

THE HISTORICAL BIOGEOGRAPHY OF FAGACEAE: TRACKING THE TERTIARY HISTORY OF TEMPERATE AND SUBTROPICAL FORESTS OF THE NORTHERN HEMISPHERE

Paul S. Manos¹ and Alice M. Stanford

Department of Biology, Box 90338, Duke University, Durham, North Carolina 27708, U.S.A.; and Division of Science and Mathematics, University of the Virgin Islands, 2 John Brewers Bay, Saint Thomas, United States Virgin Islands 00802

The angiosperm family Fagaceae is a central element of several distinct community types throughout the Northern Hemisphere and a prime candidate for modern biogeographic analysis. The rich fossil record for the family provides an unparalleled source to compare with modern distributions and evaluate hypotheses of origin, migration, and vicariance. We conducted separate phylogenetic analyses on genera with intercontinentally disjunct distributions using various noncoding regions of chloroplast and nuclear ribosomal DNA sequences. Analyses generally supported the (North America – (Europe + Asia)) pattern of area relationships. Divergence times between disjunct species were estimated to aid in the development of a comparative synthesis of historical biogeography across the family. Fully resolved phylogenies were analyzed biogeographically using three distinct approaches: dispersal-vicariance analysis (DIVA), strict vicariance, and dispersal analysis using Fitch parsimony. Ancestral area reconstructions based on DIVA were preferred because event-based inferences generally were consistent with fossil evidence for migration and estimates of divergence times. Reconstructions suggested an Asian origin for the genus *Fagus* with bidirectional migration to Europe and North America, consistent with a paraphyletic assemblage of Asian species and intercontinental exchange via the Bering Land Bridge (BLB). Reconstructions within *Quercus* generally were more ambiguous in determining a center of origin; however, one optimization pathway was consistent with the vicariance of an ancestrally widespread distribution and the initial divergence between largely North American and Asian clades. Within the North American clade, dispersal to Eurasia is inferred for section *Quercus* (white oaks). Bidirectional floristic exchange via the BLB is supported for these temperate taxa, followed by intercontinental disjunction by the mid-Miocene. In contrast, disjunctions based on living and fossil distributions within evergreen Fagaceae (e.g., *Castanopsis*, *Lithocarpus*, *Trigonobalanus*) suggest older, temporally distinct biogeographic histories involving both the North Atlantic and Bering Land Bridges.

Keywords: *Castanea*, *Fagus*, historical biogeography, phylogeny, *Quercus*.

Introduction

One of the most conspicuous features of the modern flora of the Northern Hemisphere is the preponderance of plant communities dominated by species of Fagaceae. The oak family plays a major ecological role in terms of sheer abundance of standing biomass (e.g., Soepadmo 1972; Olson et al. 1983; Whitmore 1984; Axelrod et al. 1996; Vogt et al. 1996; Zhu 1997; Delcourt and Delcourt 2000) and variety of mutualistic associations involving ectomycorrhizal fungi (Smith and Read 1997), gall-forming insects (e.g., Raman 1996; Abrahamson et al. 1998), and seed-eating vertebrates (e.g., Payne et al. 1985; Johnson and Webb 1989; Koenig and Haydock 1999; Vander Wall 2001). Not surprisingly, fossil analogs of modern Fagaceae are well represented in the Northern Hemisphere, indicating long-term presence and differential patterns of species diversification throughout the Tertiary and Quaternary (for review, see Jones 1986; Crepet 1989; Manchester 1999).

Of particular interest with regard to the biogeographical

history of the Northern Hemisphere is the relative information content provided by sets of taxa characterized by amphipacific and amphiatlantic distribution patterns (e.g., Graham 1972, 1999a; Tiffney 1985b; Wen 1999). Many of these disjunctions are the result of Tertiary range restrictions of formerly widespread paratropical and mesophytic forest communities as a response to reduction in temperature and precipitation at higher and middle latitudes (Graham 1972, 1999a; Wolfe 1975, 1985; Tiffney 1985a, 1994; Collinson 1992). Within this context, the Tertiary fossil history of a community-dominant family such as Fagaceae (fig. 1), in combination with modern phylogenetic and biogeographic analysis of its component genera, could provide a rich source of data for interpreting the complex nature of phytogeography across the Northern Hemisphere. In this article, we test hypotheses of origins, migration, and vicariance for independent examples of intercontinental disjunction within Fagaceae.

The origin and relationships of Fagaceae in light of a putative relationship with the Southern Hemisphere genus *Nothofagus* have been variously interpreted (e.g., Humphries 1981; Melville 1982; Crepet and Nixon 1989a; Nixon 1989). On the basis of multiple lines of evidence, it is clear that Fagaceae and the Southern Hemisphere genus *Nothofagus* (Nothofa-

¹ Author for correspondence; telephone 919-660-7358; e-mail pmanos@duke.edu.

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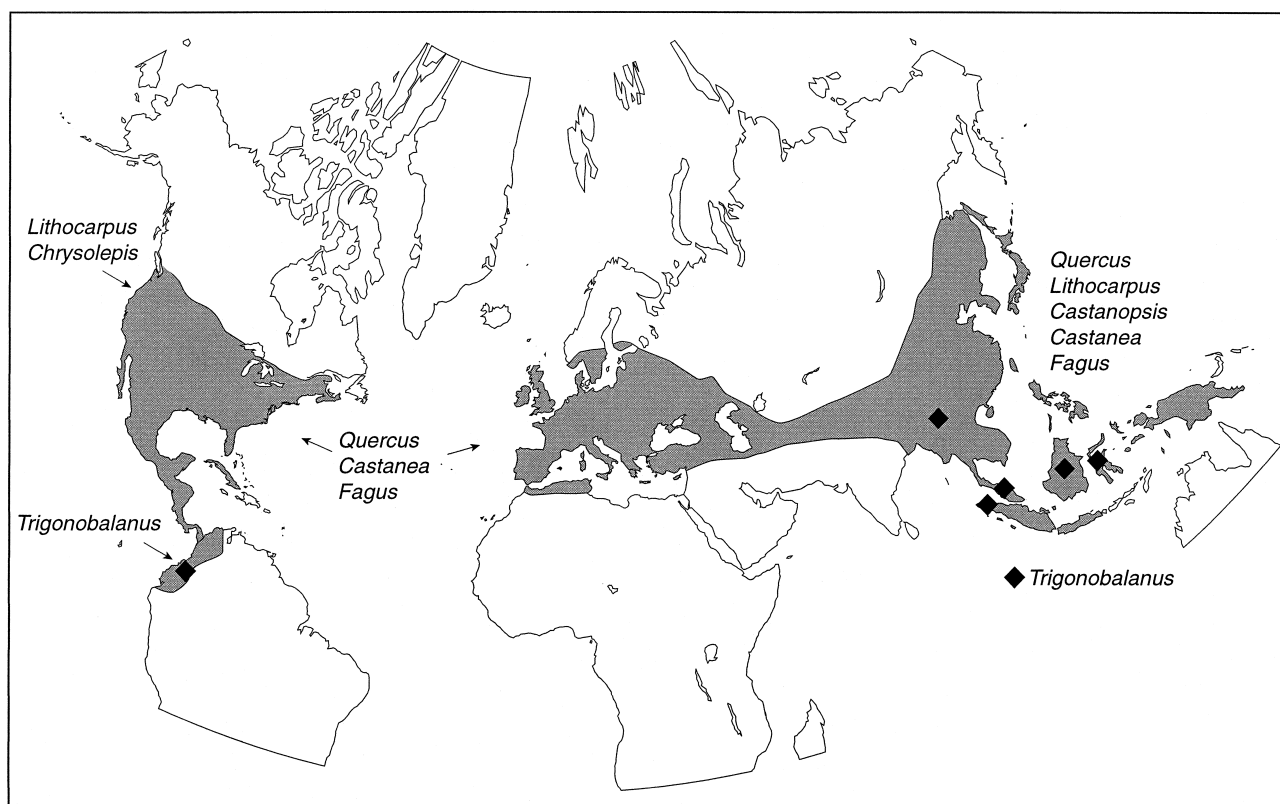


Fig. 1 Generalized distribution for Fagaceae based on Soepadmo (1972), Nixon (1997), and Nixon and Crepet (1989)

gaceae) are not sister taxa (Nixon 1989; Manos et al. 1993; Manos and Steele 1997). Genus-level diversity within Fagaceae is concentrated in the montane forests of Southeast Asia where seven of the nine currently recognized genera occur. However, the combination of transitional fossils in eastern North America and appreciable genus-level endemism in western North America indicates that North America probably was equally diverse during the Early Tertiary (Crepet 1989; Crepet and Nixon 1989a). For most genera, modern distributions essentially fall within the range of fossil ancestors, indicating fairly broad patterns of endemism. Noteworthy exceptions include Early Tertiary extinction of *Castanopsis* and *Fagus* from western North America, *Trigonobalanus* from central Europe and North America, and *Castanopsis* and *Lithocarpus* from central Europe (Crepet and Nixon 1989a; Kvaček and Walther 1989; Manchester 1994; Meyer and Manchester 1997; Walther 2000).

The extensive and well-studied fossil record for Fagaceae from Tertiary deposits of North America and Eurasia has been used to assess the relative timing of diversification within the family (Crepet and Daghljan 1980; Daghljan and Crepet 1983; Jones 1986; Crepet 1989; Crepet and Nixon 1989a, 1989b; Kvaček and Walther 1989, 1992; Manchester 1994, 1999; Walther 2000). The minimum age of Fagaceae, from Upper Paleocene to Lower Eocene (Crepet and Nixon 1989a; Palamarev and Mai 1998; Walther 2000), is roughly similar to that of fossils assignable to sister families, such as Juglandaceae, Betulaceae, and Myricaceae (Herendeen et al. 1995). Unequivocal

macrofossils of castaneoids, trigonobalanoids, quercoids, and fagoids occur by the Upper Eocene to Lower Oligocene, indicating rapid diversification within the family (Crepet 1989; Meyer and Manchester 1997). Recovery of fossilized *Quercus* leaves attributable to modern groups suggests infrageneric diversification was essentially complete by the Upper Oligocene (for review, see Axelrod 1983; Crepet 1989; Borgardt and Pigg 1999). By the Upper Oligocene to Lower Miocene, transition to cooler, more seasonal climates is thought to have promoted the spread of wind-pollinated taxa such as *Quercus* (Axelrod 1983).

