic relationships in Fagales based on DNA sequences from three genomes. *International Journal of Plant Science* 165: 311–324. http://dx.doi.org/10.1086/381920

Linder, H.P., Baeza, M., Barker, N.P., Galley, C., Humphreys, A.M., Lloyd, K.M., Orlovich, D.A., Pirie, M.D., Simon, B.K., Walsh, N. & Verboom, G.A. (2010) A generic classification of the Danthonioideae (Poaceae). *Annals of the Missouri Botanical Garden* 97: 306–364. http://dx.doi.org/10.3417/2009006

Linder, H.P. & Crisp, M.D. (1995) *Nothofagus* and Pacific biogeography. *Cladistics* 11: 5–32. http://dx.doi.org/10.1111/j.1096-0031.1995.tb00002.x

Linnaeus, C. (1753) *Species Plantarum*. Salvius, Stockholm,1200 pp.

Maddison, D.R. & Maddison W.P. (2001) *MacClade 4*. Sinauer Associates Inc. Sunderland, Massachusetts.

Manos, P.S. (1997) Systematics of *Nothofagus* (Nothofagaceae) based on rDNA spacer sequences (ITS): taxonomic congruence with morphology and plastid sequences. *American Journal of Botany* 84: 1137–1155. http://dx.doi.org/10.2307/2446156

Manos, P.S., Cannon, C.H. & Oh, S.-H. (2008) Phylogenetic relationships and taxonomic status of the paleoendemic Fagaceae of western North America: recognition of a new genus, *Notholithocarpus. Madroño* 55: 181–190. http://dx.doi.org/10.3120/0024-9637-55.3.181

Manos, P.S. & Steele, K.P. (1997) Phylogenetic analyses of "higher" Hamamelididae based on plastid sequence data. *American Journal of Botany* 84: 1407–1419. http://dx.doi.org/10.2307/2446139

Mark, A.F. & Lee, W.G. (1985) Ecology of hard beech *(Nothofagus truncata)* in southern outlier stands in the Haast ecological district, South Island, New Zealand. *New Zealand Journal of Ecology* 8: 97–121.

Martin, P.G. & Dowd, J.M. (1993) Using sequences of *rbc*L to study phylogeny and biogeography of *Nothofagus* species. *Australian Systematic Botany* 6: 441–447. http://dx.doi.org/10.1071/sb9930441

McGlone, M.S., Hall, M.J. & Wilmshurst, J. (2011) Seasonality in the early Holocene: extending fossil-based estimates with a forest ecosystem model. *The Holocene* 21: 517–526. http://dx.doi.org/10.1177/0959683610385717

McGlone, M.S., Mildenhall, D.C. & Pole, M.S. (1996) History and paleoecology of New Zealand *Nothofagus* forests. *In*: Veblen, T.T., Hill, R.S. & Read, J. (eds.) *The ecology and biogeography of* Nothofagus *forests*. Yale University Press, New Haven, pp. 83–125.

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud-Homme van Reine, W.F., Smith, G.F., Wiersema, J.H., Turland, N.J. (2012) *International Code of Nomenclature for algae, fungi and plants (Melbourne Code)*. Regnum Vegetabile 154. Koeltz Scientific Books, Koenigstein, 240 pp.

Meurk, C.D. & Hall, G.M.J. (2006) Options for enhancing forest biodiversity across New Zealand's managed landscapes based on ecosystem modelling and spatial design. *New Zealand Journal of Ecology* 30: 131–146.

Miller, D. (1754) The Gardeners Dictionary. Abridged 4th ed. John and James Rivington, London, 1582 pp.

Mirbel, C.F.B. (1827) Recherches sur la distribution géographique des Végétaux phanérogames de l'Ancien-Monde, depuis l'équateur jusqu'au pôle arctique; suivies de la description de neuf espèces de la famille des Amentacées. *Mémoires du Museum d'histoire naturelle de Paris* 14: 349–474.

Molloy, B.P.J., de Lange, P.J. & Clarkson, B.D. (1999) *Coprosma pedicellata* (Rubiaceae), a new species from New Zealand. *New Zealand Journal of Botany* 37: 383–397. http://dx.doi.org/10.1080/0028825x.1999.9512643

Mueller, F.J.H. von (1866) *Fragmenta Phytographiae Australiae* 5. Auctoritate Gubern. Coloniae Victoriae, ex officina Joannis Ferres, Melbourne, 240 pp.

