Evolution of the Madrean–Tethyan disjunctions and the North and South American amphitropical disjunctions in plants

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Abstract   The present paper reviews advances in the study of two major intercontinental disjunct biogeographic patterns: (i) between Eurasian and western North American deserts with the Mediterranean climate (the Madrean–Tethyan disjunctions); and (ii) between the temperate regions of North and South America (the amphitropical disjunctions). Both disjunct patterns have multiple times of origin. The amphitropical disjunctions have largely resulted from long-distance dispersal, primarily from the Miocene to the Holocene, with available data indicating that most lineages dispersed from North to South America. Results of recent studies on the Mediterranean disjuncts between the deserts of Eurasia and western North America support the multiple modes of origin and are mostly consistent with hypotheses of long-distance dispersal and the North Atlantic migration. Axelrod's Madrean–Tethyan hypothesis, which implies vicariance between the two regions in the early Tertiary, has been favored by a few studies. The Beringian migration corridor for semiarid taxa is also supported in some cases.
Key words   amphitropical disjunctions, biogeography, Madrean–Tethyan disjunctions, Mediterranean disjuncts, North–South American disjunctions.

Intercontinental disjunctions have long interested biogeographers (e.g. Gray, 1846; Hooker, 1853; Raven, 1963, 1972; Darlington, 1965; Thorne, 1972; Raven & Axelrod, 1974; Wen, 1999, 2001; Manos & Donoghue, 2001; Donoghue & Smith, 2004; Sanmartín & Ronquist, 2004; Xiang et al., 2004). Raven (1972) recognized several major patterns of intercontinental disjunctions as follows: (i) in the north temperate zone among eastern Asia, Europe/western Asia, eastern North America and western North America (the north temperate disjunctions); (ii) between Eurasian and western North American deserts with the Mediterranean climate (the Madrean–Tethyan disjunctions); (iii) across southern South America, Africa, and Australasia (southern Gondwanan disjunctions); (iv) between the Neotropics and Africa (transatlantic tropical disjunctions); (v) between the temperate regions of North and South America (the amphitropical disjunctions); (vi) between temperate South America and Asia; and (vii) across all major regions of the tropics (the pantropical disjunctions). Thorne (1972) undertook another review of major disjunctions in plants and recognized 16 categories with an additional 34 subcategories of biogeographically discontinuous distributions. Thorne (1972) organized these disjunctions according to continent and latitudinal occurrence, and provided selected distribution maps for each category. The 16 categories recognized by Thorne (1972) are: (i) Eurasian–North American disjunctions; (ii) amphi-Pacific tropical disjunctions; (iii) pantropical disjunctions; (iv) African–Eurasian (–Pacific) disjunctions; (v) Amphi–Indian Ocean disjunctions; (vi) Asian-Pacific disjunctions; (vii) Pacific Ocean disjunctions; (viii) Pacific–Indian–Atlantic Oceans disjunctions; (ix) American–African disjunctions; (x) North American–South American disjunctions; (xi) South American–Australasian disjunctions; (xii) temperate South American–Asian disjunctions; (xiii) circum-south temperate disjunctions; (xiv) circum-Antarctic disjunctions; (xv) subcosmopolitan disjunctions; and (xvi) anomalous disjunctions. Each of these 16 major patterns of discontinuous biogeographic distributions was further subdivided by Thorne (1972), with the third category (the temperate disjunction) having as many as 12 subcategories.

With advances in molecular phylogenetics and new tools for estimating divergence times, there is now renewed interest in studies of biogeographic disjunctions. Many analyses have been conducted on the classical temperate eastern Asian–eastern North American disjunct pattern. This disjunct pattern has also been examined in a broader framework of northern hemisphere biogeography (Wen, 1999, 2001; Manos & Donoghue, 2001; Donoghue & Smith, 2004). The tropical

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disjunctions in plants have been recently reviewed by Givnish and Renner (2004) and a few recent studies have explored the origin and evolution of the amphitropical disjunctions between North and South America (Vargas et al., 1998; Wen et al., 2002; Simpson et al., 2005; Moore et al., 2006). The Madrean–Tethyan disjunction has been examined in several studies, including those of Fritsch (1996), Liston (1997), and Hohmann et al. (2006). Classical biogeographic models, such as *Nothofagus* Blume exhibiting a southern hemisphere temperate disjunction and *Liquidambar* L. exhibiting an intercontinental disjunction among eastern Asia, western Asia/southern Europe, and eastern North America of the northern hemisphere, have also been re-examined with new analytical methods and new data sources (e.g. Cook & Crisp, 2005; Ickert-Bond & Wen, 2006).

Our understanding of northern hemisphere biogeography has progressed steadily in the past 15 years, especially with regard to the phylogenetic relationships of disjunct lineages and the timing of major biogeographic patterns (Enghoff, 1995; Wen, 1999; Donoghue et al., 2001; Sanmartín et al., 2001). Several disjunctions within the northern hemisphere have been better documented and analyzed, such as the disjunctions between eastern Asia–eastern North America (Wen, 1999, 2001), eastern Asia–western North America (Wu, 1983), the trans-Atlantic disjunction (Manchester, 1999), and eastern North America–western North America (Wen et al., 1996, 1998; Xiang et al. 1998). At present, the topic has been actively investigated by systematists, ecologists, and paleobotanists (Wen & Stuessy, 1993; Manchester, 1999; Wen, 1999, 2001; Donoghue et al., 2001; Li et al., 2001; Manos & Donoghue, 2001; Sanmartín et al., 2001; Donoghue & Smith, 2004; Qian & Ricklefs, 2004; Xiang et al., 2004; Yi et al., 2004; Li & Xiang, 2005; Nie et al., 2005, 2006a, 2006b; Ickert-Bond & Wen, 2006). These recent studies have demonstrated the complex history of migration, dispersal, and vicariance in the northern hemisphere, as well as multiple origins of the classical disjunct pattern between eastern Asia and eastern North America, and suggested morphological stasis among the disjunct lineages in the temperate zone (Wen, 1999, 2001; Ickert-Bond & Wen, 2006).

The present paper reviews advances in studies of two major disjunct patterns related to northern hemisphere biogeography, namely the Mediterranean disjunctions between the deserts of Eurasia and western North America (or the Madrean–Tethyan disjunctions) and the amphitropical disjunctions between North and South America. Despite many recent analyses of northern hemisphere biogeography, these two patterns have not been emphasized and clearly need to be investigated further. We hope that this review will stimulate additional work on these two patterns of disjunctions.

1 Madrean–Tethyan disjunctions

The Madrean–Tethyan disjunctions in plants were noted by Engler (1879), elaborated by Raven (1971, 1973) and Thorne (1972), and reviewed by Liston (1997) from a molecular perspective. This disjunct pattern refers to the discontinuous distribution of congeneric plants and sometimes conspecific taxa between Mediterranean Eurasia and coastal western North America. This pattern is sometimes known as the Mediterranean–Californian disjunction (Hohmann et al., 2006) because many western North American elements showing this disjunction are largely distributed in California. Five major regions have a Mediterranean-type climate characterized by hot, dry summers and cool, moist winters. These regions include the Mediterranean basin in southern Europe and western Asia, western North America, central Chile, the Cape region of South Africa, and southwestern and southern Australia (Raven, 1971). Among these areas, the disjunctions between Mediterranean Eurasia and California have been better documented, with approximately 35 plant genera demonstrating such a disjunct pattern and some also extending their distribution ranges to northern Africa (Thorne, 1972). Several are disjunct at the species level or at the level of species pairs (Stebbins & Day, 1967).

