Evolution of the eastern Asian and eastern North American disjunct pattern: Insights from phylogenetic studies

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This study compared the available phylogenetic analyses on taxa with an eastern Asian and eastern North American disjunct distribution, taxa with a broad disjunction in the north temperate zone, and north temperate disjunct taxa with close relatives in the tropical and subtropical regions. Taxa examined include Aralia sect. Aralia, Aralia sect. Dimorphanthus, Boykinia, Calycanthus, Cornus, Corylus, Hamamelis, the Liquidambaroideae (or Altingioideae), Magnolia sect. Rytidospermum, Nyssa, Panax, Staphylea, Styrax, Symlocarpus, Tiarella, Trautvetteria, and Trillium. Although the floristic similarity between eastern Asia and eastern North America has been traditionally emphasized since Linnaeus era and numerous presumable intercontinental species pairs were proposed, phylogenetic studies showed a general lack of direct sister species relationships between eastern Asia and eastern North America. Instead a pattern of further diversification in one or both continents is common, which suggests the antiquity of this disjunct pattern. Examinations of the phylogenetic analyses of taxa with a broad north temperate disjunct pattern showed a close biogeographic relationship between eastern North America, western North America, and eastern Asia. This biogeographic pattern is best explained by the classical hypothesis of floristic exchanges between Asia and North America via the Bering land bridge. The phylogenetic pattern in Liquidambar and Staphylea, however, is compatible with the hypothesis of the North Atlantic land bridge. Furthermore the phylogenetic studies provide important insights into the tempo and mode of evolution of the north temperate disjuncts. In the Liquidambaroideae, the tropical and subtropical Altingia and Semiliquidambar are shown to have derived from the north temperate disjunct Liquidambar. Yet Altingia and Semiliquidambar are morphologically highly distinct from Liquidambar. The morphological cohesion among the evolutionarily

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ancient species in *Liquidambar* provided evidence for the newly proposed hypothesis of morphological stasis of the disjuncts in the North temperate zone. This same phylogenetic pattern was found in *Aralia sect. Dimorphanthus*.

*Key words:* Disjunction, eastern Asia, eastern North America, biogeography, phylogenetic analyses.

The disjunct distribution of morphologically similar plants between eastern Asia and eastern North America is a classical topic in biogeography. An excellent historical account of studies on this biogeographic pattern was provided by Boufford and Spongberg (1983). An extensive symposium was held in the Missouri Botanical Garden in 1982, which resulted in a series of papers summarizing scientific data up to the early 1980's (Annals of the Missouri Botanical Garden, volume 70, numbers 3 and 4, 1983). Many previous studies focused on the general documentation of this pattern in various plant groups (Li, 1952; Koyama and Kawano, 1963; Constance, 1972; Iwatsuki, 1972; Nishida, 1972; Chen, 1983; Hong, 1983; Kato and Iwatsuki, 1983; Phipps, 1983; Wu, 1983). A few studies discussed the disjunct pattern by comparing floristic similarities between the two continents (Cheng, 1983; Ying, 1983). Some studies made comparisons of morphology, cytology, pollen morphology, secondary chemistry, and DNA sequence divergence for the disjuncts (e.g., Hara, 1952, 1956; Nowicke and Skvarla, 1981; Vogelman, 1984; Wen and Crawford, 1989; Crawford et al., 1992; Qiu et al., 1995b; Wen and Jansen, 1995). Major advances have been made in the past 15 years in enhancing our understanding of the origin and evolution of this geographical pattern from several lines of evidence including geology, fossils, phylogenetics, and molecular divergence data (McKenna, 1983; Tiffney, 1985a, b; Parks and Wendel, 1990; Lee et al., 1996; Wen et al., 1996a; Xiang et al., 1998). Several phylogenetic and biogeographic analyses have been performed for plant genera with an eastern Asian and eastern North American disjunct distribution since 1990 (e.g., Wen and Stuessy, 1993; Qiu et al., 1995a; Wen and Zimmer, 1996; Wen et al., 1996a, b; Wen and Shi, submitted). Recent molecular data not only provided additional evidence for phylogenetic reconstruction, but also for estimating the times of divergence for the intercontinental disjuncts indirectly.