Nicolson, D.D. & Fosberg, F.R. (2004) *The Forsters and the botany of the second Cook Expedition (1772–1775)*. Regnum Vegetabile 139, 759 pp.

Nixon, K.C. (1982) In support of the Nothofagaceae Kuprianova. *Botanical Society of America Miscellaneous Series* 162: 102.

Nixon, K.C. (1989) Origins of Fagaceae. *In*: Crane, P.R. & Blackmore, S. (eds.) *Evolution, systematics, and fossil history of the Hamamelidae*. Clarendon Press, Oxford, pp. 23–43.

Nixon, C. & Crepet, W.L. (1989) *Trigonobalanus* (Fagaceae): taxonomic status and phylogenetic relationships. *American Journal of Botany* 76: 828–841.
http://dx.doi.org/10.2307/2444539

Ørsted, A.S. (1871) Bidrag til Kundskab om Egefamilien i Nutid og Fortid. *Kongelige Danske Videnskabernes Selskabs Skrifter* 9: 331–538.

Peterson, K.R., Pfister, D.H. & Bell, C.D. (2010) Cophylogeny and biogeography of the fungal parasite *Cyttaria* and its host *Nothofagus*, southern beech. *Mycologia* 102: 1417–1425.
http://dx.doi.org/10.3852/10-048

Philipson, W.R. & Philipson, M.N. (1979) Leaf vernation in *Nothofagus*. *New Zealand Journal of Botany* 17: 417–421.
http://dx.doi.org/10.1080/0028825x.1979.10426911

Philipson, W.R. & Philipson, M.N. (1988) A classification of the genus *Nothofagus* (Fagaceae). *Botanical Journal of the Linnean Society* 98: 27–36.
http://dx.doi.org/10.1111/j.1095-8339.1988.tb01692.x

Phillipi, R.A. (1858) Plantarum novarum Chilensium: Centuria quarta. *Linnaea* 29: 1–47.

Phillipi, R.A. (1864) Plantarum novarum Chilensium centuriae, inclusis quibusdam Mendocinus et Patagonicis. *Linnaea* 33: 1–308.

Poeppig, E.F. & Endlicher, S.F.L. (1838) *Nova Genera ac Species Plantarum quas in Regno Chilensi Peruviano et in terra Amazonica* 2 (9–10). Sumptibus F. Hofmeister, Leipzig, pp. 61–74.

Pole, M. (1994) The New Zealand flora—entirely longdistance dispersal? *Journal of Biogeography* 21: 625–635.
http://dx.doi.org/10.2307/2846036

Poole, A.L. (1950) Studies of New Zealand *Nothofagus* species. 1. Taxonomy and floral morphology. *Transactions of the Royal Society of New Zealand* 78: 363–380.

Poole, A.L. (1958) Studies of New Zealand *Nothofagus* species. 3. The entire-leaved species. *Transactions of the Royal Society of New Zealand* 85: 551–564.

Praglowski, J. (1982) Fagaceae L.: Fagoideae. *World Pollen and Spore Flora* 11. Scandinavian University Press, Oslo, pp. 1–28.

Premoli, A.C., Mathiasen, P., Acosta, M.C. & Ramos, V.A. (2011) Phylogeographically concordant chloroplast DNA divergence in sympatric *Nothofagus* s.s. How deep can it be? *New Phytologist* 193: 261–275.
http://dx.doi.org/10.1111/j.1469-8137.2011.03861.x

Richard, A. (1832) *Essai d'une Flore de la Nouvelle-Zélande*. J.Tastu, Paris, 376 pp.

