

Int. J. Plant Sci. 165(4 Suppl.):S1–S6. 2004.
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1058-5893/2004/165054-0001\$15.00

TROPICAL INTERCONTINENTAL DISJUNCTIONS: GONDWANA BREAKUP, IMMIGRATION FROM THE BOREOTROPICS, AND TRANSOCEANIC DISPERSAL

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With the advent of molecular data, and particularly the use of molecular clocks when warranted, biogeographers have begun to reexamine the roles of Gondwana breakup, immigration from the Laurasian tropics, and transoceanic dispersal in shaping similarities among the world's tropical floras (Givnish et al. 1999, 2000; Lavin et al. 2000, 2005; Renner et al. 2000, 2001; Azuma et al. 2001; Chanderbali et al. 2001; Renner and Meyer 2001; Conti et al. 2002; Davis et al. 2002; Jobson et al. 2003; Zhang and Renner 2003; Berry et al. 2004). As increasing numbers of continental disjunctions are analyzed, it has also become possible to ask whether there are regular patterns in the directions and timing of transoceanic dispersal events (S. S. Renner, in this issue). Wind and ocean surface currents (as well as tectonics) all affect dispersal and are not randomly distributed in space and time; they should thus leave an evolutionary trace provided that they have been stable long enough to override lineage-specific differences in dispersal and establishment capability (e.g., see Muñoz et al. 2004).

Tropical intercontinental disjunctions raise issues analogous to those involving disjunct temperate floras in the Northern Hemisphere (see IJPS symposium edited by Manos and Donoghue [2001]), but the ocean gulfs are often greater and the latitudinal distributions of taxa less dynamic. Similar issues also emerge in studying the origin of island lineages (Wagner and Funk 1995; Givnish 1998; Emerson 2002). Insular groups pose special problems, especially when extraordinary divergence due to adaptive radiation makes it difficult to identify mainland ancestors or relatives. Yet intercontinental disjunctions can be even more complex to decipher, given the frequent lack of asymmetries between potential source and target areas (but see T. J. Givnish et al.; K. J. Sytsma et al.), the existence of direct connections to other landmasses at various times, and the longer and more complex tectonic histories of the terrains.

The papers collected here represent the product of a symposium held in Madison during August 2002, sponsored by the Association for Tropical Biology and the Association for Systematic Botany and honoring Robert Thorne for his outstanding contributions to biogeography and especially to the analysis of tropical plant disjunctions (Thorne 1972, 1973; R. Thorne's "reflections" at the end of this volume provide an entry into his biogeographic contributions). We invited researchers to present analyses based on molecular data for a variety of disjunctly distributed tropical lineages that, in aggregate,

display a diversity of continental disjunctions, mechanisms of dispersal, and geological age. We asked each contributor to address three questions: (1) How much information about the timing and nature of the events causing disjunctions can be obtained from molecular data? (2) What appear to be the relative roles of dispersal and vicariance, and how do these relate to events in Earth history? and (3) How can we cross-check and validate our inferences using fossils or other data?

All of the contributions calibrate the lengths of branches in molecular trees (measured as the numbers of inferred nucleotide substitutions) against the apparent age of one or more ancestral taxa (inferred from the geological age of the oldest known fossil attributed to those taxa). The absolute dates of cladogenetic events within a lineage are then inferred using one or more of several calibration models and attributed to apparent dispersal or vicariance events, which have themselves been inferred from the distributions of modern-day taxa and their phylogenetic relationships to each other. The timing of range expansions is finally tied to shifts in geography, climate, or likely pathways for dispersal during geological time, and conclusions are drawn about the likely mechanisms underlying a particular disjunct distribution. The validity of such conclusions thus hinges on the completeness of our knowledge of the fossil record, both in areal extent and in time; on uncertainties in the branch lengths inferred from particular molecular markers; on the validity of chronological calibrations based on particular models and a particular set of fossil dates; and on uncertainties regarding the distributions of ancestral taxa inferred from a molecular phylogeny, distributions of modern-day taxa, and particular models for shifts in geographic range. Nevertheless, the approaches taken by papers in this symposium, involving the complementary use of molecular and paleobotanical data, offer some of the most powerful techniques now available for assessing the age—and, hence, the mechanism—associated with a shift in the range of a lineage. Without such approaches, or comprehensive and thus perhaps unattainable fossil data bearing on the timing of a range shift, one might indiscriminately invoke long-distance dispersal, continental drift, or boreotropical migration to explain essentially any tropical disjunction. The surprising conclusion from careful analyses in this symposium and elsewhere (e.g., Cronn and Wendel 2004; Lavin et al. 2005) is that long-distance dispersal may be more pervasive than all but its most ardent advocates (e.g., Iltis 1967) had previously proposed.