Three major hypotheses have been proposed to explain the origin of the Mediterranean Eurasian and western North American disjunction (Figs. 1, 2). Axelrod (1973, 1975) proposed a nearly continuous trans-Atlantic belt of Madrean–Tethyan broadleaf evergreen sclerophyllous vegetation stretching from western North America to central Asia in the early Tertiary (from the Eocene to the late Oligocene) at low latitudes (Fig. 1). The disjunct pattern in his view is ancient and originated from floristic migration across the North Atlantic. Conversely, others (Raven, 1972; Raven & Axelrod, 1975) have argued for the origin of this disjunct pattern via convergent evolution with some disjunct taxa resulting from long-distance dispersal. Meusel (1969) also argued for the parallel evolution of disjunct taxa in Mediterranean-type climates in both western North America and western Eurasia. Stebbins and Day (1967) hypothesized that an early Beringian migration corridor in the early Miocene was available for taxa adapted for warm and semiarid climates (Fig. 2). The North Atlantic migration routes have been much better understood since the mid-1980s (Tiffney 1985; Tiffney & Manchester, 2001). In the present review, we
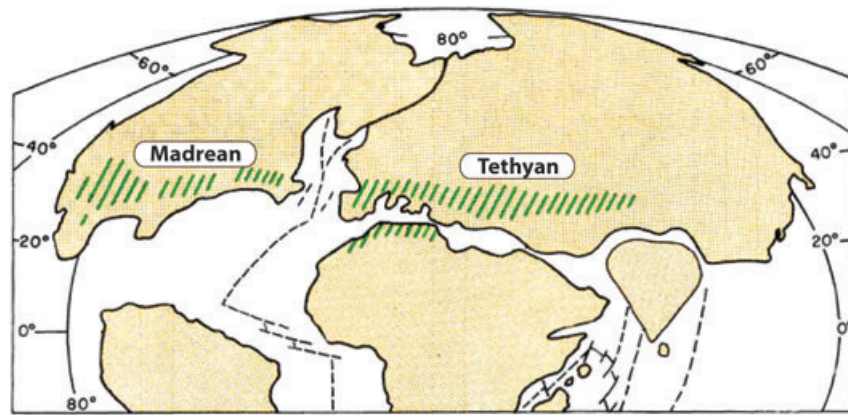
Fig. 1. Axelrod's Madrean–Tethyan hypothesis, which hypothesized a nearly continuous belt of Madrean–Tethyan broadleaf evergreen sclerophyllous vegetation stretching from western North America to central Asia in the early Tertiary (from the Eocene to the late Oligocene) at the low latitudes (modified from Axelrod, 1975).

consider the migration across the North Atlantic broadly as one pathway. Our North Atlantic migration includes the pathway implied in Axelrod's Madrean–Tethyan hypothesis, because it is difficult from the area relationships and age estimates to differentiate the two.

Liston et al. (1989, 1992) examined the disjunction in *Datisca* (Datiscaceae), which has two species, *D. glomerata* (Presl) Baill. from western North America (California and northern Baja California) and *D. cannabina* L. from the eastern Mediterranean to central Asia. The monophyly of the two disjunct species is well supported (Rieseberg et al., 1992; Swensen et al., 1994, 1998). Using 21 isozyme loci, Liston et al. (1989) estimated that the divergence time between the two intercontinental disjunct taxa was 10–40 mya. Conversely, using restriction site analysis of the chloroplast fragment corresponding to *rbc*L and *ORF106*, Liston et al. (1992) provided an estimate of 8.7 ± 1.7 mya (Fig. 3; Table 1), assuming a substitution rate of approximately 10^{-9} nucleotides per site per year for chloroplast DNA (cpDNA) (Zurawski & Clegg, 1987; Wolfe et al., 1987). Liston (1997) later reported the divergence time estimates between the two species as 36.5–50.5 mya and 42 mya based on allozyme data and *rbc*L sequences, respectively (Fig. 3; Table 1). He suggested that the ancestral populations of *Datisca* probably migrated via the North Atlantic land bridge rather than Beringia in the Eocene.

The disjunct pattern in *Styrax officinalis* L. (Styracaceae) was investigated by Fritsch (1996, 2001a, 2001b) with isozyme, chloroplast DNA restriction sites, and internal transcribed spacer (ITS) sequence data. The Mediterranean taxon was recognized as *S. officinalis* subsp. *officinalis*, whereas the Californian taxa were recognized as *S. officinalis* subsp. *fulvescens* (Eastw.) A. E. Murray and *S. officinalis* subsp. *redivivus* (Torr.)

Thorne. The ITS sequence data have shown that the two subspecies of *S. officinalis* from California form a clade with three other western North American species (*S. platanifolius* Engelm. ex Torr., *S. texanus* Cory, and *S. youngiae* Cory) and this western North American clade is then sister to *S. officinalis* subsp. *officinalis* from the Mediterranean region (Fritsch 2001a). The estimated divergence time between the Madrean and Tethyan taxa in *Styrax* is 5–13.8 mya during the middle to late Miocene (Fig. 3; Table 1). This estimate is substantially younger than the predicted age via Axelrod's Madrean–Tethyan hypothesis of the origin of this disjunct pattern of at least 25 mya (Axelrod, 1973). Yet, the monophyly of the western Asian taxon with the western North American taxa is consistent with Madrean–Tethyan migration from a common ancestor. Fritsch (1996, 2001a) argued against long-distance dispersal as an explanation in this case owing to the low dispersability of the taxa involved.

Phylogenetic and biogeographic relationships of the subfamily Arbutoideae (Ericaceae) have been constructed using the ITS region of nuclear ribosomal DNA (Hilemann et al., 2001). The subfamily is a monophyletic group within Ericaceae and consists of six genera: *Arbutus* L., *Arctostaphylos* Adans., *Arctous* Nied., *Comarostaphylis* Zucc., *Ornithostaphylos* Small, and *Xylococcus* Nutt. The members of this subfamily are dry-adapted, sclerophyllous taxa with high diversity in regions with a Mediterranean-type climate, especially western North America, Europe/western Asia, and North Africa. The analysis (Hilemann et al., 2001) suggested that *Arbutus* (approximately 11 species) was not monophyletic. The Mediterranean species are more closely related to a clade containing *Artostaphylos*, *Arctous*, *Comarostapylis*, *Ornithostaphylos*, and *Xylococcus* than to the western North American congeners of
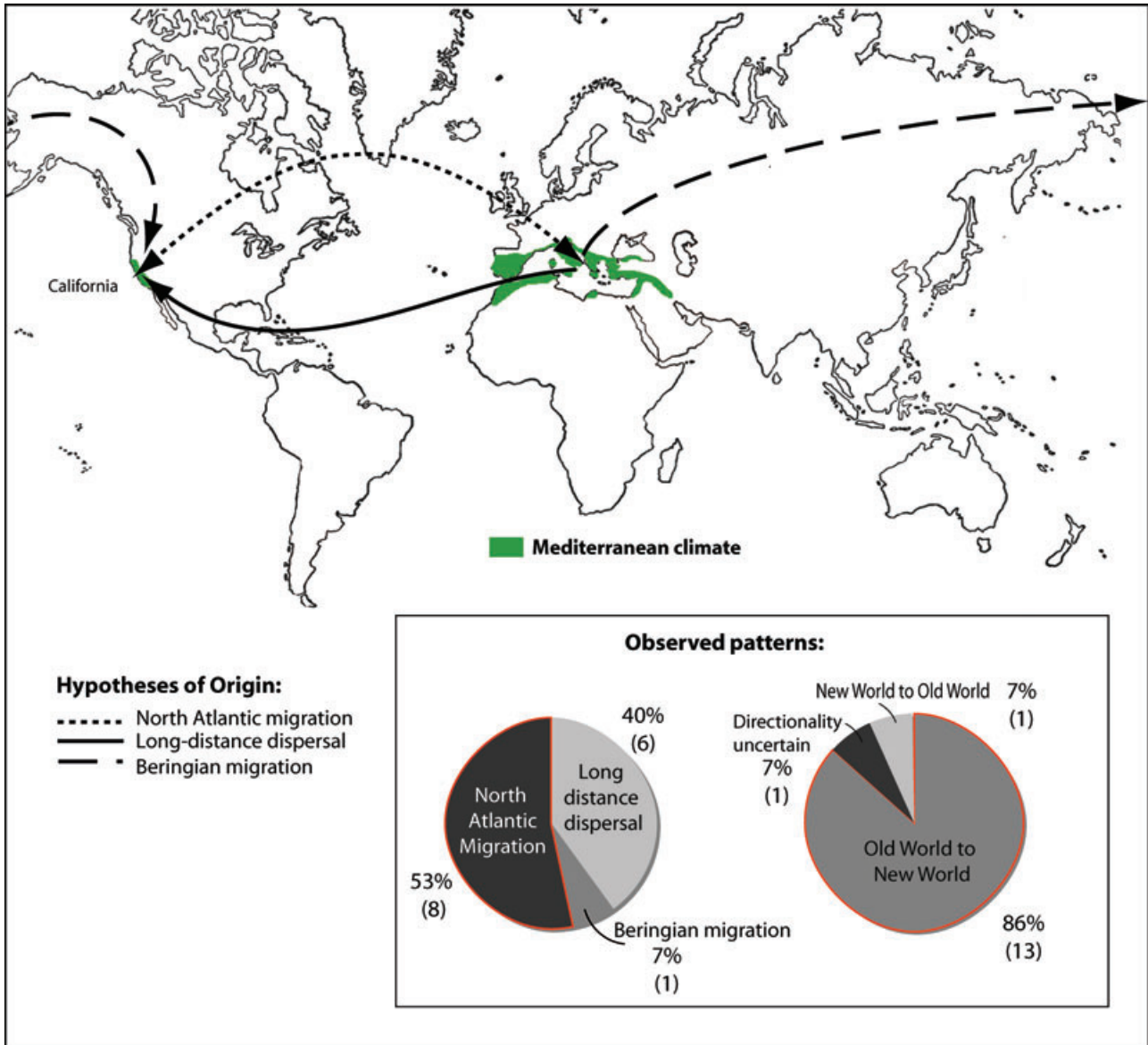
Fig. 2.   The Madrean–Tethyan disjunctions between western North America and Mediterranean southern Europe and adjacent areas in western Asia and northern Africa. Three hypotheses on the origin of such disjunctions are illustrated, namely the North Atlantic migration, long-distance dispersal, and the Beringian migration, with the observed frequencies of the hypotheses and the directionality of the migration/dispersal also shown.