Rickett, H.W. (1958) Reports of the Committee for Spermatophyta: conservation of generic names I (continued). *Taxon* 7: 184–193.
http://dx.doi.org/10.2307/1218445

Rozefelds, A.C. (1998) Stamen morphology in *Nothofagus* (Nothofagaceae). *International Journal of Plant Science* 159: 655–667.
http://dx.doi.org/10.1086/297584

Rozefelds, A.C. & Drinnan, A.N. (1998) Ontogeny and diversity in staminate flowers of *Nothofagus* (Nothofagaceae). *International Journal of Plant Science* 159: 906–922.
http://dx.doi.org/10.1086/314090

Rozefelds, A.C. & Drinnan, A.N. (2002) Ontogeny of pistillate flowers and inflorescences in *Nothofagus* subgenus *Lophozonia* (Nothofagaceae). *Plant Systematics and Evolution* 233: 105–126.
http://dx.doi.org/10.1007/s00606-002-0214-0

Russell, G.B., Bowers, W.S., Keesing, V., Niemeyer, H.M., Svenet, T., Vasanthaverni, S. & Wratten, S.D. (2000) Patterns of bioactivity and herbivory on *Nothofagus* species from Chile and New Zealand. *Journal of Chemical Ecology* 26: 41–56.

Sanmartín, I. & Ronquist, F. (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology* 53: 216–243.
http://dx.doi.org/10.1080/10635150490423430

Sauquet, H.E., Ho, S.Y.W., Gandolfo, M.A., Jordan, G.J., Wilf, P., Cantrill, D.J., Bayly, M.J., Bromham, L., Brown, G.K., Carpenter, R.J., Lee, D.M., Murphy, D.J., Sniderman, J.M.K. & Udovicic, F. (2012) Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of *Nothofagus* (Fagales). *Systematic Biology* 61: 289–313. doi:10.1093/sysbio/syr116

Setoguchi, H., Ono, M., Doi, Y., Koyama, H. & Tsuda, M. (1997) Molecular phylogeny of *Nothofagus* (Nothofagaceae) based on the *atp*B-*rbc*L intergenic spacer of the chloroplast DNA. *Journal of Plant Research* 110: 469–484.
http://dx.doi.org/10.1007/bf02506808

Spach, E. (1841) Végétaux Phanérogames Dicotylédones. *Histoire Naturelle des Végétaux* 11. Librairie encyclopédique de Roret, Paris, 444 pp.

Stecconi, M., Marchelli, P., Puntieri, J., Picca, P. & Gallo, L. (2004) Natural hybridization between a deciduous (*Nothofagus antarctica*, Nothofagaceae) and an evergreen (*N. dombeyi*) forest tree species: evidence from morphological and isoenzymatic traits. *Annals of Botany* 94: 775–786. http://dx.doi.org/10.1093/aob/mch205

Steenis, C.G.G.J. van (1952a) Preliminary account of Papuan *Nothofagus. Blumea* 7: 146–147.

Steenis, C.G.G.J. van (1952b) Errata. *Blumea* 7: 306.

Steenis, C.G.G.J. van (1953a) Results of the Archbold expeditions: Papuan *Nothofagus*. *Journal of the Arnold Arboretum* 34: 301–374.

Steenis, C.G.G.J. van (1953b) Propositions pour le Congrès de Paris. Proposal no. 39. *Taxon* 2: 177–179.

Steenis, C.G.G.J. van (1954) Additional note on *Nothofagus*. *Journal of the Arnold Arboretum* 35: 266–267.

Steenis, C.G.G.J. van (1955) Miscellaneous notes on New Guinea plants II. *Nova Guinea, new series* 6: 279–282.

Steenis, C.G.G.J. van (1971) *Nothofagus*, key genus of plant geography, in time and space, living and fossil, ecology and phylogeny. *Blumea* 19: 65–98.

Steenis, C.G.G.J. van (1972) *Nothofagus*. *In*: Steenis, C.G.G.J. van (ed.) *Flora Malesiana, series 1*, 7 (2). Noordhoff-Kolff, Djakarta, pp. 277–294.

Steenis, C.G.G.J. van (1986) An interesting new species of *Nothofagus* from New Guinea (Fagaceae). *Kew Bulletin* 41: 732. http://dx.doi.org/10.2307/4103125

Swofford, D.L. (2002) *PAUP*: Phylogenetic Analysis Using Parsimony (and other methods).* Sinauer Associates, Sunderland, Massachusetts.