Many previous studies emphasized the taxonomic and floristic similarities
between eastern Asia and eastern North America. Numerous presumable species pairs were proposed between the two geographical areas (Li, 1952, 1972). The question of whether the intercontinental species pairs represent phylogenetic sister species needs to be addressed.

Tiffney (1985a) suggested that the eastern Asian and eastern North American disjunct pattern may be a subset of the broad north temperate disjunct pattern. Hoey and Parks (1991) showed that the western Asian Liquidambar orientalis Mill. has a higher level of allozyme similarity with the eastern North American L. styraciflua L. than with the eastern Asian L. acalycina Chang and L. formosana Hance. The examination of the eastern Asian and eastern North American disjunct pattern in a broad north temperate biogeography will provide valuable insights into the evolution of the disjunct pattern, especially on the significance of the various migration routes for floristic exchanges between eastern Asia and eastern North America.

Phylogenetic and biogeographic studies of plant groups with a wider geographic distribution may also provide a test of the hypotheses on the mode of evolution among the eastern Asian and the eastern North American disjuncts. Parks and Wendel (1990) proposed that morphological stasis may be a common mode of evolution among plants disjunctly distributed in eastern Asia and eastern North America. The morphological stasis concept was applied also by Liston et al. (1989) on the evolution of Datisca L., which shows a disjunct distribution between the western North America and the Mediterranean region. Although these workers (Liston et al., 1989; Parks and Wendel, 1990; Hoey and Parks, 1991) did not explicitly define morphological stasis, it implies the slow rate of evolution at the morphological level after a long-term geographic isolation. The possible mechanism of morphological stasis may be the stabilizing selection due to the similar habitats occupied by these disjuncts. To test this hypothesis, examination of plants with a wider geographic distribution, especially those from subtropical and tropical regions, is needed. Only if plants from eastern Asia and eastern North America possess a more distant relationship and yet a higher level of morphological similarity, morphological stasis is supported.

This study compared the phylogenetic results from diverse plant groups to address the following questions: Are the species pair relationships between eastern Asia and eastern North America supported by phylogenetic analyses? Is the close floristic relationship between eastern Asia and eastern North America
suggested by the broader phylogenetic and biogeographic studies in the north temperate zone? Are there any recognizable biogeographic patterns in the north temperate zone? Is morphological stasis supported by the phylogenetic evidence?

Overview of the Phylogenetic Data


**Taxa with an eastern Asian and eastern North American disjunct distribution**

*Hamamelis* (Hamamelidaceae) ----- A phylogenetic study of *Hamamelis* was recently conducted by Wen and Shi (1998) using sequences of the internal transcribed spacer (ITS) regions of the nuclear ribosomal DNA. *Hamamelis* or the witch hazel genus consists of 4-6 species with two from eastern Asia and 2-4 species from eastern North America. Although several workers suggested the close relationship between the eastern Asian *H. japonica* Sieb. & Zucc. and the North American *H. vernalis* Sargent (Li, 1972; Meyer, 1997), the ITS phylogeny suggested that the two Asiatic species were phylogenetically basal and the North American species formed a monophyletic group (Wen and Shi, 1998). Therefore there is a lack of an intercontinental species pair relationship in *Hamamelis* between eastern Asia and eastern North America.

*Magnolia* sect. *Rytidospermum* (Magnoliaceae) ----- Qiu et al. (1995a) examined the phylogenetic relationship of *Magnolia* sect. *Rytidospermum* based on chloroplast DNA (cpDNA) restriction site variations. The section consists of six species of temperate deciduous trees, which are morphologically similar. The cpDNA analysis showed that *Magnolia* sect. *Rytidospermum* is polyphyletic. The similar leaf
morphology and wood anatomy among the Asian and North American disjuncts in this section are thus attributable to convergence. Furthermore, no direct sister species relationship was detected in this section.

