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Timing Transantarctic Disjunctions in the Atherospermataceae (Laurales): Evidence from Coding and Noncoding Chloroplast Sequences

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Abstract.—Previous studies of the small Southern Hemisphere family Atherospermataceae have drawn contradictory conclusions regarding the number of transantarctic disjunctions and role of transoceanic dispersal in its evolution. Clarification of intergeneric relationships is critical to resolving (1) whether the two Chilean species, *Laurelia sempervirens and Laureliopsis philippiana*, are related to different Austral-Pacific species, implying two transantarctic disjunctions as suggested by morphology; (2) where the group is likely to have originated; and (3) whether observed disjunctions reflect the breakup of Gondwana. We analyzed chloroplast DNA sequences from six regions (the *rbcL* gene, the *rpl16* intron, and the *trnL-trnF*, *trnT-trnL*, *psbA-trnH*, and *atpB-rbcL* spacer regions; for all six regions, 4,372 bp) for all genera and most species of Atherospermataceae, using parsimony and maximum likelihood (ML). The family's sister group, the Chilean endemic *Gomortega nitida* (Gomortegaceae), was used to root the tree. Parsimony and ML yielded identical single best trees that contain three well-supported clades (≥75% bootstrap): *Daphnandra* and *Doryphora* from south-eastern Australia; *Atherosperma* and *Nemuaron* from Australia–Tasmania and New Caledonia, respectively; and *Laurelia novae-zelandiae* and *Laureliopsis philippiana* from New Zealand and Chile, respectively. The second Chilean species, *Laurelia sempervirens*, is sister to this last clade. Likelihood ratio testing did not reject the molecular clock assumption for the *rbcL* data, which can therefore be used for divergence time estimates. The atherosperm fossil record, which goes back to the Upper Cretaceous, includes pollen, wood, and leaf fossils from Europe, Africa, South America, Antarctica, New Zealand, and Tasmania. Calibration of *rbcL* substitution rates with the fossils suggests an initial diversification of the family at 100–140 million years ago (MYA), probably in West Gondwana, early entry into Antarctica, and long-distance dispersal to New Zealand and New Caledonia at 50–30 MYA by the ancestors of *L. novae-zelandiae* and *Nemuaron*. [Biogeography; Gondwana; likelihood ratio test; maximum likelihood; molecular clock; phylogeny; *rbcL* substitution rates.]

The southern sassafrases or Atherospermataceae are a small family of trees or shrubs comprising 2 species in Chile and 12 in Australasia (Table 1; Schodde, 1969); 2 additional new species are currently being assessed in the context of a treatment of the family for the flora of Australia (D. Foreman, T. Whiffin, and R. Schodde, in prep.). Throughout temperate forests of the Southern Hemisphere, Atherospermataceae are consistent ecological associates of the Southern Beeches (*Nothofagus*, Nothofagaceae). Phylogenetically, they belong in the Laurales, where they were long included in the family Monimiaceae (e.g., Thorne, 1992; Philipson, 1993; Takhtajan, 1997). Morphological and molecular data, however, show that Atherospermataceae are only distantly related to Monimiaceae and instead are sister to a monotypic family of trees endemic in Chile, the Gomortegaceae (Schodde, 1969; Renner, 1998, 1999).

The ecological association between atherosperms and *Nothofagus* is extremely tight. In Chile, stands of *Nothofagus obliqua* and *N. alpina* regularly include the atherosperm *Laurelia sempervirens* in the understory (Donoso, 1996). Both in Chile and in Patagonia, this association is replaced at higher elevations by more cold-adapted *Nothofagus dombeyi–N. alpina–Laurelia (Laureliopsis) philippiana* stands (Veblen et al., 1996a). In New Caledonia, species of *Nothofagus* cooccur with the atherosperm *Nemuaron vieillardii* (Read and Hope, 1996). In south-eastern Australia and Tasmania, *Nothofagus cunninghamii* cooccurs with the shade-tolerant *Atherosperma moschatum* (Read and Brown, 1996; Veblen et al., 1996b), and in New Guinea, species of *Nothofagus* are associated with the atherosperm *Dryadodaphne crassa* Schodde (formerly treated as a form of *Dryadodaphne novoguineensis*; e.g., Read and Hope, 1996). The New Zealand species *Laurelia novae-zelandiae* is associated with *Podocarpus*, *Weinmannia*, and *Beilschmiedia* (Schodde, 1969). Such strikingly stable floristic associations throughout

TABLE 1. Atherospermataceae taxa and their distribution. Gomortegaceae are the sister group of Atherospermataceae (Renner, 1999) and were used to root trees.

Taxon	Geographic distribution
Atherosperma moschatum Labill.	Tasmania, Victoria, and New South Wales
Daphnandra micrantha (Tul.) Benth.	New South Wales
Daphnandra repandula (F. Muell.) F. Muell.	Queensland
Daphnandra sp. nov. (*D. apatela* Schodde, ined.)	Queensland and New South Wales
Daphnandra tenuipes Perkins	New South Wales
Doryphora aromatica (F. M. Bailey) L. S. Smith	North-east Queensland
Doryphora sassafras (Endl.) Endl.	Queensland and New South Wales
Dryadodaphne novoguineensis (Perk.) A. C. Smith	New Guinea
Dryadodaphne crassa Schodde	New Guinea
Dryadodaphne sp. nov. (*D. trachyphloia* Schodde, ined.)	Queensland
Laurelia novae-zelandiae Cunn.	New Zealand
Laurelia sempervirens (Ruiz & Pavón) Tul.	Southern Chile
Laureliopsis philippiana (Looser) Schodde	Southern Chile and Argentina
Nemuaron vieillardii (Baill.) Baill.	New Caledonia
Gomortega nitida Ruiz & Pavón (= *G. keule* (Mol.) I. M. Johnson)	Southern Chile

Austral-Pacific forests generally are thought to reflect the Gondwanan connection between South America and Australasia by way of Antarctica. Genera with similar distributions across the southern Pacific include, for example, *Araucaria*, *Podocarpus*, *Coriaria*, *Eucryphia*, *Griselinia*, *Hebe*, *Lomatia*, *Muehlenbeckia*, *Weinmannia*, and certain Proteaceae (see Thorne, 1972; Takhtajan, 1986; Veblen et al., 1996a).