Stover, L.E. & Evans, P.R. (1973) Upper Cretaceous-Eocene spore-pollen zonation, offshore Gippsland Basin, Australia. *Special Publications, Geological Society of Australia* 4: 55–72.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA 5: Molecular Evolutionary Genetics Analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28: 2731–2739. http://dx.doi.org/10.1093/molbev/msr121

Tanai, T. (1986) Phytogeographic and phylogenetic history of the genus *Nothofagus* Bl. (Fagaceae) in the southern hemisphere. *Journal of the Faculty of Science, Hokkaido University, series 4*, 21: 505–582.

Turczaninow, C.G.J. (1858) Animadversiones in secundam partem herbarii Turczaninowiani, nunc Universitatis Caesareae Charkowiensis. *Bulletin de la Société Imperiale des Naturalistes de Moscou* 31: 380–500.

Vazquez, F.M. & Rodriguez, R.A. (1999) A new subspecies and two new combinations of *Nothofagus* Blume (Nothofagaceae) from Chile. *Botanical Journal of the Linnean Society* 129: 75–83. http://dx.doi.org/10.1111/j.1095-8339.1999.tb00491.x

Wang, P.L. & Pu, F.D. (2004) *Pollen morphology and biogeography of Fagaceae.* Guangdong Science and Technology Press, Guangzhou, 158 pp.

Wardle, J. (1984) *The New Zealand beeches. Ecology, utilization and management.* New Zealand Forest Service, Christchurch, 447 pp.

Wigston, D.L. (1979) *Nothofagus* (Blume) in Britain. *Watsonia* 12: 344–345.

Wollenweber, E., Stevens, J.F., Dörr, M. & Rozefelds, A.C. (2003) Taxonomic significance of flavonoid variation in temperate species of *Nothofagus*. *Phytochemistry* 62: 1125–1131. http://dx.doi.org/10.1016/s0031-9422(02)00666-0

Zheng, Z.H., Wang, P.L. & Pu, F.D. (1999) A comparative study on pollen exine ultrastructure of *Nothofagus* and the other genera of Fagaceae. *Acta Phytotaxonomica Sinica* 37: 253–258.

Appendix 1. Morphological characters used in the phylogenetic analyses. Characters 1–22 from Jordan & Hill (1999), excluding their characters 10 and 11 (see text); characters 12–24 of Jordan & Hill (1999) were renumbered here as 10–22. Characters 23–37 were obtained from other literature.

1. Leaf vernation. 0 = plicate; 1 = planar; 2 = revolute; 3 = conduplicate. For illustrations of this character see Philipson (1979, figs. 3–6).
2. Cupule valves and fruit. 0 = valves 4, fruit 2 trimerous, 1 dimerous; 1 = valves 2, fruit 3 dimerous; 2 = valves 2, fruit 1 dimerous; 3 = valves 2, fruit 1 trimerous; 4 = valves 2–4, fruit 1 trimerous, 0–1 dimerous; 5 = valves 4, fruit 4–7. For illustrations of this character see Hill & Read (1991, figs. 1–34).
3. Cupule appendage type. 0 = glandular; 1 = lamellate. For illustrations of this character see Hill & Read (1991, figs. 1–34).
4. Peduncle length. 0 = sessile or short; 1 = long.
5. Cupule valves. 0 = woody; 1 = thin; 2 = thin and much shorter than the fruit.
6. Staminate flowers. 0 = perianth present; 1 = perianth absent, pseudanthium present. For illustrations of this character see Rozefelds & Drinnan (1998, figs. 1b–c, fig. 2e–f) and Langdon 1940, fig. 11).
7. Pollen shape in polar view. 0 = peritreme; 1 = goniotreme. For illustrations of this character see Dettmann *et al.* (1990, table 2).
8. Pollen polar to equatorial lengths (l/E). 0 = $l/E > 0.35$; 1 = $l/E < 0.3$. For illustrations of this character see Dettmann *et al.* (1990, table 2).
9. Pollen aperture thickening. 0 = annulate; 1 = heavy thickening; 2 = rimmed; 3 = unthickened. For illustrations of this character see Dettmann *et al.* (1990, table 2).
10. Stipule attachment. 0 = not peltate; 1 = peltate. For illustrations of this character see Steenis (1953, figs. 2, 4–22).
11. Phyllotaxy. 0 = distichous; 1 = spiral.
12. Glandular trichomes on cuticle. 0 = present; 1 = absent. For illustrations of this character see Hill & Read (1991, figs. 76–78).
13. Solitary unicellular trichome type A. 0 = present; 1 = absent. For illustrations of this character see Hill & Read (1991, figs. 83–84).
14. Solitary unicellular trichome type C. 0 = present; 1 = absent. For an illustration of this character see Hill & Read (1991, fig. 86).
15. Conical trichomes. 0 = present; 1 = absent; 2 = broad-based form; 3 = SUTTB or SUTTD. For an illustration of this character see Jordon & Hill (1999, fig. 1a).
16. T pieces at stomatal poles. 0 = absent; 1 = present. For illustrations of this character see Hill & Read (1991, figs. 93–96).
17. Stomatal orientation. 0 = random; 1 = mostly parallel with the midrib. For illustrations of this character see Hill & Read (1991, figs. 90–92).
18. Giant stomata on veins. 0 = present; 1 = absent. For illustrations of this character see Hill & Read (1991, fig. 78) and Jordon & Hill (1999, fig. 1b).
19. Stomatal size excluding giant stomata. 0 = more or less even; 1 = variable.
20. Upper epidermal cells over veins. 0 = more elongate than areolar cells; 1 = not distinguishable from areolar cells; 2 = thinner than areolar cells.
21. Complete fimbrial vein. 0 = absent; 1 = type 1; 2 = type 2. For illustrations of this character see Jordon & Hill (1999, figs. 1f–1h).
22. Serrations. 0 = often associated with more than two teeth; 1 = associated with one or two teeth; 2 = entire margined leaf. For illustrations of this character see Jordon & Hill (1999, figs. 1i–j).
23. Anther ornamentation. 0 = type a, non-ornamented; 1 = type b, isomorphic, and consisting of a single papilla on each epidermal cell; 2 = type c1, heteromorphic, with striated papillae in ridges and/or on the apex, weakly defined papillose ridges along sides of anthers and lacking prominently striated cells on the

