

DISPERSAL-VICARIANCE ANALYSES OF INTERCONTINENTAL DISJUNCTS: HISTORICAL BIOGEOGRAPHICAL IMPLICATIONS FOR ANGIOSPERMS IN THE NORTHERN HEMISPHERE

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Ten North Temperate taxa representing diverse angiosperm lineages were analyzed for biogeographic histories using the dispersal-vicariance analysis method to gain insights into the origin and evolution of disjunct distributions in the Northern Hemisphere. Results indicate four general biogeographic patterns: (1) origin and speciation in eastern Asia with subsequent expansion into North America and/or Europe (e.g., *Aralia* sect. *Aralia*, *Symplocarpus*, and possibly *Asarum*, *Aesculus*, and *Chrysosplenium*); (2) origin in eastern Asia and western North America with subsequent spread into eastern North America (e.g., *Calycanthus* and *Boykinia*); (3) a disjunct origin in eastern Asia and eastern North America with subsequent dispersal from eastern Asia into eastern North America (e.g., *Panax*); and (4) a widespread origin in the Northern Hemisphere with subsequent fragmentation by intercontinental vicariance (e.g., *Cornus* and *Trautvetteria*). Although there are caveats, the results indicate that the disjunct distributions of angiosperm lineages in the Northern Hemisphere cannot be explained with a simple vicariance model. Most lineages may have been restricted ancestrally to one or two adjacent areas and then secondarily expanded their ranges via dispersal. A noteworthy finding was the one-way intercontinental plant exchange from the Old World to the New World and biased dispersal within each continent. There was more dispersal from the west to the east in North America but more dispersal from the east to the west in Eurasia. Such asymmetrical dispersal has also been documented in animals. The results also indicate that eastern Asia and western North America were the centers of origin for a majority of lineages examined, implying that these two areas were important sources of temperate angiosperm evolution in the Northern Hemisphere. The results further support a complex evolutionary history of angiosperms in the Northern Hemisphere and suggest pseudocongruence among lineages in phylogenetic relationships and distributional patterns.

Keywords: angiosperms, biogeography, disjunction, dispersal, vicariance.

Introduction

A striking characteristic of angiosperm biogeography in the Northern Hemisphere is the intercontinental disjunct distributions of closely related species (Thorne 1972; Raven and Axelrod 1974). Numerous temperate angiosperm genera exhibit a disjunct distributional pattern in two or more of the following areas: eastern Asia, eastern North America, western North America, western Asia, and southeastern Europe (Wood 1972; Wu 1983; Wen 1999), with the eastern Asian–eastern North American disjunction most prominent. The origin and evolution of this phytogeographic pattern has puzzled botanists for centuries (see Graham 1972; Boufford and Spongberg 1983; and reviews in Wen 1999, 2001; Tiffney and Manchester 2001). Modern consensus considers the disjunctions of temperate taxa in the Northern Hemisphere the result of range restriction of a once more widely distributed ancient flora, the mixed mesophytic forest (e.g., Li 1952; see Wood 1971, 1972; Graham 1972; Wolfe 1975; Tiffney 1985a, 1985b) descended

from the “boreotropical flora” (Wolfe 1975; Tiffney 1985a, 1985b).

The boreotropical flora was hypothesized to consist of taxa originating from several different centers at different latitudes that spread quickly to occupy the two continents via the North Atlantic Land Bridge, the Bering Strait, and the Tethys Sea Way (Wolfe 1975; Tiffney 1985a). This boreotropical flora was later gradually shaped into a mixed mesophytic forest by subsequent climatic fluctuation in the later Oligocene and Miocene via diversification of cool-adapted taxa that were selected from the boreotropical flora or that evolved during this period (Leopold and MacGinitie 1972; Wolfe 1975; Tiffney 1985a). This mixed mesophytic forest was once more or less continuously distributed throughout the Northern Hemisphere and was subsequently fragmented due to the extreme cooling of climate in the later Tertiary (the late Miocene and Pliocene) and Quaternary and the development of grassland in central North America resulting from the uplift of the Rocky Mountains. Thus, the floristic elements displaying the various disjunct distributions in temperate regions of the Northern Hemisphere represent relicts of the mixed mesophytic forest community now surviving in only a few “refugia,” including eastern Asia,

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southeastern Europe and western Asia, western Europe, eastern North America, and western North America.

This concept of a boreotropical flora and hypothesized range reduction of the mixed mesophytic forest implies a complex history of the North Temperate flora. This hypothesis is considered likely by most modern authors and is supported by several lines of evidence (Li 1952, 1972; Graham 1972; Leopold and MacGinitie 1972; Wood 1972; Tiffney 1985*a*, 1985*b*; Manchester 1999; Wen 1999). For example, fossil evidence suggests that families containing lineages showing disjunct distributions in eastern Asia and eastern North America evolved in different geological times, and many disjunct taxa had a wider distributional range in the past than are observed today (Tiffney 1985*a*, 1985*b*; Manchester 1999). This vicariance-based hypothesis implies an origin of the disjunct lineages and a wide distribution of their ancestors in the Northern Hemisphere before the Late Miocene. Furthermore, it implies a time of isolation of sister taxa in the Late Miocene or later.

Although the time of origin and ancestral distributions of most lineages are unknown, the prediction of this hypothesis for the time of isolation of sister taxa appears to be congruent with most recent molecular estimates of divergence times of isolated sister species (e.g., species pairs in eastern Asia and eastern North America; Xiang et al. 1998*b*, 2000; also see Qiu et al. 1995; Donoghue et al. 2000; Li et al. 2000). Exceptions included a few lineages mostly found in three or more unit areas that have multiple divergent species in one or more areas (i.e., *Aralia* sect. *Aralia*, *Aesculus*, *Pachysandra*, and *Cornus*). In these lineages, the sister taxa in isolated areas diverged earlier in the Tertiary, according to molecular data (Wen et al. 1998; Xiang et al. 1998*a*, 1998*b*, 2000). These results suggest that the climate cooling and the development of grassland in central North America during the later Tertiary and Quaternary were the causes for the disjunction of many, but not all, of the temperate taxa in the Northern Hemisphere. Other historical events occurring in the earlier Tertiary might have caused the disjunction of other taxa. These earlier events may have especially affected those older lineages that later diverged into multiple species and now occupy more widespread areas. In addition, long-distance dispersal may have been responsible for the disjunct distribution of some lineages with recently diverged sister species (see Qiu et al. 1995; Xiang et al. 2000). This evidence indicates that areas of the Northern Hemisphere have complex histories, and the disjunct patterns of temperate taxa observed today are more complex in their origins than previously thought. This conclusion is further supported by evidence from phylogenetic analyses, which revealed that not all taxa exhibiting the same disjunct pattern share a congruent phylogenetic pattern, and some taxa showing congruent phylogenetic and distributional patterns may represent pseudocongruence (Hafner and Nadler 1990; Page 1990, 1991; Cunningham and Collins 1994; Wen et al. 1996*b*; Xiang et al. 1998*b*; Wen 1999). It is clear that all available evidence supports a more complex nature of the floristic disjunctions of angiosperms in the Northern Hemisphere than previously envisioned in the simple vicariance-based hypothesis. However, for most individual taxa displaying the disjunctions, the biogeographic history, such as the time and place of origin and the migration route used to obtain a distribution in the two continents, has remained uncertain. It is also unclear whether

