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PHYLOGENETIC PATTERNS IN NORTHERN HEMISPHERE PLANT GEOGRAPHY

Michael J. Donoghue,[1,*] Charles D. Bell,* and Jianhua Li†

*Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520, U.S.A.; and †Arnold Arboretum of Harvard University, 125 Arborway, Jamaica Plain, Massachusetts 02130, U.S.A.

Geological and climatological processes that have impacted the biota of the Northern Hemisphere during the Tertiary are expected to yield little resolution when area cladograms are compared without taking the timing of diversification into account. In an attempt to establish a set of appropriate phylogenetic comparisons, we distinguished between a Pacific track involving (minimally) China, Japan, and eastern North America but not Europe, and an Atlantic track involving China, Europe, and eastern North America but not Japan (or, in most cases, western North America). Within the two Atlantic-track taxa considered here—*Liquidambar* and *Cercis*—European and North American species are more closely related to one another than they are to the Asian species. Within a set of five Pacific-track taxa—*Hamamelis*, *Weigela-Diervilla*, *Triosteum*, *Buckleya*, and *Torreya*—we see all possible relationships involving China, Japan, and eastern North America. Estimates of minimum divergence times between Old World and New World lineages, based on molecular and fossil evidence, differ markedly between the two Atlantic-track clades. Among the Pacific-track taxa, we find no correlation between pattern of area relationships and estimated divergence times of the Old World–New World disjuncts. Instead, we see a wide range in the timing of these splitting events among and within phylogenetic patterns. Despite the existence of a variety of patterns, inferred ancestral areas and divergence times can be explained by assuming initial diversification within Asia in a number of lineages, followed by iterative trans-Beringian dispersion and vicariance.

Keywords: biogeography, dispersal, vicariance, phylogeny, Northern Hemisphere, North America, Asia.

Introduction

The historical biogeography of the Northern Hemisphere has long been of interest to botanists. Close relationships between species in eastern Asia and eastern North America have been highlighted (Li 1952; Graham 1972; Wood 1972; Tiffney 1985*b*; Wen 1999), following Asa Gray's seminal treatment of the problem (Gray 1840, 1859; Boufford and Spongberg 1983), but other connections have also been noted, such as between Eurasia and western North America (Axelrod 1975; Liston 1997). In recent years, the number of phylogenetic studies of taxa with species in three or more Northern Hemisphere centers of endemism has grown to the point that vicariance biogeographic analyses are now feasible. Enghoff (1995) and Sanmartin et al. (2001) have conducted such analyses based on phylogenetic trees for Northern Hemisphere animal clades. Their studies have documented an array of patterns that are difficult to reconcile, suggesting a complex biogeographic history involving vicariance events spanning time intervals from the Cretaceous onward.

Botanical studies along these lines have so far been limited for the Northern Hemisphere (in contrast to the Southern Hemisphere: see Crisp et al. 1995; Linder and Crisp 1995). A number of authors have discussed the biogeographic implication of their phylogenetic studies of individual clades (e.g., Fritsch 1996; Wen and Zimmer 1996; Kelly 1998; Wen et al. 1998; Xiang et al. 1998*a*; Gould and Donoghue 2000), but few attempts have been made to identify general patterns by comparing area cladograms. Recently, Xiang et al. (1998*b*, 2000) moved in this direction in their analyses of several plant taxa with endemic species in eastern Asia, western North America, and eastern North America. These studies yielded a clear pattern in which eastern North American and western North American species are more closely related to one another than they are to the species from eastern Asia. However, based on several chloroplast DNA restriction site data sets (Xiang et al. 1998*b*) and analyses of *rbc*L sequences calibrated using *Cornus* (Xiang et al. 2000), they found a wide range in the timing of relevant speciation events across more than a dozen clades (from less than 1 million years B.P. in *Menispermum* to over 12 million years B.P. in *Pachysandra*). These findings imply "pseudocongruence" (Cunningham and Collins 1994) in some instances. That is, the same phylogenetic pattern appears to have been achieved at different times, presumably in response to different vicariance events.

Our work on this problem is oriented by the expectation that any vicariance biogeographic analysis attempting to extract a single general pattern from phylogenetic trees of all Northern Hemisphere taxa is highly likely to yield confusing and misleading results. The main reason for this is that diversification within some lineages will have coincided with a particular set of vicariance events, whereas these same events will have been irrelevant for groups that diversified during other (earlier or later) time periods. If speciation in a particular group occurred prior to a set of geological/climatological vi-

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[1] Author for correspondence; e-mail michael.donoghue@yale.edu.

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cariance events, then the distribution of species among the resulting areas of endemism is a function of the sorting of species into these regions. This is sometimes viewed as the biogeographic analog of lineage sorting (or deep coalescence) of gene trees with respect to a species tree (see Maddison 1997; Page and Charleston 1998). However, if the speciation events within a clade postdated a particular set of vicariance events, then the distribution of these species among the areas of endemism reflects either long-distance dispersal among regions (analogous to the lateral transfer of a gene) or dispersion and vicariance events that influenced these regions at a later date. In such cases, simultaneous analysis of all potentially relevant phylogenies, without some initial sorting by age of diversification, will conflate patterns that took shape at different times and had different underlying causes. Grande (1985) developed a similar view, stressing the importance of absolute time control in sorting out dispersal and vicariance in areas with complex histories. And, although not focused specifically on the timing of splitting events, similar concerns appear to underly some recent developments in cladistic biogeography, such as the identification of "paralogy-free subtrees" (Nelson and Ladiges 1996).

Ideally, one would begin a phylogenetic analysis of Northern Hemisphere biogeography with a large set of phylogenetic trees for which the absolute timing of the relevant splitting events had already been established with confidence. This would allow the sorting of clades into age classes within which the search for a single vicariance pattern might be productive. Lacking such knowledge at the outset of our own studies, however, we began by assigning taxa to either an "Atlantic track" or a "Pacific track" based on specific differences in their distributions across the major areas of endemism (fig. 1). We assigned to an Atlantic track those clades with extant representatives in eastern Asia, Europe (and western Asia), and eastern North America but not in Japan/Korea or (in some cases) western North America. In contrast, we assigned to a Pacific track those groups with extant species in eastern China (west to the Himalayas), Japan/Korea, western North America (perhaps only as fossils), and/or eastern North America but not in western Asia or Europe. Note that Asia is here subdivided into two long-recognized areas of endemism; in many clades, species in Japan, Korea, and northeastern China are distinct from those occurring in southern China and west to the Himalayas.

Our rationale in making this distinction was that groups showing the Atlantic track may have had available to them a dispersion pathway north of the Tethys seaway and across the North Atlantic through the Eocene (Tiffney 1985*a*; Sanmartin et al. 2001), or possibly (especially for more vagile and deciduous groups) into the Miocene (Tiffney 2000). In contrast, groups showing the Pacific track might well have migrated more recently between the Old World and New World via Beringia (Tiffney 1985*a*, 1985*b*; Sanmartin et al. 2001), which has been periodically available for dispersion by some plant groups up until the present. On this basis, we might expect intercontinental disjunctions in Atlantic-track plants to date to the Miocene or before, whereas we might find more recent splitting events among Pacific-track taxa.