distal connective protrusion; 3 = type c2, heteromorphic, with striated papillae in ridges and/or on the apex, papillose ridges along sides of anthers and epidermal papillae on the distal connective protrusion are larger and strongly differentiated from other epidermal cells; 4 = type c3, heteromorphic, with striated papillae in ridges and/or on the apex, prominent lateral papillose ridges, and epidermal cells on distal connective protrusion are not strongly differentiated from other epidermal cells; 5 = type c4, heteromorphic, with striated papillae in ridges and/or on the apex, papillose ridges along sides of anthers and epidermal papillae on distal connective protrusion smaller than other epidermal cells. Data from Rozefelds (1998). For illustrations of this character see Rozefelds (1998, figs. 1–4).

24. Filaments free or connate. 0 = free; 1 = connate. Data from Rozefelds (1998) and Rozefelds & Drinnan (2002). For illustrations of this character see Rozefelds & Drinnan (1998, fig. 9g).
25. Stamen number. 0 = <20; 1 = usually >20. Data from Rozefelds (1998).
26. Pollen aperture ends. 0 = U-shaped; 1 = V-shaped. Data from Manos (1997) character 10. For illustrations of this character see Dettmann *et al.* (1990, table 2).
27. Epidermal cell walls. 0 = not granular; 1 = granular. Data from Hill & Read (1991) character 16.
28. Stamen development. 0 = centripetal; 1 = pseudocentrifugal. Data from Rozefelds & Drinnan (1998). For illustrations of this character see Rozefelds & Drinnan (1998, figs. 1–2).
29. Staminate perianth lobe number. 0 = 4; 1= 6–14. Data from Rozefelds & Drinnan (1998). For illustrations of this character see Rozefelds & Drinnan (1998, figs. 1–2).
30. Staminate perianth shape. 0 = narrowly campanulate; 1 = broadly campanulate; 2 = tubular. Data from Rozefelds & Drinnan (1998). For illustrations of this character see Rozefelds & Drinnan (1998, figs. 1–2).