Arbutus. The divergence between the Mediterranean and western North American relatives is dated from 21.2 to 39.2 mya (Fig. 3; Table 1). The phylogenetic pattern and age estimate are consistent with the Madrean–Tethyan hypothesis proposed by Axelrod (1973), as preferred by Hilemann et al. (2001).

The Old World and New World *Senecio* L. sect. *Senecio* was analyzed using nuclear ribosomal ITS sequences (Coleman et al., 2003). This section includes two striking disjunct species: (i) *Senecio flavus* Sch. Bip. disjunct between the Mediterranean basin/northern

Africa and South Africa (Namibia; Liston & Kadereit, 1995); and (ii) *S. mohavensis* A. Gray between western North America (subsp. *mohavensis*) and southwestern Asia (subsp. *breviflorus* (Kadereit) M. Coleman). The two subspecies of *S. mohavensis* form a well-supported monophyletic group in the ITS trees and show no variation in ITS sequences, supporting their divergence during the past 0.15 mya (Fig. 3; Table 1). *Senecio mohavensis* subsp. *mohavensis* is the only North American member of a Mediterranean subclade, supporting long distance dispersal in the direction from the Old
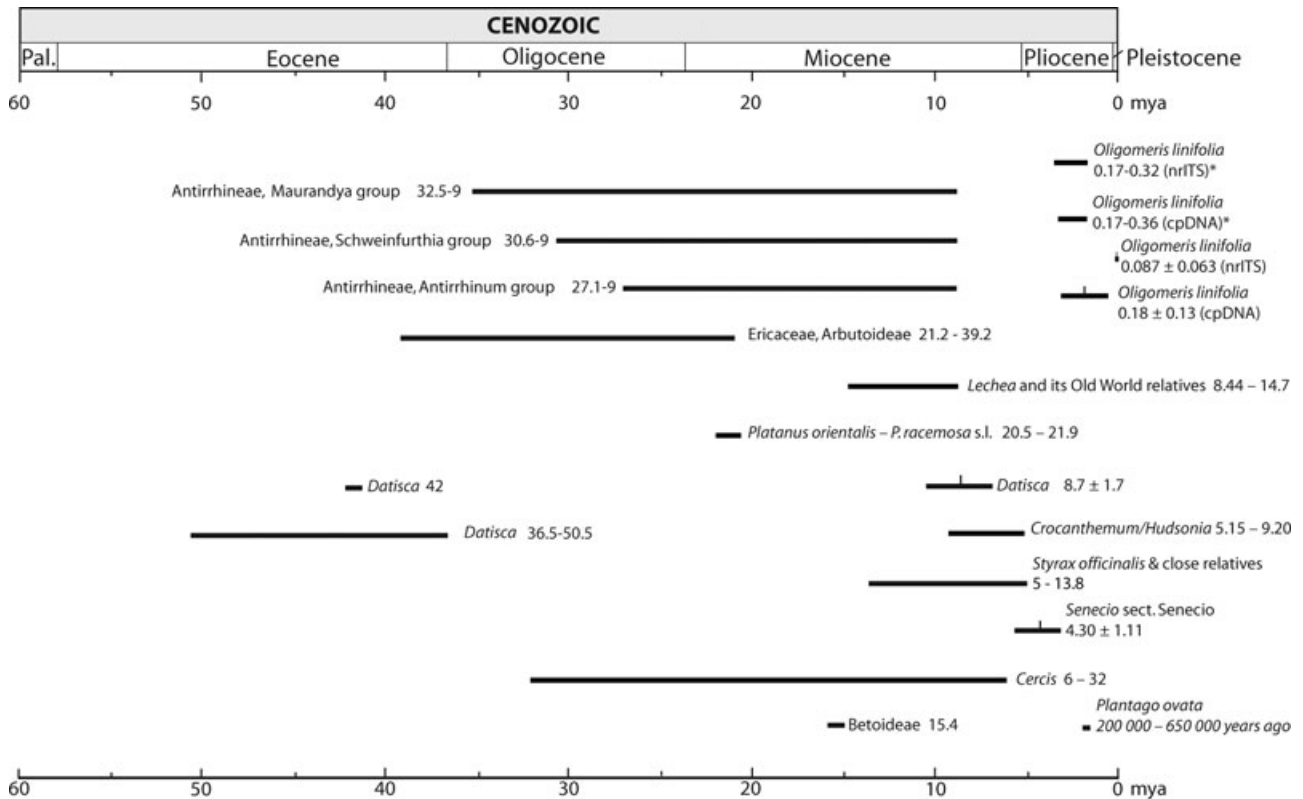
Fig. 3.   Overview of divergence times in the Madrean–Tethyan disjuncts based on available studies (see Table 1 for details).

World to western North America, as also suggested by Liston et al. (1989). The recent divergence via long-distance dispersal was consistent with Raven's hypothesis on the origin of this disjunct pattern (Raven, 1972, 1973).

Cercis L. (Fabaceae) contains approximately 10 species disjunctly distributed in four areas of the north temperate zone, namely the eastern US to northeastern Mexico, western North America, the Mediterranean region to central Asia, and eastern Asia. *Cercis* occurs in the mesic through arid zones in both North America and Eurasia. Davis et al. (2002) estimated its phylogeny with the nuclear ribosomal ITS and chloroplast *ndh*F gene sequences. The eastern North American *C. canadensis* L. is more closely related to *C. siliquastrum* L. from western Eurasia than to the western North American *C. occidentalis* Torr. ex A. Gray. The adaptation to the arid climate was inferred to have originated once in *Cercis* from mesophytic ancestors. The possible divergence time for the North American and western Eurasian lineages ranged from 6 to 32 mya (Fig. 3; Table 1) depending on the placement of the oldest *Cercis* fruit fossil. The estimate used a molecular clock, because the clock could not be rejected. The oldest estimate was consistent with the Madrean–Tethyan hypothesis and the youngest requires an explanation via long-distance dispersal.

The Mediterranean intercontinental disjuncts of mosses account for 5% of the mosses of Pacific North America (Schofield, 1984). This pattern was recently analyzed by Shaw et al. (2003), who focused on three species of mosses, namely *Claopodium whippleanum* (Sull.) Ren. & Card., *Dicranoweisia cirrata* (Hedw.) Linb., and *Scleropodium touretii* (Brid.) L. F. Koch, disjunct between western North America and Mediterranean Eurasia and adjacent northern Africa and western Asia. That study documented the differentiation of the disjunct taxa at both the morphological and molecular levels. Quantitative measurements of morphological characters did not reveal significant differentiation between Old and New World disjunct populations in any of the three species studied. Conversely, molecular data showed some geographic patterning between the two continents. In *Claopodium*, five Old World populations shared a mutation that distinguished them from all New World populations. In *Dicranoweisia*, a clade of nine western North American populations shared five mutations, but the other 12 North American populations are identical to five Old World populations in ITS haplotypes. The authors regarded the well-marked clade