_Nyssa_ (Cornaceae) ---- Wen and Stuessy (1993) performed a phylogenetic analysis of _Nyssa_ based on morphological characters. _Nyssa_ consists of eight species with four species from eastern Asia, three species from eastern North America, and one from Costa Rica. Two phylogenetic connections were detected between Asia and the Americas. The presumable species pair relationship between _N. sylvatica_ Marshall from eastern North America and _N. sinensis_ Oliver from eastern Asia (Eyde 1963) was not supported by the phylogenetic analysis. _N. sinensis_ formed a sister species relationship with _N. shweiensis_ (W. W. Smith) Airy Shaw from eastern Asia. _N. sylvatica_ is basal to the _N. shweiensis_- _N. sinensis_ clade. _N. sylvatica_ is diversified into at least two varieties: var. _sylvatica_ and var. _ursina_ (Small) Wen et Stuessy.

_Panax_ (Araliaceae) ---- The phylogeny of _Panax_, the ginseng genus, was constructed by Wen and Zimmer (1996) using the nuclear ITS sequences. _Panax_ consists of approximately 12 species with about ten from eastern Asia and two from eastern North America. Of the two eastern North American species, _P. quinquefolius_ L. and _P. trifolius_ L., _P. quinquefolius_ was suggested to be more closely related to the eastern Asian species in the ITS tree, while _P. trifolius_ was phylogenetically isolated. Although _P. ginseng_ C. A. Meyer from eastern Asia was regarded to be most closely related to _P. quinquefolius_ from eastern North America (Li, 1942, 1952; Zhou et al., 1975; Hoo and Tseng, 1978), the ITS tree suggested that _P. ginseng_ formed a sister species relationship with _P. japonicus_ C. A. Meyer from Japan. No intercontinental species pairs were thus found in Panax. The Himalayas and central and western China are the present center of diversity of the ginseng genus. The low ITS sequence divergence and a close relationship among species in that region suggested that rapid evolutionary radiation may have created such a diversity of _Panax_ in the Himalayas and in central and western China. In addition, a discrepancy between the sequence divergence pattern and the phylogenetic pattern was observed in _Panax_, suggesting the need for caution in using sequence divergence data alone in inferring biogeographical patterns.

_Symlocarpus_ (Araceae) ---- Chloroplast DNA variation was surveyed with 20 restriction endonucleases for _Symlocarpus_, which has three species with two from eastern Asia and one from eastern North America (Wen et al., 1996b).
The cpDNA phylogeny revealed a sister group relationship between *S. foetidus* (L.) Nutt. from eastern North America and *S. renifolius* Schott ex Miquel from eastern Asia. The cpDNA divergence between the two intercontinental sister species is 0.61%, which suggests an estimated divergence time of 6.1 million years ago during the late Miocene.

**Taxa with a wide distribution in the north temperate zone**

*Aralia* sect. *Aralia* (Araliaceae) —— *Aralia* sect. *Aralia* consists of approximately eight species disjunctly distributed in Asia and North America, with about five species from eastern Asia, one from the Himalayas, one from eastern North America, one subspecies from southwestern North America, and one species from western North America. *A. cordata* Thunb. from eastern Asia and *A. racemosa* L. from eastern North America were suggested to form an intercontinental species pair (Li, 1952, 1972). Phylogenetic analyses using the nuclear ITS sequences (Wen et al., 1998) did not support the intercontinental species pair relationship. *A. racemosa* from eastern North America was sister to *A. californica* S. Wats. from western North America in the ITS phylogeny. *A. cordata* was cladistically basal within the section. Biogeographical analyses of *Aralia* sect. *Aralia* suggested a close area relationship between eastern North America and western North America, with eastern Asia basal to the North American clade. This biogeographic pattern of the eastern Asian and eastern North American connection via the western North America is compatible with the hypothesis of the origin of the eastern Asian and eastern North American disjunct pattern in *Aralia* sect. *Aralia* via the Bering land bridge (Hopkins, 1967).

*Boykinia* (Saxifragaceae) —— *Boykinia* is composed of seven species with one species from eastern North America, one from eastern Asia, and five from western North America. The phylogenetic analyses by Xiang et al. (1998) using cpDNA restriction sites and nuclear ITS sequences placed the eastern Asian species basal to the North American clade. Within the North American clade, the ITS tree suggests that *B. rotundifolia* Parry from western North America is basal to the clade consisting of the eastern North American *B. aconitifolia* Nutt. and the remaining western North American species. The cpDNA tree suggested a trichotomy among *B. aconitifolia*, *B. rotundifolia*, and the remaining species.