31. Staminate perianth lobes. 0 = prominent; 1 = reduced. Data from Rozefelds & Drinnan (1998). For illustrations of this character see Rozefelds & Drinnan (1998, figs. 1–2).
32. Anther distal connective protrusion. 0 = absent; 1 = present, weakly or strongly developed. Data from Rozefelds (1998) and Rozefelds & Drinnan (1998).
33. Cupule vestiture. 0 = simple trichomes; 1 = densely covered with simple trichomes; 2 = glabrous. Data from Hill & Read (1991).
34. Pollen aperture length. 0 = 4–11 µm; 1 = >15 µm. Data from Manos (1997).
35. *Cyttaria* (Ascomycota, Leotiomycetes) lineage A of Peterson *et al*. (2010). 0 = absent; 1 = present.
36. *Cyttaria* (Ascomycota, Leotiomycetes) lineage B of Peterson *et al*. (2010). 0 = absent; 1 = present.
37. *Cyttaria* (Ascomycota, Leotiomycetes) lineage C of Peterson *et al*. (2010). 0 = absent; 1 = present.

Appendix 2. Morphological matrix for phylogenetic analysis of *Fuscospora, Lophozonia, Nothofagus, and Trisyngyne*.

Fagus	03?01000000000000000???0???1000?1000
Betulaceae	0????????0001000001000?00?????????000
N. antarctica	0010100101001101111000000010000000110
N. nitida	1010100101001101110100000000000000010
N. pumilio	03?0100101001131111000000010000000110
N. betuloides	10?0100101001101111000000000000000110
N. dombeyi	1010100101001101110000000000000000110
F. alessandri	0510100110000110011001000010001000000
F. gunnii	0010100110010100011001000010001000000
F. solandri	2410100110010110011012000010001000000
F. fusca	2010100110000100011011000010001000000
F. truncata	2010100110000110011011000010001000000
T. grandis	3210101121001110000202310000021120000
T. brassii	3111101121001110000202410000021120000
T. perryi	3111101121001110000101310000021120000
T. resinosa	3210201121001100000211210000021120000
T. balansae	3110001121101110000211510000021120000
T. aequilateralis	311000112110110000020 2?10000021120000
L. alpina	0000111030001000011000101111110011001
L. glauca	0000111030001000011000001101110011011
L. obliqua	0000111030001000011000101111110011011
L. cunninghamii	1000111030001020001101001101110011001
L. menziesii	1000111030001020011120001101110011001
L. moorei	1000111030001020011120101101110011001

Appendix 3. Taxa and GenBank numbers for *rbc*L sequences used for analysis of between- and within-genus genetic variation. Taxon names are as they appear in GenBank records except for genera of Nothofagaceae. Some species have sequence variation and we have included this in the analysis and so some species are represented by more than one accession.