Table 1   Origin and evolution of the Madrean–Tethyan disjunctions

Taxon	Estimated age	Most plausible hypothesis on origin	References
Asteraceae, *Senecio mohavensis* subsp. *mohavensis*, and subsp. *breviflorus*	0.15 mya	Long-distance dispersal from Old World to western North America	Coleman et al., 2003
Chenopodiaceae, Betoideae	15.4 (18.7) mya	Fragmentation of a Beringian ancestral range	Hohmann et al., 2006
Cistaceae, *Crocanthemum/Hudsonia*	5.15–9.20 mya	Migration from Old World to New World	Guzmán & Vargas, 2009
Cistaceae, *Lechea* and its Old World relatives	8.44–14.7 mya	Migration from Old World to New World	Guzmán & Vargas, 2009
Datiscaceae, *Datisca*	36.5–50.5 mya (allozyme data) 42 mya (*rbcL* sequences) 8.7 ± 1.7 mya (cpDNA restriction sites)	Migration via the North Atlantic land bridge in the Eocene; no directionality hypothesized	Liston et al., 1989, 1992; Liston, 1997
Ericaceae, Arbutoideae	21.2–39.2 mya	Madrean–Tethyan vicariance; migration from New World to the Mediterranean Basin	Hilemann et al., 2001
Fabaceae, *Cercis*	6–32 mya	Madrean–Tethyan hypothesis or long-distance dispersal; likely from Old World to New World	Davis et al., 2002
Plantaginaceae, *Plantago ovata*	200 000–650 000 years ago	Likely long-distance dispersal via epizoochory, from Asia to North America	Meyers & Liston, 2008
Plantanaceae, *Platanus orientalis – P. racemosa* s.l.	20.5–21.9 mya	Madrean–Tethyan hypothesis	Feng et al., 2005
Resedaceae, *Oligomeris linifolia*	0.18 ± 0.13 mya (cpDNA) and 0.087 ± 0.063 mya (ITS) using the penalized likelihood approach 0.17–0.32 mya (ITS) and 0.17–0.36 mya (cpDNA) using a molecular clock	Long-distance dispersal from Old World to south-western North America	Martín-Bravo et al., 2009
Scrophulariaceae, Antirrhineae, Antirrhinum group	27.1–9 mya	North Atlantic migration, most likely from Eurasia to New World, with seeds in dehiscent capsules presumably not suitable for long-distance dispersal	Vargas et al., 2004
Scrophulariaceae, Antirrhineae, Schweinfurthia group	32.5–9 mya	North Atlantic migration, most likely from Eurasia to New World, with seeds in dehiscent capsules presumably not suitable for long-distance dispersal	Vargas et al., 2004
Scrophulariaceae, Antirrhineae, Maurandya group	30.6–9 mya	North Atlantic migration, most likely from Eurasia to New World, with seeds in dehiscent capsules presumably not suitable for long-distance dispersal	Vargas et al., 2004
Styracaceae, *Styrax officinalis* & close relatives	5–13.8 mya	Madrean–Tethyan migration, with low dispersability arguing against dispersal	Fritsch, 1996, 2001a
Bryophyte, *Claopodium whippleanum*	Recent	Long-distance dispersal, directionality uncertain	Shaw et al., 2003
Bryophyte, *Dicranoweisia cirrata*	Recent	Long-distance dispersal, directionality uncertain	Shaw et al., 2003
Bryophyte, *Scleropodium touretii*	Recent	Long-distance dispersal, most likely from Old World to New World	Shaw et al., 2003

cpDNA, xxx; ITS, internal transcribed spacer.

from North America as a possible derivative of the ancestral haplotypes of the New and Old World plants. The ITS haplotype network suggests that the species dispersed to Mexico, rather than northward dispersal into North America from the Old World. In *Scleropodium*, the New and the Old World populations are differentiated at the molecular level, but one population from California lacks the mutations that characterize the New World populations. The Old World populations form a paraphyletic grade from which the New World populations were derived. In all three disjunct species, North American species possessed higher levels of nucleotide

diversity compared with their Old World counterparts. The differentiations between the disjunct populations in all three genera are nevertheless minor and thus the results are not consistent with a Madrean–Tethyan hypothesis to explain the disjunct distribution because the hypothesis would require a divergence time of more than 20–25 mya (Axelrod, 1973, 1975). Shaw et al. (2003) regard recent long-distance dispersal as the most likely explanation for intercontinental disjunctions in these genera.

Vargas et al. (2004) detected three independent disjunctions between western America and the western

Mediterranean Basin in the tribe Antirrhineae (Scrophulariaceae). The three lineages displayed similar levels of ITS sequence divergence. Based on a general molecular clock, as calibrated in Richardson et al. (2001), and the average pairwise Kimura-2 parameter distance of the ITS regions, the authors estimated the divergence times in these three lineages to be between 9 and 11 mya in the mid-Miocene. The maximum divergence times, obtained by applying the most conservative ITS sequence substitution rate of 1.72×10^{-9}, were 30.6–9 mya in the Maurandya group, 32.5–9 mya in the Schweinfurthia group, and 27.1–9 mya in the Antirrhinum group (Fig. 3; Table 1). Vargas et al. (2004) preferred migration through an Atlantic track. Based on the phylogenetic trees of Vargas et al. (2004), the direction of migration seems to be from the Old World to the New World.

Feng et al. (2005) conducted phylogenetic analyses of six species of *Platanus* L. (Platanaceae) with sequences of the ITS regions, the 3′ region of the second intron of *LEAFY*, and the chloroplast *trnT–trnL* intergenic spacer. Their analysis identified a semiarid clade of *P. orientalis* L. from the eastern Mediterranean Europe and *P. racemosa* Nutt. from western North America. The combined data and a pruned combined dataset were shown to follow a clock-like evolutionary pattern. The authors used fossil calibrations within *Platanus* and estimated the divergence of the *P. orientalis–P. racemosa* node to range from 20.5 to 21.9 mya (Fig. 3; Table 1). The Madrean–Tethyan hypothesis was preferred by the authors to explain the disjunction.

Subfamily Betoideae of Chenopodiaceae consists of five genera, namely *Beta* L., *Aphanisma* Nutt. Ex Moq., *Hablitzia* M. Bieb., *Oreobliton* Dur. & Moq., and *Patellifolia* A. J. Scott, B. V. Ford-Lloyd & J. T. Williams as circumscribed by Hohmann et al. (2006), which is a modified classification of Ulbrich (1934). *Aphanisma* occurs in western North America, whereas the other four genera are from Mediterranean Eurasia and adjacent North Africa. The phylogeny of Betoideae was constructed using *ndhF*, *matK*, *trnL-F* intergenic spacer, and ITS sequences and this phylogeny was used to explore the origin and evolution of the Mediterranean–Californian disjunction (Hohmann et al., 2006). The monophyly of Betoideae sensu Hohmann et al. (2006) was supported and the western North American *Aphanisma* was found sister to the Mediterranean *Oreobliton* in all markers examined. This intercontinental disjunction was estimated to range between 8.1 and 15.4 (18.7) mya using the penalized likelihood method (Sanderson, 2002, 2003; Fig. 3; Table 1) with each of the four molecular datasets individually and constraining the molecular phylogeny with three fossils in the *ndhF* and *matK* data, and with calibra-

tion of the basal-most node using the *ndhF* estimates in the case of the smaller ITS and *trnL-F* data. Based on the estimates of the divergence times, Hohmann et al. (2006) have argued that it was unlikely for Betoideae to have achieved the disjunction via the North Atlantic migration route. Instead, they concluded that the western Eurasian–western North American disjunction between *Oreobliton* and *Aphanisma* is more likely to have resulted from the fragmentation of a Beringian ancestral range, as postulated by Stebbins and Day (1967). The adaptation to dry habitats of the disjuncts then took place in parallel in western Eurasia and western North America.

Plantago ovata Forssk. (Plantaginaceae) is a disjunct species that occurs in the deserts along the Mediterranean Sea and southwestern Asia extending from the Canary Islands to western India in the Old World, and in the Sonoran and Mohave deserts of the southwestern US, Baja California, northwestern Mexico, as well as in coastal California, the Channel Islands of California, and Mexico in the New World (Meyers & Liston, 2008). Stebbins and Day (1967) detected cytological and morphological differences of plants grown from the Old and New Worlds and recognized two species, *P. ovata* from the Old World and *P. fastigiata* Morris in the New World. Meyers and Liston (2008) used sequence data from the chloroplast *trnL-F*, *trnS-G*, and *psbA–trnH* regions and the nuclear ribosomal ITS and a putative *CYCLOIDEA*-like gene and suggested that the introduction of *P. ovata* from the Old World to North America occurred 200 000–650 000 years ago during the Pleistocene (Fig. 3; Table 1). Their dating was based on molecular clocks for both the chloroplast (2.5×10^{-9} substitutions per site per year) and nuclear ITS (4.27×10^{-9} substitutions per site per year) data. The mechanisms for introduction were hypothesized to be likely dispersal via epizoochory. The authors recognized four varieties of *P. ovata* and the North American *P. ovata* was shown to be a hybrid between Old World varieties.