Although not as impressive or as well-studied as that of *Nothofagus*, the fossil record of Atherospermataceae goes back at least to the Upper Cretaceous (discussed below), and because of this and their disjunct South American–Australasian distribution and ecological association with other Gondwanan relict groups, the family has long been seen as having had a fundamentally vicariant history, with dispersal having played but a limited role (Schodde, 1969; and in e-mail, 1998). Schodde (1969:543) suggested that

> The close, presumably monophyletic relationship between *Dryadodaphne*, *Nemuaron*, and *Laurelia* [with widely disjunct distributions] suggests either earlier land continuity of one kind or another or long-distance dispersal between the regions in which they now occur. . . . Because of the unlikelihood that atherospermataceous nutlets can be transported by wind for great distances or that they are viable after immersion in sea water, the former alternative is the more likely.

Atherosperm diaspores are small hairy achenes with persistent long-plumose styles (Fig. 1) that are wind-dispersed.

Particularly striking is the disjunction between *Laurelia novae-zelandiae* from New Zealand and its morphologically closest relative *L. sempervirens* from Chile. New Zealand began to rift from Australia/Antarctica around 90–82 million years ago (MYA) and had reached its present position some 2,000 km from the Australian and Antarctic coasts by 60 MYA (Stevens, 1989). Arrival of the ancestors of *L. novae-zelandiae* over land would therefore imply an age for the lineage

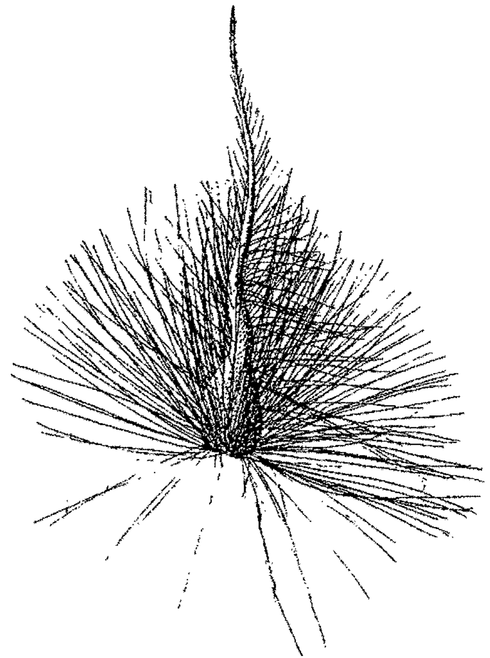

FIGURE 1. Fruitlet of *Laureliopsis philippiana* (Looser) Schodde (from Mart´nez-Laborde, 1983a); total length ~1.2 cm.

of at least 86 million years and is hard to reconcile with the absence of atherosperm pollen in older fossil layers on New Zealand that have been studied (discussed below). An arrival of *L. novae-zelandiae* after 86 MYA, on the other hand, would imply long-distance dispersal of seeds—in conflict with Schodde's view of a limited role of overwater dispersal in Atherospermataceae.

Besides the New Zealand–Chile disjunction between *L. novae-zelandiae* and *L. sempervirens*, systematic treatments of Atherospermataceae (Schodde, 1969; Philipson, 1993) postulate a second transantarctic disjunction within the family. Traditionally, the two Chilean species of atherosperms, *L. sempervirens* and *L. philippiana*, had been seen as closely related (Perkins [1911:47], where *L. serrata* R. Philippi non Bert. [=*L. philippiana* Looser] is treated as a synonym of *L. sempervirens*). However, after a careful morphological analysis of all species, Schodde removed *L. philippiana* from *Laurelia*, placing it in a new genus as *Laureliopsis philippiana* (Looser) Schodde (in Mart´nez-Laborde, 1983b). *Laureliopsis* differs from other atherosperms in the degree to which the inner staminodes become elongated and lignified in fruit. Schodde saw *Laureliopsis* as closest to the Tasmanian–southeastern Australian *Atherosperma moschatum* and formalized this view in his re-circumscription of the two subgroups traditionally recognized in the family (e.g., Bentham and Hooker, 1880). In Schodde's classification, *Laureliopsis* and *Atherosperma* together form a subfamily. Based on an a priori weighting of morphological and wood anatomical characters as either primitive or advanced (following Baileyan ideas), Schodde concluded that *Laureliopsis* possessed the greatest number of unspecialized characters and thus was the most primitive member of the family.