only vicariance has been involved in the disjunction of all taxa. Did all lineages have a wide ancestral distribution before they diverged into different species found in isolated unit areas as hypothesized based on the vicariance model? If dispersal was involved, what is the relative timing of the vicariant and dispersal events? Further studies are needed to answer these questions before the biogeographic history of angiosperms in the Northern Hemisphere may be clearly understood.

We reconstructed the biogeographic histories of 10 temperate taxa (including both deciduous woody and perennial herbaceous taxa) showing intercontinental disjunctions in the Northern Hemisphere using a phylogenetic framework and the method of dispersal-vicariance analysis (Ronquist 1996, 1997). Our goals are several: (1) evaluate whether vicariance and dispersal have been involved in the formation of present-day disjunct distributions, (2) infer the geographic center of origin of a disjunct lineage, (3) infer the migration routes and direction of migration, and (4) identify possible historical events associated with the disjunctions.

Material and Methods

Various analytical biogeographic methods have been available for assessing the likelihood of alternative biogeographic hypotheses (see reviews in Morrone and Crisci 1995). However, most of the biogeographic methods used today are based on the search for a single branching relationship among areas of endemism (i.e., area cladogram) (see Morrone and Crisci 1995). Although area cladograms allow the testing of hypotheses of general patterns, the fundamental assumption of a single hierarchical relationship among areas can be easily violated given that areas may have multiple histories and reticulate relationships. In addition, most methods available either do not treat dispersal and extinction explicitly or treat them unsatisfactorily (see Morrone and Crisci 1995; Ronquist 1996, 1997). To overcome these problems, Ronquist (1997) and Hovenkamp (1997) proposed two alternative methods that are event-based and do not rely on area cladograms (i.e., do not require an analogy between taxa and areas). However, Hovenkamp's (1997) method considers only vicariance to resolve biogeographic history, whereas the method of Ronquist, dispersal-vicariance analysis (DIVA), considers not only vicariance but also dispersal and extinction.

DIVA reconstructs ancestral distributions in a given phylogeny without any prior assumptions about area relationships and treats dispersal and extinction explicitly (Ronquist 1996, 1997). The method searches for the optimal reconstruction of ancestral distributions by assuming a vicariant explanation (i.e., allopatric speciation) but incorporating the potential contribution of dispersal and extinction in shaping the current distributional pattern. The optimal solutions are those that minimize dispersal and extinction events under a parsimony criterion. According to Ronquist (1996), one of the advantages of DIVA is that it does not restrict widespread distributions to terminals or force ancestral distributions to single areas as do other parsimony-based algorithms (e.g., Fitch optimization). In addition, DIVA estimates the direction of dispersal events and provides more parsimonious solutions than cladistic biogeographic methods (Ronquist 1996, 1997). It is useful for examining individual taxon biogeography and also for testing

hypotheses about general biogeographic events among lineages occurring in the same set of unit areas (Ronquist 1996; Sanmartin et al. 2001). Given these advantages of DIVA, we applied this method to study long-standing problems of biogeographic history of angiosperms in the Northern Hemisphere.

We chose 10 taxa for which strongly supported and well-resolved molecular phylogenies are available (table 1). These taxa represent diverse angiosperm lineages and exhibit different disjunct patterns. *Symplocarpus* (Araceae) and *Panax* (Araliaceae) represent the eastern Asian–eastern North American disjunction; *Aralia* sect. *Aralia* (Araliaceae), *Boykinia* (Saxifragaceae), the big-bracted dogwoods (*Cornus* subg. *Cynoxylon*, subg. *Syncarpea*) (Cornaceae), *Calycanthus* (Calycanthaceae), and *Trautvetteria* (Ranunculaceae) represent the eastern Asian–eastern North American–western North American disjunction; and *Aesculus* (Hippocastanaceae), *Asarum* s.s. (Aristolochiaceae), and one lineage of *Chrysosplenium* (Saxifragaceae) represent the eastern Asian–eastern North American–western North American–European disjunction.

For each lineage, the trees derived from previous phylogenetic studies were used as the framework for the reconstruction of optimal ancestral distributions using DIVA 1.1 (Ronquist 1996, 1997; <http://www.ebc.uu.se/systzoo/research/diva/diva.html>). Six unit areas were defined to cover distributions of all lineages and their outgroups: eastern Asia (A), eastern North America (B), western North America (C), Central America (D), southeastern Europe (E), and South America (F). A species was coded for presence or absence in each unit area of the genus distribution. Outgroups have an important impact on DIVA optimization. For each genus, we therefore chose outgroups based on the results of broad phylogenetic analyses that included the disjunct lineages and their close relatives. The sister taxa or sometimes a few successive sister lineages of the disjunct lineage in question were chosen as the outgroups. The selected outgroups were generally the same as those used in previous phylogenetic analyses. The distributions of outgroups were determined from previous phylogenetic studies and information in the literature (e.g., Mabblerley 1997).

For taxa occurring in three or fewer areas, we conducted the analyses without imposing a constraint on the number of areas allowed for an ancestral distribution. For taxa occurring

in four areas (e.g., *Asarum* s.s., *Aesculus*, and one lineage of *Chrysosplenium*), we performed the analyses in several different ways: without constraint on the number of unit areas in the ancestral distribution and with constraints on the number of unit areas set to four, three, or two. The “maxareas” option of the “optimize” command in DIVA was used to impose this constraint on number of unit areas allowed in ancestral distributions.