Allocasuarina muelleriana (Miq.) L.A.S.Johnson, U06839; *Allocasuarina torulosa* (Aiton) L.A.S.Johnson, AY033850; *Allocasuarina verticillata* (Lam.) L.A.S.Johnson, X69527; *Alnus cremastogyne* Burkill, JF940705; *Alnus ferdinandi-coburgii* C.K.Schneid., FJ844570; *Alnus glutinosa*, FN689372; *Alnus glutinosa* (L.) Gaertn., HE574600; *Alnus incana* (L.) Moench, HM849757; *Alnus japonica* Siebold & Zucc., FJ844577; *Alnus nepalensis* D.Don, FJ844581; *Annamocarya sinensis* (Dode) J.-F.Leroy, AY263935; *Betula alleghaniensis* Britton, GU373373; *Betula ermanii* Cham., GU373374; *Canacomyrica monticola* Guillaumin, DQ310504; *Carpinus betulus* L., JN893226; *Carpinus viminea* Wall. ex Lindl., HQ427161; *Carya cordiformis* (Wangenh.) K.Koch, HQ590020; *Carya cordiformis* (Wangenh.) K.Koch, HQ590021; *Carya ovate* (Mill.) K.Koch, AY263931; *Castanea sativa* Mill., AY548965; *Castanea sativa* Mill., HM849869; *Castanea sativa* Mill., JN891651; *Castanea sativa* Mill., M94936; *Castanea seguinii* Dode, AY263937; *Castanopsis carlesii* (Hemsl.) Hayata, HQ427175; *Castanopsis cuspidata* Schottky var. *cuspidata*, AB060563; *Castanopsis fargesii* Franch., JF941175; *Castanopsis fissa* Rehder & E.H.Wilson, JF941176; *Castanopsis hystrix* Miq., JF941182; *Castanopsis hystrix* Miq., JF941183; *Castanopsis hystrix* Miq., JF941184; *Castanopsis indica* A.DC., JF941185; *Castanopsis inermis* Benth. & Hook.f., AB125011; *Castanopsis lamontii* Hance, JF941191; *Castanopsis remotidenticulata* Hu, JF941204; *Castanopsis rockii* A.Camus, JF941207; *Castanopsis sclerophylla* (Lindl. & Paxton) Schottky, JF941212; *Castanopsis sieboldii* (Makino) Hatus, AB060564; *Castanopsis tibetana* Hance, AY147096; *Casuarina collina* J.Poiss. ex Pancher & Sebert, AY033856; *Casuarina equisetifolia* L., GU135200; *Casuarina glauca* Spreng., GU135181; *Casuarina littorea* Oken L01893; *Casuarina obesa* Miq., AY033853; *Ceuthostoma terminale* L.A.S.Johnson, AY033860; *Chrysolepis sempervirens* (Kellogg) Hjelmq., AF206750; *Comptonia peregrina* (L.) J.M.Coult., AJ626756; *Comptonia peregrina* (L.) J.M.Coult., DQ310505; *Comptonia peregrine* (L.) J.M.Coult., X69529; *Corylus avellana* L., FN689371; *Corylus avellana* L., HM849918; *Corylus avellana* L., JN890946; *Corylus avellana* L., JN891389; *Corylus cornuta* Marshall, X56619; *Cyclocarya paliurus* (Batal.) Iljinsk., AY263942; *Engelhardia fenzelii* Merr., AY147095; *Fagus Americana* Sweet, L13338; *Fagus crenata* Blume, AB060567; *Fagus grandifolia* Ehrh. AY935745; *Fagus grandifolia* subsp. *mexicana* Martinez) A.E.Murray, FJ348713; *Fagus hayatae* Palib., JF941503; *Fagus hayatae* Palib., JF941505; *Fagus japonica* Maxim., AB060566; *Fagus longipetiolata* Seemen, JF941508; *Fagus lucida* Rehder & E.H.Wilson, JF941510; *Fagus sylvatica* L., JN641795; *Fagus sylvatica* L., JN891396; *Fuscospora alessandri* (Espinosa) Heenan & Smissen, AY605489; *Fuscospora alessandri* (Espinosa) Heenan & Smissen, L13341; *Fuscospora fusca* (Hook.f.) Heenan & Smissen, L13351; *Fuscospora gunnii* (Hook.f.) Heenan & Smissen, AY605493; *Fuscospora gunnii* (Hook.f.) Heenan & Smissen, L13354; *Fuscospora solandri* (Hook.f.) Heenan & Smissen, AY605497; *Fuscospora solandri* (Hook.f.) Heenan & Smissen, L13362; *Fuscospora truncata* (Colenso) Heenan & Smissen, AY605498; *Fuscospora truncata* (Colenso) Heenan & Smissen, L13363; *Gymnostoma leucodon* (J.Poiss.) L.A.S.Johnson, AY033865; *Gymnostoma nobile* (Whitmore) L.A.S.Johnson, AY033866; *Gymnostoma sumatranum* (Jungh. ex de Vriese) L.A.S.Johnson, AY033870; *Hamamelis mollis* Oliv. ex Forb. & Hemsl., L01922; *Juglans cinerea* L., HQ590142; *Juglans nigra* L., AF206785; *Juglans nigra* L., HQ590143; *Juglans nigra* L., U00437; *Juglans regia* L., GQ436392; *Lithocarpus glaber* Nakai, AB060568; *Lithocarpus glaber* Nakai, HQ427174; *Lithocarpus henryi* Rehder & E.H.Wilson, AY147097; *Lithocarpus lucidus* (Roxb.) Rehder, AB125014; *Lithocarpus wallichianus* (Lindl. ex Hance) Rehder, AB125015; *Lophozonia alpina* (Poepp. & Endl.) Heenan & Smissen, L13342; *Lophozonia cunninghamii* (Hook.f.) Heenan & Smissen, AY605490; *Lophozonia cunninghamii* (Hook.f.) Heenan & Smissen, L13348; *Lophozonia glauca* (Phil.) Heenan & Smissen, AY605492; *Lophozonia glauca* (Phil.) Heenan & Smissen, L13352; *Lophozonia menziesii* (Hook.f.) Heenan & Smissen, AY605494; *Lophozonia menziesii* (Hook.f.) Heenan & Smissen, AY605495; *Lophozonia menziesii* (Hook.f.) Heenan & Smissen, L13355; *Lophozonia menziesii* (Hook.f.)