The genus *Quercus* accounts for roughly half of the species within Fagaceae (fig. 2), has the most extensive living and fossil distribution, and is broadly represented by both evergreen and deciduous species. Infrageneric diversity is highest in Central and North America (300 spp.). Axelrod (1983) used the taxonomy of the genus and its rich fossil history to suggest that the major oak groups evolved *in situ*, with mostly localized radiations and rare instances of monophyletic groups with transcontinental distributions. Phylogenetic studies generally support this concept (Manos et al. 1999), yet the entire phylogenetic breadth of the genus has not been subject to biogeographic analysis. With roughly similar amounts of species diversity and strong fossil records in both hemispheres (MacGinitie 1941; Bones 1979; Manchester 1981), *Quercus* appears to have achieved a widespread distribution during the Upper Eocene to Lower Oligocene. Therefore, a phylogenetic pattern of reciprocal monophyly between Asian and North

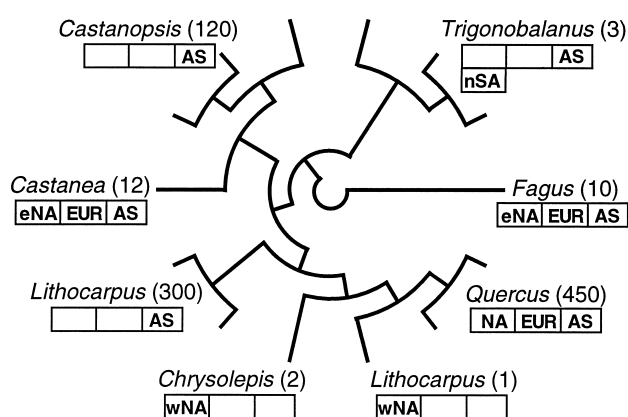


Fig. 2 Phylogenetic relationships within Fagaceae based on parsimony analysis of chloroplast (*matK*) and ITS DNA sequences (Manos et al. 2001). Within-genus branches refer to the number of species sampled. Number of species within genera generally follows Mabberley (1990). Geographic range appears under the genus name: AS = Asia; eNA = eastern North America; wNA = western North America; EUR = Europe; nSA = north South America.

American taxa might be expected based on long-term isolation and divergence brought about by the vicariance of an ancestral distribution. The widespread distribution of section *Quercus* (white oaks), however, is suggestive of more recent connections between Asia and North America, perhaps involving the Bering Land Bridge (BLB). Fossil data generally support a North American origin during the Oligocene (Daghlian and Crepet 1983) with later appearance in China in the Upper Miocene (Zhou 1992, 1993). In this case, a phylogenetic pattern of Eurasian white oaks nested within North American lineages would be expected given the probable direction of migration.

Although no single distribution within Fagaceae exactly matches the classic eastern Asia and eastern North America pattern of disjunction known in other families (Wen 1999), both the comparatively smaller and exclusively deciduous genera *Castanea* and *Fagus* occur in these areas, as well as in the relict mesophytic forests of western Asia (figs. 1, 2). *Fagus* has an excellent fossil record around the northern Pacific Basin and throughout Europe (Brown 1937; Chaney and Axelrod 1959; Chandler 1963; Tanai 1974; Kvaček and Walther 1992; Liu et al. 1996; Meyer and Manchester 1997; Hably et al. 2000). A continuous distribution spanning Asia, North America, and Europe was achieved during the Oligocene, leading to the formulation of evolutionary scenarios including a hypothesized center of origin. An origin at middle to high latitudes in Asia has been proposed with migrations to Europe, Japan, and North America (Tanai 1974; Kvaček and Walther 1992). Phylogenetic support for this hypothesis would show that European and American species are more closely related to different sets of Asian species.

The Early Tertiary history of *Castanea* is unfortunately ambiguous because distinguishing characters (e.g., locule and style number) have not been found and its pollen is too general to be of diagnostic value (Crepet and Daghlian 1980; Jones 1986). Pollen assigned to *Castanea* has been reported throughout the Northern Hemisphere (Chmura 1973; Muller 1981),

and Eocene leaves and cupules with strong affinities to modern species suggest long-term presence in at least eastern North America (Crepet and Daghlian 1980; Jones 1986). While no worker has proposed specific hypotheses to account for the distribution of *Castanea*, a shared distribution and similar pattern of worldwide species diversity with *Fagus* suggest a temporally congruent biogeographic history. Disjunctions within *Fagus*, *Castanea*, and section *Quercus* provide an opportunity to evaluate the growing phylogenetic support for intercontinental connections via the BLB (e.g., Wen et al. 1998; Wen 1999; Wen and Shi 1999; Xiang et al. 2000).

Exclusively evergreen Fagaceae provide a good temporal contrast because their modern distributions appear to reflect older disjunctions and potentially different biogeographic histories. In one of the most striking recent discoveries of floristic disjunction involving southernmost extensions of the Northern Hemisphere flora, Lozano et al. (1979) described *Trigonobalanus excelsa* from northern montane forests of Colombia (fig. 1). This area is well known for its tropical taxa with amphipacific or American-Malayan distributions and fossil records in the Tertiary Holarctic flora (Van der Hammen and Cleef 1983). The distribution of the modern *Trigonobalanus* relative to putative fossil ancestors from Europe and eastern North America suggests tropical amphipacific biogeographic connections spanning the Northern Hemisphere, with subsequent extinction throughout most of this range (Van der Hammen and Cleef 1983; Crepet and Nixon 1989a; Kvaček and Walther 1989; Walther 2000).

A clearly different type of biogeographic pattern is shown by the genus *Lithocarpus* (fig. 1). This genus appears to have evolved in Southeast Asia, with fossils indicating western range expansion to central Europe (Kvaček and Walther 1989) and eastern BLB connection to western North America. *Castanopsis* occurs within the same general tropical to warm temperate Asian distribution as *Lithocarpus*, with a similar fossil history of western range extension to central Europe and eastern BLB connection to western North America based on Eocene fossils (Kvaček and Walther 1989; Manchester 1994). Two western North American species formerly placed within *Castanopsis*, but now recognized as the genus *Chrysolepis*, also provide anecdotal evidence for a common biogeographic history with *Lithocarpus*.

Comparisons between modern and fossil distributions provide one general approach to assess differential patterns of diversification and extinction within various disjunct plant genera, whereas stratigraphy and the comparative morphology and diversity of fossils have been used to hypothesize origins, migration patterns, and former distributions (e.g., Manchester 1999). Species diversity within contemporary patterns of disjunction also has been used as an explicit means to understand the interface between the shared historical component of community structure and evolutionary response following vicariance (Guo et al. 1998; Guo 1999; Guo and Ricklefs 2000). Phylogenetic and biogeographic studies of modern taxa with exceptional fossil histories have the potential to provide critical, independent lines of evidence to test and evaluate hypotheses based on comparative diversity, stratigraphy, and land-area relationships (Tiffney 1985a, 1985b, 2000; Tiffney and Manchester 2001). Here, we specifically address the following questions: (1) Is there support for the various explicit

hypotheses of origins and migration routes of mesophytic Fagaceae based on phylogenetic pattern and biogeographic analysis? (2) How does sequence divergence compare across evergreen and deciduous disjunct examples within Fagaceae? (3) What can we infer about the historical biogeography of these taxa in the context of the growing phylogenetic database on Tertiary disjunctions and improved understanding of land-area relationships?

Material and Methods

Analyses were based on plant material collected from natural populations or cultivated plantings (see appendix). Intensive sampling of Asian species of section *Quercus* was supplemented by using cultivated material with well-established source-location data. Methods for extracting DNA, PCR, and sequencing generally follow Manos et al. (1999, 2001) and Manos and Steele (1997). Noncoding regions of chloroplast DNA (cpDNA) were sequenced for *Fagus* (*rbcL*/*atpBE* intergenic spacer; 5' *trnK* intron), *Castanea* (*rbcL*/*atpBE* intergenic spacer; 5' *trnK* intron; 3' *trnK* intron), section *Quercus* (*rbcL*/*atpBE* intergenic spacer; 3' *trnK* intron), and *Trigonobalanus* (5' *trnK* intron; 3' *trnK* intron). Primer sequences for amplifying and sequencing the flanking regions of the *matK* gene followed Manos and Steele (1997). Primers for the *rbcL*/*atpBE* intergenic spacer followed Hodges and Arnold (1994). We also sequenced the ITS region for *Fagus* using the methods of Manos et al. (1999).

Five data sets were generated for the following taxa: (1) *Quercus sensu lato* – ITS; (2) *Fagus* – ITS + cpDNA; (3) *Quercus* section *Quercus* – cpDNA; (4) *Castanea* – cpDNA; (5) *Trigonobalanus* – cpDNA. The ITS data set for *Quercus* is based on two previously published analyses (Manos et al. 1999, 2001), and neither explicitly explored biogeographic methods. A pruned data set is used here to maintain species representation from all major clades and biogeographic areas. Alignments were performed manually due to generally high levels of sequence similarity among interspecific sequences. Outgroups were selected on the basis of previous studies within Fagaceae (Manos and Steele 1997; Manos et al. 2001). Sets of most parsimonious phylogenetic trees were constructed using PAUP* (Swofford 2000) with 100 random addition sequences and BRANCH and BOUND. Relative branch support was estimated using conventional bootstrapping (Felsenstein 1985) in full heuristic searches of 1000 pseudoreplicates saving all trees.

Biogeographic analysis using three general approaches was performed on the resulting phylogenies concentrating mostly on those with reasonable resolution and over three taxa (see Fritsch 1999 for discussion). Dispersal-vicariance analysis (DIVA ver. 1.1; Ronquist 1996, 1997) is a hybrid method that permits both vicariance and dispersal. DIVA optimizes area data, scored as presence/absence, onto fully bifurcating trees by permitting vicariance at no cost while explicitly optimizing ancestral areas by minimizing equally costly events such as dispersal. In contrast, a strict vicariance approach (Nelson and Platnick 1981; Page 1990) assumes hierarchical relationships by implicitly constructing widespread component areas at internal nodes that, in theory, could be the result of hierarchical relationships, dispersal to an area (reticulation), or both (Ron-

quist 1997; Fritsch 1999). Dispersal analysis using Fitch optimization (Maddison et al. 1992) represents an extreme approach that emphasizes dispersal from source areas by coding areas as a single multistate character and optimizing states on a tree. Ambiguously optimized nodes are not equivalent to ancestrally widespread areas, therefore inferences derived from this method show only partial overlap with those derived from DIVA and have little in common with the reconstruction of component areas in vicariance biogeography.