Oligomeris linifolia (Vahl) J. F. Macbr. (Resedaceae) is a widespread species in arid regions in southwestern Asia to northern Africa, as well as in deserts of southwestern North America, and has also been reported in the upper Yangtze river valley in China by Lu and Turland (2001). Martín-Bravo et al. (2009) used the penalized likelihood approach (Sanderson, 2002, 2003) with the ITS and plastid *rbcL–matK–trnL-F* sequences and suggested a relatively recent origin of *O. linifolia* (0.18 ± 0.13 mya, cpDNA; 0.087 ± 0.063 mya, ITS). A second molecular clock estimate resulted in the maximum age of the disjunction as 0.17–0.32 mya (ITS) and 0.17–0.36 mya

(cpDNA; Fig. 3; Table 1). Thus, the results support a recent long-distance dispersal event from the Old World to southwestern North America in the Quaternary.

From the studies presented in this review (also see Table 1), the origin of the Madrean–Tethyan disjunction seems to be highly complex, involving long-distance dispersal, the North Atlantic migration, and the Beringian migration (Figs. 2, 3). Convergent evolution may have reinforced the floristic similarity during adaptation to the semiarid Mediterranean-type climate after the formation of the disjunction (Wolfe, 1975; Liston, 1997; Hohmann et al., 2006), such as in the case of some morphologically similar members of *Pinus* L. in the Mediterranean and the New World (Liston et al., 1999). The Madrean–Tethyan hypothesis as postulated by Axelrod (1973; Fig. 2) predicts early divergence of the intercontinental disjuncts. A number of recent studies (see Table 1) obtained estimates largely younger than 25 mya, which was the upper boundary of the direct vicariance between the two floristic regions (Axelrod, 1975). Thus, the long-distance dispersal hypothesis has been favored by a few recent studies. Nevertheless, the Madrean–Tethyan migration has been preferred by a number of analyses (Table 1; Fig. 2). The complex origin of this disjunct pattern may also reflect the highly dynamic paleogeologic history in the Tertiary of the Mediterranean region, which, in general, included the western Mediterranean, North Africa, Balkans–Anatolia, Middle East, Caucasus, the Iranian Plateau, and central Asia (Sanmartín, 2003). It has been noted that the directionality of the migration/dispersal was inferred to be mostly from the Old World to the New World (Table 1; Fig. 2). This pattern certainly needs to be tested further with additional analyses.

2   Amphitropical disjunctions

Plant disjunctions between North and South America have been discussed by botanists for over a century (Gray & Hooker, 1880; Engler, 1882; Bray, 1898, 1900; DuReitz, 1940; Raven, 1963; Ochyra & Buck, 2003). Many botanists have studied this intercontinental disjunction, and an entire volume of the *Quarterly Review of Biology* was devoted to amphitropical disjunctions (Constance, 1963). Many different plant groups were documented to demonstrate such a disjunct pattern, and a few hypotheses have been proposed to explain this pattern. Raven (1963) distinguishes three unique classes of amphitropical disjuncts (Fig. 4): (i) a bipolar pattern; (ii) a pattern among temperate taxa; and (iii) desert disjunctions. These disjuncts may also be grouped based on their taxonomic and phylogenetic complexities. Many cases with the amphitropical disjunctions are identical or closely related species (Raven, 1963; Moore et al., 2006; Holmes et al., 2008). A second class of amphitropical disjuncts has groups that are well differentiated in
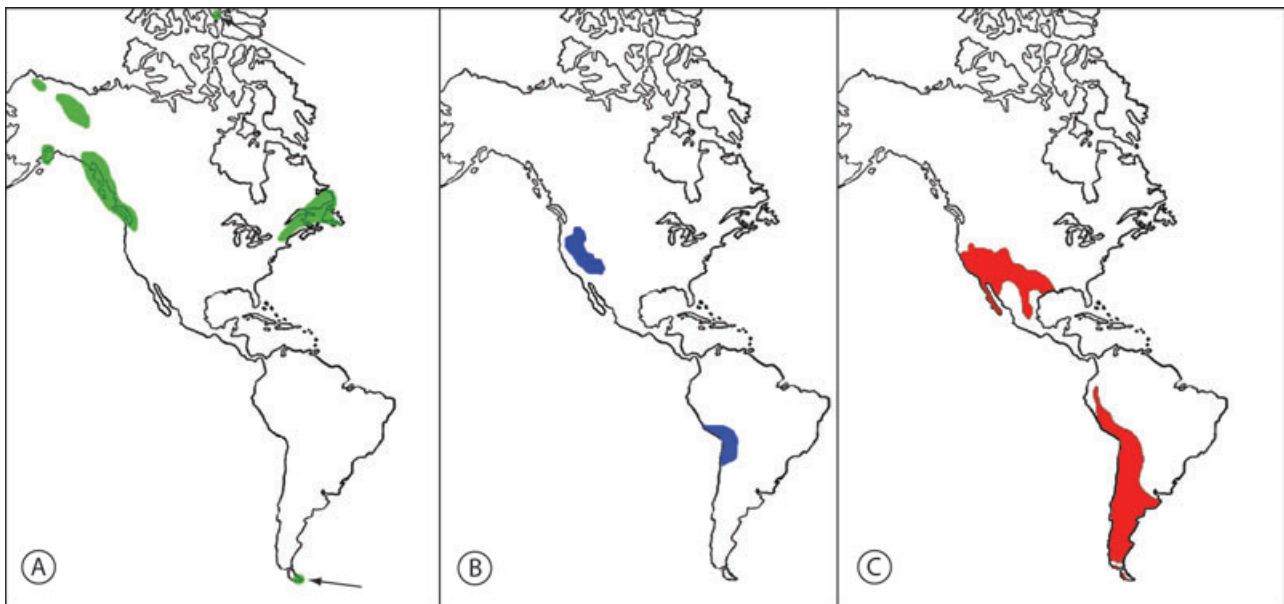

Fig. 4.   Three types of amphitropical disjunctions between North America and South America. **A,** The bipolar pattern, exemplified by distribution of the bipolar moss disjunct *Arctoa fulvella* (Dicks.) Bruch & Schimp. (adapted from Ochyra & Buck, 2003). **B,** Temperate disjunction, exemplified by the *Phacelia* Juss. distribution (modified from Solbrig, 1972). **C,** Desert disjunction, as illustrated by distribution of *Ephedra* L. (modified from Caveney et al., 2001).

both continents, such as *Astragalus* L. (Scherson et al., 2008), *Ephedra* L. (Ickert-Bond et al., 2009), and *Hoffmanseggia* Cav. (Simpson et al., 2005). Bipolar disjunctions are mostly of widely distributed species from high latitudes. These disjuncts belong to a very small proportion of the circumboreal flora, rather than the most dominant members of the floras in the two disjunct regions. Raven (1963) suggests that these disjuncts attained their current distribution no earlier than the late Pliocene or Pleistocene via long-distance dispersal. Some examples of approximately 30 species of bipolar disjunct plants are *Arctoa fulvella* (Dicks.) Bruch & Schimp., *Botrychium lunaria* (L.) Swartz, *Cryptogramma crispa* (L.) R. Br. var. *acrostichoides* (R. Br.) C. B. Clarke, *Deschampsia caespitosa* (L.) Beauv., *Lathyrus japonicus* Willd., and *Plantago maritima* L. subsp. *juncoides* (Lam.) Hultén.

Temperate disjuncts are most common in the amphitropical distributional pattern. Raven (1963) lists 130 examples, of which 95 are restricted to the western part of North America. Many hierarchical levels are involved in this pattern, such as at the generic level (e.g. *Astragalus* L., *Galium* L., *Haplopappus* Cass., *Lesquerella* S. Wats., *Microseris* D. Don, *Phacelia* Juss., *Stachys* L., *Verbena* L., and *Osmorhiza* Raf.) and in species and species groups (e.g. *Azolla filiculoides* Lam., *Dalea leporina* (Aiton) Bullock, *Petunia parviflora* Juss., and *Baccharis glutinosa* Pers.). Most temperate disjuncts have an autogamous breeding system and a widespread distribution occurring in open habitats. The timing of this disjunct pattern was suggested to date back at least to the Pliocene, whereas the evolution of the herbaceous members may have occurred later (Raven, 1963; Wen et al., 2002). In addition, very few animal groups show this distributional pattern, except for some insect genera showing temperate disjuncts. Some examples of temperate amphitropical disjunct plant species include *Amsinkia menziesii* (Lehm.) Nels. & Macbr., *Androsace occidentalis* Pursh., *Crypthantha minima* Rydb., *Erigeron dendroideum* (Nutt.) S. Stokes, *Lepidium nitidum* Nutt., *Osmorhiza depauperata* Phil., *Osmorhiza berteroi* DC., *Pellaea andromedifolia* Fée, *Phacelia affinis* A. Gray, *Polystichum lemmonnii* Underw., *Sanicula graveolens* Poepp. ex DC., and *Sanicula crassicaulis* Poepp. ex DC.