In this article, we include discussion of two Atlantic-track groups on which we have worked (*Liquidambar* and *Cercis*) but focus primary attention on six seed-plant clades representing the Pacific track (*Hamamelis*, *Weigela-Diervilla*, *Triosteum*, *Buckleya*, and *Torreya*). Specifically, we ask whether the latter show a common phylogenetic pattern involving China, Japan, and eastern North America and whether the timing of splitting events between the Old World and New World closely

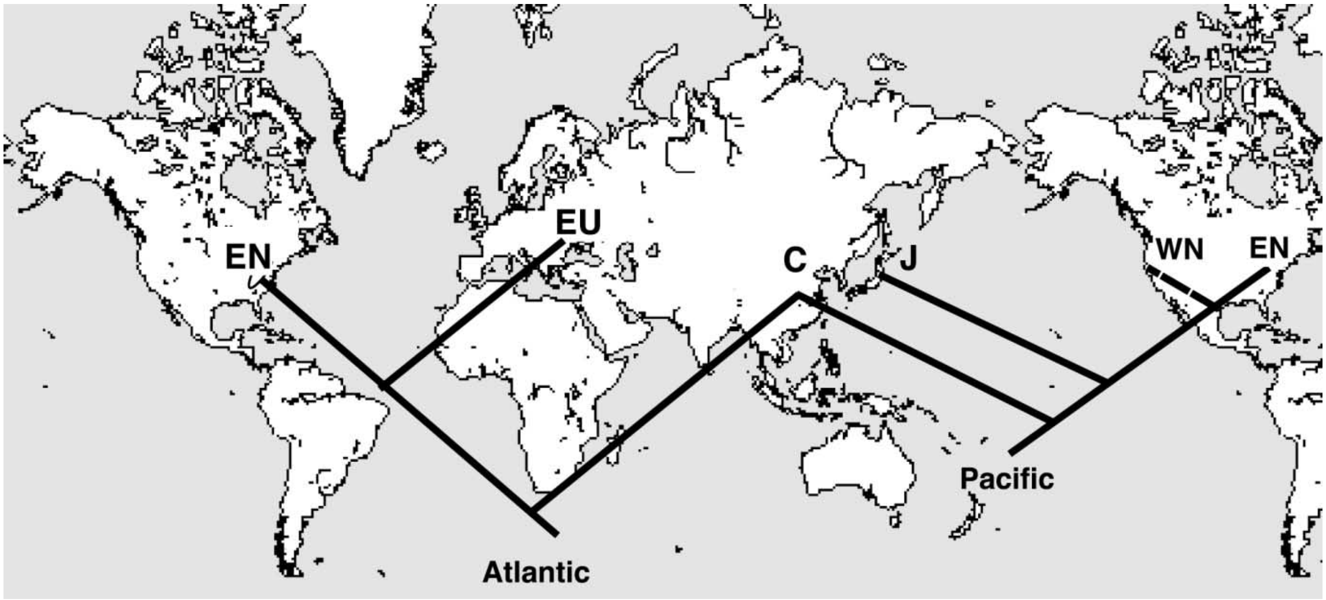

Fig. 1 Hypothetical relationships in a clade with an Atlantic track (present, minimally, in China, Europe, and eastern North America but not in Japan) and a second clade with a Pacific track (present, minimally, in China, Japan, and North America but not in Europe). Atlantic-track taxa may have older divergence times than many Pacific-track taxa.

correspond to phylogenetic patterns. Finally, we consider historical scenarios to account for both inferred dispersal and vicariance events and for a set of divergence-time estimates.

Phylogenetic Hypotheses and Area Cladograms

Our analyses build on phylogenetic studies that we have conducted over the past several years. These studies are published or are in press, and the data sets and trees can be obtained from TreeBASE (http://www.herbaria.harvard.edu/treebase). The individual studies should be consulted for additional details, including relevant taxonomic and nomenclatural information, additional fossil and geographic information, and specifics on the underlying data sets and analyses. In this section, we briefly summarize the results of each of these analyses as they pertain to the Northern Hemisphere biogeographic problem and then compare the set of implied area cladograms ("taxon-distribution cladograms," as opposed to "areagrams," *sensu* Swenson et al. 2001).

Atlantic-Track Clades

***Liquidambar* (Hamamelidaceae; Li and Donoghue 1999).** Our analyses, based on a combination of *mat*K (Li et al. 1997), nrDNA ITS, *trn*L intron, and GBSS (*waxy*) sequences (3164 characters; 298 variable, 39 parsimony informative) from four accessions representing four species of *Liquidambar* and one accession each of the outgroups *Mytilaria* and *Exbucklandia* (see Li et al. 1997, 1999*a*, 1999*b*), support the conclusion that the North and Central American species *Liquidambar styraciflua* is more closely related to *Liquidambar orientalis* of Europe and western Asia (bootstrap = 86%) than it is to the eastern Asian species *Liquidambar acalycina* and *Liquidambar formosana* (bootstrap = 100%). These results are consistent with those obtained by Hoey and Parks (1991) based on isozyme data and by Li et al. (1997) based on *mat*K sequences alone. Shi et al. (1998) derived similar results based on ITS sequences, although their analyses also linked the Asian species *Altingia chinensis* and *Semiliquidambar cathayensis* with *L. formosana*.

***Cercis* (Leguminosae; Davis et al. 2001).** A parsimony analysis of combined ITS and *ndh*F sequences (1396 characters; 194 variable, 29 parsimony informative) from 11 accessions (representing six species) of *Cercis* and one accession of an outgroup *Bauhinia faberi* supports a tree in which the two North American species, *Cercis canadensis* of eastern North America and *Cercis occidentalis* from western North America, form a clade with the European and western Asian species, *Cercis siliquastrum* (bootstrap = 93%), to the exclusion of three Chinese species, *Cercis chinensis*, *Cercis gigantae*, and *Cercis chingii*. Within the Europe–North America clade, *C. siliquastrum* may be more closely related to the eastern *C. canadensis* than it is to the western *C. occidentalis*, but support for this conclusion is weak.

Pacific-Track Clades

***Hamamelis* (Hamamelidaceae; Li et al. 2000).** Our analyses of a combination of ITS, *trn*L-F, *mat*K, and GBSS (*waxy*) sequences (3146 characters; 123 variable, 18 parsimony informative) from five accessions representing five species of *Hamamelis* and one accession of an outgroup *Fothergilla major* (Li et al. 1999*a*, 1999*b*) support the conclusion that the three North American species, *Hamamelis virginiana*, *Hamamelis vernalis*, and *Hamamelis mexicana*, form a clade (bootstrap = 98%) that is more closely related to the Japanese species, *Hamamelis japonica* (bootstrap = 83%), than it is to the Chinese species, *Hamamelis mollis*. Wen and Shi (1998) obtained the same basic result (*H. japonica* sister to the North American species; bootstrap = 64%) with a parsimony analysis of ITS sequences alone.