Because these analyses require fully resolved topologies, several plausible resolutions were examined for certain taxa. Topologies also were modified to allow for different outgroup

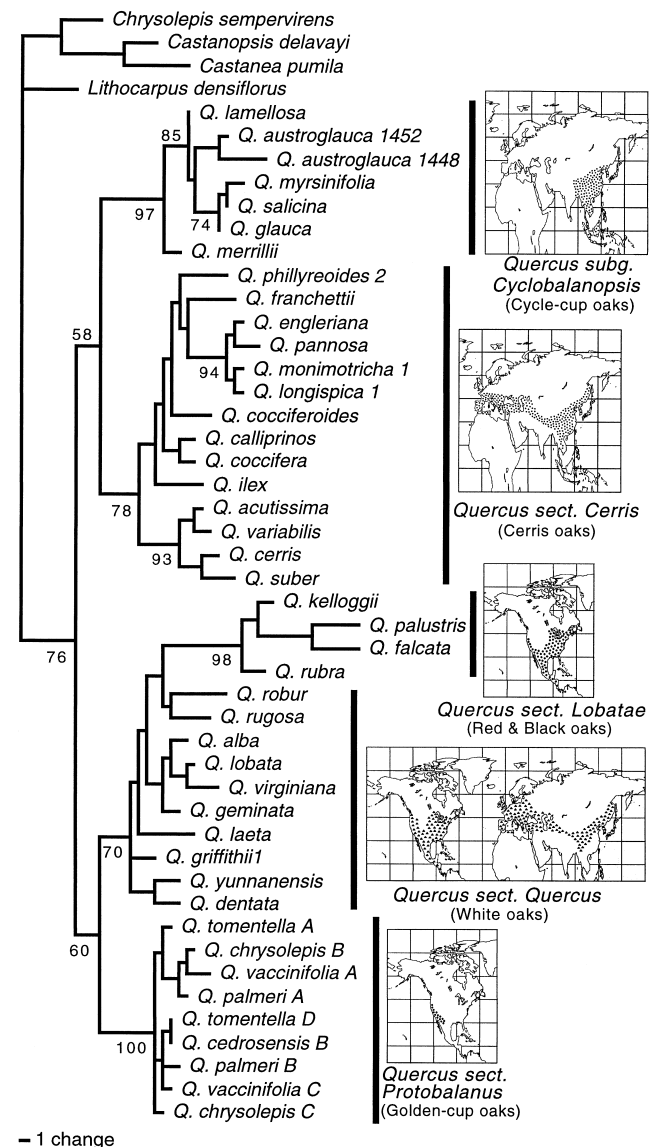


Fig. 3 Representative phylogram based on parsimony analysis of ITS sequences of *Quercus* and outgroups. Bootstrap values (above or below branches) are based on 1000 pseudoreplicates. Taxonomy follows Nixon (1993), except for the circumscription of section *Quercus*, which generally follows Camus (1934–1954) and the results of Manos et al. (1999).

combinations because optimizations using DIVA and dispersal analysis can be affected by outgroup areas (Xiang and Soltis 2001). We also explored constraints on the number of areas used in the optimization of ancestral distributions at basalmost nodes. Using DIVA, this is done by reducing the maximum areas or “maxareas” as a means to hypothesize centers of origin (Xiang and Soltis 2001). Where possible, the fossil record for Fagaceae was used to evaluate the various hypotheses resulting from each analysis.

Results

Patterns of Sequence Variation

Nucleotide variation for noncoding cpDNA intergenic spacer regions generally was low in interspecific comparisons of *Fagus*, *Castanea*, and *Quercus* section *Quercus* as measured by the two-parameter method of Kimura (1980) implemented in PAUP*. Pairwise sequence divergence values ranged from roughly 0.1%–1.3%. Consistently higher values (1.6%–2.2%) were obtained among *Trigonobalanus* species. Divergence among *Fagus* species for ITS sequences also was comparably low and within the range observed for cpDNA noncoding regions. Divergence among *Quercus* species based on ITS sequences was as high as 7.4% in comparisons between different sections of the genus.

Phylogenetic Analyses

Parsimony analysis of each data set generally yielded low numbers of equally parsimonious trees and reasonably well-resolved consensus trees in all but one case (figs. 3, 4). For *Fagus*, analyses were derived from 12 accessions representing nine species and 24 informative characters, including four indels coded as presence/absence data, drawn from a total of 2576 aligned sites (ITS+cpDNA). Congruence among the three data sets was high ($P = 0.54$), as determined by the partition homogeneity test (Farris et al. 1995) implemented in PAUP*. Using *Trigonobalanus verticillata* as the outgroup, a single tree was recovered (fig. 4A; length [L] = 364; consistency index [CI] = 0.93; retention index [RI] = 0.94). Accessions representing *Fagus crenata* were not found to be monophyletic, whereas sampling within *Fagus lucida* and *Fagus japonica* resulted in species-specific clades. Distinct clades of European and North American species were found to be nested within a paraphyletic grade of Asian taxa.

For *Quercus*, parsimony analysis of 44 species and four outgroups using 96 informative characters from 643 aligned sites identified a single island of 180 equally parsimonious trees (L = 265; CI = 0.44; RI = 0.76). The strict consensus resolved two major clades, as well as subclades that correspond to most of the traditionally recognized groups, except for *Quercus* section *Quercus*. A representative phylogram presents relative branch lengths, branch support, and taxon distribution (fig. 3). Additional species of section *Quercus* were analyzed using a total of 37 accessions and 15 informative characters from 1182 aligned sites. The single tree (fig. 4B; L = 24; CI = 1.0; RI = 1.0) resolved two clades: one included 12 accessions representing nine species from throughout North America and Mexico, and the other included 25 accessions representing 10 species from throughout Europe and Asia.

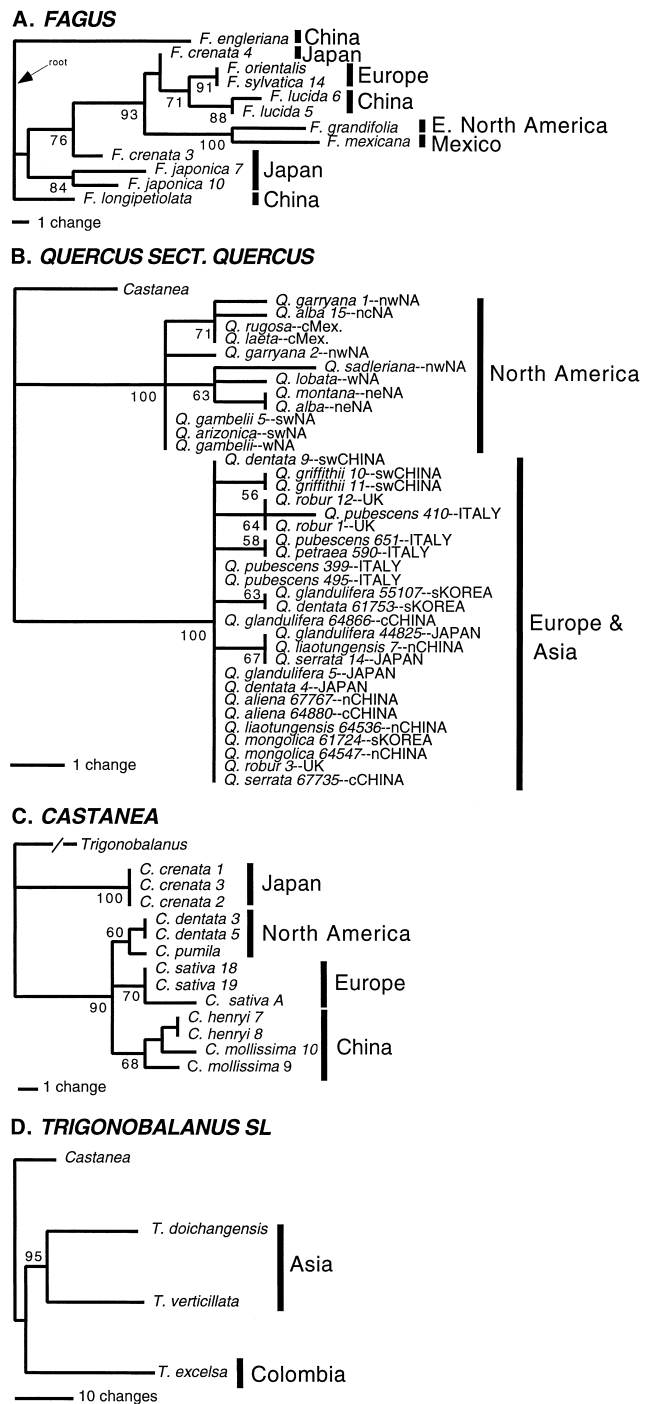


Fig. 4 A–D, Phylograms for disjunct taxa within Fagaceae. Bootstrap values (above or below branches) are based on 1000 pseudoreplicates.

There was no apparent geographic or taxonomic structure within either clade.

For *Castanea*, analysis of 13 accessions representing six species based on 21 informative characters, including five indels coded as presence/absence data, drawn from 2597 aligned sites produced two equally parsimonious trees (L = 62; CI =

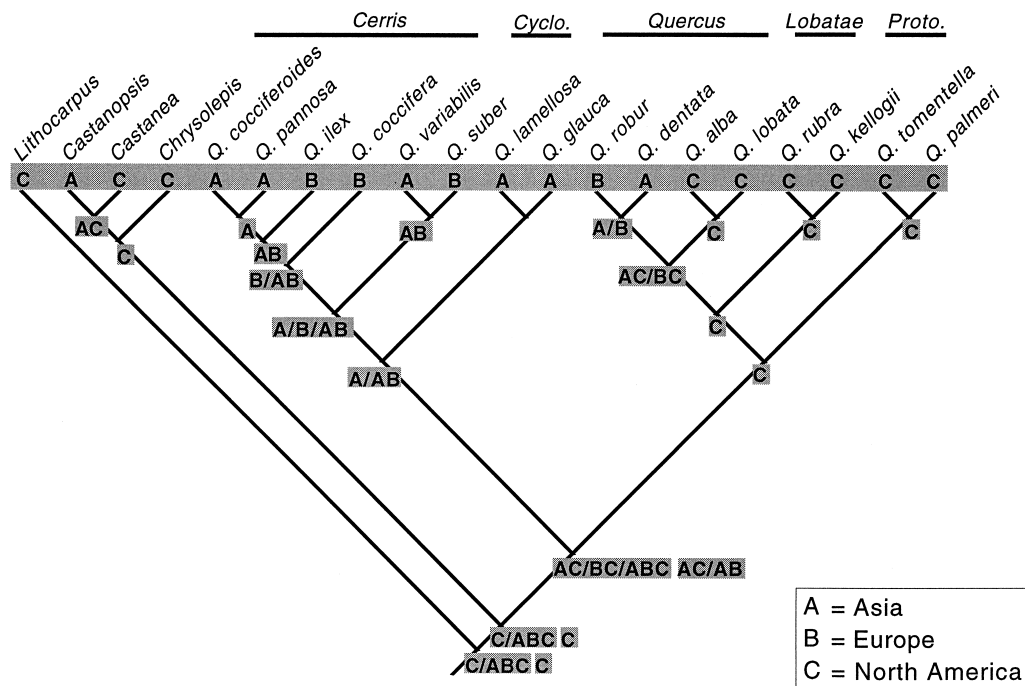


Fig. 5 Ancestral area reconstructions based on DIVA for the phylogeny of *Quercus* (see fig. 3), including only biogeographically distinct taxa. Area designations separated by slashes represent equally parsimonious reconstructions. Areas designations separated by a space indicate optimization results based on the “maxareas” – 1 function.

0.82; RI = 0.90). One of the trees is consistent with the strict consensus showing lack of resolution among three clades of taxa representing specific areas (fig. 4C), whereas the other supports the monophyly of North American and Chinese species.

Relationships among the three species of *Trigonobalanus* were analyzed based on five informative characters out of 2086 aligned sites that produced a single tree (fig. 4D; L = 69; CI = 0.83; RI = 0.80).