Desert amphitropical disjunctions include many plants from the Sonoran and Chihuahuan deserts in North America with similar habitats in the deserts of northern Chile and northern Argentina in South America. In contrast with the mainly herbaceous members of the bipolar and temperate disjuncts, there are many more woody members, some of which may have originated from tropical ancestors (*Acacia* L., *Caesalpinia* L., *Condalia* Cav., and *Pithecellobium* Mart.).

Conversely, other woody members (e.g. *Gutierrezia* Laq., *Helietta* Tul., *Hoffmanseggia*, *Menodora* Humb. & Bonpl., *Lippia* L., and *Lycium* L.) may have their biogeographic origin in temperate mesic forests prior to the development of the arid and semiarid habitats in these two disjunct regions. Some temperate disjuncts also include suffructescent herbs (e.g. *Fagonia* L.). No vertebrates have desert disjunct distributional patterns, and the insects of North and South America are also very different. The origin of the deserts is generally assumed to be recent, because the mesic Neotropical–Tertiary Geoflora (Axelrod, 1958) did not disappear until after the Oligocene. Raven (1963) concludes that most of the desert disjuncts seem to have originated in South America and have arrived in North America via long-distance dispersal, generally having diverged from tropical ancestors, whereas both bipolar and temperate disjuncts seem to have originated in the North and arrived in South America via long-distance dispersal.

The recency of many amphitropical disjunctions was supported by Chambers (1963) and Moore and Raven (1970). Both studies presented cytological evidence from crossing experiments that demonstrated the variability of reproductive isolation ranging from fully interfertile hybrids in intercontinental disjuncts to major chromosomal repatterning in intercontinental hybrids of *Camissonia dentata* Reiche and *Microseris* D. Don. In a study comparing the amphitropical disjunct pattern in grasses, Peterson and Ortíz-Diaz (1998) presented results from analysis of allozyme data in *Muehlenbergia* Schreb. (Poaceae) and confirmed an earlier assumption that this disjunction is of rather recent origin due to long-distance dispersal from North to South America. They found less allelic variation in the South American populations of *M. torreyi* Hitchcock ex Bush than those in North America. Similar conclusions on recency of origin and the dispersal from North to South America were reached in several grass lineages (Table 2). Peterson and Ortíz-Diaz (1998) did point out that the amphitropical disjunct grass genus *Erioneuron* Nash dispersed from South America to North America. Unlike the other examples of grasses cited in Table 2, this genus had its center of diversity in South America.

Linanthus Benth. (Polemoniaceae), with 44 species, occurs throughout western North America with one species, *L. pusillus* (Benth.) Greene, endemic to Chile. Most species are endemic to the Californian floristic province and occupy various habitats throughout the state (Bell & Patterson, 2000). The Chilean *L. pusillus* is found to be nested within the Letosiphon clade of *Linanthus*. Using the *matK* data set, Bell and Patterson (2000) estimated that the clade containing *L. pusillus* and its 14 close relatives diversified and

Table 2   Origin and evolution of amphitropical disjunctions between North and South America

| Taxon	Estimated age	Most plausible hypothesis of the origin	References
Apiaceae, *Osmorhiza berteroi*	Very recent within 1 mya	Long-distance dispersal from North to South America	Wen et al., 2002
Apiaceae, *Osmorhiza depauperata*	Very recent within 1 mya	Long-distance dispersal from North to South America	Wen et al., 2002
Apiaceae, *Sanicula crasssicaulis*	1 mya	Long-distance dispersal from temperate western North America to southern South America Fruits with hooked spines, likely bird-mediated dispersal	Vargas et al., 1998
Apiaceae, *Sanicula graveolens*	2 mya	Long-distance dispersal from temperate western North America to southern South America	Vargas et al., 1998
Asteraceae, *Agoseris*	Quite recent, but pre-Pleistocene	Disjunction between *Agoseris coronopifolia* from southern South America and *A. heterophylla* from south-western North America Long-distance dispersal from North to South America	Chambers, 1963
Asteraceae, *Microseris*	Middle or late Pliocene	Disjunction between *Microseris pymaea* from Chile and *M. bigelovii* from North America Long-distance dispersal from North to South America	Chambers, 1963
Boraginaceae, *Tiquilia* subg. *Tiquilia*, the *T. plicata* clade	3–6 mya	Different datasets supporting conflicting dispersal histories, but from North America to South America and Galápagos	Moore et al., 2006
Boraginaceae, *Tiquilia* subg. *Tiquilia*, the *T. palmeri* species group	3–6 mya	Long-distance dispersal from North to South America, radiation due to novel pollinators	Moore et al., 2006
Boraginaceae, *Tiquilia* subg. *Tiquilia, T. nuttallii*	Recent colonization within the last few thousand years	Long-distance dispersal from North to South America	Moore et al., 2006
Brassicaceae, *Rorippa*, the *R. philippiana – R. curvisiliqua* lineage	Low sequence divergence suggesting very recent dispersal	Long-distance dispersal via migrating birds; directionality unknown	Bleeker et al., 2002
Empetraceae, *Empetrum*	Not available, but indicated to be very recent	Long-distance dispersal from the northern hemisphere to South America	Li et al., 2002
Ephedraceae, *Ephedra*, the New World clade	ca. 25 mya	Long-distance dispersal from North to South America, perhaps mediated by birds (endozoochory)	Ickert-Bond et al., 2009
Fabaceae, *Astragalus*, South American clade F	1.89 mya	Likely long-distance dispersal from North to South America	Scherson et al., 2008
Fabaceae, *Astragalus*, South American clade G	0.98 mya	Likely long-distance dispersal from North to South America	Scherson et al., 2008
Fabaceae, *Hoffmannseggia*, suffrutescent clade S1	Late Miocene or later	Dispersal from South to North America via birds	Simpson et al., 2005
Fabaceae, *Hoffmannseggia*, suffrutescent clade S2	Late Miocene or later	Dispersal from South to North America via birds and radiation within North America	Simpson et al., 2005
Fabaceae, *Hoffmannseggia*, herbaceous clade H2	Late Miocene or later	Dispersal from South to North America via birds and northward movement	Simpson et al., 2005
Fabaceae, *Hoffmannseggia, H. glauca* in herbaceous clade H3	Perhaps Pleistocene	Long-distance dispersal via birds of the disjunct species *H. glauca* from South to North America (from coastal Peru into Mexico, then to western US)	Simpson et al., 2005
Fabaceae, *Lupinus*, the Andean crown node	1.47–1.93 mya	Long-distance dispersal from North to South America	Hughes & Eastwood, 2006
Fabaceae, *Prosopis*	Not available	Long-distance dispersal from North to South America perhaps mediated by birds	Bessega et al., 2006
Fabaceae, *Prosopis glandulosa*	Very recent	Long-distance dispersal from South to North America	Bessega et al., 2006
Fabaceae, *Prosopis velutina*	Very recent	Long-distance dispersal from South to North America	Bessega et al., 2006
Poaceae, *Chaboissaea*	Recent	Long-distance dispersal from Mexico to South America	Peterson & Herrera, 1995; Sykes et al., 1997
Poaceae, *Erioneuron*	Recent	Long-distance dispersal from South to North America	Peterson & Ortíz-Diaz, 1998
Poaceae, *Lycurus setosus*	Recent	Long-distance dispersal from North to South America	Peterson & Morrone, 1997
Poaceae, *Muehlenbergia torreyi*	Late Tertiary	Long-distance dispersal from North America to the Andes	Peterson & Ortíz-Diaz, 1998
Poaceae, *Scleropogon brevifolius*	Recent	Long-distance dispersal from North to South America	Peterson & Columbus, 1997
Polemoniaceae, *Linanthus pusillus/ L. felipes*	2 mya	Long-distance dispersal from North to South America	Bell & Patterson, 2000

Table 2   (continued)

Taxon	Estimated age	Most plausible hypothesis of the origin	References
Portulacaceae, *Calandrinia*		Possible disjunction in *Calandrinia*	Hershkovitz & Zimmer, 2000
Solanaceae, *Lycium*, one older lineage	Late Tertiary	Long-distance dispersal from South to North America	Fukuda et al., 2001
Solanaceae, *Lycium*, the lineage containing *L. americanum*, *L. elongatum*, and *L. carolinianum*	Quaternary	Long-distance dispersal likely from North to South America	Fukuda et al., 2001
Valerianaceae, *Plectritis*	No age estimate available on the disjunction; likely in the late Tertiary	Dispersal from western South America to western North America	Bell & Donoghue, 2005
Zygophyllaceae, *Fagonia*	Long-distance dispersal possibly during the Pleistocene	Vicariance led to the split of *Fagonia* into New and Old World groups, dispersal from North to South America	Beier et al., 2004
Zygophyllaceae, *Larrea*	Late Neogene (8.4–4.2 mya)	Dispersal from South America to North America	Cortes & Hunziker, 1997; Hunter et al., 2001; Lia et al., 2001

speciated extensively in the timeframe from 1.6 to 5 mya (Fig. 5; Table 2). *Linanthus pusillus* is found to be sister to *L. filipes* (Benth.) Greene from western North America in the *mat*K strict consensus and in the ITS maximum likelihood tree. The estimated divergence time between *L. pusillus* and *L. filipes* is approximately 2 mya. The Chilean distribution of *L. pusillus* is consistent with a dispersal event.