Ideally, fossil species of each lineage should be added to the phylogenetic framework for accurate optimizations. However, for the lineages we examined, there either are no fossils or the exact relationships of fossils to extant species is uncertain. Because of this limitation, we did not include fossils in the analyses.

Results

The Eastern Asian–Eastern North American Disjunct Pattern

Panax. The optimal solution of DIVA indicates that the ancestor of *Panax* was distributed in eastern Asia and eastern North America. Thus, the ancestor of *Panax* either evolved in eastern Asia and subsequently dispersed into eastern North America or vice versa. Alternatively, the ancestor was first more widely distributed in the Northern Hemisphere but later became extinct in Europe or in western North America or both. Two independent vicariant events fragmenting eastern Asia and eastern North America, with an intervening dispersal event from eastern Asia to eastern North America, were involved in the disjunct pattern (fig. 1a).

Symplocarpus. Three alternative optimal solutions were obtained for the genus *Symplocarpus* (fig. 1b). The ancestral area of *Symplocarpus* was suggested to be either eastern Asia or both eastern Asia and eastern North America. The latter hypothesis requires the extinction of the ancestor in either Europe or western North America or a prior long-distance dispersal of the ancestor from one area to the other. Thus, an ancestral distribution in eastern Asia is more likely. Based on this solution, the genus first diverged into two lineages in eastern Asia; one of them spread into eastern North America. A

Table 1

Distributional Patterns and Sources of Phylogenies of 10 Taxa Included in the Biogeographic Analysis

Disjunct pattern	Taxa	Family	Phylogenetic study
A, B	<i>Panax</i> L.	Araliaceae	Wen and Zimmer 1996: ITS
A, B	<i>Symplocarpus</i> Salisb. ex W. Barton	Araceae	Wen et al. 1996a: cpDNA R.S.
A, B, C	<i>Aralia</i> sect. <i>Aralia</i> Wen	Araliaceae	Wen et al. 1998: ITS
A, B, C	<i>Boykinia</i> Nutt.	Saxifragaceae	Xiang et al. 1998b: ITS
A, B, C	<i>Calycanthus</i> Schumann.	Calycanthaceae	Wen et al. 1996b: cpDNA R.S.
A, B, C, D	<i>Cornus</i> subg. <i>Cynoxylon</i> Raf., <i>C.</i> subg. <i>Syncarpea</i> (Nakai) Xiang	Cornaceae	Xiang et al. 1996: cpDNA R.S.
A, B, C	<i>Trautvetteria</i> Fischer & C. Meyer	Ranunculaceae	Xiang et al. 1998b: ITS, <i>matK</i>
A, B, C, E	<i>Asarum</i> L.	Aristolochiaceae	Kelly 1998: ITS, morphology
A, B, C, E	<i>Aesculus</i> L.	Hippocastanaceae	Xiang et al. 1998a: ITS
A, B, C, E, F	<i>Chrysosplenium</i> L.	Saxifragaceae	Soltis et al. 2001: <i>matK</i>

Note. A = eastern Asia, B = eastern North America, C = western North America, D = Central America, E = Europe, and F = South America.

subsequent vicariance fragmented the lineage into eastern Asian and eastern North American parts.

The Eastern Asian–Eastern North American–Western North American Disjunct Pattern

Aralia sect. Aralia. The optimal solution suggested eastern Asia as the ancestral area of *Aralia* sect. *Aralia*. The lineage first diverged into two sublineages in eastern Asia, with one of the two subsequently spreading into western North America, which later became fragmented by a vicariant event separating eastern Asian and western North American floras. The clade in western North America subsequently spread eastward into eastern North America and later became isolated in eastern and western North America by a vicariant event. At least two vicariance and two dispersal events were involved (fig. 1c).

Boykinia and Calycanthus. The ancestral distributions of both *Boykinia* and *Calycanthus* were suggested to be eastern Asia and western North America. A vicariant event fragmented the geographic range of the ancestor of each genus into two portions, each restricted to one of the two areas that later diverged into two lineages. The lineage in western North America spread eastward into eastern North America, followed by a subsequent vicariance event that fragmented the North American flora, resulting in the isolation of species in eastern and western North America (fig. 1d, 1e). Two vicariance events and one dispersal event were required to explain the disjunction given the phylogenetic pattern of these taxa.

Cornus subg. Cynoxylon, subg. Syncarpea. Two alternative optimal solutions were suggested for the big-bracted dogwoods. Both involve three vicariant events and one dispersal event, with a wide ancestral distribution of the lineage in eastern Asia and North America. The first vicariant event involved separation of eastern Asia and North America. This event was followed by dispersal from North America to Central America. The second vicariant event was either the separation of eastern North America–Central America from western North America or North America from Central America, depending on relationships among *Cornus disciflora*, *Cornus florida*, and *Cornus nuttallii* (fig. 1f₁, 1f₂). The third vicariant event involved the isolation between either eastern North America and Central America or between eastern North America and western North America (fig. 1f₁, 1f₂).

Trautvetteria. The optimal solution for *Trautvetteria* suggests a wide ancestral distribution of the genus in both eastern Asia and North America. The disjunction of the genus involved only two vicariant events: the isolation between eastern Asia and North America followed by the isolation between eastern and western North America (fig. 1g).

The Eastern Asian–Eastern North American–Western North American–European Disjunct Pattern

Aesculus. Optimization without constraint on number of areas resulted in 12 alternative solutions that mainly differed in the ancestral areas for the root of *Aesculus* and the root of the lineage consisting of species from Japan, Europe, and North American (referred to as JENA hereafter). Three alternative distributions (ABE, ACE, ABCE) (A: eastern Asia, B: eastern North America, C: western North America, E: Europe)

were suggested for the former and six alternative distributions (BE, ABE, CE, ACE, BCE, ABCE) were suggested for the latter. When the maximum areas were constrained to four in the optimization, eight alternative solutions were obtained. The root of *Aesculus* was suggested to be ACE or ABE, and the root of JENA was reduced to four alternatives (BE, ABE, CE, ACE). When the number of areas was limited to three, 44 alternative solutions resulted. Six alternative solutions for the root of *Aesculus* (A, AB, AC, AE, ABE, ACE) and six solutions for the root of JENA (AB, AC, BE, ABE, CE, ACE) were suggested. If the maximum number of areas was restricted to two, there was a single solution for the root area of *Aesculus* (A) and two solutions for the root of JENA (AB or AC) (fig. 1h).