Biogeographic Analyses

Phylogenies of *Fagus* and *Quercus* provided ample resolution to serve as case studies for biogeographic analysis, whereas analysis of *Castanea* did not resolve relationships in a critical clade containing taxa from Europe, North America, and China. For *Quercus*, we used a simplified version of the phylogenetic framework shown in figure 3 but also treated section *Quercus* as monophyletic on the basis of morphological evidence and previous molecular analysis (Nixon 1993, 1997; Manos et al. 1999). Additional resolution within section *Quercus* was achieved by constraining the topology based on the results of cpDNA analysis so that North American and Eurasian species, for which exemplars were present in the ITS tree, form reciprocally monophyletic subclades (see fig. 4B). We also considered the possibility that subgenus *Cyclobalanopsis* is sister to the rest of the genus as supported by morphological cladistic analysis (Nixon 1985).

DIVA: *Quercus*. Using a pruned phylogeny of *Quercus* (17 spp.), dispersal-vicariance analysis with three areas (A: Asia, B: Europe, C: North America) resulted in numerous com-

binations of equally optimal reconstructions at eight nodes and inferred a total of eight dispersal events (fig. 5; table 1). The ingroup node was reconstructed to include three out of the four possible combinations of areas to the exclusion of AB (Asia + Europe). Reducing the maximum areas (“maxareas”) criterion to two areas resulted in fewer area combinations at the outgroup/ingroup node and a subset, AC (Asia + North America) or BC (Europe + North America), of possible ingroup node optimizations. When outgroups were constrained to “Asia” and “maxareas” set to two, only AC (Asia + North America) was reconstructed for the ingroup node. Overall, an initial vicariance within a formerly widespread distribution involving all land area or pairs of areas is supported with equally parsimonious scenarios of subsequent dispersal along internodes within the *Quercus* clade.

Using a slightly modified tree depicting *Cyclobalanopsis* as sister to the rest of the genus, optimization of the ingroup node changed to AB/AC/ABC and “maxareas” constraints optimized a single ancestral area of AC, a result also obtained when all outgroups were treated as “Asia.” Under these conditions, the node uniting (*Cerris* – (*Protobalanus* – (*Lobatae* + *Quercus*))) was reconstructed to BC, while the node for the ancestral distribution of section *Cerris* was assigned to B.

Vicariance and dispersal: *Quercus*. Under strict vicariance (see table 1), the relevant components included ingroup node to ABC; node for *Cerris* + *Cyclobalanopsis* to AB; node for (*Protobalanus* – (*Lobatae* + *Quercus*)) to ABC; nodes for *Lobatae* + *Quercus* and section *Quercus* to ABC; and node for *Quercus robur* + *Quercus dentata* to AB. The assignment of

Table 1
Ancestral Area Reconstructions Based on Three Methods (DIVA, Strict Vicariance, and Dispersal) for
Biogeographically Relevant Nodes Resolved by Phylogenetic Analysis of *Quercus* and *Fagus*

	DIVA	Vicariance	Dispersal
<i>Quercus</i> :			
Ingroup	AC/BC/ABC*	ABC	C
(<i>Cerris</i> + <i>Cyclobalanopsis</i>)	A/AB*	AB	A/B/C*
<i>Cerris</i>	A/B/AB*	AB	A/B*
(<i>Q. coccifera</i> – (<i>Q. ilex</i> – (<i>Q. cocciferoides</i> + <i>Q. pannosa</i>)))	B/AB*	AB	A/B*
(<i>Protobalanus</i> – (<i>Lobatae</i> + <i>Quercus</i>))	C	ABC	C
(<i>Lobatae</i> + <i>Quercus</i>)	C	ABC	C
<i>Quercus</i>	AC/AB*	ABC	C
((<i>Q. alba</i> + <i>Q. lobata</i>) + (<i>Q. robur</i> + <i>Q. dentata</i>))	AC/BC*	ABC	C
(<i>Q. robur</i> + <i>Q. dentata</i>)	A/B*	AB	A/B/C*
<i>Fagus</i> :			
Ingroup	A	ABCD	A
(<i>F. longipetiolata</i> + <i>F. spp.</i>)	A	ABCD	A
(<i>F. japonica</i> + <i>F. spp.</i>)	A	ABCD	A
(<i>F. crenata2</i> + <i>F. spp.</i>)	A	ABCD	A
(<i>F. spp.</i> – (<i>F. mexicana</i> + <i>F. grandifolia</i>))	AC/AD/ACD*	ABCD	A
(<i>F. crenata1</i> – (<i>F. spp.</i>))	A	AB	A
(<i>F. lucida</i> – (<i>F. sylvatica</i> + <i>F. orientalis</i>))	AB	AB	A
(<i>F. mexicana</i> + <i>F. grandifolia</i>)	CD	CD	A/C/D*

Note. A = Asia; B = Europe; C = North America; and D = Mexico. Asterisks indicate optimization of the node is equivocal, and slashes separate equally likely area-state assignments.

component areas was not affected by outgroup distribution and alternative ingroup topology.

Dispersal analysis using Fitch parsimony and the 17-taxon tree shown in figure 5 resulted in a single most parsimonious tree of seven steps. The ingroup and *Lobatae* + *Quercus* nodes were optimized to C, whereas the *Cerris* + *Cyclobalanopsis* node was ambiguous for all three areas. Five of the seven steps could be mapped onto the phylogeny in more than one way. Overall, an origin in C (North America) is supported with dispersal to A and B occurring multiple times within the *Cyclobalanopsis* + *Cerris* clade and once each within the (*Protobalanus* – (*Lobatae* + *Quercus*)) clade. When the outgroup areas were modified to reconstruct the outgroup/ingroup node to A (Asia), the ingroup and *Cyclobalanopsis* + *Cerris* nodes retained the area state of A, while most of the nodes within *Cerris* were ambiguously optimized for areas B and C. Within the other clade, dispersal from A to C unambiguously defined the (*Protobalanus* – (*Lobatae* + *Quercus*)), while dispersal back to A and B was optimized equivocally for the node uniting the tip clade *Q. robur* + *Q. dentata*.

Dispersal analysis using a modified tree depicting *Cyclobalanopsis* as sister to the rest of the genus resulted in only one ambiguous node (*Q. robur* + *Q. dentata*) and maintained area C at both the ingroup and the (*Protobalanus* – (*Lobatae* + *Quercus*)) nodes. Under this scenario, dispersal from C to A accounted for the distribution of *Cyclobalanopsis*, whereas dispersal from C to B was inferred for the *Cerris* node, in addition to two subsequent dispersals to A within *Cerris*. With the outgroup/ingroup node constrained to A or “Asia,” the ingroup retained A, but all other nodes subtending biogeographically variable terminal branches were reconstructed ambiguously.

DIVA: *Fagus*. Using the phylogeny of *Fagus* (nine spp.), dispersal-vicariance analysis with five areas (A: Asia, B: Eu-

rope, C: North America, D: Mexico, E: Japan) resulted in two or more combinations of equally optimal reconstructions at six nodes while inferring a total of five dispersal events (fig. 6A). The ingroup node was reconstructed to include two possible combinations (AE/ABCDE). Reducing the maximum areas (“maxareas”) criterion to four areas produced optimizations of area A (China) for both the outgroup/ingroup and ingroup nodes. Other interior nodes were affected similarly with optimizations reduced to include AE (China + Japan) or E (Japan). Multiple optimizations at critical nodes were in part due to the three distinct placements of Japanese taxa within the tree.

When Japan and China were treated as a single area, A (Asia), the ingroup and the three most basal nodes were optimized to A, while inferring a total of three dispersal events (fig. 6B). The node uniting (*Fagus spp.* – (*Fagus mexicana* + *Fagus grandifolia*)) remained ambiguous but was reduced to AC (Asia + North America), AD (Asia + Mexico), or ACD (Asia + North America + Mexico). The (*Fagus crenata1* – (*F. spp.*)) node was reduced to A (Asia). Under DIVA, reconstructions with five areas constrained to four, and with treating Asia as single area, implied an origin in Asia with subsequent dispersal involving some combination of B (Europe), C (North America), and D (Mexico). Subsequent to an initial dispersal, an alternative interpretation would involve vicariance of ACD followed by dispersal from A (Asia) to B (Europe) and then vicariance of AB. Only the four-area dispersal-vicariance analysis was used to make comparisons with the results of the other methods.

Vicariance and dispersal: *Fagus*. Under strict vicariance (see table 1), the relevant components included: ingroup and basalmost nodes to ABCDE, node for (*F. crenata1* – (*F. spp.*)) to ABE, node for (*Fagus lucida* – (*Fagus sylvatica* + *Fagus orientalis*)) to AB, and node for (*F. mexicana* + *F. grandifolia*) to