Further support for the recency of amphitropical disjunctions was provided by Wen et al. (2002)

in their study of *Osmorhiza* (Apiaceae). The absence of ITS sequence divergence between the North and South American populations of *O. depauperata* and low divergence in *O. berteroi* support the recent origin of this disjunction in both disjunct species (Fig. 5; Table 2). The genus-wide phylogeny suggests dispersal from North to South America. The spiny fruit morphology and an autogamous breeding system of both species may have facilitated long-distance dispersal via birds.
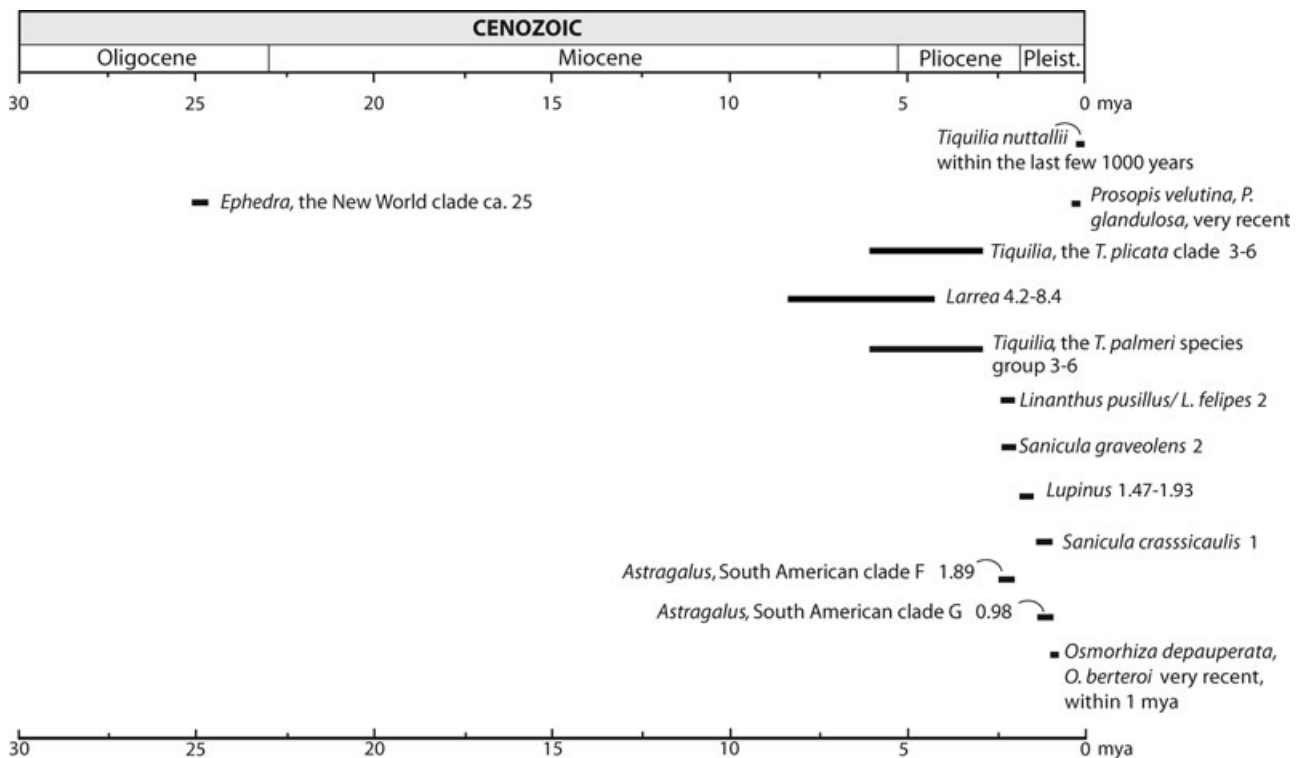
Fig. 5. Overview of divergence times of North and South American amphitropical disjuncts based on available studies (see Table 2 for details).

In their study using sequence data from the plastid *trnL* intron and nuclear ribosomal ITS DNA, Beier et al. (2004) also provide support for dispersal from North to South America in the shrub genus *Fagonia* L. (Zygophyllaceae), possibly during the Pleistocene. Another example from the Zygophyllaceae with this classical amphitropical disjunct pattern is the genus *Larrea*, which has four species distributed in South America and one species, *L. tridentata* (DC.) Coville, widely distributed from the Chihuahuan desert west to the Mohave desert in North America. Using sequence data from *rbcL* and nuclear ribosomal ITS with a molecular clock hypothesis of sequence evolution, Lia et al. (2001) dated the arrival in North America of *L. tridentata* to the late Neogene (8.4–4.2 mya; Fig. 5; Table 2). Furthermore, the distribution of ploidy races within North American *Larrea* has been demonstrated to increase with aridity from east (diploid in the Chihuahuan desert) to west (hexaploid in the Mohave desert) and to be a post-glacial phenomenon (Hunter et al., 2001).

Although a number of studies have demonstrated long-distance dispersal from North to South America as a hypothesis for explaining an amphitropical disjunctional pattern, several studies have also documented dispersal from South to North America. Simpson et al. (2005), using nuclear and chloroplast sequence data, illustrate a South American origin for *Hoffmannseggia*, with at least four long-distance dispersal events to North America (Table 2). Two hypothesized dispersal events occurred within the suffrutescent clade: one established *H. drummondii* Torr. & Gray in Texas, whereas the other originated in Peru and dispersed across the Andes into Baja California and North America. Two additional dispersal events occurred in the two herbaceous clades of *Hoffmannseggia*. One of these two dispersal events involves *Hoffmannseggia glauca* (Ortega) Eifert, the only individual species of *Hoffmannseggia* with an amphitropical distribution. The second dispersal event in the herbaceous clade gave rise to a low-elevation coastal taxon in South America and an ancestor that was able to disperse to North America. The exact timing of these dispersal events was not given, but it was hypothesized that these long-distance dispersal events occurred at different times from the late Miocene to the Pliocene.

Fukuda et al. (2001) reconstructed the biogeographic history of *Lycium* L. (Solanaceae), a genus disjunctly distributed in temperate to subtropical regions of South America, North America, Eurasia, southern Africa, and Australia (Table 2). The authors suggested at least three independent dispersals between South and North America, most likely via long-distance dispersal (see also Levin & Miller, 2005). It appears that there was at least one dispersal event from South America to North America during the late Tertiary. It seems that there was a recent dispersal from North America to South America likely in the Quaternary (Fukuda et al., 2001).

Moore and Jansen (2006) and Moore et al. (2006) used relaxed molecular clock approaches (Renner, 2005), in particular penalized likelihood methods (Sanderson, 2002, 2003), to test hypotheses of the origin of the amphitropical desert disjunct *Tiquilia* Pers. subg. *Tiquilia* (Boraginaceae). Using data from both the chloroplast and nuclear genomes, Moore and Jansen (2006) and Moore et al. (2006) demonstrated a North American origin for *Tiquilia* that required multiple long-distance dispersal events from North to South America. The two subgenera, namely *Eddya* A. T. Richardson with an exclusive North American distribution and *Tiquilia*, which contains taxa in both North and South America, diverged ca. 33 mya shortly after the great aridification event of the late Eocene/early Ologocene. The divergence of the seven major lineages dates to the early-to-mid Miocene (ca. 23–13 mya). Dispersal-vicariance analysis (DIVA, Ronquist, 1997) analysis of *Tiquilia* subg. *Tiquilia* suggests at least three dispersals from North to South America. *Tiquilia nuttallii* colonized the Monte region of Argentina directly from North America and the ancestor of the blue-flowered group of the *T. palmeri* clade was dispersed from North America to South America. The evolution of the disjunction in the *T. plicata* group was less resolved due to the topological incongruence among the different markers for the group. The cpDNA tree suggested two dispersals from North America: one to South America and one to the Galápagos Islands. Two dispersals were required by the ITS data to explain the distribution of the *T. plicata* clade. However, whether the initial dispersal was to South America or to the Galápagos Islands remain unresolved. The *T. nutallii* dispersal was very recent, perhaps in the last few thousand years, as indicated by the sequence uniformity across all markers and the current restricted distribution of the taxon in Argentina. The other disjunct lineages were not directly dated, but seemed to range from 3 to 6 mya (Fig. 5; Table 2).