Laureliopis-like fossil wood has been described from Campanian (76–71 MYA) formations on James Ross Island just off the northeastern coast of the Antarctic Peninsula (Poole and Francis, 1999) as well as from Lower Oligocene (33 MYA) to Upper Miocene strata in Chile (Nishida, 1984; Nishida et al., 1988). Paleocene (65–55 MYA) formations on Seymour, an island next to James Ross Island, have yielded *Laurelia*-like wood (Poole and Gottwald, in press) leaves representing *Laurelia* or *Laureliopsis* (Dusén, 1908; Schodde, 1969:531), and leaves that show a perfect resemblance in venation and marginal teeth to those of extant *Laureliopsis philippiana* have been described from mid-Tertiary Patagonian sediments found near Rio Pichileufú in the eastern foothill of the Andes at ~41°-S (Berry, 1935; Schodde [1969:530–531] discusses the resemblance of the fossil leaves, *L. guinazui* Berry, to extant *L. philippiana* leaves; see Markgraf et al. [1996] for a recent description of the fossil floras at Rio Pichileufú). Atherosperm fossil wood is furthermore known from Upper Eocene deposits in Germany (35 MYA; Gottwald, 1992) and Lower Oligocene deposits in Egypt and the Cape province (Kräusel, 1939; Mädel, 1960; Müller-Stoll and Mädel, 1962). Recently, B. Mohr (Palaeontological Institute, Natural History Musem, Berlin, pers. comm.) has found *Laurelia*-like pollen in Kerguelen plateau material (Ocean Drilling Program, leg 120) dated to the Coniacian at 86–88 MYA. Atherospermataceae pollen is unusual among basal angiosperms in being dicolpate or meridionosulcate, and it is well studied and securely identifiable as to family (Sampson, 1975, 1996; Sampson and Foreman, 1988).

The fossil record of the family in New Zealand and Tasmania, by contrast, is much shorter. Late Pliocene–Early Pleistocene leaves of *Atherosperma moschatum* are the oldest record of the family from Tasmania (Hill and MacPhail, 1985), and pollen of *Laurelia novae-zelandiae*, today an abundant forest species, is known from the Oligocene (33–24 MYA) of New Zealand, albeit with some doubt (Couper, 1960). Mildenhall (1980; and pers. comm., Feb. 1999) indicates that this pollen differs somewhat in appearance from present-day *Laurelia* pollen, which does not appear in New Zealand until the Pliocene. No fossils are known from Australia. The earliest record of the sister group of atherosperms, Gomortegaceae, is fossil wood from Late Oligocene–Early Miocene (24–21 MYA) deposits in Chilean Patagonia (Nishida et al., 1989).

To address the question as to whether Atherospermataceae indeed harbor two transantarctic sister-group relationships among their 14 species, we have accumulated DNA sequences from six plastid regions: the *rbcL* gene, the *rpl16* intron, and the *trnL- trnF*, *trnT-trnL*, *psbA-trnH*, and *atpB-rbcL* spacer regions. Nuclear (internal transcribed spacer, ITS) sequences are

extremely divergent from each other and align dubiously with *Gomortega* (Renner and Won, unpubl.). We used parsimony and maximum likelihood (ML) analyses to reconstruct phylogeny and explored the possibility of dating divergence events, using a molecular clock approach and employing the fossils to calibrate substitution rates. The relatively good fossil record of Atherospermataceae, and Laurales in general, makes them a model system for comparing estimates of gene rates derived from fossil calibrations with those based on geological or other yard sticks.

MATRERIALS AND METHODS

Taxon Sampling, Rooting, and DNA Isolation and Amplification

The species used in this study and their source or voucher information are provided in the Appendix. Sister group relationships in Laurales are well understood (Renner, 1998, 1999), and higher-level molecular phylogenetic analyses based on the same six DNA regions used here confirm that the closest relative of Atherospermataceae are Gomortegaceae (Schodde, 1969), which include only *Gomortega nitida* from Chile. The closest relative of Atherospermataceae + Gomortegaceae are Siparunaceae, a family with 65 species in one genus in South America and a second monotypic genus in West Africa (Renner, 1999). Atherospermataceae comprise 12 described and a few undescribed species (Table 1; Schodde, 1969; Foreman et al., in prep.). We obtained sequences from 10 of the described and 2 of the undescribed species (Appendix). Because species of *Doryphora* and *Daphnandra* yielded spacer and intron sequences that were nearly or completely identical to those of congeners, for the final analyses we restricted sampling to one species per genus, choosing *Doryphora sassafras* and *Daphnandra repandula* as representatives. For *rbcL*, we sequenced one species per genus.

Total DNA was isolated from silica gel–dried or herbarium leaves by using DNeasy plant mini kits (QIAGEN) according to the manufacturer's instructions. Polymerase chain reaction (PCR) amplification followed standard protocols, with 32 cycles of 94°C for 30 sec, 52°C for 30–60 sec, and 72°C for 60 sec. The *rbcL* gene was amplified by using primers developed by Fay et al. (1997). The large intron that interrupts the *rpl16* gene was amplified by using primers 1067F and 18R designed by C. B. Asmussen (1999). To amplify the *trnT-trnL* and *trnL-trnF* intergenic spacer regions, we used the universal primers a, b, e, and f of Taberlet et al. (1991). The *atpB-rbcL* spacer (Golenberg et al., 1993) was amplified by using the forward primer "oligo 2" of Manen et al. (1994). A primer complementary to the *rbcL* forward primer 1F (Fay et al., 1997) was used for the reverse reaction. The *psbA-trnH* intergenic spacer was amplified by using the forward and reverse primers designed by Sang et al. (1997). PCR products were purified either by running the entire product on a low-melting point agarose gel and then recovering the amplified DNA with the help of QIAquick gel extraction kits (QIAGEN) or by using the QIAquick PCR purification columns directly without a prior purification on gel step. Cycle sequencing of the amplified products was conducted with the ABI Prism Dye Terminator Cycle Sequencing Ready Reaction kit (Perkin-Elmer, Norwalk, CT), using 2.5 ng of primer in a 5-μl reaction volume. Sequencing reactions were purified by ethanol precipitation and run on ABI 373 or ABI 377 automated sequencers (University of Missouri DNA Core Sequencing Facility). Both strands of DNA were sequenced and used to generate a consensus sequence by using Sequencher software (version 3.1; GeneCodes Corp., Ann Arbor, MI). All alignment was done manually, and except for the 3′ end of the *psbA-trnH* spacer, no problematic regions were encountered that would have warranted exclusion from the analysis.