***Weigela-Diervilla* (Diervilleae, Caprifoliaceae; Kim and Kim 1999).** Based on analyses of 21 ITS region sequences (representing 11 species of *Weigela*, three species of *Diervilla*, and three Caprifoliaceae s.s. outgroups) with 51 parsimony-informative characters (621 nucleotide sites, 98 variable), Kim and Kim (1999) found *Weigela* to be paraphyletic. Specifically, *Weigela middendorfiana* and *Weigela maximowiczii* (sections *Calyptrostigma* and *Weigelastrum*, respectively; *sensu* Hara 1983) from Japan appear to be more closely related to the eastern North American *Diervilla* (*Diervilla lonicera*, *Diervilla sessilifolia*, and *Diervilla ribularis*; bootstrap = 99%) than they are to the other species of *Weigela* from China, Korea, and Japan. Bootstrap support for *W. middendorfiana* + *Diervilla* is, however, only 56%, and the association of *W. maximowiczii* with this clade is even less clearly resolved. In connection with estimating splitting times (see below), we reanalyzed the Kim and Kim (1999) data together with other Caprifoliaceae ITS sequences and obtained the same basic results within the *Weigela-Diervilla* clade.

***Triosteum* (Caprifoliaceae; Gould and Donoghue 2000).** An analysis of 11 accessions representing six species of *Triosteum* and seven outgroup accessions from species of *Symphoricarpos*, *Lonicera*, and *Leycesteria* scored for 1522 ITS and GBSS (*waxy*) characters (117 parsimony informative) recovered a clade consisting of the three eastern North American species, *Triosteum aurantiacum*, *Triosteum angustifolium*, and *Triosteum perfoliatum* (bootstrap = 100%), which is sister (bootstrap = 87%) to two Chinese species, *Triosteum himalayanum* and *Triosteum pinnatifidum* (bootstrap = 98%). The Japanese species *Triosteum sinuatum* is sister to the clade containing all of the other species. For the purpose of estimating divergence times (see below), the *Triosteum* ITS data were combined with ITS sequences from other Caprifoliaceae *sensu lato*.

***Buckleya* (Santalaceae; Li et al. 2001*a*).** Our analysis of nine accessions representing five species of *Buckleya* and one accession of the outgroup *Thesium* (see Nickrent et al. 1998), scored for 767 ITS characters (257 variable, 94 parsimony informative), indicates that the eastern North American species *Buckleya distichophylla* is more closely related to the Chinese species *Buckleya graebneriana* (bootstrap = 100%) than it is to a Japanese and Chinese species complex (bootstrap = 100%) consisting of *Buckleya lanceolata* (Japan) and *Buckleya henryi* (China).

***Torreya* (Taxaceae; Li et al. 2001*b*).** Our analysis based on nrDNA ITS nucleotide sequences (1214 aligned nucleotide sites; 225 variable, 184 parsimony informative) obtained from 14 accessions representing seven species of *Torreya* and one accession of the outgroup *Amentotaxus argotaeda* (see Cheng et al. 2000) indicates that all of the Asian species (*Torreya* *fargesii*, *Torreya grandis*, *Torreya jackii*, and *Torreya yunnanensis* from China; *Torreya nucifera* from Japan) form a clade (bootstrap = 75%) that is sister to a lineage containing the two North American species (bootstrap = 95%), *Torreya taxifolia* (Florida and Georgia) and *Torreya californica* (California).

Area Cladograms

Reduced-area cladograms (redundant areas removed) for our two Atlantic-track and five Pacific-track clades are shown in figure 2. The Atlantic-track cladograms for *Liquidambar* and *Cercis* indicate that the North American species are more closely related to the European/western Asian species than they are to the eastern Asian species (fig. 2*a*, 2*b*). In contrast, in the case of the Pacific-track taxa, we have recovered examples of each of the possible relationships among Japan, China, and eastern North America (fig. 2*c*–2*g*). In *Hamamelis* and *Weigela-Diervilla* (fig. 2*c*, 2*d*), eastern North American and Japanese species form a clade exclusive of the Chinese species. In *Triosteum* and *Buckleya* (fig. 2*e*, 2*f*), eastern North America and China are united to the exclusion of Japan. Additionally, in *Torreya* (fig. 2*g*), China and Japan are united to the exclusion of North America.

How can the differences among Pacific-track patterns be explained? Perhaps one of the three phylogenetic patterns correctly reflects a series of vicariance events that also impacted the diversification of the other clades. In this case, one either needs to suppose that there were errors in phylogenetic inference in some cases or that some other factors (e.g., extinction, dispersal, etc.) resulted in apparent incongruence. Errors in phylogenetic inference are certainly possible; although, as noted above, bootstrap support for the key relationships is strong in most cases. If we felt compelled to reconcile the entire set of trees—in effect, choosing among the three patterns—we could attempt to identify one that minimized some quantity, such as the number of extinction and/or dispersal events (see Page and Charleston 1998). In this particular case, however, two of the patterns are equally represented, and, in view of the small sample, any such choice would be unconvincing.

An alternative explanation supposes that the different area relationships reflect dispersal-vicariance events that occurred at different times. For example, the basal Old World–New World split in *Torreya* might reflect an early vicariance event that did not impact the other taxa, perhaps because transcontinental distributions had not yet been established in these groups. Likewise, the other two patterns might reflect responses to vicariance events at later times.

To help distinguish among these alternatives, estimates of the relevant divergence times are needed. If transcontinental divergence estimates were comparable for all of the clades, then reconciliation (yielding a single pattern of relationship among areas) would be a justified goal. In this case, further resolution would require additional relevant area cladograms. If, on the other hand, divergence times differed markedly among clades, then a series of temporally distinct vicariance events that differentially impacted diversification in these groups would be favored. In this case, general patterns might still be identified by comparing area cladograms in which divergence events appeared to be roughly the same age.