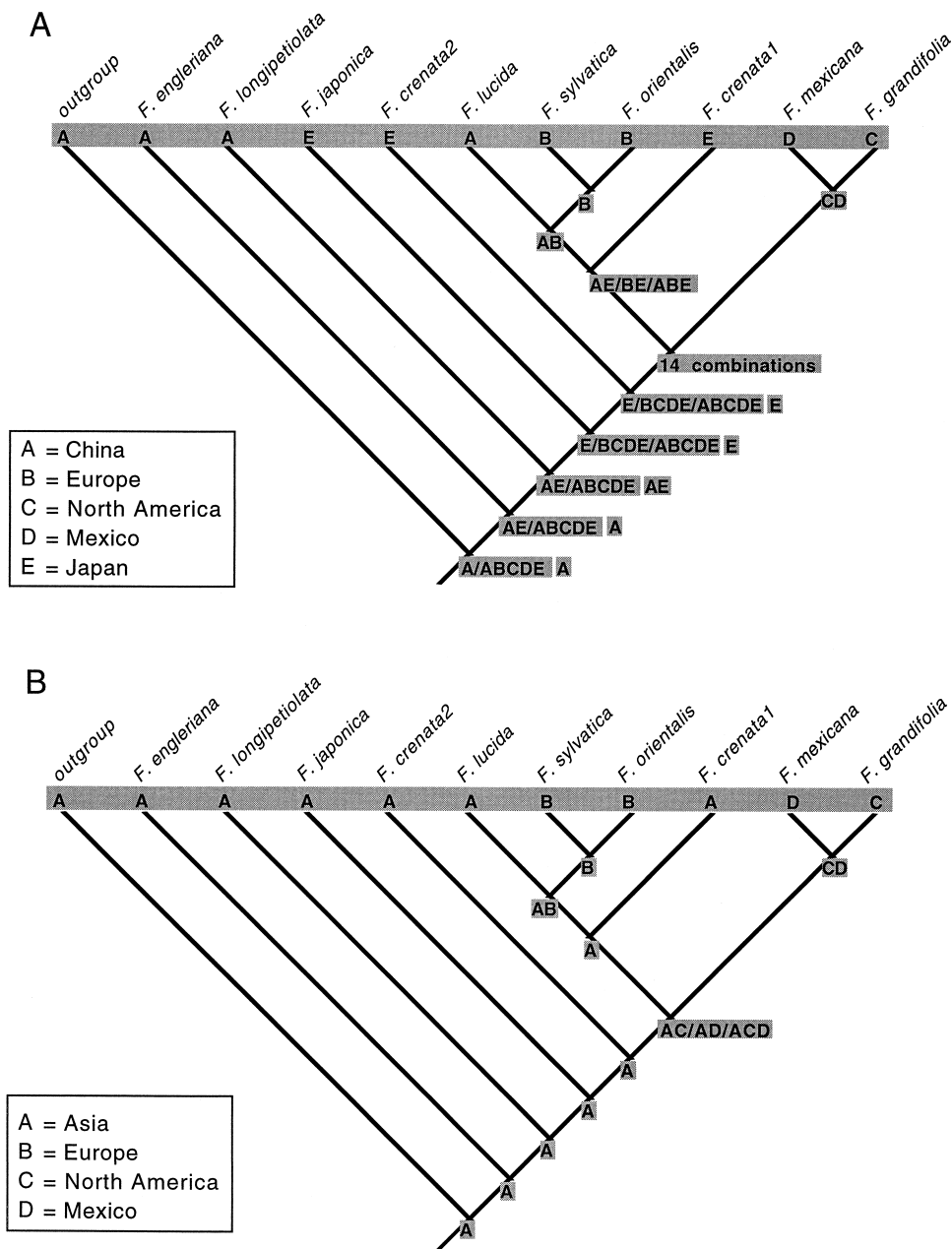


Fig. 6 A, Ancestral area reconstructions based on DIVA, subdividing areas within Asia, for the phylogeny of *Fagus* (see fig. 4a). Area designations separated by slashes represent equally parsimonious reconstructions. Area designations separated by a space indicate optimization results based on the “maxareas” – 1 function. B, Ancestral area reconstructions based on DIVA, treating Asia as a single area, for the phylogeny of *Fagus* (see fig. 4a).

CD. With only four areas, the biogeographic components have Asia in place of Japan and China, but the ancestral distributions at the nodes remain essentially the same (table 1).

Dispersal analysis with five areas designated resulted in a single most parsimonious tree of five steps with two ambiguously reconstructed nodes. An origin in China is supported followed by dispersal to Japan and subsequent independent dispersal events from Japan to North America, Mexico, Europe, and back to China. With only four areas, dispersal analysis resulted in a single most parsimonious tree of three steps

with one ambiguously reconstructed node. An origin in Asia is supported with independent dispersal events to Europe, North America, and Mexico.

Discussion

Overview of Interspecific Phylogeny

Regarding the general pattern of species relationships in *Fagus*, *Quercus*, and section *Quercus*, we find support for a close

relationship between European and Asian taxa (fig. 4). Specifically for *Fagus*, North American taxa form the sister group to a clade containing both European and Asian species. Wen (1999) has suggested that this lack of direct intercontinental sister species is the result of additional speciation before or after vicariance. Interestingly, *Fagus* species from Europe and western Asia are sister to *Fagus lucida* from southwestern China. The general pattern of relationships has implications for interpreting the migration and evolution of the genus, especially in light of data from both the fossil record and estimates of divergence times (see below).

One of the major issues confounding our ability to confidently infer species-level relationships is infraspecific variation and the general observation that gene trees may not track organismal relationships (Doyle 1992; Rieseberg et al. 1996; Wendel and Doyle 1998). For the disjuncts studied here, we generally find that sampling a single individual per species is adequate to infer species phylogeny for subsequent biogeographic analysis, as good examples of phylogenetically distinct taxa from disjunct areas are seen within *Castanea* and throughout most of *Fagus* (fig. 4A, 4C). While it is reasonable to find that species of *Fagus* from Japan are not monophyletic (see fig. 4A), infraspecific cpDNA variation within *Fagus crenata* illustrates one source of uncertainty in calculating divergence times and assigning area designations for biogeographic analysis.

Inferring interspecific phylogeny within the white oaks (section *Quercus*) was problematic, consistent with previous studies using cpDNA (Whittemore and Schaal 1991; Petit et al. 1993; Dumolin-Lapegue et al. 1997; Manos et al. 1999). For oak species, notorious for their lack of reproductive isolating mechanisms, it is clear that transspecific polymorphisms are maintained through the combined forces of cytoplasmic introgression and incomplete lineage sorting, thus precluding any attempt to infer species phylogeny (see fig. 4B). Phylogenetic analyses based on nuclear ribosomal (ITS) sequences were unable to resolve interspecific relationships as well (Manos et al. 1999, 2001). We also observed few examples of area-specific haplotypes, and this too could be related to cytoplasmic introgression brought about through postglacial colonization (Dumolin-Lapegue et al. 1997; Petit et al. 1997; Ferris et al. 1998). As a general result, area relationships must be generalized to a simple two-area case (North America + Eurasia). This pattern, however, remains biogeographically informative and useful with respect to possible interpretations based on the resulting cladistic structure. Interestingly, ITS sequences have not sorted out intercontinentally (see fig. 3), suggesting reproductive isolation as measured by biparental markers takes longer to produce patterns of reciprocal monophyly (Manos et al. 1999, 2001). This makes biological sense for several reasons, including wind-dispersed pollen, higher effective population size for nuclear alleles, and appreciable ITS allelic diversity documented within *Quercus* species (Manos et al. 1999; Muir et al. 2001).

The phylogenetic pattern within *Castanea* is based on cpDNA sequences as well, but in contrast to section *Quercus*, it shows stronger correspondence to geography (fig. 4C). Resolution of species-specific clades suggests long-term maintenance of populations with no evidence of cytoplasmic introgression between species with nonoverlapping distributions.

Interfertility among *Castanea* species is well known (Jaynes 1974; Johnson 1988); therefore, the pattern of cpDNA relationships among Chinese species may be more similar to that seen in the white oaks after more sampling.

Overview of Interspecific Divergence

One general observation within Fagaceae is that sequence divergence among and within genera is fairly low. This is based on a variety of sources, including the cpDNA genes, *rbcl* and *matK* (Frascaria et al. 1993; Manos and Steele 1997), and the ITS region (Manos et al. 1999, 2001). The various noncoding regions of cpDNA sequenced in this study also reveal appreciably low levels of sequence divergence between disjunct species of most of the genera, except *Trigonobalanus*. Estimating divergence times between species with low sequence divergence can be problematic because of low statistical power of relative rate tests and high levels of standard error (Sanderson 1997; Schnabel and Wendel 1998; Wen 1999). Nevertheless, estimates of divergence times between species of disjunct Northern Hemisphere genera have suggested that many classic temperate zone examples fitting the eastern Asia–eastern North America pattern appear to be Miocene (ca. 5–22 million years B.P. in age and associated with connections via the BLB [for review, see Wen 1999; Xiang et al. 2000]). The low sequence divergence observed among disjunct species of *Fagus*, *Castanea*, and section *Quercus* generally fits this pattern.

Calculation of divergence times using the highest estimate of the rate of synonymous changes for *rbcl* (3×10^{-10}) in Fagaceae (Frascaria et al. 1993), calibrated using fossil data for the minimum divergence time of *Castanea* and *Quercus* (60 million years B.P.; see Crepet 1989), provides a rough guide to estimate divergence times based on the noncoding cpDNA sequences examined here. To explore the relationship between cladistic pattern and divergence time, we used the following examples within *Fagus*, *Quercus*, and *Trigonobalanus* to provide temporal context for further discussion involving biogeographic analyses and the fossil record.

For *Fagus*, where roughly equal amounts of nucleotide variation were obtained for cpDNA noncoding and ITS regions, we calculated divergence times using the same substitution rate across the total amount of sequence. The low of 0.22% and high of 1.31% sequence divergence between species suggests minimum and maximum divergence between species of 3.6 million years B.P. and 22 million years B.P., respectively. Comparisons of disjunct pairs of species that share a most recent common ancestor (MRCA) suggest that *Fagus sylvatica* + *Fagus orientalis* diverged from the Asian species *F. lucida* around 3.6 million years B.P., while the North American species, *Fagus grandifolia* and *Fagus mexicana*, diverged ca. 7 million years ago. Examples of intercontinental disjunction involving either *F. grandifolia* or *F. mexicana* and several species from its sister clade roughly yield divergence times of 10–11.3 million years B.P. The higher values of time since divergence within *Fagus* generally involve the Asian species *Fagus engleriana* and *Fagus japonica* relative to *F. sylvatica*, *F. grandifolia*, and *F. lucida*, suggesting older speciation events within the genus had occurred in Asia prior to intercontinental vicariance (see Wen 1999).

In the case of *Quercus*, we focused on the analysis within

section *Quercus* because it is based strictly on noncoding cpDNA sequences, thus maintaining a standard source of data across the family. In section *Quercus*, intercontinental disjunction can be generalized such that an average of 1.0% sequence divergence roughly characterizes the amount of nucleotide substitution between any two members from each clade, resulting in an estimate of time since divergence of ca. 17 million years B.P.

The evergreen genus *Trigonobalanus* provides a single, yet important data point in evaluating the biogeographic history of Fagaceae. Thus far, we have shown that *Fagus*, section *Quercus*, and perhaps *Castanea* fit the pattern of BLB connections followed by vicariance during the Miocene. Exceptions to this pattern appear to be rare among widespread deciduous temperate elements (but see Li and Donoghue 1999). This could also be due to the lack of focus on paratropical taxa (Tiffney and Manchester 2001). Along these lines, *Trigonobalanus* represents paratropical Fagaceae, and both its modern and extensive fossil distribution suggest an older biogeographical history (Van der Hammen and Cleef 1983). We find 2.21% sequence divergence between Asian species and the New World relict *Trigonobalanus excelsa* to roughly estimate a divergence time of 37 million years B.P. This data point is significant in that intercontinental vicariance within *Trigonobalanus* apparently occurred earlier than estimated within either *Fagus* or section *Quercus*. The combination of fossil and modern distributions with molecular dating suggests the continuous distribution of *Trigonobalanus* most likely was achieved via the North Atlantic Land Bridges (NALB) during the Paleocene before the complete formation of the Turgai Strait (Tiffney and Manchester 2001). Unfortunately, there is no fossil record for the genus and its allies in Asia to assist in the interpretation of its migration to current relict localities. If vicariance occurred as early as the Lower Oligocene, this amphipacific pattern potentially characterizes floristic exchange via the NALB, and similar disjunctions represent other examples of peripheral relicts of a formerly widespread, Early Tertiary paratropical flora (Van der Hammen and Cleef 1983; Fritsch 1999).

Overview of Biogeographic Analyses

A general outcome of our focus on Fagaceae is that biogeographical analysis involves as few as two and no more than five distinct areas. Upon treating Asia and North America more generally, the patterns generally consist of just three areas, Europe, North America, and Asia, and thus are limited in overall information content. Our ability to evaluate congruence in area relationships also is somewhat hampered by the lack of adequate phylogenetic resolution within certain taxa, such as *Castanea* and section *Quercus*. Phylogenies of particular Fagaceae occurring in all three areas generally support the (North America – (Europe + Asia)) pattern, but knowledge of area relationships based on extant taxa alone often provides an incomplete view of biogeographic history (Manchester 1999; Manchester and Tiffney 2001). As mentioned earlier, there are many positive aspects of concentrating on the biogeographical history of Fagaceae, and of these, high-quality fossil data stand out because they serve as a key independent

data source to evaluate the results of biogeographical analyses and estimates of divergence times.