Phylogenetic Analyses

Phylogenetic analyses of the aligned sequences were conducted with test version 4.0b.2 of PAUP* (Swofford, 1998). Analyses were performed by using exhaustive searches. Characters were unweighted and unordered, and gaps were treated as missing data. Nonparametric bootstrap support (Felsenstein, 1985) for each clade was estimated on the basis of 1,000 replicates, each with 100 random taxon addition replications, TBR swapping, and MULPARS. The COLLAPSE, but not the STEEPEST DESCENT, options of PAUP were in effect during these searches, and character changes were interpreted under ACCTRAN optimization.

Most-parsimonious trees were generated independently for the six data sets, followed by bootstrap analyses, to assess whether any strongly supported (i.e., with >50% bootstrap support) conflict was present among data sets—which was not expected, because the chloroplast genome is inherited as a unit. In the absence of such conflict, the data were combined in a global analysis. Species for which a particular marker did not amplify (*Atherosperma moschatum for trnL-trnF*; *Laurelia sempervirens* for *trnT-trnL*) were scored as missing.

ML analyses were performed by using the general-time-reversible model (GTR; Yang, 1994), which assumes that all substitution probabilities are independent. This model accounts for unequal base frequencies, a possible transition/transversion bias, and variable substitution rates among sites, which are described by a gamma distribution with four rate categories. The proportions of invariable sites and the shape parameters α of the gamma distributions were estimated, the latter by the method of Yang and Kumar (1996) as implemented in PAUP*. Starting trees for ML searches were obtained by neighbor joining; the swapping strategy used was TBR swapping.

Likelihood Ratio Tests and Divergence Time Estimation

Having obtained single best trees with the same topology from ML and parsimony, we decided to estimate age ranges for divergence events in the atherosperm tree by alternately using fossils and geological events to calibrate *rbcL* substitution rates. To assess the severity of rate heterogeneity among sequences, we used likelihood ratio tests (Felsenstein, 1981; Sanderson, 1998; Lewis, 1998) that compared the likelihoods of clock and nonclock versions of trees obtained under the same model. (Clock and nonclock analyses of the *rbcL* data supported single optimal trees.) If lineages accumulate mutations highly unequally, nonclock models will have significantly greater likelihoods than models that assume a constant substitution rate. To conduct this analyses, we first excluded two ambiguous characters by using the character set exclusion option in PAUP. Heuristic searches were then run with the same estimation and search strategy as used in the ML phylogenetic reconstruction. The likelihood ratio test (LRT) statistic is calculated as $-2\ (\ln L_0 - \ln L_1)$, where L_0 and L_1 are the likelihoods under the null (clock) and alternative (nonclock) hypotheses, respectively. The significance of this value is judged by comparing it to a χ^2 distribution with n degrees of freedom (df), where n is the difference in the number of free parameters between the null and the alternative model. In our case, df $= 7$, because nucleotide substitution rates are estimated for 15 branches in the unconstrained analysis, whereas the rates of only 8 branches are estimated under a clock constraint.

RESULTS

Data Characteristics and Phylogenetic Analyses

Fifty-five sequences were generated for this study or its precursor (Renner, 1999) and have been deposited in GenBank (Appendix). The data matrices are available at the Society of Systematic Biologists web site, and each of the six sequenced regions is characterized in Table 2. Overall, 4,372 characters (nucleotides) were sampled, yielding 283 variable positions (6.5%) and 47 phylogenetically informative characters (1.1%). The *rbcL* data set comprised 1,434 nucleotides, from positions 29 to 1,395 of the coding region plus 67 bp following the 3′ terminus (i.e., the stop codon at position 1,396). The completed *rpl16* alignment (with three short gaps) comprised 918 positions. The aligned *trnT-trnL* data set (with nine gaps) comprised 715 positions, whereas the *trnL-trnF* alignment (also with seven gaps) comprised 401 positions. The completed *atpB-rbcL* alignment (with four gaps) comprised 724 positions. Only the first 180 nucleotides of the *psbA-trnH* data set were used in the analyses, because of alignment difficulties toward the 3′ end of this rapidly evolving marker; the portion of the *psbA-trnH* alignment that we used contained one gap. Of the 24 sequence length mutations (indels, gaps), 3 were potentially phylogenetically informative. Averaged over all genome regions, the mean divergence between the outgroup and the ingroup species was 3% (Table 2). As expected, most of this divergence was accumulated in the *trnL-trnF* and *psbA-trnH* spacer regions. The ratio of transitions to transversions across all

TABLE 2. Characterization of cpDNA sequences (coding and noncoding).

Region	Aligned length (bp)	% divergence from outgroup[a]	Substitutions[b]	Indels[c]
Intergene spacers				
atpB-rbcL	724	3.0	46:5	4 (1)
trnL-trnF	401	5.4	37:7	7 (0)
trnT-trnL	715	4.5	67:7	9 (1)
psbA-trnH	180	4.5	19:6	1 (1)
Intron				
rpl16	918	2.6	63:8	3 (0)
Gene				
rbcL	1,434	2.1	51:14	0
Total	4,372	3.0	283:47	24 (3)

[a]Calculated as the mean absolute nucleotide differences between ingroup and outgroup (*Gomortega nitida*) sequences divided by the length of the sequenced region.
[b]Ratio of variable sites (autapomorphies) to parsimony-informative substitutions (synapomorphies).
[c]Number of indels (insertions or deletions); number of potentially informative indels in parentheses.

sequences was essentially 1, with very little variation among regions.

Parsimony analysis of the combined cpDNA (chloroplast DNA) data resulted in a single shortest tree (length = 394 steps; consistency index = 0.90; retention index = 0.48), which is shown as a phylogram in Figure 2. Bootstrap support along the backbone of the tree is weak, except for the early-branching *Daphnandra* + *Doryphora* clade (76% bootstrap support). Two relatively derived clades also are supported, one comprising *Laurelia novaezelandiae* and *Laureliopsis* (75%), the other *Nemuaron* and *Atherosperma* (84%).