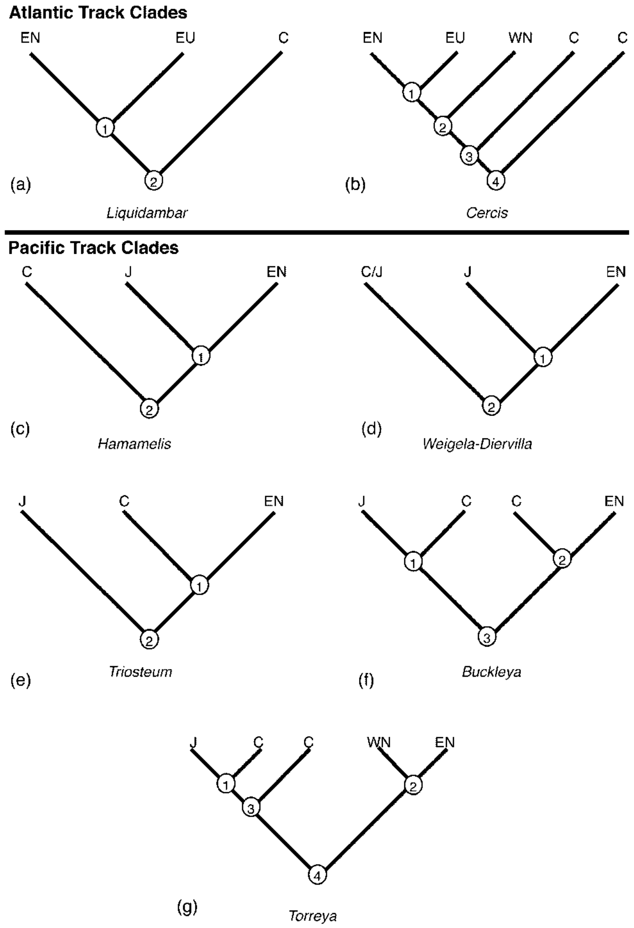

Fig. 2 Reduced-area cladograms (redundant areas omitted) for two Atlantic-track clades and five Pacific-track clades. Age estimates and inferred geographic areas for numbered nodes are given in table 1. *EU* = Europe/western Asia; *C* = China; *J* = Japan/Korea; *WN* = western North America; *EN* = eastern North America.

Estimating Disjunction Times

To estimate the ages of transcontinental disjunctions, we reanalyzed DNA sequence data from the seven studies discussed above, using the reported alignments. To make the best use of fossil information, we analyzed ITS sequences from *Triosteum* and *Weigela-Diervilla* together (see below); sequences in the concatenated data set were readily aligned by eye, and the data set and trees are available in TreeBASE.

Maximum likelihood methods were used to estimate phylogenetic relationships and branch lengths for each of the data sets. All analyses recovered trees that were in agreement with previously published results, which were derived using maximum parsimony. Maximum likelihood searches were conducted with PAUP* 4.0 beta8 (Swofford 2001) using either branch-and-bound or heuristic (TBR branch swapping, 100 random addition replicates) algorithms, depending on the number of taxa.

To determine the best-fitting model of DNA substitution for each data set, a series of hierarchical likelihood ratio tests

(Felsenstein 1981; Goldman 1993) was performed using a program written in PYTHON for the LINUX operating system (Bell 2001). The parameters for the corresponding models were estimated with tree topologies obtained from maximum parsimony analyses. Trees recovered from minimum evolution distance searches and those constructed with the Neighbor-Joining algorithm for a variety of corrected distances (i.e., Jukes-Cantor, logDet paralinear, Kimura 2-parameter) were also used to determine the best-fitting model.

We used trees resulting from maximum likelihood searches to test for rate constancy among lineages (i.e., the presence of a molecular clock) using $2[-\ln L_1 - (-\ln L_0)]$ as a test statistic. This was compared to a χ^2 distribution (with $n-2$ degrees of freedom, where $n =$ number of taxa) to assess significance. When the presence of a clock could not be rejected (*Liquidambar*, *Cercis*, *Hamamelis*, and *Buckleya*), we used branch-length estimates (obtained with maximum likelihood on clock-parameterized trees) as proportional to time to estimate divergence times for clades of interest. When a clock was rejected (P value < 0.05; *Weigela-Diervilla*, *Triosteum*, and *Torreya*), we used Sanderson's (1997) nonparametric rate-smoothing algorithm to estimate divergence times.

To estimate standard errors associated with divergence dates, we used a strategy similar to the three-step procedure of Baldwin and Sanderson (1998). Baldwin and Sanderson (1998) used a nonparametric procedure to estimate the stochastic error caused by having sampled only a finite number of nucleotide characters. We have used a parametric bootstrapping approach as follows: (1) 100 data sets were simulated with the computer software Seq-Gen version 1.2.3 (Rambaut and Grassly 1997); (2) the resulting data sets were imported into PAUP*, and divergence times were estimated on the original tree topology using the sequence model and parameters estimated from the original data; and (3) the resulting branch-length estimates from the simulated data sets were used to calculate the variance in divergence time estimates. These error estimates, thus, reflect the stochastic error associated with the molecular evolution process.

To calibrate rates of molecular evolution, we used fossil data from the literature, when available, to estimate minimum ages for particular clades. For *Buckleya*, where fossils are lacking, we used ITS substitution rates from the literature. The following paragraphs provide further details on age estimates for each clade.

Atlantic-Track Clades

***Liquidambar*.** The *Liquidambar-Altingia* lineage is inferred to have been in existence in the Late Cretaceous, at least 90 million years B.P. (Friis and Crane 1989; Endress and Friis 1991; Zhou et al. 2001). Based on fossil pollen (Muller 1981; Wang 1992) and leaves (Manchester 1999) from the Middle Eocene, which we interpret to be nested within crown *Liquidambar*, we infer that *Liquidambar* itself probably existed by the beginning of the Eocene (ca. 55 million years B.P.). Using these dates and the combined data set of Li and Donoghue (1999), we estimate that the divergence between Eurasian *Liquidambar orientalis* and North American *Liquidambar styraciflua* occurred by 34.99 ± 5.5 million years B.P. This is substantially older than estimates of between 7 and 13 million years B.P. for this split based on isozyme data (Hoey and Parks 1991).

***Cercis*.** Davis et al. (2001) reviewed the fossil record of *Cercis* (see references therein) and calibrated their estimates of divergence times using the oldest reliable fossil, namely fruiting material from the Oligocene (ca. 32 million years B.P.) of Oregon (Manchester and Meyer 1987; Herendeen et al. 1992). By placing this fossil at a range of positions within *Cercis*, they obtained ages for the disjunction between the Eurasian *Cercis siliquatrum* and the eastern North American *Cercis canadensis* ranging from 9.1 to 32 million years B.P. On the basis of its winged fruits and its geographic location, the fossil might best be interpreted as belonging within the crown clade that includes all *Cercis* species except *Cercis chingii* (which has unwinged fruits). Assigning an age of 32 million years B.P. to this node yields an estimate of 15.41 ± 2.3 million years B.P. for the intercontinental disjunction.

Pacific-Track Clades

***Hamamelis*.** Crown Hamamelidaceae, and within it the Hamamelidoideae line, probably existed by the Late Cretaceous (Endress and Friis 1991; Zhou et al. 2001). The clade including *Hamamelis* and the Fothergilleae (Shi et al. 1998; Li et al. 1999*a*, 1999*b*) might also have originated in the Cretaceous but certainly was in existence by the mid-Eocene, judging by fossils that can be assigned with confidence to related clades (*Corylopsis*, *Fortunearia/Sinowilsonia*; Manchester 1999; also see Friis and Crane 1989 for discussion of older fossils less securely assigned to *Disanthus* and *Rhodeoleia*). Fossil leaves have been assigned to *Hamamelis* itself from the Paleocene onward (references in Li et al. 2000), but these are often difficult to distinguish from related groups. If we accept, conservatively, the existence of the *Hamamelis*-Fothergilleae clade by the mid-Eocene (ca. 44 million years B.P.), the split between *Hamamelis japonica* and the North American clade is estimated to have occurred by 18.87 ± 3.7 million years B.P. If the Cretaceous flowers of Endress and Friis (1991) turn out to represent *Hamamelis* itself or if Paleocene or Eocene fossil leaves can be linked to the Japan–New World clade within *Hamamelis* (see Li et al. 2000), then the divergence-time estimate for the intercontinental disjunction would shift farther back in time.