Bell and Donoghue (2005) reconstructed the biogeographic history of Valerianaceae (Dipsacales), which has approximately 350 species widely distributed in the alpine and subalpine zones (Table 2). The family appears to have originated in Asia, most likely in the Himalayan region, then dispersed several times to Europe and to the New World. Through several colonization events, the North American taxa of Valerianaceae colonized South America likely in the Miocene. The genus *Plectritis* has five recognized species, four of which are from western North America, ranging from Baja
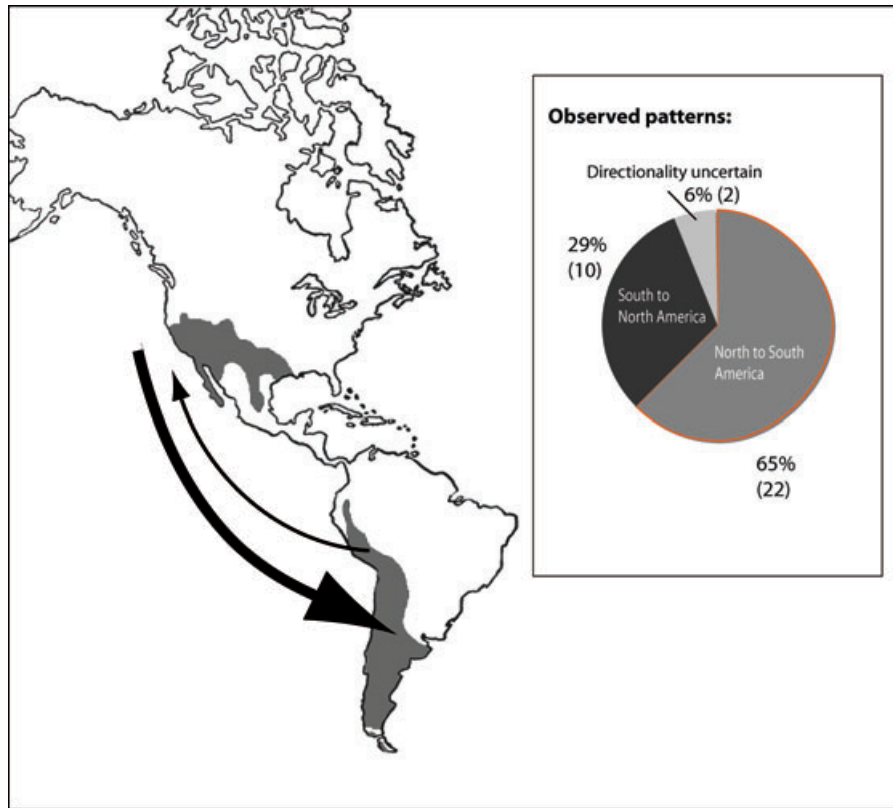
Fig. 6. Frequency and directionality of dispersal events for North and South American amphitropical disjuncts (see Table 2 for details).

California, Mexico, to British Columbia, Canada, and one species in Chile. Bell and Donoghue (2005) were not able to sample the Chilean species. The three western North American species of *Plectrilis* sampled formed a clade nested within *Valeriana* L. from western South America. The authors suggested dispersal from western South America to western North America, most likely in the late Tertiary.

Lupinus L. (Fabaceae) comprises approximately 275 species having an amphiatlantic distribution, with most species from the New World. Within the New World there are two main centers of species diversity: (i) western North America (approximately 100 spp.); and (ii) the Andes (approximately 85 spp.). Using the nuclear ITS and *CYCLOIDEA* gene sequences, Hughes and Eastwood (2006) detected two well-supported New World clades, one from the eastern New World and the other from western North America, Mexico, and the Andes. The Andean species form a subclade, which exhibits diverse life forms and ecologies. The authors also detected a subclade of species from Mexico sister to the Andean subclade. The western North American species are paraphyletic with a subclade of taxa from Mexico and the Andes nested within it. The crown Andean

subclade was estimated to be 1.47–1.93 mya (Fig. 5; Table 2). This phylogenetic pattern suggests dispersal in the late Tertiary in the direction from North America to the Andes in the formation of the amphitropical disjunction in this clade of New World *Lupinus*.

Empetrum L. of Empetraceae (Moore et al., 1970; Anderberg, 1994; Li et al., 2002) has a disjunct distribution between the northern hemisphere and southern South America. The genus is taxonomically difficult, with highly controversial species delimitations, yet two species groups are generally accepted: (i) the red fruited; and (ii) black or purple fruited (Anderberg, 1994). Li et al. (2002) used sequences of the chloroplast *matK* gene and nuclear ribosomal ITS regions to resolve the relationships in the Empetraceae. The monophyly of the genus *Empetrum* from both the northern and southern hemispheres was strongly supported, rejecting the hypothesis of the independent origins of the amphitropical disjuncts in the genus. The results showed recent divergence of the southern hemisphere species from the northern hemisphere taxa, supporting long-distance dispersal as the most likely scenario (Table 2). No age estimates were provided for the amphitropical disjuncts by Li et al. (2002).

In summary, the amphitropical disjunctions between North and South America are a common and well-known biogeographic pattern (Raven, 1963; Barbour, 1969; Hunziker et al., 1977; Cortés & Hunziker, 1997, Lia et al, 2001). Available evidence supports long-distance dispersal in most cases analyzed and has shown a dominant direction of dispersal from North to South America (Table 2; Fig. 5). The amphitropical disjunctions seem to have evolved multiple times and many recent estimates are in the late Tertiary to the Holocene (Table 2; Fig. 6). Many lineages showing very recent divergence between North and South America were suggested to have involved birds as the dispersing agents. Some large genera, such as *Ephedra*, were shown to have dispersed from North America to South American deserts with a single event (Ickert-Bond et al., 2009); yet, at least four dispersal events were inferred in *Tiquila* subg. *Tiquila* with the same direction (Moore et al., 2006). It is certainly premature to make generalizations at present because only a few lineages have been analyzed and the taxa showing the disjunctions are highly diverse in ecology (Fig. 4). Many of the analyses examined simple systems with a few species or species-level disjuncts or species pairs. More studies need to examine species-rich groups using rigorous analytical biogeographic methods (Simpson et al., 2005; Moore et al., 2006).

3   Future directions

It will be important to carry out careful analyses using various newly developed tools in analytical biogeography, especially concerning more rigorous methods in the estimation of the divergence time of lineages (Sanderson, 2002; Thorne & Kishino, 2002; Drummond et al., 2006; Drummond & Rambaut, 2007) as well as inference of geographic range evolution (Ree et al., 2005; Nylander et al., 2008; Ree & Smith, 2008). Global biogeographic analyses are needed in studying intercontinental disjunctions, such as the Madrean–Tethyan and the amphitropical patterns. Early biogeographic work emphasized lower-level analyses with limited sampling. Our insights into the evolution of the biogeographic disjunctions will be limited if our sampling is restricted to certain continents or in the northern hemisphere or just in the southern hemisphere.

Integration of evidence from phylogeny, ecology, morphology, and fossils should provide a comprehensive perspective on the diversification of various plant lineages through time and space. So far only a few biogeographic studies have incorporated evidence from ecology. Most analyses have only used fossils to the degree of providing calibration points. Recently, a few studies (e.g., Manchester & Tiffney, 2001; Xiang et al., 2006; Feng et al., 2009; Harris et al., 2009) integrated fossils in phylogenetic and biogeographic analysis, and these studies reported results that may differ substantially depending on whether fossils are included or excluded in biogeographic analysis. The phylogenetic and divergence time uncertainties need to be taken into account in biogeographic interpretations (Smith, 2009). It is important to emphasize integrative analysis to better understand plant diversification processes. The spatial and temporal processes need to be interpreted in both local ecological and large-scale contexts (Ackerly, 2003, 2009; Wiens & Donoghue, 2004).

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