*Calycanthus* (Calycanthaceae) —— *Calycanthus* contains three species distributed
in eastern North America (*C. floridus* L.), western North America (*C. occidentalis* Hooker et Arnott) and eastern Asia (*C. chinensis* Cheng et S. Y. Chang). *Calycanthus floridus* demonstrates a high degree of morphological variability and two varieties are recognized based on leaf pubescence, var. *floridus* and var. *glaucus* (Willd.) Torrey et Gray. Parsimony analyses of forty-eight cpDNA restriction site changes produced a single most parsimonious tree with 48 steps and a consistency index of 1.0 (Wen et al., 1996a). The genus is strongly supported as a monophyletic group. The eastern Asian *C. chinensis* is cladistically basal and the eastern and western North American species form a sister group.

*Coruus* (Cornaceae) ----- *Coruus* or the dogwood genus consists of approximately 55 species, seven of which comprise a monophyletic group known as the big-bracted dogwoods (Xiang et al., 1998). This group is disjunctly distributed in eastern Asia (4 spp.), eastern North America (1 sp.), western North America (1 sp.), and Central America (1 sp.). Analysis of combined rbcL-matK-cpDNA restriction site data showed that the eastern Asian species formed a monophyletic group, which was sister to the North American clade.

*Staphylea* (Staphyleaceae) ----- *Staphylea* consists of approximately 10 species distributed disjunctly in the north temperate region with five species from eastern Asia, one from the Himalayas and western Asia, one from western Asia, one from Europe, one in eastern North America, and one in western North America. The monophyly of *Staphylea* is supported by synapomorphies of bladder-like capsules and the alternate arrangement between petals and stamens. The nuclear ITS regions were used to construct the phylogeny of *Staphylea* using *Euscaphis* Sieb. et Zucc. as the outgroup (J. Wen, unpublished). The total length of ITS1, 5.8S and ITS2 regions of Staphylea ranged from 625-635 bases, with an ITS1 of 263-269 bases, a 5.8S of 164-168 bases and an ITS2 of 204-210 bases. Few gaps were detected in aligning the sequences. Two accessions were sequenced for three (*S. bumatla* (Thunb.) DC., *S. holocarpa* Hemsl. and *S. trifolia* L.) of the seven species and little (*S. holocarpa* with one nucleotide substitution) or no infraspecific sequence variation was found. The interspecific sequence divergence was estimated to be 1.3-11.6%. Treating gaps as missing data, the parsimony analyses generated two equally most parsimonious trees with a length of 172 steps and a CI of 0.90, a RI of 0.89, and a RC of 0.80. Treating gaps as a fifth state did not change the tree topology. The Himalayan and western Asian *S. emodi* Wall. constituted a sister group relationship.
with the eastern North American *S. trifolia*. The two North American species (*S. trifolia* and *S. bolanderi* Gray) formed a monophyletic group with the Asian species (*S. emodi* and *S. holocarpa*). The western Asian *S. colchica* Stev. was sister to the European *S. pinnata* L. The eastern Asian *S. bumaIa* was highly diverged from other species with 35 autapomorphies and was most closely related to *S. colchica* from western Asia and *S. pinnata* from Europe.

*Styrox* (Styracaceae) —— Fritsch (1996) presented a phylogenetic hypothesis of 23 taxa of *Styrox* using the parsimony analysis of combined nuclear ITS sequences and the cpDNA restriction site variations from two gene regions (various regions within rpoCl, rpoC2, trnK, and flanking regions). The five species sampled from eastern North America formed a monophyletic group. The western North American *S. jaliscanus* S. Wats. was basal to the eastern North American clade. Species from eastern Asia constituted two major clades, which formed a trichotomy with the above mentioned North American clade. Furthermore, Five additional taxa from western North America formed a monophyletic group with the Mediterranean *S. officinalis* L. ssp. *officinalis*.