All of these solutions required three vicariance events and one to three dispersal events to explain the disjunction. The single optimal solution resulting from optimization limiting the ancestral distribution in two areas was also one of the optimal solutions from optimization limiting ancestral distribution in three areas. This solution suggests that the genus evolved in eastern Asia and diverged into two major lineages. One of the major lineages likely spread eastward to western North America. (Although eastern North America was suggested as an alternative, it is not adjacent to eastern Asia. Thus, the dispersal from eastern Asia to eastern North America is less likely than a dispersal from eastern Asia to the adjacent western North America.) This lineage was later fragmented into New World (C) and Old World (A) components. The New World clade subsequently spread from western North America to eastern North America and diverged into two lineages. A latter vicariant event separating eastern and western North America fragmented both lineages into two parts each. The eastern Asian clade spread westward into Europe and was subsequently fragmented by a vicariance resulting in sister species now isolated in eastern Asia and southeastern Europe.

Asarum s.s. Similar to the results for *Aesculus*, multiple alternative optimal solutions were obtained for *Asarum* when ancestral distributions were not limited or were limited in three or four areas, while only a single optimal solution was obtained when limiting the ancestral distribution to only two unit areas (fig. 1i). According to this optimal solution, the ancestral distribution of *Asarum* s.s. was in eastern Asia. Three vicariance and three dispersal events were required to explain the disjunct pattern observed in the genus. The genus likely first spread from eastern Asia into western North America (although eastern North America was suggested as the alternative, it is less likely given that eastern North America is not adjacent to eastern Asia; fig. 1i). After the isolation between eastern Asia and western North America, two subsequent dispersal events occurred. One was from eastern Asia to Europe and the other from western North America to eastern North America. The other two vicariant events involved the isolation of sister species of the lineage in eastern Asia and Europe and the isolation of species of the North American lineage in eastern and western North America (fig. 1i).

Chrysosplenium. The optimization with constraint of ancestral distribution in two areas resulted in one optimal solution for *Chrysosplenium* and indicated the root area of the lineage representing the eastern Asia–eastern and western North America–Europe disjunct pattern to be eastern Asia.

The lineage spread westward into Europe (E), which was subsequently fragmented by a vicariant event. The European portion later spread into eastern North America (B), followed by vicariance separating B and E. The eastern North American portion further spread into western North America (C), which was followed by vicariance separating B and C (fig. 1j). Three vicariance and three dispersal events were involved.

Discussion

The optimal biogeographic pathways were estimated for disjunct angiosperm lineages in the Northern Hemisphere using DIVA. These estimates are limited by two factors. One important consideration is the accuracy of the molecular phylogenies. Most of the phylogenies used were only single gene or single genome based (table 1), and although internal support of relationships is generally high, the reliability of these phylogenies is unknown. A second factor is the assumptions of DIVA. DIVA assumes that current distributions were the result of vicariant events. It assigns cost only for dispersal and extinction and no cost for vicariance. The optimal solution is the one minimizing the occurrence of dispersal and extinction. Thus, the results may underestimate the number of dispersal and extinction events involved with each taxon. In fact, extinction events never appear in DIVA reconstructions when using the default cost assignments because there are always more parsimonious solutions without extinctions (F. Ronquist, personal communication). Nonetheless, assuming that the molecular phylogeny of each lineage examined closely represents the actual species phylogeny and that the parsimony principle applies to biogeography (both are nearly impossible to test without observing the evolutionary history of the taxa), the results from DIVA provide estimates on (1) a minimum number of interarea dispersal events and their directions in each lineage, (2) the maximum number of vicariance and the relative timing of one to another, and (3) the relative timing between dispersal and vicariant events in a lineage.

It must also be noted that DIVA optimizations often provide a wide ancestral distribution at the root of the tree as a result of a wide distribution encoded for widespread outgroups. The coding of wide distribution for widespread outgroups in the optimizations is due to the lack of information on ancestral distribution of the outgroups. Consequently, the entire distribution of the outgroups was encoded. However, in most cases, the ancestral distribution of outgroups is likely to be much more restricted than their entire distribution. This disadvantage affected only a few of the lineages we examined that have widespread outgroups, including *Symplocarpus*, *Cornus*, *Trautvetteria*, and *Panax*. For these lineages, the entire distribution of their outgroups was encoded in the analyses (fig. 1a, 1b, 1f, 1g). Therefore, it is possible that the ancestral distribution at the root of these lineages may actually be more restricted than what was reconstructed. The outgroups of all other taxa examined are either small lineages restricted to only a single area (e.g., *Boykinia*, *Calycanthus*, *Aesculus*) or the ancestral distributions of the sister outgroups known from a broader and detailed phylogeny including the sister and deeper outgroups (e.g., *Chrysosplenium*, *Aralia* sect. *Aralia*, and *Asarum* s.s.) (fig. 1c–1e, 1h–1j).

For three widespread lineages that occur in four areas

(*Chrysosplenium*, *Aesculus*, and *Asarum* s.s.), the optimizations without constraints or with constraints of three or four unit areas resulted in multiple optimal solutions with various wide ancestral distributions at the root. In contrast, only one of these multiple optimal solutions was obtained in the optimization with a constraint of ancestral distribution in two areas. The two-area constraint solutions for these lineages were also found in the optimization of limiting ancestral distributions in three unit areas and are congruent with the solutions optimized using the Fitch algorithm on MacClade (Maddison and Maddison 1992). We base the following discussion of these three taxa on these two-area constraint solutions described in the results above.