The single tree resulting from the ML analysis (Fig. 3) has the same topology as the parsimony-derived tree.

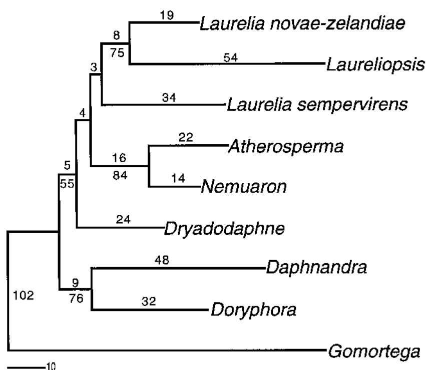

FIGURE 2. Phylogram of the cpDNA parsimony tree for Atherospermataceae (length = 394, CI = 0.90, RI = 0.48). Branch lengths (above branches) were determined under ACCTRAN optimization; bootstrap precentages (below branches) are based on 1,000 pseudoreplicates, each with 100 random taxon addition sequences.

Molecular Clock Analyses

A likelihood ratio test on the *rbcL* data set found that clock and nonclock analyses did not have significantly different likelihoods ($\chi^2 = 7.1$, df $= 8$, $P > 0.1$). This result justifies the use of *rbcL* sequence divergences in the ingroup to estimate absolute divergence times from branch lengths. Branch lengths were measured as Kimura distances and thus were corrected for multiple substitutions and transition/transversion biases. We chose Kimura distances, rather than GTR distances, because most published *rbcL* substitution rates have used this distance measure, and we wanted to compare atherosperm rate estimates with those for other woody angiosperms.

Pairwise Kimura two-parameter (K2P) differences among all *rbcL* sequences are shown in Table 3. These raw distances were used

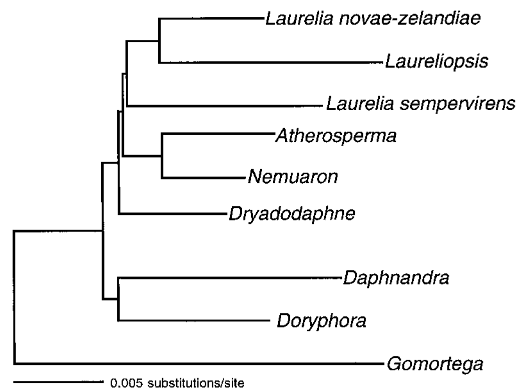

FIGURE 3. Maximum likelihood tree obtained for Atherospermataceae (using the GTR model of nucleotide substitution with rate variation across sites).

TABLE 3. Kimura two-parameter distances of Atherospermataceae *rbcL* sequences.

	1	2	3	4	5	6	7	8	9
Atherosperma	—								
Daphnandra	0.011	—							
Doryphora	0.012	0.013	—						
Dryadodaphne	0.014	0.015	0.013	—					
Laurelia novae-zelandiae	0.009	0.010	0.011	0.013	—				
Laurelia sempervirens	0.009	0.011	0.011	0.012	0.008	—			
Laureliopsis	0.011	0.013	0.011	0.014	0.008	0.010	—		
Nemuaron	0.006	0.011	0.011	0.011	0.008	0.006	0.008	—	
Gomortega	0.021	0.025	0.024	0.025	0.018	0.021	0.020	0.021	—

to compute the average distances shown in Table 4 between members of clades A through D in Figure 4. For example, node D consists of *Atherosperma* and *Nemuaron*. The Kimura distance of their *rbcL* sequences is 0.006. This value is used in Table 4 (column D) to calculate a rate of 0.00009 substitutions per site per million years (SSMY) under the assumption that node D is minimally 65 MY old, by dividing 0.006 by 65. Standard deviations for the genetic distances were calculated as follows. The number of nucleotide substitutions (S) is equal to the product of the total number of nucleotides in a sequence (N) times the proportion of nucleotides substituted (p; i.e., K2P distances). Thus, $S = Np$. The standard deviation of the number of nucleotides substituted divided by the total number of nucleotides is the standard deviation of the proportion of nucleotide substi- tutions. Thus, $\mathrm{SD}(p) = [p(1-p)/N]^{1/2}$.

We explored four alternative calibrations, two relying on fossils and two on geological events.

1. Given the 88–86 MY old atherosperm pollen from the Kerguelen plateau material (B. Mohr, pers. comm.), we assumed a minimum age for the family of 90 MY; that is, we fixed node A at 90 MYA. This calibration pushes nodes B–D to 38–25 MYA, making them almost 30 MY younger than the oldest fossils associated with nodes B and C (Fig. 4).
2. Given 65- to 55-MY-old *Laurelia/Laureliopsis* leaves (Dusén, 1908) and *Laurelia*-like wood (Poole and Gottwald, in press) and even older *Laureliopsis*-like wood (Poole and Francis, 1999), we assumed a minimum age of 65 MY for node B, which yields an *rbcL* divergence rate of 0.00014 SSMY (Table 4). This yields 157 MY for node A (age of family), 57 MY for node C (arrival in New Zealand), and 43 MY for node D (arrival in New Caledonia).
3. To allow for overland entry into New Zealand, we fixed node C, the divergence between Chilean *Laureliopsis* and its New Zealand sister species *L. novae-zelandiae*, at 80 MYA. This pushes the minimum age of the family back to 220 MY.
4. To allow for an overland entry of the ancestors of *Nemuaron* into New Caledonia from either Australia or Antarctica, we set the age of node D at 65 MY, which yields an age of 244 MY for the family.