***Weigela-Diervilla* and *Triosteum*.** *Weigela* seeds have been described from several Miocene localities (references in Manchester and Donoghue 1995); fossils of *Triosteum* are unknown. In the context of Dipsacales phylogeny, we can make use of other fossils to establish the age of the most recent common ancestor of these two groups. Morphological and molecular studies of Dipsacales phylogeny (Judd et al. 1994; Backlund and Donoghue 1996; Pyck et al. 1999; M. J. Donoghue, T. Eriksson, P. A. Reeves, and R. G. Olmstead, unpublished data) have recovered three major clades situated near the base of the Caprifoliaceae (*sensu* Judd et al. 1994; M. J. Donoghue, T. Eriksson, P. A. Reeves, and R. G. Olmstead, unpublished data): (1) Caprifolieae, which includes *Triosteum*, *Lonicera*, *Symphoricarpos*, *Leycesteria*, and probably *Heptacodium*; (2) Diervilleae, including *Weigela* and *Diervilla*, and (3) the remainder of the Caprifoliaceae s.l., including the Linnaeeae (*Linnaea*, *Abelia*, *Kolkwitzia*, and *Dipelta*), Morinaceae, Valerianaceae, and Dipsacaceae. Although relationships among these clades have not yet been convincingly resolved, either the Caprifolieae or the Diervilleae are sister to the remaining two lineages. A direct relationship between Caprifolieae and Diervilleae is not supported by the data. *Dipelta* (Linnaeeae) is known from fruits of the Late Eocene of England (Reid and Chandler 1926), and its extinct sister group *Diplodipelta* is found in the Eocene and Miocene of western North America (Manchester and Donoghue 1995). If the split between these two groups occurred by ca. 35 million years B.P., then the basal Dipsacales splitting event must also have occurred before this time, probably before the middle of the Eocene (ca. 44 million years B.P.). This is consistent with reports of fossil pollen of the *Lonicera* type and various leaf fossils from the early Tertiary (reviewed in Manchester and Donoghue 1995). Assigning an age of 44 million years B.P. to the most recent common ancestor of *Weigela-Diervilla* and *Triosteum*, we estimate the intercontinental disjunction in *Weigela-Diervilla* to be 5.19 ± 0.5 million years B.P. and in *Triosteum* to be 10.06 ± 1.5 million years B.P.

Buckleya. Fossils of *Buckleya*, or of closely related plants, are presently unknown. Li et al. (2001*a*) estimated divergence times within *Buckleya* using the slowest known rate of substitution for ITS (from Winteraceae; Suh et al. 1993) and the fastest rate (from *Robinsonia*, Asteraceae; Sang et al. 1995). The slowest rate was dismissed on the grounds that it predicted pre-Cretaceous divergence times for *Buckleya*. The *Robinsonia* rate yielded a split between the Chinese *Buckleya graebneriana* and the eastern North American *Buckleya distichophylla* of ca. 5 million years B.P. Although this might be justified on the grounds that nucleotide substitution rate may be elevated in parasitic and hemiparasitic plants (Nickrent et al. 1998), here we have made a more conservative estimate based on the somewhat slower substitution rate (3.94×10^{-9}) obtained by Sang et al. (1994) for *Dendroseris* (Asteraceae), which is similar to estimates made for *Gossypium* by Wendel et al. (1995). This yields an estimated intercontinental disjunction time of 9.64 ± 1.8 million years B.P.

Torreya. *Torreya* and its sister group *Amentotaxus* (Cheng et al. 2000) are both well known from fossil material. *Torreya* fossils are reported from the middle Jurassic, and *Amentotaxus* fossils are reported from the Late Cretaceous (Florin 1963). If the divergence between these lineages is dated at 165 million years B.P. (Jurassic), the Old World–New World disjunction is estimated at 19.14 ± 3.4 million years B.P. (Li et al. 2001*b*). In view of uncertainty about the identification of Jurassic material, and age estimates for deeper splitting events within Taxaceae (Cheng et al. 2000), we have estimated divergence times based on the assumption that *Torreya* and *Amentotaxus* were separated by the beginning of the Cretaceous, 144 million years B.P. On this basis, we obtain an estimate for the intercontinental disjunction of 16.70 ± 3.0 million years B.P.

Our age estimates are summarized in table 1 and figure 3. It is important to stress that these results depend directly on the assumptions specified above, which are more secure in some cases than in others, and that these are estimates of minimum divergence time (see below). More refined estimates await new fossil material or reinterpretation of existing fossils.

Despite the preliminary nature of this exercise, however, several general results are noteworthy. First, the prediction that intercontinental disjunctions are older in Atlantic-track taxa than those in Pacific-track taxa is only partially corroborated. Our estimated intercontinental disjunction times for *Liquidambar* and *Cercis* differ considerably, and the divergence in *Cercis* is more similar to several Pacific-track taxa (see further discussion below). Second, our Pacific-track clades show a wide range of minimum divergence times, from ca. 5 million years B.P. (in *Weigela-Diervilla*) to more than 18 million years B.P. (in *Hamamelis*). Third, there is wide variation in timing even within particular Pacific-track phylogenetic patterns (fig. 3). Thus, within the (China(Japan,E.N.A.)) pattern, the Old World–New World split is estimated at over 18 million years B.P. for *Hamamelis* and at only ca. 5 million years B.P. for *Weigela-Diervilla*. We see the same area relations in *Viburnum* section *Pseudotinus* (M. J. Donoghue and J. Li, unpublished data) but with almost no ITS nucleotide differences between the Japanese *Viburnum furcatum* and the eastern North American *Viburnum lantanoides*. This implies an even more recent intercontinental disjunction. In contrast, in our two representatives of the (Japan(China,E.N.A.)) pattern, *Triosteum* and *Buckleya*, the minimum times for intercontinental disjunction are estimated at around 10 million years B.P., implying that vicariance in these taxa may have been caused by the same factors. Finally, the split in *Torreya*, with the (N.A.(Japan, China)) pattern, is estimated around 17 million years B.P. Although no pattern comparable to *Torreya* exists among the clades discussed here, our preliminary study of *Stewartia* (J. Li, P. Del Tredici, S. Yang, and M. J. Donoghue, unpublished data) shows similar area relationships and an Old World–New World split during the same general time period. Xiang et al. (1998*b*, 2000) have estimated much more recent divergence times for several groups with this phylogenetic pattern.