Center of Origin and Direction and Route of Migration

The optimization of ancestral distributions using DIVA suggests that the biogeographic pathways of the lineages examined may be classified into four general patterns: (1) origin and speciation in eastern Asia with subsequent expansion into North America and/or Europe (this pattern was suggested for several lineages, including *Aralia* sect. *Aralia*, *Asarum* s.s., *Aesculus*, *Chrysosplenium*, and possibly *Symplocarpus*) (fig. 1a, 1c, 1h–1j); (2) origin in eastern Asia and western North America with subsequent spread into eastern North America (this pattern was suggested for *Calycanthus* and *Boykinia*) (fig. 1d, 1e); (3) a disjunct origin in eastern Asia and eastern North America with subsequent dispersal from eastern Asia into eastern North America (this pattern was suggested for *Panax*); and (4) a widespread origin in the Northern Hemisphere with subsequent fragmentation by intercontinental vicariance (this pattern was suggested for *Cornus* and *Trautvetteria*) (fig. 1f, 1g). Although a wider ancestral distribution for *Asarum* s. s., *Aesculus*, and the disjunct lineage of *Chrysosplenium* is possible, as discussed above, these results clearly indicate that not all disjunct lineages had their ancestors widely distributed in the Northern Hemisphere, as implied by the simple vicariance explanation. Divergence of species prior to a wide distribution in the Northern Hemisphere and dispersal out of the ancestral range for secondary range expansion occurred in many lineages (fig. 1a, 1c–1e, 1h–1j). Extinction of ancestors in one or two unit areas may have also occurred in some lineages, such as in *Cornus* and *Trautvetteria* in Europe and *Panax* in Europe and western North America, although it was not inferred by DIVA. The results suggest eastern Asia and western North America as centers of origin for several lineages examined, implying that these two areas may be important sources of temperate angiosperm evolution in the Northern Hemisphere.

A noteworthy finding from DIVA was the one-way plant exchange between the two continents. Six intercontinental dispersals involving six lineages (*Panax*, *Symplocarpus*, *Aralia* sect. *Aralia*, and likely *Aesculus*, *Asarum* s.s., and *Chrysosplenium*) were inferred, all of which were from the Old World to the New World. Although the direction of dispersal in *Symplocarpus* may be the reverse (if its ancestor had a disjunct distribution in eastern Asia and eastern North America [fig. 1b]), this scenario is less likely (see “Results” section). Three of these intercontinental dispersals were from eastern Asia to western North America (e.g., in *Asarum*, *Aesculus*, and *Aralia* sect. *Aralia*; fig. 1c, 1h, 1i), one from Europe to eastern North

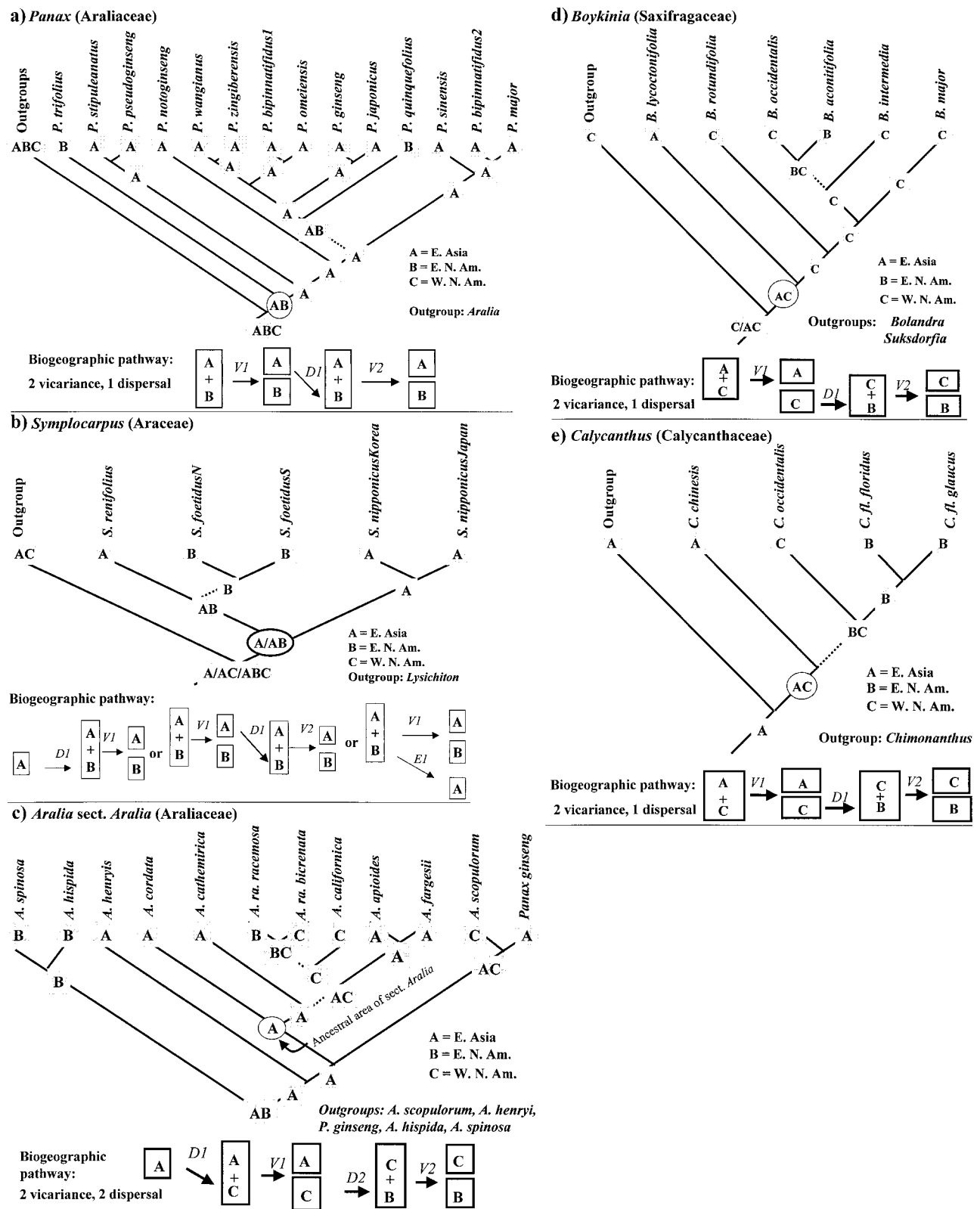
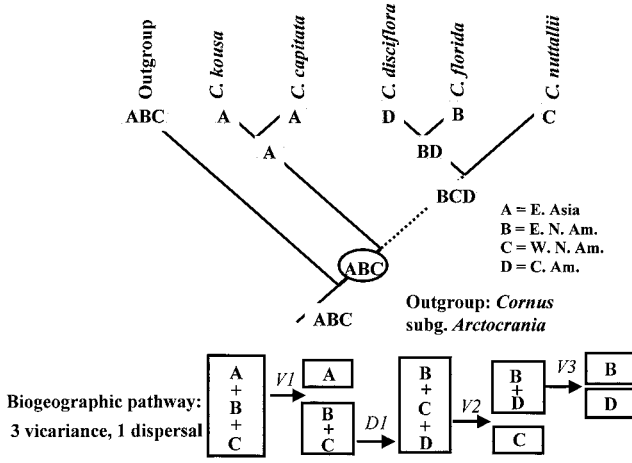
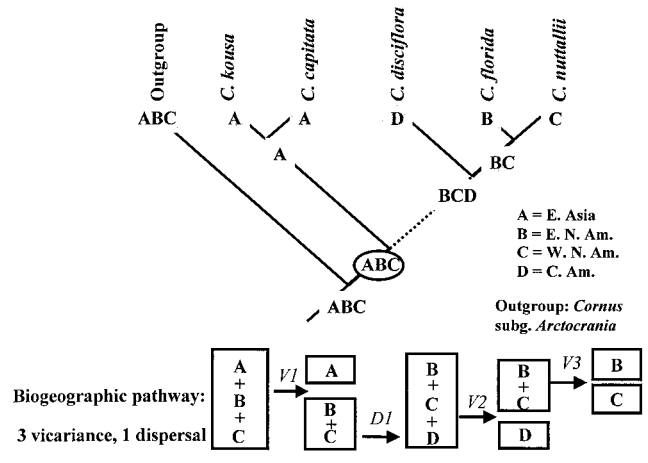