TABLE 4. Estimated minimum ages (in millions of years [MY]) of divergence events A, B, C, and D in the phylogeny of Atherospermataceae (Fig. 4) under different calibrations of *rbcL* sequence divergences. Divergence events associated with fossils (A, B) or geological events (C, D) and used for calibration are shown in italics. Compare with Kimura distances in Table 3.

	Nodes			
	A	B	C	D
Average Kimura distances	0.022 ± 0.0024 SD	0.009 ± 0.0025 SD	0.008 ± 0.0024 SD	0.006 ± 0.0025 SD
A: 90 MY, rate = 0.00024/MY	*90*	38 ± 10	33 ± 11	25 ± 6
B: 65 MY, rate = 0.00014/MY	157 ± 17	*65*	57 ± 19	43 ± 12
C: 80 MY, rate = 0.00010/MY	220 ± 24	90 ± 23	*80*	60 ± 16
D: 65 MY, rate = 0.00009/MY	244 ± 26	100 ± 25	89 ± 29	*65*

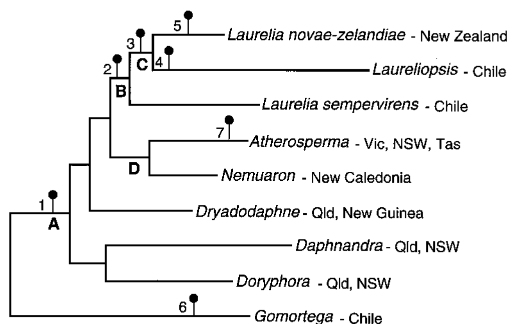

FIGURE 4. Phylogenetic hypothesis for Atherospermataceae with key divergence events labeled A–D. Lollipops indicate the following fossils: 1, Atherosperm pollen in Kerguelen plateau material dated to the Coniacian, 88–86 MYA (B. Mohr, pers. comm.); 2, *Laurelia* or *Laureliopsis* leaves from the Paleocene (Dusén, 1908 and Laurelia-like wood from the Eocene of Seymour (Poole and Gottwald, in press)); 3, *Laureliopis*-like wood from James Ross Island, Campanian, 76–71 MYA (Poole and Francis, 1999); 4, *Laureliopsis* leaves from Patagonia, Mid-Tertiary (Berry, 1935); 5, *Laurelia novae-zelandiae*-like pollen from New Zealand, Oligocene, 37–25 MYA (Couper, 1960; Mildenhall, 1980); 6, *Gomortega* wood from Patagonia, Late Oligocene-Miocene (Nishida et al., 1989); 7, *Atherosperma moschatum* leaves from Tasmania, Late Pliocene–Early Pleistocene, 3–1 MYA (Hill and MacPhail, 1985). Atherosperm fossil wood is also known from Upper Eocene deposits in Germany (Gottwald, 1992) and Lower Oligocene deposits in Egypt and the Cape province (Kräusel, 1939; Mädel, 1960; Müller-Stoll and Mädel, 1962). Geographic distribution of terminal taxa is given to the right: NSW = New South Wales, Tas = Tasmania, Qld = Queensland, Vic = Victoria.

DISCUSSION

Relationships Within Atherospermataceae

In his monograph of the family, Schodde (1969) recognized two ubfamilies of Atherospermataceae, Atherospermateae (*Atherosperma* and *Laureliopsis*) and Laurelieae (the remaining genera), and concluded that

> (1) *Laureliopsis*, confined to primary temperate rainforest, is the most primitive member of the family whereas *Daphnandra*, adapted to life in subtropical rainforest seres, is the most advanced, and (2) there are two arcs of distribution, one subantarctic for the Atherospermateae in south-east Australia and Chile, and the other tropical montane-subtropical for the Laurelieae, extending from New Guinea (*Dryadodaphne*) into eastern Australia on one side, and New Caledonia, New Zealand, and Chile on the other.

Neither conclusion is supported by molecular data. *Atherosperma* is not close to *Laureliopsis*, but instead to *Nemuaron* (84% bootstrap support), and *Laureliopsis*, rather than being basal, is sister to *Laurelia novae-zelandiae*. Older morphological studies placed *Laureliopsis* in a genus with *Laurelia sempervirens* and *L. novae-zelandiae*, based on resemblance in habit, leaves, and inflorescences (Perkins, 1911). In support of his view of a close relationship between *Laureliopsis* and *Atherosperma*, Schodde (1969) and, following him, Philipson (1993) listed centrifixed (stellate) hairs on the lower leaf surface, slender truncate stamens with rather elongate staminal glands, and relatively shallow receptacles with the tepals, stamens, and staminodes attached successively down their inner face towards the carpels. The remaining genera were characterized by basifixed hairs, apiculate anthers with shorter glands, and deeper receptacles with the tepals and stamens/staminodes attached well above the carpels on a well-defined, outward-facing rim of the receptacle. However, *Laureliopsis* has both types of hairs on the leaf surfaces (Mart´nez-Laborde, 1988), and truncate anthers are also found in *Daphnandra* (Schodde, 1969:79; and S.S.R. pers. obs.). As noted by Schodde (also Renner, 1999), the configuration of the receptacle is strikingly plastic throughout the Laurales, and there are several transitions from perigynous to epigynous flowers. The sister group to Atherospermataceae, Gomortegaceae, has epigynous flowers, and their next closest relatives, Siparunaceae, have perigynous flowers. It is thus possible that the relatively flat receptacles of *Atherosperma* and *Laureliopsis* evolved independently within atherosperms, rather than representing an ancestral condition as assumed by Schodde.

The deepest divergence in Atherospermataceae, according to molecular data, appears to separate the Australian endemics *Daphnandra* and *Doryphora* from the remaining genera, although this conclusion is weakened by the poor statistical support of the tree's basal nodes. *Daphnandra*, *Doryphora*, and *Dryadodaphne* have bisexual flowers, as does *Nemuaron*, whereas *Atherosperma*, *Laureliopsis*, and *Laurelia* have various proportions of unisexual flowers and are monoecious or andromonoecious (rarely polygamous). The molecular tree suggests that these breeding systems evolved within atherosperms.