In general, our results are similar to those of Xiang et al. (2000), who used a substitution rate for *rbc*L sequences calibrated by fossils in *Cornus*, in that we see a significant range of intercontinental disjunction times across clades (also see table 2 in Wen 1999). However, Xiang et al. (2000) reported several intercontinental divergence times much younger than we have found in our analyses (e.g., *Menispermum*, at less than 1 million years B.P.). In fact, in most of their taxa, disjunctions are estimated in the Pliocene, with an average age of ca. 5 million years B.P. With the exception of *Weigela-Diervilla*, at ca. 5 million years B.P., our taxa show older splitting times than reported by Xiang et al. (except for their estimate for *Pachysandra* at ca. 12 million years B.P.). Taking all of these analyses together, we see a range from less than 1 to more than 18 million years B.P. This, we believe, implies response in different clades to vicariance events at a number of different times during the Tertiary and especially during the Neogene. As predicted, intercontinental splits in the Pacific-track taxa appear to be too young (taking our minimum-age estimates at face value) for the North Atlantic dispersion pathway to be relevant. Beringian dispersion appears more likely.

Finally, the observation of a wide range of divergence times for taxa showing the same area relationships implies that there are instances of pseudocongruence (Cunningham and Collins 1994). Just as interestingly, we also see the inverse. That is, during the same general time period, we find taxa exhibiting different area relationships. For example, despite differences

Table 1

Age Estimates and DIVA Inferences for Area Cladograms in Figure 2

Clade/node	Estimated divergence times (million years B.P.)	DIVA reconstructions (unconstrained)	DIVA reconstructions (constrained)
Liquidambar:			
1	34.99 ± 5.5	EN-EU	EN-EU
2	55*	EN-EU-C	EN-C, EU-C
Cercis:			
1	15.41 ± 2.3	EN-EU	EN-EU
2	15.42 ± 3.1	EN-EU-WN	EU-WN, EN-WN
3	32*	EN-EU-WN-C	WN-C, EU-C, EN-C
4	46.39 ± 9.6	EN-EU-WN-C	C, WN-C, EU-C, EN-C
Hamamelis:			
1	18.87 ± 3.7	J-EN	J-EN
2	23.32 ± 4.6	C-J-EN	C-J, C-EN
Weigela-Diervilla:			
1	5.19 ± 0.5	J-EN	J-EN
2	6.94 ± 1.2	C-J-EN	C-J, C-EN
Triosteum:			
1	10.06 ± 1.5	C-EN	C-EN
2	17.67 ± 3.2	C-J-EN	C-J, J-NE
Buckleya:			
1	5.84 ± 0.6	C-J	C-J
2	9.64 ± 1.8	C-EN	C-EN
3	23.85 ± 5.1	C, J-EN, C-J-EN	C
Torreya:			
1	7.63 ± 0.9	C-J	C-J
2	7.19 ± 0.9	EN-WN	WN-EN
3	8.90 ± 1.0	C	C
4	16.70 ± 3.0	C-WN-EN, J-WN-EN, C-J-WN-EN	C-WN, C-EN

Note. Estimated divergence dates for intercontinental disjunctions are underlined; underlined DIVA reconstructions contain geographically adjacent areas (see text). * = fossil calibration; EU = Europe; C = China; J = Japan; EN = eastern North America; WN = western North America.

in phylogenetic pattern, divergence estimates overlap for *Hamamelis* and *Torreya* in the 15–18 million years B.P. interval.

Historical Scenarios

How can these evidently complex findings be accounted for? One possibility is that the seemingly chaotic situation reflects a series of independent, uncoordinated, long-distance dispersal events. Alternatively, a series of vicariance events, from the mid-Tertiary onward, may have impacted different plant lineages in different ways. To explore the latter possibility, we reconstructed ancestral areas for each area cladogram, using Ronquist's dispersal-vicariance approach (Ronquist 1997) as implemented in DIVA (Ronquist 1996).

The results of our DIVA analyses are summarized in table 1, showing inferred areas for the numbered nodes in figure 2, along with our age estimates for each splitting event. Several DIVA analyses were conducted, differing in the constraints imposed. In all cases, we used DIVA's default event costs: 0 for vicariance and 1 for each inferred dispersal or extinction event. In our initial analyses (table 1, "unconstrained"), areas were inferred without inclusion of outgroup-area information and without constraints on the number of areas inferred at internal nodes. In this case, DIVA inferred the basal node to be widespread, as anticipated (Ronquist 1996, 1997). For each of the taxa under consideration here, outgroups are most likely distributed in China. Adding this information to our analyses yielded results identical to those obtained without outgroups. On the grounds that none of the modern species are distributed across multiple areas of endemism, a third DIVA analysis used the "maxareas" option to restrict the number of inferred areas at internal nodes (as suggested by Ronquist 1996, 1997), in this case to two areas (table 1, "constrained"). Finally, to further eliminate ambiguity, we chose to focus discussion (see below) on those two-area reconstructions in which areas are geographically adjacent to one another (underlined in table 1). For example, we preferred China-Japan (C-J), which are adjacent in Asia, over China–eastern North America (C-EN). This last approach is not supported in DIVA, though it might be implemented by treating areas as an ordered set of states in a DIVA three-dimensional cost matrix (cf. Ronquist 1998).

In the remainder of this section, we consider possible historical scenarios to account for our area cladograms, age estimates, and DIVA ancestral area inferences. In doing so, our aim is not so much to account for the specifics in our own data, which we think are too limited at this stage to deserve a more detailed analysis. Instead, on the view that our findings are representative of those that will accumulate as other clades

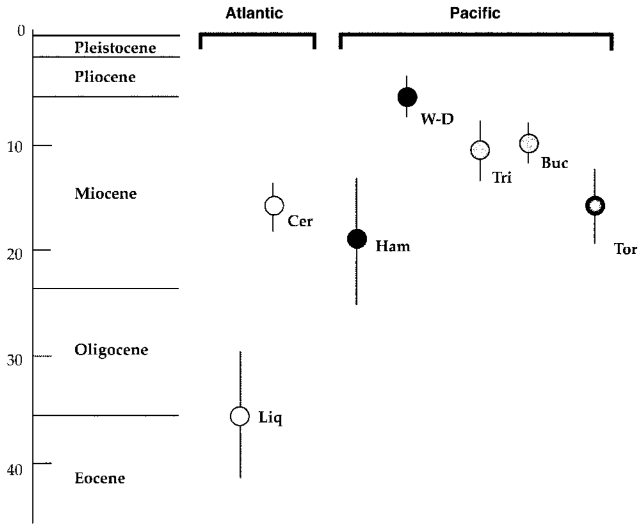

Fig. 3 Estimated divergence times for seven taxa discussed in the text (see fig. 2; table 1) plotted against Tertiary time in millions of years B.P. Atlantic-track taxa: *Liq* = *Liquidambar*; *Cer* = *Cercis*. Pacific-track taxa: *Ham* = *Hamamelis*; *W-D* = *Weigela-Diervilla*; *Tri* = *Triosteum*; *Buc* = *Buckleya*; *Tor* = *Torreya*. Dot shading indicates phylogenetic pattern: open = C(EU,EN); black = C(J,EN); gray = J(C,EN); stippled = (C,J)EN.

are studied in detail, our aim is only to highlight the processes that might account for such patterns.