Fig. 1 Results of optimizations for ancestral distributions and the inferred biogeographic pathways of the disjunct lineages from DIVA. Phylogenies used were from previous molecular studies (see table 1). The reconstruction of the ancestral distribution of disjunct lineages in question is circled and the dispersal events are indicated by dashed lines. The results for *Aesculus*, *Asarum*, and *Chrysosplenium* are from optimizations using constraints of maxareas = 2. a, *Panax*; b, *Symplocarpus*; c, *Aralia* sect. *Aralia*; d, *Boykinia*; e, *Calycanthus*; f₁ and f₂, *Cornus* subg. *Cynoxylon*, subg. *Syncarpea*; g, *Trautvetteria*; h, *Aesculus*; i, *Asarum*; j, *Chrysosplenium*.

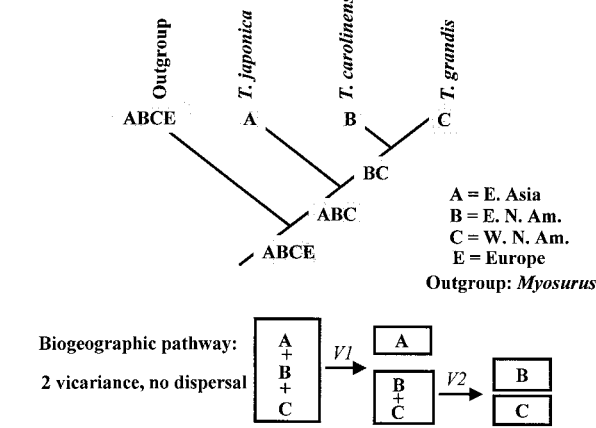
f₁) *Cornus* subg. *Cynoxylon*, subg. *Syncarpea* (Cornaceae)



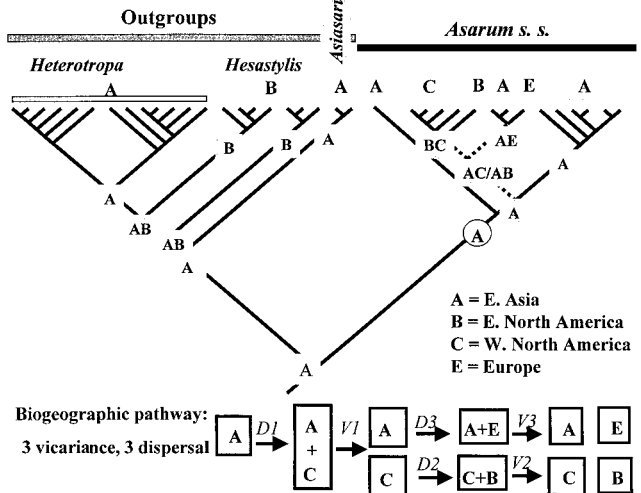
f₂) *Cornus* subg. *Cynoxylon*, subg. *Syncarpea* (Cornaceae)



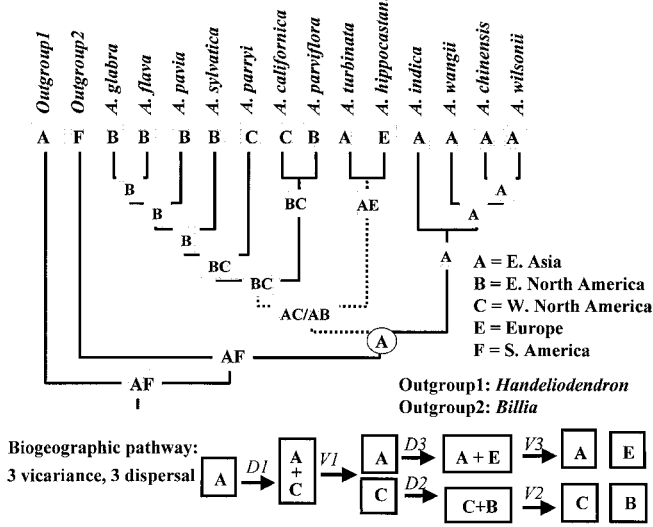
g) *Trautvetteria* (Ranunculaceae)



i) *Asarum* s. s. (Aristolochiaceae)



h) *Aesculus* (Hippocastanaceae)



j) *Chrysosplenium* (Saxifragaceae)

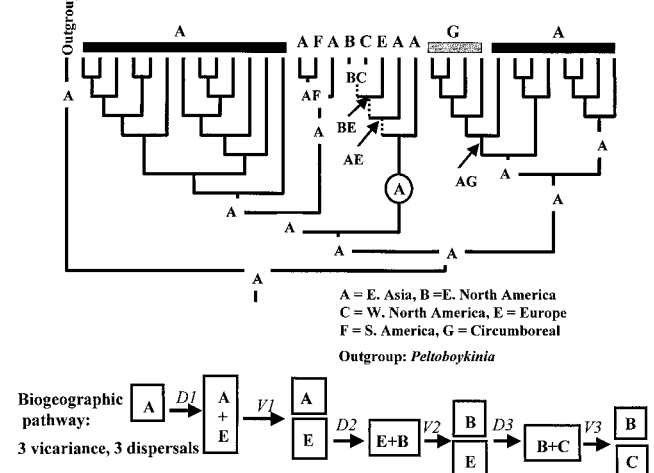


Fig. 1 (Continued)

America (e.g., in *Chrysosplenium*; fig. 1j) and two from eastern Asia to eastern North America (e.g., in *Panax* and *Symplocarpus*) (fig. 1a, 1b), indicating more interadjacent-area (or paleocontinental) dispersals than disjunct dispersals. This asymmetry of more paleocontinental dispersals than disjunct dispersals was similarly revealed in the study of 57 animal groups by Sanmartin et al. (2001) using DIVA.