*Tiarella* (Saxifragaceae) —— There are three species in *Tiarella* disjunctly distributed in eastern North America, western North America, and eastern Asia. Although the genus was suggested to be polyphyletic by several chloroplast markers (Soltis et al., 1991), morphology and nuclear ITS sequences indicated its monophyly (Soltis and Kuzoff, 1995). Soltis and Kuzoff (1995) explained the incongruence to be due to chloroplast capture. The ITS phylogeny supported the sister species relationship between the two North American species and a basal position of the eastern Asian *T. polypylla* D. Don (Xiang et al., 1998).

*Trautvetteria* (Ranunculaceae) —— Xiang et al. (1998) conducted a phylogenetic analysis of *Trautvetteria*, which consists of three species disjunctly distributed in eastern Asia, eastern North America, and western North America, using the ITS and matK sequences. The eastern Asian *T. japonica* Sieb. & Zucc. was shown to be basal to the North American clade of *T. carolinensis* (Walt.) Vail and *T. grandis* Nutt.

*Trillium* (Liliaceae) —— *Trillium* is composed of 46 species disjunctly distributed in eastern Asia (10 species), eastern North America (29 species), and western North America (seven species). A chloroplast DNA phylogeny was provided for 25 species of *Trillium* with restriction site analysis (Kato et al., 1995). The phylogeny showed a lack of direct sister species relationships between eastern
Asia and eastern North America. The Japanese *T. kamtschaticum* Pallas was suggested to be basal to the eastern North American clade of the *Erectum* subgroup. A clade comprising the eastern and western North American species was detected. These biogeographic pattern needs to be further tested by sampling additional taxa of *Trillium* because only a few species from eastern Asia were included.

**Disjunct taxa with close relatives in the tropical and subtropical regions**

*Aralia* sect. *Dimorphanthus* (Araliaceae) —— The phylogeny of *Aralia* sect. *Dimorphanthus* was constructed with the ITS sequence data (Wen et al., 1996a). The section consists of 25 species with one species from North America and 24 from eastern and South Asia. Based on morphology, Wen (1991) recognized three taxonomic series within *Aralia* sect. *Dimorphanthus*: series *Chinensis* Wen, series *Dimorphanthus*, and series *Foliolosa* Wen. Series *Dimorphanthus* is disjunctly distributed in eastern Asia and eastern North America and species from series *Chinensis* and series *Foliolosa* are from subtropical and tropical Asia. The ITS study sampled 16 species from all the three series. Li (1942, 1952, 1972) suggested a presumable species pair relationship between the North American *A. spinosa* L. and the eastern Asian *A. chinensis* L. Li *A. chinensis* was actually not the same as the one described by Linnaeus. *A. chinensis* sensu Li includes two taxonomic entities: the widely distributed Asiatic *A. elata* Miquel and *A. stipulata* Franchet from western China.

The ITS data suggested that series *Chinensis* and series *Foliolosa* were derived from series *Dimorphanthus*. The paraphyly of the eastern Asian and eastern North American disjunct series *Dimorphanthus* suggested that series *Dimorphanthus* is older than the subtropical and tropical series *Chinensis* and series *Foliolosa*. Yet series *Chinensis* and series *Foliolosa* are morphologically quite divergent and were thus recognized as distinct taxonomic series. Species of the older series *Dimorphanthus* are morphologically similar to each other, suggesting that morphological stasis may have occurred in the evolution of this group of species. The paraphyly of the disjunct series indicated that the morphological similarity of the disjunct group is due to the dominance of symplesiomorphies, i.e., shared primitive morphological similarities.

Li (1952, 1972) recognized the species pair relationship between the Chinese *A. stipulata* and the eastern North American *A. spinosa*. Our ITS phylogeny suggested instead the monophyly of the eastern Asian species and a basal

The Liquidambaroideae (Hamamelidaceae) ------ The Liquidambaroideae consists of three genera: Liquidambar (4 spp.) from the north temperate zone, Altingia Noronha (7 spp.) from tropical and subtropical Asia, and Semiliquidambar Chang (approximately 3 spp.) from subtropical China. Liquidambar is a well-known genus and has been used to study the biogeography of the north temperate zone (Hoey and Parks, 1991, 1994; Shi et al., 1997; Li et al., 1998). Our recent phylogenetic analysis suggested that Liquidambar is paraphyletic (Shi et al., 1997). The two subtropical and tropical Asiatic genera of the Liquidambaroideae: Altingia and Semiliquidambar were derived from the temperate Liquidambar.