Atlantic-Track Clades

For *Liquidambar*, it would be reasonable to postulate dispersion along the North Tethys during the Eocene (Tiffney 1985*a*), followed by differentiation between Chinese and Eurasian/North American forms, and then divergence between the European and the North American species by the Early Oligocene. In contrast, although *Cercis* may have been widespread around the Northern Hemisphere by the beginning of the Oligocene, we infer that differentiation between the Chinese and the European/North American species did not occur until the Miocene. Likewise, the split in *Cercis* between the European and North American species occurred much later than in *Liquidambar* (fig. 3), implying either continued exchange across the North Atlantic or extinction and long-distance dispersal between eastern North America and Europe. Although geological and climatological reconstructions argue against North Atlantic dispersion for most plants after the Eocene, Tiffney (2000; also see Manchester 1999) highlighted similarities between the biotas of Europe and eastern North America during the Oligocene and Miocene and the possibility of continued exchange into the Miocene for plants that could tolerate higher-latitude climates. Tiffney (2000) further suggested that such exchange may have been most likely from east to west (with the prevailing winds) for plants with wind-dispersed fruits. This might apply to *Cercis* (see Davis et al. 2001).

Studies of other possible Atlantic-track taxa are needed to test whether disjunctions between Europe and North America were rare or common into the Miocene and whether there are life-history or dispersal correlates of the *Cercis* pattern. Alternatively, it may emerge that some modern Atlantic-track distributions were established partly via Beringian dispersion. For *Cercis*, this possibility is suggested by some of the constrained DIVA optimizations.

Pacific-Track Clades

Two of the patterns—C(J,EN) and J(C,EN)—suggest some diversification within Asia prior to the Old World–New World split. Our constrained DIVA analyses are consistent with the genesis of these two patterns as illustrated in figure 4, where panels *a*, *b*, *c*, and *d* show a sequence of events resulting in C(J,EN), and panels *a*, *b*, *e*, and *f* yield J(C,EN). These patterns are similar in envisioning differentiation within Asia between a more southern and western Chinese species and a more northern and eastern Japanese, Korean, and northeastern Chinese species. They also both involve vicariance through Beringia, probably in response to a climate shift that eliminated northern and western North American populations. They differ in whether dispersion through Beringia involved the Japanese/Korean species (fig. 4*c*) or the Chinese species (fig. 4*e*).

Our age estimates appear to rule out the possibility that the two different phylogenetic patterns reflect vicariance events that occurred at two different time periods. Although the J(C,EN) pattern seen in *Triosteum* and *Buckleya* could reflect response to a single vicariance event, the C(J,EN) pattern appears to have been established at quite different times in *Hamamelis* and in *Weigela-Diervilla*. In this case, at least, the data suggest iterated dispersion/vicariance through Beringia of a Japanese/Korean species. Although we do not see evidence in our present data set of the C(J,EN) and the J(C,EN) pattern being established during the same time period (i.e., fig. 4*c* and 4*e* occurring more or less simultaneously), we see no reason why this could not happen and expect such examples to be recovered in future studies.

To account for the *Torreya* pattern—(C,J)(WN,EN)—and similar patterns reported by Xiang et al. (1998*b*, 2000), dispersion and vicariance through Beringia may have occurred first, before diversification within either the Old World or the New World. In *Torreya*, we infer that dispersion occurred in the same general time period as it did in *Hamamelis* (and *Cercis*), but it should be clear that this pattern could also have originated at other times, whenever climate shifts allowed dispersion.

Although the Pacific-track events that we have just outlined may seem complex, they reduce to a fairly simple general process. Beringian vicariance events are envisioned during several different time periods, acting on geographic distributions attained in different ways and at different times in different clades. The idea of iterative dispersion and vicariance through Beringia recalls the "East of Eden" hypothesis (or, perhaps more intuitively, what might be called the "out of Asia" hypothesis) developed by Beard (1998) to explain area cladograms for a variety of placental mammal clades. Although our models are similar in structure, it is important to appreciate that Beard's (1998) examples involve earlier time periods (late Paleocene to early Eocene). Taken together, our findings suggest that geological and climatic shifts have promoted repeated episodes of biotic interchange and isolation between Asia and North America throughout the Tertiary. For the plant groups