Phylogeny and historical biogeography of Quercus. Our analysis of a worldwide sample of *Quercus* using ITS data suggests two major clades within the genus that largely correspond to a geographic split between New and Old World groups. An interesting exception within the New World clade is the widespread, annual fruiting white oaks of section *Quercus* (see below). In contrast to the ITS data presented here, previous analyses have shown that cpDNA restriction site data provide no hierarchical information within the genus (Manos et al. 1999). Our results generally support Axelrod's (1983) hypothesis that all major oak groups essentially evolved in the areas where they occur today. While there are reports of fossilized *Quercus* from the Eocene (45–50 million years B.P.) (MacGinitie 1941; Bones 1979; Manchester 1981, 1994; Zhou 1992, 1993; reviewed by Jones 1986), the earliest unequivocal evidence of modernized forms is from the Oligocene (ca. 30 million years B.P.) of Huntsville, Texas (Daghlian and Crepet 1983). The totality of fossil data basically supports a widespread ancestral *Quercus* that by most accounts appeared to be evergreen based on leaf types with affinities to modern *Cyclobalanopsis* and particular members of the *Cerris* and *Lobatae* groups. Biogeographic hypotheses based on DIVA and under the assumption that the MRCA of *Quercus* was widespread support an initial vicariance between North America and Asia with subsequent diversification and dispersal restricted to the middle latitudes (figs. 3, 5).

Although biogeographic inferences based on modern distribution of the *Cyclobalanopsis* + *Cerris* clade generally suggest diversification within Asia and multiple dispersals within *Cerris* back to Europe, the pattern within the (*Protobalanus* – (*Lobatae* + *Quercus*)) clade is more tractable. According to DIVA, the ancestral area of this clade is North America with dispersal to Asia and then Europe as a likely explanation for the widespread distribution of section *Quercus*. Strict vicariance (table 1), on the other hand, suggests a widespread ancestor for the (*Protobalanus* – (*Lobatae* + *Quercus*)) clade, as well as for several internal nodes within the clade. Under this model, the presence of section *Quercus* in Eurasia has the effect of generalizing the interpretation of biogeography for the clade. The hypothesis suggested by DIVA is in agreement with the general pattern of species diversity (125 spp. in North America and Mexico vs. 20 spp. in Eurasia) and the appearance of older fossils in North America (Zhou 1992, 1993). As Axelrod (1983) had postulated, only the deciduous ancestors of section *Quercus*, most likely those of the chestnut oak group, were capable of migrating via land bridges during the Oligocene. Therefore, the estimated time of divergence, roughly 17 million years B.P. between Old and New World clades of section *Quercus*, is consistent with an Upper Oligocene migration to Eurasia. Subsequent intercontinental vicariance during the Miocene is supported by the extinction of populations adjacent to the BLB. Fossilized pollen data from northwestern Canada and Alaska of thermophilous species, including *Quercus* and *Fagus*, provide evidence for global temperature decline starting at ca. 15 million years B.P. (White et al. 1997). The time to reciprocal monophyly for cpDNA is clearly less than 17 million years B.P. in this case, thus elimi-

nating any genetic signature of historical migration from North America to Asia.

The center of origin for the genus *Quercus* and overland migration route used by its ancestors to achieve a continuous distribution remain intriguing questions. Vicariance analysis was not intended for such questions, whereas dispersal analysis is, in part, influenced by the distribution of outgroups (table 1). DIVA, like strict vicariance, suggests a widespread ancestral distribution for *Quercus* but with equally likely optimizations for restriction to all pairwise combinations of the three areas (fig. 5). While support for two major clades is modest at best, a single vicariance event within a continuous, widespread ancestral distribution provides the most conservative and general explanation for the phylogenetic pattern of reciprocal monophyly between Eurasian + North American clades.

Our inability to designate a specific area of origin using fossil data and biogeographic analyses makes it impossible to discriminate among potential migration routes. Assuming genus-level diversification within Fagaceae originated within the Tropics of Asia, one possible scenario would suggest that ancestral evergreen *Quercus* migrated via the NALB during the Upper Eocene to Lower Oligocene after the retreat of the Turgai Strait (Tiffney and Manchester 2001). Following the inferences provided by phylogeny, an initial vicariance between North America and Eurasia may have resulted from closure of the NALB. Subsequent cooling and drying trends during the Oligocene may have promoted infrageneric diversification within the genus, ultimately leading to the patterns of endemism observed in the modern oak flora (Axelrod 1983).

Phylogeny and historical biogeography of Fagus. Our analysis of nine species of the genus *Fagus* suggests appreciable cladistic structure (fig. 4A). The rooted tree supports the basal placement of several Asian taxa, notably *F. engleriana*, *F. longipetiolata*, and *F. japonica*. As mentioned earlier, the placement of the Japanese taxon *F. crenata* is ambiguous due to the mixed phylogenetic signal of the two accessions sampled. *Fagus crenata*4 is strongly supported within a biogeographically diverse clade including *F. sylvatica*, *F. lucida*, and *F. grandifolia*. While there are no previous cladistic studies of the genus, morphometric analyses using venation type, marginal dentation, type and size of stomata, and cupule morphology and size provided groupings among extant species (Kvaček and Walther 1992). East Asiatic *Fagus*, as represented by *F. engleriana*, *F. longipetiolata*, and *F. japonica*, formed a group defined mostly by long pedunculate cupules. An alternative rooting of our analysis, between *F. crenata*3 and *F. japonica*, would provide support for this assemblage. The remaining extant species were placed in three marginally distinct groups that all seem to share comparatively larger cupules on short to medium length peduncles, in general agreement with the resolution of the species forming the biogeographically diverse clade. It also seems likely that the ancestor of this clade was widespread at high latitudes and by the Lower Miocene became distinct from an ancestral Asian assemblage that may have occupied middle latitudes.

Biogeographic hypotheses using DIVA and area designations that recognize Japan and China generally support ancestral *Fagus* as widespread, in agreement with strict vicariance and the fossil record of the genus (fig. 6B). Simplifying the component areas within Asia (fig. 6B), in addition to using the

“maxareas” constraint (fig. 6A), reconstructs a hypothesis for an Asian origin, consistent with previous investigations based on pollen and narrative biogeographical insights (Van Steenis 1971; Hanks and Fairbrothers 1976; Takhtajan 1982). In contrast to section *Quercus*, where the resulting topology within the sample did not suggest a source and direction of migration, bidirectional migration to Europe and North America within *Fagus* is supported by a paraphyletic Asian assemblage of species, in agreement with the expectations based on modern phylogeographic models (Avice 2000).

The pollen record indicates that dispersal to North America and Europe apparently occurred during the Upper Oligocene to Lower Miocene (Brown 1994; Walther 1994). Vicariance between both Europe and Asia, and North America and Mexico, completes the sequence of biogeographic events. On the bases of both node depth and estimates of divergence time, the initial vicariance between Asian and North American taxa is older (10–11.5 million years B.P.) than the inferred vicariance events between both Europe and Asia (3.6 million years B.P.) and North America and Mexico (7 million years B.P.). This sequence is consistent with the phylogenetic pattern and pollen record for *Fagus* in northwestern Canada and Alaska (White et al. 1997). The occurrence of *Fagus* and other temperate elements in northern Latin America has recently been revisited by analysis of several palynofloras. These data suggested a relatively recent Pliocene migration of some of these taxa, including *Fagus* (Graham 1999b). Our estimate of divergence (7 million years B.P. or Upper Miocene) between *F. mexicana* and *F. grandifolia* suggests a slightly earlier migration and subsequent vicariance. In spite of the possible sources of error associated with each type of dating procedure, the palynological hypothesis of a recent migration of *Fagus* into northern Latin America is generally upheld by sequence-based dating.

Biogeographic patterns of other fagaceous genera. Combining the results of previous phylogenetic studies among the genera within Fagaceae (Manos et al. 2001) with the infrageneric focus presented here provides the context for a comprehensive biogeographic synthesis for the family. New data on the phylogenetic relationships of relict Fagaceae also have clarified several aspects of the phylogeny and biogeography of the family (Manos et al. 2001; fig. 2). Most important, the distribution of evergreen Fagaceae suggests two distinct patterns of Early Tertiary connections. While each is limited in terms of area relationships, together they provide critical comparative context for developing a biogeographic overview of the family.

Tiffney (2000) has argued that evergreen angiosperm connections through the BLB are probably rare and possible only during the Eocene or before because high latitude and extended periods of darkness were likely to have precluded exchange of thermophilic evergreen taxa (but see Wolfe 1994). The distributions of the evergreen castaneoid genera, *Lithocarpus* and *Castanopsis*, bear on this point. It is now clear that the western North American genus *Chrysolepis* is not sister to the Asian genus *Castanopsis* (fig. 2). Therefore, this previously used example of BLB connection and subsequent vicariance no longer provides an adequate biogeographic explanation for the relict distribution of *Chrysolepis*. However, evidence from the Eocene Nut Beds Flora of Oregon (Manchester 1994) unequivocally shows that *Castanopsis* occurred in North America.

Amphi-Pacific disjunction within *Lithocarpus* further suggests Eocene BLB evergreen connections; however, phylogenetic analysis does not support the monophyly of the genus (Manos et al. 2001; fig. 2).

One explanation for this result is the great antiquity of the disjunction within *Lithocarpus*. An ancient vicariance event, perhaps as early as the Late Cretaceous, involving the closing of the BLB to evergreen taxa could explain the loss of synapomorphic nucleotide sites at the genus level as a product of long-term isolation. Based on the presence of both living and extinct lineages of largely Asian evergreen Fagaceae in western North America, it seems likely that evergreen Fagaceae migrated via the BLB during the Late Cretaceous to Lower Eocene. While there is support for the general observation that western North America is home to relict Fagaceae, a vicariant relationship with Asian taxa does not fully explain the presence of all relict Fagaceae in the area. For example, *Chrysolepis* may have had greater affinities to extinct transitional castaneoids documented in the macrofossil record from the Paleocene/Eocene boundary of eastern North America (Crepet and Daghljan 1980; Crepet and Nixon 1989a, 1989b). This assemblage of early castaneoids might have been biogeographically contemporaneous with the widespread genus *Trigonobalanus*. In summary, modern elements of the evergreen castaneoid radiation, the bulk of which are paratropical and Asian in distribution, and the biogeography and relative timing of vicariance within *Trigonobalanus* provide a comparative basis to support floristic exchange via both the BLB and NALB during the Early Tertiary.

Synthesis of Biogeographic Patterns

The family Fagaceae provides a wide variety of examples to consider in the development of a modern synthesis of the historical dynamics of Northern Hemisphere phytogeography (Tiffney 1985a, 2000; Tiffney and Manchester 2001). Because Fagaceae occur in range of floristic types, our studies provide general support for several emerging phytogeographic patterns based on data from climatology, geology, paleobotany, and phylogeny.