Timing of Biogeographic Events

Atherospermataceae harbor two widely disjunct species pairs, *Laureliopsis philippiana* (Chile) and *L. novae-zelandiae* (New

Zealand), and *Atherosperma moschatum* (New South Wales, Victoria, Tasmania) and *Nemuaron vieillardii* (New Caledonia). A molecular clock approach can be used to address whether these disjunctions are more likely to have resulted from dispersal or from vicariance (i.e., the breakup of Gondwana).

Atherospermataceae are nested within Laurales (Renner, 1999), an order known to be at least 110 MY old (Drinnan et al., 1990; Crane et al., 1994; Eklund and Kvacek, 1998). The fossil history of Atherospermataceae themselves goes back at least 85 MYA (Poole and Francis, 1999; B. Mohr, pers. comm.). Given their fossil presence in Egypt, the Cape Province, and Europe (Kräusel, 1939; Mädel, 1960; Müller-Stoll and Mädel, 1962; Gottwald, 1992); the 88- to 82-MY-old pollen from the Kerguelen plateau; and the presence of the relatively derived *Laurelia/Laureliopsis* clade in Antarctica at 65–55 MYA, by the time of the Lower Tertiary, Atherospermataceae clearly were distributed throughout West Gondwana and Antarctica. A possible age of 140 MY for the family, as obtained when *rbcL* distances were calibrated with a Tertiary age for node B, is thus less outrageous as it may seem. The atherosperm sister group, *Gomortega*, is known only from Late Oligocene–Early Miocene wood from southwestern Patagonia (Nishida et al., 1989), but given its floristic affinities, Nishida et al. expect *Gomortegoxylon* also to have occurred in Antarctic forests.

Based on the wide distribution of Atherospermataceae in the Tertiary, an overland entry of the ancestors of *L. novae-zelandiae* and *Nemuaron vieillardii* from Antarctica or Australia into New Zealand and New Caledonia is conceivable (although no atherosperm fossils are known from Australia). Antarctica and Australia remained connected through the Tasman Rise until the Eocene-Oligocene boundary, and the Antarctic coastline and Transantarctic Mountains are known to have supported *Nothofagus* forests well into the mid-Miocene (15–13 MYA; Truswell, 1989). Atherosperms and Gomortegaceae even today grow in association with *Nothofagus, Podocarpus, Drimys,* and Araucariaceae (*Araucaria, Wollemia*), and the fossil record implies that forests formed by these plants have existed continuously since Cretaceous times, albeit not necessarily in any one place. New Zealand began to rift from eastern Australia 95–82 MYA (Stevens, 1989; van der Lingen et al., 1994), resulting in the opening of the Tasman Basin, and is believed to have reached its present position some 1,850 km from Australia by the Early Tertiary. New Caledonia rifted from Australia beginning at ~65 MYA and reached its present position, some 1,800 km east of Australia, by ~50 MYA. The key issues thus are the time of arrival in New Zealand of *L. novae-zelandiae* and in New Caledonia of *Nemuaron vieillardii* (nodes C and D in the phylogenetic tree for the family, both of which have solid bootstrap support). Calibration of nodes C and D with 80 and 65 MY ages, respectively, to allow for overland arrival in New Zealand or New Caledonia (or both), pushed the estimated minimal age of the family back into the Jurassic (estimates ranged between 220 and 244 MYA; Table 4). Calibration with the Lower Tertiary leaf and wood fossils of *Laurelia* and *Laureliopsis,* which are associated with nodes B and C (Fig. 4), implied a possible age for the family of 157 ± 17 MY, an arrival of the ancestor of *L. novae-zelandiae* in New Zealand at ~57 MYA (Table 4), and an arrival of *Nemuaron* in New Caledonia at ~43 MYA. Calibration with a pollen-based minimal family age of 90 MY, finally, implied arrivals of *L. novae-zelandiae* in New Zealand at ~33 MYA and of *Nemuaron* in New Caledonia at ~25 MYA.

Laurelia-like pollen first appears in the fossil record of New Zealand in the Oligocene (37 MYA) and definitely modern *Laurelia* pollen is present in the Pliocene (Couper, 1960; Mildenhall, 1980, and pers. comm., Feb. 1999). *Nemuaron* has no fossil record, and its sister species, *Atherosperma moschatum,* is first known from the Late Pliocene–Early Pleistocene (Hill and MacPhail, 1985). As argued by the biogeographers Fleming (1963), Pole (1994), and MacPhail (1997) it seems unlikely that a species could have been present in New Zealand (or New Caledonia) for millions of years without leaving a pollen record when its pollen is abundant in younger layers (and when atherosperm pollen elsewhere is preserved in layers dated to the Coniacian at 88–86 MYA; B. Mohr, pers. comm.; see above). Taken together, the relatively short fossil record of *L. novae-zelandiae* and the small genetic divergences of *L. novae-zelandiae* and *Nemuaron vieillardii* from their respective closest relatives are more consistent with their arrival by wind dispersal from

the coasts of Antarctica or Australia sometime during the past 50–30 MY than with an overland arrival in New Zealand and New Caledonia during Gondwanan times.