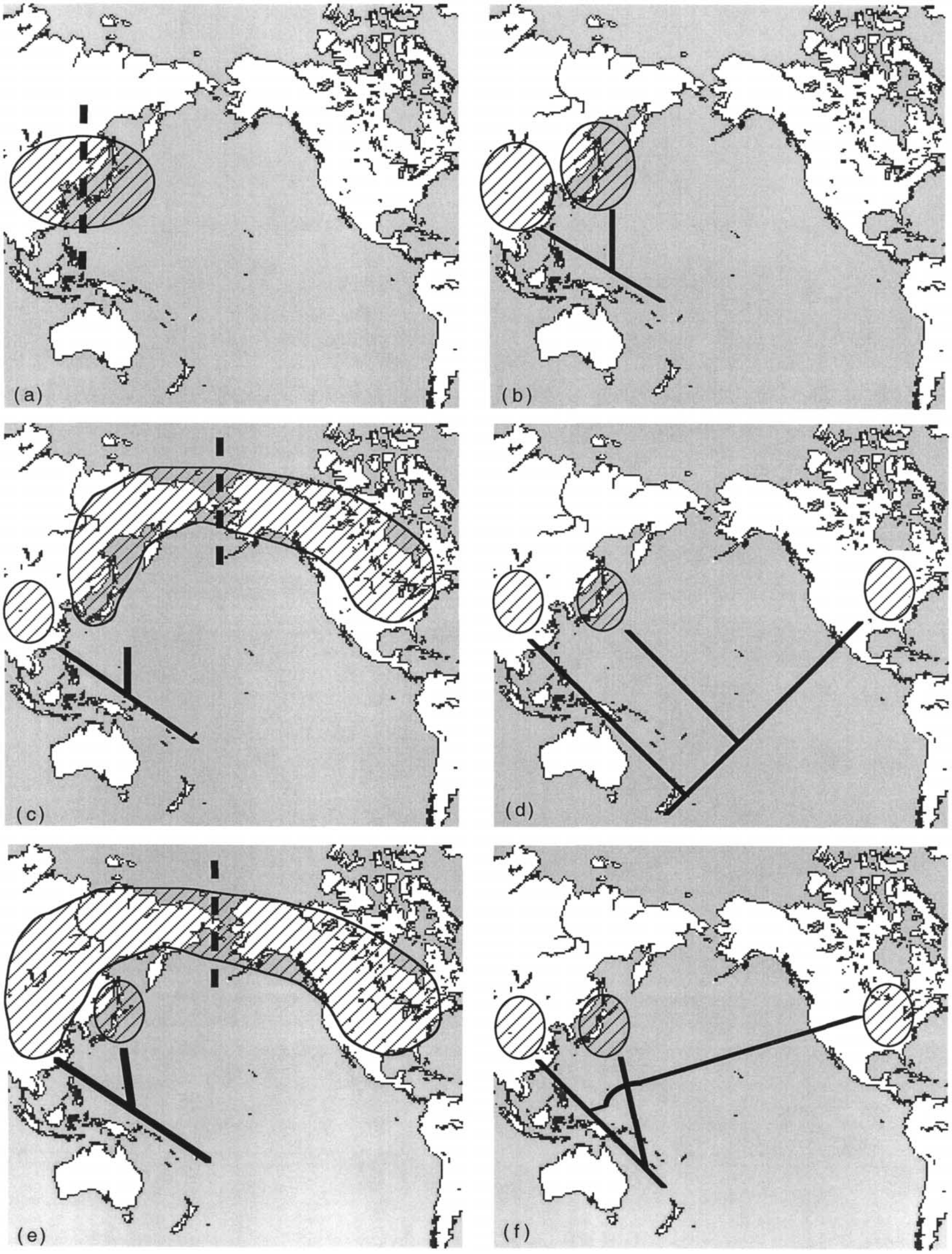

Fig. 4 Hypothetical events yielding area cladograms C(J,EN) and J(C,EN). Both sequences begin with diversification within Asia (*a*, *b*). Dispersion and vicariance involving a Japanese species results in C(J,EN) (*c*, *d*). Dispersion and vicariance involving a Chinese species results in J(C,EN) (*e*, *f*). Dispersion and vicariance may or may not have occurred at the same time in *a*, *c*, and *e*.

we have considered, and those discussed by Xiang et al. (1998*b*, 2000), the relevant time period appears to be from the Oligocene onward and, even more importantly, from the Miocene. However, we would not be surprised if other lineages showed even earlier connections. Similarly, we anticipate the discovery of more recent interchanges in mammals and other animal groups.

Discussion and Conclusions

The seven phylogenetic studies summarized here demonstrate a wide range of relationships among major areas of endemism around the Northern Hemisphere. The two Atlantic-track taxa are similar in that the European and North American species are more closely related to one another than they are to the Asian species. However, only the age estimates for *Liquidambar* are readily accommodated by prevailing ideas on the availability of the North Atlantic dispersion pathway. Among the Pacific-track clades, we have recovered examples of each of the possible relationships involving China, Japan, and eastern North America. Furthermore, and consistent with previous findings (Xiang et al. 1998*b*, 2000), our age estimates indicate significant variation within and among the phylogenetic patterns, with Old World–New World divergence times occurring from the early Miocene to the Pliocene. These results confirm the expectation based on geological, climatological, and paleoecological evidence that the history of the Northern Hemisphere has been complex, with repeated shifts in the factors responsible for vicariance. They also highlight the possibility, for both the Atlantic and Pacific tracks, of significant intercontinental exchange occurring more recently than is often implied in the paleontological literature.

We note that although theoretical and empirical vicariance biogeographic studies have tended to downplay knowledge of the absolute timing of divergence events (e.g., note the lack of discussion in recent reviews, such as Morrone and Crisci 1995 and Humphries and Parenti 1999), we believe that such information is crucial (also see Grande 1985; Sanmartin et al. 2001). This is especially the case where, as in the Northern Hemisphere, diversification in different clades appears to have spanned a long and repeating series of vicariance events. In future studies, we hope it will be possible to sort clades into categories for comparison based directly on age estimates, as opposed to the initial sorting done here on the basis of geographical tracks, which evidently provides too rough of a surrogate for actual ages. We also look forward to the development of better methods to identify general patterns across sets of area cladograms for which age estimates have been made (for a start along these lines, see Sanmartin et al. 2001).

It is important to stress, however, that conclusions about timing rest directly on the accuracy of estimated ages. Methods for estimating divergence times have, fortunately, received renewed attention (e.g., see Sanderson 1997, 1998; Huelsenbeck et al. 2000), but there is much work to be done. In the present context, it is critical to bear in mind that we are estimating minimum divergence times, which means that actual splitting events might have occurred well before the estimated ages. While a maximum bound can confidently be set in some cases by reference to well-documented Earth history events (e.g., we might reject estimated ages for angiosperm clades that predate evidence of life on land), in practice this relies on extension over long time periods of locally estimated rates of molecular evolution. Our experiments with such an approach are somewhat troubling. Even when a molecular clock cannot be rejected, we have sometimes found that realistic placement of a well-studied fossil yields rates of evolution that, when extended backward in time, lead to unrealistically old branching events. For example, placement of the *Cercis* fossil at any node in the *Cercis* tree implies pre-Cretaceous origination for the major lineages of legumes (also see Davis et al., 2001). This problem may be quite general (e.g., conflicts involving the Cambrian explosion and the timing of the evolution of birds and mammals; see Cooper and Fortey 1998) and could indicate significant changes in the rate of molecular evolution associated with the radiation of major clades.

Although our results rule out any simple explanation, we remain optimistic about achieving a coherent historical account for all of the evidence. As we have shown, a scenario involving initial diversification within Asia, followed by iterated episodes of migration and vicariance, can bring order to a pattern that initially appears chaotic. Testing this model, and establishing the number and timing of dispersal-vicariance episodes, will require many additional phylogenetic studies of taxa with species endemic to the relevant areas. Fortunately, there are many appropriate clades remaining to be examined (e.g., see Li 1952; Wen 1999), many of which also have a fossil record (e.g., see Manchester 1999).

With respect to evaluating such scenarios, however, it will be especially important to bear in mind the possible impacts of extinction. For example, although we have highlighted the idea of some diversification taking place within Asia before dispersion to the New World, it is possible that the relevant phylogenetic patterns instead reflect undetected extinction of the New World representatives of basal clades. Clearly, the most compelling results will be obtained when a reasonable fossil record exists and when fossil species can be placed with confidence in a phylogenetic context.

Finally, our studies highlight limitations in our knowledge of potential vicariance events, especially within Asia over the last 30 million years. More detailed geographic range maps are also badly needed, especially for Asian species, as these, in the context of GIS analyses, should allow a far more sophisticated decomposition of different patterns. So, for example, we are hopeful that alternative tracks will be distinguishable through detailed comparisons of current geographic ranges (cf. the method of Tiffney 1994). In eastern North America, the more northern and high-elevation distributions (e.g., extending down the Appalachians) may imply more recent arrival through Beringia, whereas the more southern, lower-elevation patterns (e.g., on the piedmont and coastal plain of the southern United States) may indicate older North Atlantic dispersion. Likewise, it may be possible to document geographic and ecological correlates of dispersion-vicariance episodes at different times, with some periods allowing migration of plants with a wide range of life forms and tolerances and some accommodating a much more limited set.

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