Discussion

The rare occurrence of direct intercontinental sister species relationships between eastern Asia and the eastern North America

At present phylogenetic analyses have been reported for six taxa disjunctly distributed in eastern Asia and eastern North America including Aralia sect. Dimorphanthus (Wen et al., 1996a), Hamamelis (Wen and Shi, 1998), Magnolia sect. Rytidospermum (Qiu et al., 1995a), Nyssa (Wen and Stuessy, 1993), Panax (Wen and Zimmer, 1996), and Symlocarpus (Wen et al., 1996b). Although intercontinental species pairs between eastern Asia and eastern North America were largely emphasized by previous workers (e.g., Li, 1972), phylogenetic analyses did not reveal this type of close relationship in five of the six taxa including Aralia sect. Dimorphanthus, Hamamelis, Magnolia sect. Rytidospermum, Nyssa, and Panax. Only Symlocarpus showed a direct intercontinental sister species relationship (Wen et al., 1996b). Linnaeus (Halenius, 1750) and Gray (1846, 1859, 1878) regarded many of the disjuncts as conspecific. Li (1952, 1972) and many later workers recognized numerous species pairs between eastern Asia and eastern North America. The general lack of the phylogenetic sister species relationships...
suggested the antiquity of the disjunct pattern. Species apparently underwent further speciation events after the formation of the disjunct pattern and thus further diversification of species occurred in one or both continents.

The polyphyly and paraphyly of some disjunct taxa

Molecular phylogenetic studies suggested that some traditionally recognized disjunct taxa including *Aralia* sect. *Aralia* (Wen et al., 1998) and *Magnolia* sect. *Rytidospernum* (Qiu et al., 1995a) are polyphyletic. The morphological similarity in these polyphyletic disjunct groups is perhaps attributable to evolutionary convergence. Qiu et al. (1995a) discussed the general habitat similarity of the taxa in eastern Asia and eastern North America. The similar habitats may have caused stabilizing selection, which led to the superficial morphological similarity, even though the disjuncts have been separated for a long period of time. These polyphyletic phylogenetic patterns provided evidence for morphological stasis via convergence.

The eastern Asian and the eastern North American disjunct *Aralia* series *Dimorphanthus* is paraphyletic, from which two subtropical series were derived. The North Temperate disjunct *Liquidambar* was also shown to be paraphyletic, and the subtropical and tropical *Altingia* and *Semiliquidambar* were derivatives of *Liquidambar*. The paraphyly of *Aralia* series *Dimorphanthus* and *Liquidambar* suggested that the morphological similarities used to define these two taxa were symplesiomorphies.

The phylogenetic evidence on the floristic exchanges between eastern Asia and eastern North America

Two major migration routes were recognized between eastern Asia and eastern North America based on fossil and geological evidence. They are: (1) the Bering land bridge (Hopkins 1967), and (2) the North Atlantic land bridge (McKenna 1983; Tiffney 1985b). There exist four generalized pathways between eastern Asia and eastern North America: (1) eastern Asia-western North America-eastern North America, (2) eastern Asia-western Asia-eastern North America, (3) eastern Asia-Europe-eastern North America, and (4) eastern Asia-arctic regions-eastern North America.