Numerous other taxa on New Zealand are thought to have colonized the island after successful overwater dispersal, including many with small and seemingly vulnerable seeds (Pole, 1994; and references therein). For example in Compositae, disjunctions between South American and Australasian sister species in *Cotula*, *Microseris*, *Centipeda*, *Lagenophora*, *Abrotanella*, and other genera of Senecioneae (Bremer, 1993; Bremer and Humphries, 1993; Swenson and Bremer, 1997) must have resulted from long-distance dispersal, because Asteraceae are not old enough to have reached Australia and New Zealand over land. In work on these groups, Bremer and his students have concluded that South America is likely to have been the ancestral area for several and that species must have dispersed from South America to Australasia along the coastline of Antarctica and from there to New Zealand. On the other hand, Raven (1972) has suggested that the prevailing westerly winds of the Southern Hemisphere may play a role in the dispersal of wind-borne seeds. He illustrated this using the example of a balloon released at Christchurch, New Zealand, and tracked by satellite; it circled Antarctica eight times in the 108 days it was tracked and traveled from South America to Australia in 7 to 9 days, albeit at an altitude of 12,000 m.

Plastid DNA Substitution Rates in Atherosperms Compared with Those in Other Angiosperms

Substitution rates of the *rbcL* gene have been calculated in various ways, making comparisons problematic. Estimates are available for rates of sequence divergence, rates of total nucleotide substitutions per taxonomic lineage (half the rate of divergence), and rates for synonymous and nonsynonymous substitutions. Estimates have been based on corrected distances (e.g., K2P) or uncorrected distances (e.g., Bousquet et al., 1992; Wendel and Albert, 1992; Bremer and Gustafsson, 1997; Eyre-Walker and Gaut, 1997; Gaut et al., 1997). We initially calculated nucleotide substitution rates also for the *rpl16* intron and *atpB-rbcL* intergenic spacer region to compare them with published rates for these regions (e.g., Schnabel and Wendel [1998] for *rpl16*; Hurr et al. [1999] for *atpB-rbcL*), but as pointed out by a reviewer of this paper, current evidence contradicts assumptions of clock-like accumulation of nucleotide substitutions by noncoding regions. Introns and spacers have been found to be susceptible to frequent length mutations of multiple origins, nonindependent character evolution, and regions of high mutability (Kelchner and Clark; 1997; Sang et al., 1997; Cho and Palmer, 1999). Such effects and poor calibration may be responsible for discrepancies between DNA-divergence–based age estimates and the fossil record (e.g., in *Gleditsia*; see Wendel and Albert, 1992).

Our estimates of rates between 1.4 and 2.4×10^{-4} SSMY for *rbcL* in the woody Atherospermataceae are based on K2P distances divided by the ages of 65- or 90-MY-old fossils. These values may be compared with Albert et al.'s (1994) estimate of an average rate of 1.0×10^{-4} SSMY in 38 woody seed plants and Wendel and Albert's (1992) estimate of 2.5×10^{-4} to 3.5×10^{-4} SSMY in herbaceous *Gossypium*. (Albert et al. explored various corrections for multiple substitutions and found them to have small effects; Wendel and Albert used Nei-and-Tajima, as opposed to Kimura, distances.) Among the seed plant sequences on which Albert et al.'s estimate is based are several from Calycanthaceae, one of seven families in the Laurales and thus in the same order as Atherospermataceae (Renner, 1998, 1999). Using Kimura distances and *rbcL* sequences of the four species of Calycanthaceae in GenBank, we estimated a rate of 1.3×10^{-4} SSMY for that family, assuming that the divergence between *Idiospermum* and the remaining genera dates back 120 MY. (The 120 MY is a minimum age for Calycanthaceae; the issue of lauralean divergence times will be dealt with elsewhere; Renner, in prep.). The relatively low *rbcL* substitution rates in the Laurales families Atherospermataceae and Calycanthaceae, compared with those in *Gossypium*, support the hypothesis that species with long generation times may have low substitution rates, although this may be confounded by the degree of relative phylogenetic advancement.

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APPENDIX

Sources of plant material or DNA sequences used, and GenBank accession numbers. For species' author names see Table 1. Herbarium acronyms after the voucher citation follow Holmgren et al. (1990). For leaves that came from cultivated plants, botanical garden accession numbers are cited instead of a voucher.

	Chloroplast regions						
Species	*rpl16*	*trnT-trnl*	*trnL-trnF*	*atpB-rbcL*	*psbA-trnH*	*rbcL*	Source or voucher
Atherosperma moschatum	AF127249	AF129013	—	AF127603	AF129044	AF121362	Qiu 92007 (NCU)
Daphnandra micrantha	AF198496	—	AF040668	AF198495	—	—	Melbourne BG 504037
Daphnandra repandula	AF127251	AF129022	AF040670	AF127608	AF129049	AF052195	B. Hyland 13324 (QRS)
Daphnandra sp. nov.	AF198497	—	AF040669	—	—	—	Canberra BG 702451
Doryphora aromatica	—	AF198494	AF040671	AF198493	—	L77211	B. Gray 7671 (QRS) *rbcL*: Ablett et al. 1997
Doryphora sassafras	AF127252	AF129023	AF040672	AF127609	AF129050	—	Sydney BG 18026
Dryadodaphne sp. nov.	AF127253	AF129024	—	—	—	AF121363	B. Gray 4853 (LTB)
Dryadodaphne novoguineensis	—	—	AF040673	AF127610	AF129051	—	Takeuchi 7095 (MO)
Laurelia novae-zelandiae	AF127254	AF129032	AF040674	AF127618	AF129059	AF052196	WELTU 19730 (WELTU)
Laurelia sempervirens	AF127255	—	AF012402	AF127619	AF129060	AF052612	Edinburgh BG 19931681
Laureliopsis philippiana	AF127256	AF129033	AF040675	AF127620	AF129061	AF040662	Landrum & Landrum 8160 (MO)
Nemuaron vieillardii	AF127257	AF129039	AF040676	AF127625	AF129066	AF121366	McKee 12800 (K)
Gomortega nitida	AF127260	AF264020	AF012404	AF127612	AF129053	D89561	Rodriguez 3070 (CONC) *rbcL*: Ueda et al., 1997