Although DIVA suggests that all intercontinental dispersal events were from the Old World to the New World, the specific mechanism involved in the dispersal events remains unclear. For example, it is not clear whether the dispersal occurred via gradual migration across existing land bridges or via long-distance dispersal. Distinguishing the two requires information on the availability of land bridges connecting the Old World and New World floras, divergence times of sister lineage isolated on the two continents, and the biological characteristics of sister lineages as well. It is known that the Bering Land Bridge connected eastern Asia and western North America at one time or another throughout the late Cretaceous and the Tertiary and was available for floristic exchanges until ~3.5 Ma (see Tiffney 1985a, 1985b; Wen 1999). The North Atlantic Land Bridge connected northwestern Europe and northeastern North America and was available for plant exchanges from the early Tertiary to possibly as late as the Early Miocene (Tiffney 1985a).

Divergence times of sister taxa have been estimated for three lineages involving intercontinental dispersals using molecular data (*Aesculus*, *Aralia* sect. *Aralia*, and *Symplocarpus*; Wen et al. 1996a, 1998; Xiang et al. 1998a). These estimates suggest that in *Aesculus*, the intercontinental disjunct taxa diverged in the mid-Eocene, whereas in *Aralia* sect. *Aralia* the sister taxa in eastern Asia and North America diverged in the Oligocene, and in *Symplocarpus* it was in the Late Miocene (Wen et al. 1996a, 1998; Xiang et al. 1998a). The time frame of these estimates falls in a range during which plant exchanges via land connections were still possible. Thus, these results do not reject the migration hypothesis. Therefore, the dispersal of *Aesculus* and *Aralia* sect. *Aralia* from eastern Asia to western North America as inferred from DIVA likely involved migration across the Bering Land Bridge in the early Tertiary. The dispersal of *Symplocarpus* from eastern Asia to eastern North America also may have involved migration via the Bering Land Bridge in the Late Tertiary. A poor long-distance dispersal capability of the genus (seeds dispersed by rodents) and a modern distribution of *Symplocarpus* extending into the boreal region including Siberia and Canada are consistent with this hypothesis (see Wen et al. 1998).

Dispersal mechanisms in the other four lineages could not be vigorously evaluated. However, both *Chrysosplenium* and *Asarum* have relatively poor long-distance dispersal capabilities. For example, *Chrysosplenium* produce small capsules and small ridged or papilose seeds, and *Asarum* produce ant-dispersed seeds that are highly prone to desiccation (see Spongberg 1972; Kelly 1998). Therefore, it is likely that these lineages expanded their distribution out of the ancestral distribution via gradual migration. However, given that the seeds of *Chrysosplenium* are small, long-distance dispersal is also possible. The phylogenetic pattern of the genus indicated possible long-distance dispersal from eastern Asia into South America (Soltis et al. 2001). The spread of *Chrysosplenium*

from Europe to eastern North America might have involved the North Atlantic Land Bridge, and the spread of *Asarum* from eastern Asia to western North America should have involved migration across the Bering Land Bridge. Given that the dispersal of *Panax* from eastern Asia to eastern North America occurred after a first vicariance separating eastern Asian and eastern North American floras as inferred by DIVA (fig. 1a), this dispersal was either a long-distance dispersal resulting in the occurrence of *Panax quinquefolius* in eastern North America or a gradual migration when there was reconnection of the two floras (fig. 1a). Both the Bering Land Bridge and the North Atlantic Land Bridge were interrupted for plant exchanges at different times during the Tertiary (see Tiffney 1985a; Wen 1999). Overall, these data suggest that both the Bering Land Bridge and the North Atlantic Land Bridge played roles in plant exchange across the two continents, and the Bering Strait was probably more important than the North Atlantic Land Bridge for the temperate taxa, which was also proposed by Tiffney (1985a, 1985b).

DIVA infers nine interarea dispersals within continents involving six lineages (*Aralia* sect. *Aralia*, *Calycanthus*, *Boykinia*, *Asarum*, *Aesculus*, and *Chrysosplenium*) (see fig. 1c–1e, 1h–1j), six of which occurred within the North American continent and three of which were within Eurasia. The dispersal within North America was two-directional and the dispersal within Eurasia is one-directional. Within North America all dispersal events except that in *Chrysosplenium* were from western North America to eastern North America. In *Chrysosplenium* the dispersal was from eastern North America to western North America (fig. 1j). Dispersal within Eurasia occurred in *Aesculus*, *Asarum*, and *Chrysosplenium*; all were from eastern Asia to Europe. These directions of dispersal further support the conclusion that eastern Asia and western North America may have served as two major sources of temperate angiosperm evolution. The bias in directions of dispersal is congruent with the findings in animals (Sanmartin et al. 2001).

The biogeographic pathways inferred from DIVA provide information not only on directions of dispersal events but also on the relative timing of dispersal and vicariant events involved in each lineage. According to the inferred biogeographic pathways, all of the intercontinental dispersals occurred before the vicariance isolating these lineages on the two continents, except the dispersal in *Panax*, which occurred after the first intercontinental vicariant event (fig. 1a). All interarea dispersal within continents occurred after the vicariance isolating floras on the two continents, which was followed by within-continent vicariance.

Historical Events and Vicariance

The same vicariance involving the same two areas but two or more different lineages may be caused by independent historical events occurring at different times. This phenomenon of “pseudocongruence” was observed in this investigation. For example, DIVA optimization suggests two independent vicariances between eastern Asia and eastern North America for *Panax* (and probably also for *Symplocarpus*) (fig. 1a, 1b). The optimized biogeographic pathway of *Chrysosplenium* indicates that the eastern-western North American vicariance oc-

curred after the European–eastern Asian vicariance in the genus (fig. 1j), whereas in *Aesculus*, the order of these two vicariant events was the reverse, based on estimates of divergence times using a molecular clock (Xiang et al. 1998a; fig. 1b), suggesting that one or both of these vicariant events in the two genera involved different historical events.