Recent phylogenetic analyses provided evidence for the strong biogeographic connection among eastern Asia, western North America, and eastern North America, which support the Bering land bridge hypothesis to explain the floristic
similarity between eastern Asia and eastern North America. A common biogeographic pattern of a close relationship among taxa from eastern North America and western North America with eastern Asia basal to the North American clade was observed in several genera including *Aralia* sect. *Aralia* (Wen et al. 1998), *Boykinia* (Xiang et al. 1998), *Calycanthus* (Wen et al. 1996a), *Cornus* (Xiang et al. 1998), *Corylus* (J. Wen, unpublished), *Styrax* (Fritschi 1996), *Tiarella* (Xiang et al. 1998), *Trautvetteria* (Xiang et al. 1998), and *Trillium* (Kato et al. 1995). A close floristic relationship between eastern North America and western North America has not been emphasized (Good 1974) because of the existence of biogeographic barriers. North American Mid-Continental Seaway separated eastern and western North America in the late Cretaceous and retreated to the north and south by the Paleocene. This regression occurred concomitantly with the uplifting of the Rocky Mountains in the early Tertiary. The Central North American epicontinental seaway and the subsequent rising of the Rockies created biogeographic barriers for floristic exchange between eastern and western North America (Tiffney 1985b). Phylogenetic evidence from the diverse plant genera exhibiting the close biogeographic relationship between eastern and western North America and their connection to eastern Asia suggested that the floristic relationship between the eastern and the western North America is stronger than previously thought. This biogeographic pattern further supported the importance of the Bering land bridge in the evolution of the disjunct pattern between eastern Asia and eastern North America.

The floristic connection between eastern North America and eastern Asia via western Asia was detected in *Liquidambar* (Hoey and Parks 1991; Li et al. 1998) and *Staphylea* (J. Wen, unpublished), which provided support for the North Atlantic land bridge hypothesis. Present phylogenetic data thus support the multiple origins of the eastern Asian and the eastern North American disjunction via both the Bering land bridge and the North Atlantic land bridge. Additional genera need to be examined to gain insights into the relative importance of the two major migration routes.

**Lack of correlation between sequence divergence values and phylogenetic positions**

Recently Wen et al. (1996a) and Wen and Zimmer (1996) reported discrepancies between sequence divergence pattern and phylogenetic pattern in *Aralia* and *Panax*, two genera showing a disjunct pattern between eastern Asia and eastern North America. Taxa with a high overall sequence similarity may not
have a close phylogenetic relationship. This discrepancy was also found in Magnolia sect. Rytidospermum (Qiu et al. 1995a, b). This incongruence suggests the importance of a phylogenetic framework in biogeographic analyses. The high level of similarities among the disjuncts may be due to the dominance of synapomorphies, which do not contribute to phylogenetic relationships.

**Morphological stasis among the north temperate disjuncts**

Morphological stasis refers to the little morphological divergence of species after a long time separation. Parks and Wendel (1990) first applied morphological stasis as a common mode of evolution in the disjunct genus Liriodendron. Observing the high level of allozyme divergence between the morphologically similar eastern Asian L. chinense (Hemsley) Sargent and eastern North American L. tulipifera L., they suggested that the two species may have undergone morphological stasis. Morphological stasis was proposed as a common mode of evolution among the Asian and North American disjunct plants (Parks and Wendel, 1990; Hoey and Parks, 1991; Qiu et al., 1995a, b) and needs to be tested. One method to test the morphological stasis is to conduct phylogenetic analyses of the eastern Asian and eastern North American disjuncts and their close relatives in the tropical and subtropical regions. Morphological stasis among the eastern Asian and eastern North American disjuncts predicts a uniform morphology among the eastern Asian and eastern North American disjuncts and a high level of morphological divergence from their tropical and subtropical derivatives.

The subtropical and tropical members of Aralia sect. Dimorphanthus and Liquidambar were suggested to be derived from the temperate group (Wen et al., 1996a; Shi et al., 1997). However, the temperate group are morphologically cohesive and their tropical and subtropical relatives are morphologically much more distinct, thus being recognized taxonomically. The tropical and subtropical derivatives of Liquidambar are Altingia and Semiliquidambar. The temperate members of Aralia sect. Dimorphanthus gave rise to Aralia series Chinensis, and Aralia series Foliolosae. The paraphyly of Aralia ser. Dimorphanthus and Liquidambar suggested that the high level of morphological similarity is contributed by the dominance of synapomorphies. This phylogenetic pattern highlights the importance of examining the evolution of the eastern Asian and eastern North American disjuncts in the context of a global biogeography. In addition, Qiu et al. (1995a, b) provided evidence that morphological similarity in
Magnolia sect. Rytidospermum was due to evolutionary convergence. Additional phylogenetic and morphological analyses are needed to conclude upon morphological stasis.

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