Neogene vicariance (2–22.5 million years B.P.). Starting with apparently more recent biogeographic discontinuities of the Tertiary, our analyses suggest that the “cradle” for *Fagus* is Asia and that bidirectional migration from Asia to both North America and Europe is responsible for its widespread modern distribution. Vicariance events between North America and Asia and within North America date to the mid-Miocene, whereas that between Europe and Asia is approximately Pliocene in age. A center of origin in Asia also is supported by the presence of older fossils and greater species diversity. Using phylogeny, Xiang and Soltis (2001) also provide biogeographical analyses that generally support an Asian origin for other Miocene disjunctions (e.g., *Aralia* sect. *Aralia*, *Asarum*, *Panax*, *Symplocarpus*), and while species diversity within these genera is usually higher in Asia, lack of complementary fossil data coupled with likely extinctions of European taxa limit the informativeness of these examples. Thus, valid testing of the Miocene BLB pattern requires phylogenetic analysis of taxa with species representation in at least three areas.

The genus *Castanea* would have provided a biogeographic check on the pattern in *Fagus*, especially in light of the contradictory biogeographical pattern, (Asia – (North America + Europe)), based on phylogenies of *Liquidambar* (Li and Donoghue 1999) and *Cercis* (Davis et al., in press). This latter pattern suggests NALB connections and generally older estimates of vicariance (Lower Miocene to Upper Oligocene), emphasizing alternative explanations exist for certain mesophytic disjunct genera.

Although phylogenetic relationships within section *Quercus* and *Fagus* support the (North America – (Europe + Asia)) pattern, section *Quercus* provides a counterexample to the “cradle” in Asia scenario. Because the white oaks most likely evolved within North America and migrated west via the BLB, it appears that floristic exchange involving this migration route was bidirectional. While we cannot rule out the notion that a majority of woody disjunct taxa of temperate North America are predominantly Asian in origin, additional examples of taxa following an eastern BLB migration pattern might better characterize the Miocene floristic exchange. Higher extinction rates in North America throughout the Neogene also may contribute to the apparent asymmetry of this exchange (Guo and Ricklefs 2000).

Paleogene vicariance (23–65 million years B.P.). Evidence for comparatively older vicariance patterns occurring within Fagaceae involves both the mesophytic genus *Quercus* and thermophilic genus *Trigonobalanus*, taxa that became widespread, most likely via the NALB, by at least the Lower Oligocene. Both genera are wind pollinated and seemingly well suited to seasonal climates. Unequal patterns of diversification between the two genera appears to be associated with the greater xeric tolerance of *Quercus* during the Oligocene and thereafter. Within *Trigonobalanus*, divergence time estimates are larger than any values estimated between Asian and North American *Quercus* (P. S. Manos, unpublished data), suggesting that vicariance may have occurred quite early during the Oligocene. Barrier formation around the NALB may have affected these genera differentially, leading to temporally incongruent scenarios of vicariance (Xiang et al. 1998; Tiffney 2000). This seems likely considering *Trigonobalanus* is associated with other taxa that share a paratropical amphi-Pacific pattern of distribution.

Under the assumption that vicariance promoted the initial phylogenetic split within *Quercus*, the evolution of modern taxa during the Oligocene generally supports vicariance prior to the Miocene. The magnitude of divergence between *Trigonobalanus* species and their modern distribution is suggestive of comparatively older vicariance (Upper Eocene to Lower Oligocene). In contrast to *Trigonobalanus*, *Lithocarpus* and *Castanopsis* do not appear to have ever been present in eastern North America. Therefore, by combining modern and fossil distributions and considering that North American *Lithocarpus* appears to have diverged well before other disjunctions within the family, we hypothesize an Asian origin for each genus, with migrations to central Europe and western North America occurring by at least the mid-Eocene. Evidence supporting BLB exchange and resulting amphi-Pacific disjunctions involving thermophilic Fagaceae agrees with Tiffney’s (2000) assertion that evergreen connections were rare after the Eocene. The cryptic nature of evergreen floristic exchange via the

BLB during the Paleocene to Eocene is, in part, explained by the well-characterized extinction of thermophilic taxa from North America (Manchester 1999).

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Appendix

DNA Sources

DNA sources include species, locality, and GenBank accession number (¹ITS/5.8S accession, ²5' *trnK*, ³3' *trnK*, and ⁴*rbcL/latpBE* accession).

Castanea crenata Sieb. & Zucc.; 1. U.S.A.: Conn. Connecticut Agricultural Research Station. *Stanford R7T7* (UNC-CH); ²AY042428, ³AY042415, ⁴AY042441.

Castanea crenata Sieb. & Zucc.; 2. Japan. C.R. Parks CP1; ²AY042430, ³AY042417, ⁴AY042443.

Castanea crenata Sieb. & Zucc.; 3. U.S.A.: Mass. Arnold Arboretum, accession no. 225-97, seed source = Connecticut Agricultural Research Station; ²AY042429, ³AY042416, ⁴AY042442.

Castanea dentata (Marshall) Borkh.; 3. U.S.A.: Conn. Connecticut Agricultural Research Station. *Stanford R1T18* (UNC-CH); ²AY042431, ³AY042418, ⁴AY042444.

Castanea dentata (Marshall) Borkh.; 5. U.S.A.: Tenn., Short Springs. *Stanford SS3* (UNC-CH); ²AY042432, ³AY042419, ⁴AY042445.

Castanea henryi (Skan) Rehd. & E. H. Wilson; 7. China: Lushan. C.R. Parks 1-86-L2-6; ²AY042437, ³AY042424, ⁴AY042450.

Castanea henryi (Skan) Rehd. & E. H. Wilson; 8. China: Lushan. C.R. Parks 2-86-L2-6; ²AY042438, ³AY042425, ³AY042426, ⁴AY042451.

Castanea mollissima Bl.; 9. U.S.A.: Conn. Connecticut Agricultural Research Station. *Stanford R1T15* (UNC-CH); ²AY042439, ³AY042426, ⁴AY042452.

Castanea mollissima Bl.; 10. U.S.A.: Conn. Connecticut Agricultural Research Station. *Stanford R3T7* (UNC-CH); ²AY042440, ³AY042427, ⁴AY042453.

Castanea pumila (L.) Miller; A. U.S.A.: Conn. Connecticut Agricultural Research Station. *Stanford 17-R2T2* (UNC-CH); ¹AY040394, ²AY042433, ³AY042420, ⁴AY042446.

Castanea sativa L.; 18. U.S.A.: Conn. Connecticut Agricultural Research Station. *Stanford R3T2* (UNC-CH); ²AY042434, ³AY042421, ⁴AY042447.

Castanea sativa L.; 19. U.S.A.: Conn. Connecticut Agricultural Research Station. *Stanford R3T3* (UNC-CH); ²AY042435, ³AY042422, ⁴AY042448.

Castanea sativa L.; A. U.S.A.: Mass. Arnold Arboretum, accession no. 12924, seed source = Orleans, France; ²AY042436, ³AY042423, ⁴AY042449.

Castanopsis delavayi Franchet; China: Yunnan. Simao; *Manos & Zhou 1393* (DUKE); ¹AY040371.

Chrysolepis sempervirens (Kell.) Hjelmquist; U.S.A.: Calif. San Bernardino Co., Black Mountain; *Manos 160* (BH); ¹AF389087.

Colombobalanus excelsa (Lozano, Hdz-C. & Henao) Nixon & Crepet (*Trigonobalanus excelsa* Lozano, Hdz-C. & Henao); Colombia: Virolin; *Nixon 4655* (BH); ²AY042456, ³AY040492.

Fagus crenata Bl.; 3. U.S.A.: Mass. Arnold Arboretum, accession no. 2122C; ¹AY040508, ²AY042399, ⁴AY042411.

Fagus crenata Bl.; 4. Japan. Nikko Botanical Garden; *J. Wen 2501 W*; ¹AY040501, ²AY042392, ⁴AY042404.

Fagus engleriana Seemen; U.S.A.: Mass. Arnold Arboretum, accession no. 383-27A; ¹AY040500, ²AY042391, ⁴AY042403.

Fagus grandifolia Ehrh. U.S.A.: N.Y. Tompkins Co.; *Manos 114* (BH); ¹AY040509, ²AY042400, ⁴AY042412.

Fagus japonica Maxim.; 7. U.S.A.: Mass. Arnold Arboretum, accession no. 5277B; ¹AY040503, ²AY042394, ⁴AY042406.

Fagus japonica Maxim.; 10. Japan. Nikko Botanical Garden; *J. Wen 2502 W*; ¹AY040504, ²AY042395, ⁴AY042407.

Fagus longipetiolata Seemen; China. C.R. Parks 92-C6-2; ¹AY040511, ²AY042402, ⁴AY042414.

Fagus lucida Rehd. & E. H. Wilson; 5. U.S.A.: Mass. Arnold Arboretum, accession no. 7418A; ¹AY040507, ²AY042398, ⁴AY042410.

Fagus lucida Rehd. & E. H. Wilson; 6. U.S.A.: Mass. Arnold Arboretum, accession no. 23033A; ¹AY040506, ²AY042397, ⁴AY042409.

Fagus mexicana Camp; U.S.A.: N.C. Wade Co., North Carolina State Arboretum; ¹AY040510, ²AY042401, ⁴AY042413.

Fagus orientalis Lipsky; Turkey. C.R. Parks 92-TF-17; ¹AY040505, ²AY042396, ⁴AY042408.

Fagus sylvatica L. U.K. C.R. Parks B-6, HHB; ¹AY040502, ²AY042393, ⁴AY042405.

Formanodendron doichangensis (A. Camus) Nixon & Crepet (*Trigonobalanus doichangensis* Forman); China: Yunnan. Menglian; *Manos & Zhou 1400* (DUKE); ²AY042454, ³AY040499.

Lithocarpus densiflorus (Hooker & Arnott) Rehder; U.S.A.: Calif. *Nixon 4585* (BH); ¹AF389086.