Heenan & Smissen, L13356; *Lophozonia obliqua* (Mirb.) Heenan & Smissen, AY605496; *Lophozonia obliqua* (Mirb.) Heenan & Smissen, L13358; *Morella caroliniensis* (Mill.) Small, GQ248648; *Morella cerifera* (L.) Small, AJ626759; *Morella faya* (Aiton) Wilbur, HM850183; *Morella quercifolia* (L.) Killick, AJ626760; *Myrica gale* L., JN890811; *Myrica gale* L., JN893091; *Myrica gale* L., X69530; *Myrica hartwegii* S.Watson, DQ310503; *Nothofagus antarctica* (G.Forst.) Oerst., AY263939; *Nothofagus antarctica* (G.Forst.) Oerst., L13343; *Nothofagus betuloides* (Mirb.) Oerst., L13345; *Nothofagus dombeyi* (Mirb.) Oerst., L13350; *Nothofagus nitida* (Phil.) Krasser, AY745881; *Nothofagus nitida* (Phil.) Krasser, L13357; *Nothofagus pumilio* (Poepp. & Endl.) Krasser, L13360; *Ostrya virginiana* K.Koch, HQ590197; *Ostrya virginiana* K.Koch, X56620; *Ostryopsis davidiana* Decne., AF081515; *Ostryopsis intermedia* B.Tian & J.Q.Liu, JF942745; *Ostryopsis nobilis* Balf.f. & W.W.Sm., JF942747; *Ostryopsis nobilis* Balf.f. & W.W.Sm., JF942749; *Platycarya strobilacea* Siebold & Zucc., AY263933; *Platycarya strobilacea* Siebold & Zucc., HQ427158; *Pterocarya fraxinifolia* (Poir.) Spach, AJ235790; *Pterocarya rhoifolia* Siebold & Zucc., U00439; *Quercus acutissima* Carruth., AB060578; *Quercus alba* L., EU676966; *Quercus alba* L., EU676967; *Quercus cerris* L., AB125017; *Quercus crenata* Lam., FN675732; *Quercus dentata* Thunb., AB060579; *Quercus garryana* Douglas ex Hook., HQ184325; *Quercus gemelliflora* Blume, AB125019; *Quercus hemisphaerica* Bartram ex Willd., AF119176; *Quercus hondae* Makino, B060583; *Quercus macrocarpa* Michx., EU676971; *Quercus macrocarpa* Michx., HQ590229; *Quercus ngira* L., EU002284; *Quercus phillyraeoides* A.Gray., HQ427176; *Quercus pubescens* Willd., FN675720; *Quercus robur* L., FN675733; *Quercus rubra* L., AB125026; *Quercus rubra* L., EU676973; *Quercus rubra* L., N689354; *Quercus serrata* var. *brevipetiolata* (A.DC.) Nakai, HQ427171; *Quercus suber* L., AB125027; *Quercus variabilis* Blume, AB060574; *Quercus virginiana* Mill., AF119175; *Rhoiptelea chiliantha* Diels & Hand.-Mazz., AF017687; *Ticodendron incognitum* Gómez-Laur. & L.D.Gómez, AB015455; *Ticodendron incognitum* Gómez-Laur. & L.D.Gómez, AF061197; *Trigonobalanus verticillata* Forman, AB084767; *Trigonobalanus verticillata* Forman, AJ235812; *Trisyngyne balansae* Baillon, L13344; *Trisyngyne brassii* (Steenis) Heenan & Smissen, L13346; *Trisyngyne codonandra* Baillon , L13347; *Trisyngyne discoidea* Baum.-Bod., L13349; *Trisyngyne grandis* (Steenis) Heenan & Smissen, L13353; *Trisyngyne perryi* (Steenis) Heenan & Smissen, L13359; *Trisyngyne resinosa* (Steenis) Heenan & Smissen, L13361.