Identifying specific historical events responsible for a particular vicariance in a given lineage requires information on divergence times of sister taxa isolated in adjacent unit areas. Several lineages examined in this study have been estimated for divergence times using molecular clocks as mentioned above, which may be useful for identifying potential historical events creating the divergence (or vicariance) of species. According to the divergence times estimated using molecular data, the vicariance separating eastern Asian and North American lineages of *Aesculus* occurred in the mid-Eocene; a similar vicariance in *Aralia* occurred in the Oligocene (see Wen et al. 1998; Xiang et al. 1998a). This time frame suggests that the disjunction of *Aesculus* between the two continents might have been the consequence of the disruption of both the Bering Land Bridge and the North Atlantic Land Bridge in the mid-Eocene, whereas the disjunction of *Aralia* was the result of the climatic cooling in the Oligocene (Wolfe 1975; Tiffney 1985a). In addition, estimates of divergence times for *Cornus*, *Symplocarpus*, *Boykinia*, and *Calycanthus* indicated that the intercontinental vicariance in these genera occurred in different periods of the later Tertiary (Wen et al. 1996a; Xiang et al. 1998b), suggesting that other historical events, such as the periodic climatic cooling in the later Tertiary, may have caused the intercontinental vicariance between eastern Asia and North America in these lineages. This analysis indicates that it is possible to sort out historical events and the affected taxa via synthesis of divergence times and paleontological data of the Northern Hemisphere.

Congruent Patterns versus Common Histories

Biogeographic analyses using DIVA indicate that disjunct lineages showing the same disjunct pattern do not necessarily share the same phylogenetic pattern and biogeographic histories. For example, *Panax* and *Symplocarpus* both exhibit an eastern Asian–eastern North American disjunction. However, phylogenetic and biogeographic analyses reveal different evolutionary and biogeographic histories for the two genera (fig. 1a, 1b). *Panax* evolved in eastern Asia and eastern North America. The eastern Asian part diverged into three lineages after the first vicariance event separating eastern Asia and eastern North America. One of these lineages subsequently spread into eastern North America. Thus, the two eastern North American species had a completely different history. One species (*Panax trifolius*) was derived from the original vicariance isolating the ancestor in the two continents and the other (*P. quinquefolius*) involved a dispersal from eastern Asia to North America and another vicariance between eastern Asia and eastern North America. In contrast, *Symplocarpus* evolved in eastern Asia or, less likely, in eastern Asia and eastern America (i.e., the ancestor of the genus was restricted in eastern Asia or disjunctly distributed in eastern Asia and eastern North America). The two eastern North American species had a single origin deriving from the vicariance separating eastern Asia

and eastern North America. Similar examples are also found among taxa showing the other two disjunct patterns (fig. 1c–1j).

Results of DIVA further suggest that taxa displaying the same distributional and phylogenetic patterns have also undergone different biogeographic pathways that involved different numbers of vicariant and dispersal events (see fig. 1c–1g, 1h–1j). For example, among the several genera with the eastern Asia–eastern and western North American disjunct distributions (i.e., *Aralia* sect. *Aralia*, *Boykinia*, *Calycanthus*, *Cornus* subg. *Cynoxylon*–subg. *Syncarpea*, and *Trautvetteria*), all genera shared a similar phylogenetic pattern: species from North America were more closely related to one another than they were to the eastern Asian species (fig. 1c–1g). However, results of DIVA did not suggest the same biogeographic pathways for these taxa (fig. 1c–1g). A similar phenomenon was also observed among taxa restricted to the four areas (e.g., *Aesculus*, *Chrysosplenium*, and *Asarum*; see fig. 1h–1j). These results further support pseudocongruence among disjunct lineages and suggest caution in interpreting biogeographic histories using conventional historical biogeographic approaches.

Conclusions

Our study demonstrates the utility of DIVA in reconstructing biogeographic history and provides insights into dispersal and vicariance events involved in the disjunction of temperate angiosperms in the Northern Hemisphere. Although there are caveats, the results clearly suggest that the disjunct distribution of various angiosperm lineages in the Northern Hemisphere could not be explained with a simple vicariant model. At least three independent historical events occurring at different geological times may have involved the intercontinental disjunctions in different lineages examined. Most lineages might have an ancestral distribution restricted to one or two adjacent areas and then might have secondarily expanded their ranges via dispersal out of the original ancestral distribution. Although there was not enough information on divergence times to evaluate gradual migration versus long-distance dispersal for all lineages, the evidence available did not refute gradual migration in all lineages, with divergence times of sister taxa estimated using molecular clocks. Results from DIVA indicate that intercontinental dispersal of temperate taxa was biased toward one way, from the Old World to the New World, and might have occurred mostly via migration across the Bering Land Bridge, although migration via the North Atlantic stepping stones has also been suggested for some lineages. Dispersal within continents was also asymmetrical, mostly from the west to the east in North America, but mostly from the east to the west in Eurasia. The results also suggest that eastern Asia and western North America may have served as centers of origins of many temperate angiosperm lineages. Our study also demonstrates that it is possible to sort out the biogeographic history of angiosperms in the Northern Hemisphere by accurately reconstructing the biogeographic history of individual lineages using appropriate analytical methods and data from phylogeny and divergence times. An accurate phylogeny is a prerequisite for biogeographic analysis. Our analyses using DIVA were solely based on phylogenies of extant species. Ideally, reliable fossil species should be included in the phylogenetic analyses.

Given the difficulties in determining the affinity of fossils to extant species and the problems with molecular clocks, the recently developed methods for estimating divergence times without a molecular clock (i.e., without requiring a clocklike sequence evolution among lineages) (e.g., Sanderson 1997; Thorne et al. 1998; Huelsenbeck et al. 2000; and Kishino et al. 2001) would be particularly valuable tools for providing estimates of divergence times in historical biogeographic analysis of any taxa. By using DIVA and these new methods for estimating divergence times, we may be able to reconstruct a detailed biogeographic history of angiosperms in the Northern Hemisphere with the aid of information from the geological

and climatic history of the earth and ecological and biological properties of species.

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