- Quercus acutissima* Carruth.; U.S.A.: N.Y. Tompkins Co., Cornell University Plantations; *Manos s.n.* (BH); ¹AF098428.
- Quercus alba* L.; U.S.A.: N.Y. Tompkins Co.; *Manos s.n.* (BH); ¹AF098419, ³AY042464, ⁴AY042501.
- Quercus alba* L.; 15. U.S.A.: Mich., Grand Rapids. *J. McLachlan* MI32; ³AY042469, ⁴AY042506.
- Quercus aliena* Bl.; 67767. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 67767, seed source = China: Shaanxi; ³AY042481, ⁴AY042518.
- Quercus aliena* Bl.; 64880. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 64880, seed source = China: Hubei; ³AY042482, ⁴AY042519.
- Quercus arizonica* Sarg. U.S.A.: Ariz. Pima Co. north of Tucson; *Manos* 1225 (DUKE); ³AY042491, ⁴AY042528.
- Quercus austoglauca* (Y.T. Chang ex Y.C. Hsu & H.W. Jen) Y.T. Chang; China: Yunnan. Da Wei Shan; *Manos* & *Zhou* 1452 (DUKE); ¹AY040455.
- Quercus austoglauca* (Y.T. Chang ex Y.C. Hsu & H.W. Jen) Y.T. Chang; China: Yunnan. Da Wei Shan; *Manos* & *Zhou* 1448 (DUKE); ¹AY040461.
- Quercus calliprinos* Webb.; U.S.A.: Calif. Yolo Co., Shields Grove Arboretum; *Manos* 933; ¹AF098429.
- Quercus cedrosensis* Muller; B. Mexico: Baja California. Santo Tomas; *Manos* 716 (BH); ¹AF098450.
- Quercus cerris* L.; U.S.A.: Calif. Yolo Co., Shields Grove Arboretum; *Manos* 935 (BH); ¹AF098430.
- Quercus chrysolepis* Liebm.; B. U.S.A.: Calif. Del Norte Co. east of Hamburg; *Manos* 954 (BH); ¹AF098439.
- Quercus chrysolepis* Liebm.; C. U.S.A.: Ariz. Coconino Co., Oak Creek Canyon; *Manos* 771 (BH); ¹AF098440.
- Quercus coccifera* L.; U.S.A.: Calif. Yolo Co., Shields Grove Arboretum; *Manos* 931 (BH); ¹AF098431.
- Quercus cocciferoides* Hand.-Mazz.; China: Yunnan. *Zhou. s.n.* (KUN); ¹AY040466.
- Quercus dentata* Thunberg; 9. China: Yunnan. Western Hills; *Manos* 1304 (DUKE); ³AY042465, ⁴AY042502.
- Quercus dentata* Thunberg; 4. U.S.A.: Mass. Arnold Arboretum, accession no. 1590-52, seed source = Japan: Honshu; ³AY042480, ⁴AY042517.
- Quercus dentata* Thunberg; U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 61753, seed source = Korea: Myon; ³AY042479, ⁴AY042516.
- Quercus engleriana* Seeman; China: Yunnan. *Zhou. s.n.* (KUN); ¹AY040465.
- Quercus falcata* Michaux; U.S.A.: Fla. Alachua Co.; *Cavender-Bares* FA-19; no voucher; ¹AY040482.
- Quercus franchettii* Skan.; China: Yunnan. Kunming Botanical Garden; *Manos* 1286 (DUKE); ¹AY040464.
- Quercus gambelii* Nutt.; 5. U.S.A.: Ariz., Cochise. Ramsay Canyon; *Manos* 1250 (DUKE); ³AY042462, ⁴AY042499.
- Quercus gambelii* Nutt. U.S.A.: Utah, Snow Bird. *J. McLachlan s.n.* (DUKE); ³AY042492, ⁴AY042529.
- Quercus garryana* Douglas ex Hooker; 1. U.S.A.: Oreg., Corvallis. *Manos s.n.* (DUKE); ³AY042458, ⁴AY042495.
- Quercus garryana* Douglas ex Hooker; 2. U.S.A.: Oreg., Corvallis. *Manos s.n.* (DUKE); ³AY042459, ⁴AY042496.
- Quercus geminata* Small; U.S.A.: Fla. *L. Robbins s.n.* (BH); ¹AF098426.
- Quercus glandulifera* Bl.; 55107. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 55107, seed source = Korea: Kyong Gi Do Ongjin Gun; ³AY042475, ⁴AY042512.
- Quercus glandulifera* Bl.; 64866. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 64866, seed source = China: Hubei; ³AY042476, ⁴AY042513.
- Quercus glandulifera* Bl.; 44825. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 44825, seed source = Japan: Nikko; ³AY042477, ⁴AY042514.
- Quercus glandulifera* Bl.; 5. U.S.A.: Mass. Arnold Arboretum, accession no. 1264-80, seed source = Japan: Nagasaki; ³AY042478, ⁴AY042515.
- Quercus glauca* Thunb.; China: Yunnan. Kunming Botanical Garden; *Manos* 1340 (DUKE); ¹AY040458.
- Quercus griffithii* Hook.f. & Thompson ex Miq.; 10. China: Yunnan. Bei-Shui; *Manos* 1321 (DUKE); ¹AY040490, ³AY042466, ⁴AY042503.
- Quercus griffithii* Hook.f. & Thompson ex Miq.; 11. China: Yunnan. Bei-Shui; *Manos* 1322 (DUKE); ³AY042467, ⁴AY042504.
- Quercus ilex* L.; U.S.A.: Calif. Santa Barbara Co., University of California, Santa Barbara Campus; *Manos* 412 (BH); ¹AF098432.
- Quercus kelloggii* Newb.; U.S.A.: Calif. Riverside Co., Banning; *Manos* 123 (BH); ¹AF098416.
- Quercus laeta* Liebm.; Mexico: Morelos. Taxco; *Manos et al.* 563 (BH); ¹AF098421, ³AY042494, ⁴AY042531.
- Quercus lamellosa* (Smith) Oersted; China: Yunnan. Kunming Botanical Garden; *Manos* 1283 (DUKE); ¹AY040454.
- Quercus liaotungensis* Koidz.; 7. U.S.A.: Mass. Arnold Arboretum, accession no. 15-95, seed source = China: Beijing; ³AY042483, ⁴AY042520.
- Quercus liaotungensis* Koidz.; 64536. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 64536, seed source = China: Beijing; ³AY042484, ⁴AY042521.
- Quercus lobata* Nee.; U.S.A.: Calif. Santa Barbara Co.; *Manos* 999 (BH); ¹AF098422, ³AY042461, ⁴AY042498.
- Quercus longispica* A. Camus; 1. China: Yunnan. Lijiang; *Manos* 1329 (DUKE); ¹AY040473.
- Quercus merrillii* von Seemen; Borneo: Malaysia. Sarawak; *Cannon* 126 (DUKE); ¹AY040456.
- Quercus mongolica* Fisch.; 61724. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 61724, seed source = Korea: Tae-Dok San; ³AY042485, ⁴AY042522.
- Quercus mongolica* Fisch. 64547. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 64547, seed source = China: Beijing; ³AY042486, ⁴AY042523.
- Quercus monimotricha* Hand.-Mazz.; 1. China: Yunnan. Gang-Ha-Ba; *Manos* 1313 (DUKE); ¹AY040467.
- Quercus montana* Willd.; U.S.A.: N.C. *Manos s.n.* (DUKE); ³AY042463, ⁴AY042500.
- Quercus myrsinifolia* Bl.; U.S.A.: Ga. USDA Coastal Research Station, Savannah; *Manos s.n.* (BH); ¹AF098414.
- Quercus palmeri* Engelm.; A. U.S.A.: Calif. San Luis Obispo Co., Peachy Canyon Rd; *Nixon* 4590 (BH); ¹AF098446.
- Quercus palmeri* Engelm.; B. U.S.A.: Ariz. Coconino Co., Oak Creek Canyon; *Manos* 777 (BH); ¹AF098447.
- Quercus palustris* Muench.; U.S.A.: N.Y. Tompkins Co.; *Manos s.n.* (BH); ¹AF098417.
- Quercus pannosa* Hand.-Mazz.; China: Yunnan. Lijiang; *Zhou* 0064 (KUN); ¹AY040469.

- Quercus petraea* Liebl.; 590. Italy: Monte Terlago. S. *Fineschi DNA no. EL 590*; ³AY042472, ⁴AY042509.
- Quercus phillyreoides* Gray; 2. China: Yunnan. Babao; *Ming 0036 (KUN)*; ¹AY040462.
- Quercus pubescens* Willd.; 399. Italy: Poggio Bustone. S. *Fineschi DNA no. EL 399*; ³AY042473, ⁴AY042510.
- Quercus pubescens* Willd.; 410. Italy: Cori. S. *Fineschi DNA no. EL 410*; ³AY042470, ⁴AY042507.
- Quercus pubescens* Willd.; 495. Italy: S. Agata Militello. S. *Fineschi DNA no. EL 495*; ³AY042474, ⁴AY042511.
- Quercus pubescens* Willd.; 651. Italy: Novafeltria. S. *Fineschi DNA no. EL 651*; ³AY042471, ⁴AY042508.
- Quercus robur* L.; 1. U.K.: Wales. J. *McLachlan s.n. (DUKE)*; ³AY042488, ⁴AY042525.
- Quercus robur* L.; 3. U.K.: England, Egham. J. *McLachlan s.n. (DUKE)*; ³AY042487, ⁴AY042524.
- Quercus robur* L.; 12. U.S.A.: N.Y. Tompkins Co., Cornell University Campus; *Manos s.n. (BH)*; ¹AF098424, ³AY042468, ⁴AY042505.
- Quercus rubra* L.; U.S.A.: N.Y. Tompkins Co., Cornell University Campus; *Manos s.n. (BH)*; ¹AF098418.
- Quercus rugosa* Nee.; Mexico: Morelos. *Manos et al. 570 (BH)*; ¹AF098425, ³AY042493, ⁴AY042530.
- Quercus sadleriana* R. Brown; U.S.A.: Calif. Del Norte Co.; *Manos s.n. (DUKE)*; ¹AY040489, ³AY042460, ⁴AY042497.
- Quercus salicina* Bl.; U.S.A.: North Carolina. Orange Co., Parks Nursery; *Manos s.n. (DUKE)*; ¹AY040457.
- Quercus serrata* Thunb.; 14. Japan: Oofuento City. C.R. *Parks Q3H-6*; ³AY042490, ⁴AY042527.
- Quercus serrata* Thunb.; 67735. U.S.A.: Washington, D.C., U.S. National Arboretum, accession no. 67735, seed source = China: Shaanxi; ³AY042489, ⁴AY042526.
- Quercus suber* L.; U.S.A.: Calif. Santa Barbara Co., Orella St.; *Manos 423 (BH)*; ¹AF098434.
- Quercus tomentella* Engelm.; A. U.S.A.: Calif. San Diego Co., San Clemente Island; *Manos 684 (BH)*; ¹AF098435.
- Quercus tomentella* Engelm.; D. U.S.A.: Calif. Ventura Co., Anacapa Island; *Manos 545 (BH)*; ¹AF098436.
- Quercus vaccinifolia* (Kell.) Curran; A. U.S.A.: Calif. El Dorado Co., Echo Lake; *Manos 909 (BH)*; ¹AF098452.
- Quercus vaccinifolia* (Kell.) Curran; C. U.S.A.: Calif. Trinity Co., Scott Mountain; *Manos 945 (BH)*; ¹AF098454.
- Quercus variabilis* Bl.; China: Yunnan. Kunming Botanical Garden; *Zhou 069 (KUN)*; ¹AY040463.
- Quercus virginiana* Miller; U.S.A.: Fla. T. *Engstrom s.n. (BH)*; ¹AF098427.
- Quercus yunnanensis* Franchet.; China: Yunnan. Lijiang; *Zhou 0050 (KUN)*; ¹AY040491.
- Trigonobalanus verticillata* Forman; U.K.: Royal Botanical Gardens, Edinburgh, U.K.; RBG 1967-421; ²AY042455, ³AY042457.

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