S. Magallón sets the stage by reviewing recent methods for dating nodes in molecular trees, including those that permit among-lineage rate variation and calibration against multiple fossil dates or constraints. Under several conditions, cross-verified penalized likelihood (Sanderson 2002), used by many authors in this symposium, outperforms both the traditional, one-rate molecular clock (Langley and Fitch 1973, 1974) and nonparametric rate smoothing (Sanderson 1997). Bayesian approaches to the estimation of divergence times that, like penalized likelihood, relax the assumption of equal rates between sister groups and permit multiple calibration points but also allow the use of different models for different data partitions came into wider use only after our symposium (Thorne and Kishino 2002; Yang and Yoder 2003; Renner 2004; Renner and Zhang 2004). Magallón also addresses the problem of identifying the first appearance of particular lineages versus individual morphological traits in the fossil record. The construction of stratigraphic confidence intervals from the temporal distribution and abundance of known fossils may, to a limited extent, help compensate for inherent uncertainties in the fossil record.

S. S. Renner updates Thorne's (1973) classic analysis of angiosperm genera with disjunct ranges on both sides of the tropical Atlantic, finding 110 amphi-Atlantic genera that are now considered to be monophyletic. Molecular calibrations for the disjunction events, including several presented in this issue, are now available for 12 cases (more are about to be added by Lavin et al. [2005]). Among the 12 calibrated cases summarized by Renner, three of four cases of dispersal from South America to Africa involved wind, while dispersal from Africa to South America primarily involved sea currents. A somewhat less skewed mix of dispersal events via water emerges when all 110 amphi-Atlantic genera are considered, with apparent dispersal from South America to Africa in Vochysiaceae (K. J. Sytsma et al.), *Andira*, *Drepanocarpus*, *Hernandia*, *Hymenaea*, *Sacoglottis*, and *Thalia*. Because of the relatively recent origin of genera, generic disjunctions are likely to reflect dispersal rather than continental drift or boreo-tropical invasions (but see Jobson et al. 2003 for *Genlisea*). Overall, water dispersal appears to have been involved in a large number of dispersal events across the tropical Atlantic, reflecting the existence of one large, reliable east-flowing current and two large, reliable west-flowing currents. Wind dispersal is rarer and more problematic given the absence of regular wind avenues connecting Africa and South America, although rare cases of strong winds blowing in either direction across the tropical Atlantic are known. In accord with expectations, Muñoz et al. (2004) have just shown that, among the temperate landmasses of the Southern Hemisphere, floristic similarity among wind-dispersed mosses, liverworts, lichens, and ferns is more closely coupled to connectivity based on prevailing winds than on geographic proximity.

T. J. Givnish et al. dissect two of the simplest cases of amphi-Atlantic disjunctions, involving single species of the Neotropical families Bromeliaceae and Rapateaceae endemic to West Africa. Analyses are based on cross-verified penalized likelihood, calibrated against six fossil dates stratified across the monocots. In Bromeliaceae and Rapateaceae, the African species (*Pitcairnia feliciana*) and genus (*Maschalocephalus dinklagei*) are the results of long-distance dispersal from

South America no earlier than the past 7 to 12 million years (m.yr.), even though both inhabit sandstone regions that abutted the Guayana Shield of South America before the Atlantic rifted at ca. 90 Ma. It appears that, for both families, the nutrient-poor substrate favoring them is vicariant, even though they themselves are not. The relatively moist conditions associated with the Cameroon mountains and nearby sandy, wet savannas along the coast from Liberia to Côte d'Ivoire may have enabled bromeliads and rapateads to have survived in Africa during the past cycles of climatic aridification. Within South America, these families arose at low elevations and then speciated rapidly upon invasion of dissected montane regions; this habitat shift may have been facilitated by the evolution of CAM photosynthesis, tank habit, and plumose seeds associated with epiphytism in Bromeliaceae.

J. A. Doyle et al. explore much deeper and more complex branching events in Annonaceae and Myristicaceae. Both families are pantropical and are members of order Magnoliales, one of the earliest divergent clades of angiosperms, extant for at least the last 100–120 m.yr. Fossils and calibrated molecular phylogenies converge on a fairly consistent account for Annonaceae, involving continental drift and long-distance dispersal. The group appears to have arisen in South America and/or Africa at ca. 82 Ma. Continental drift (or dispersal across a narrow Atlantic) is inferred to account for the amphi-Atlantic range of *Anaxagorea* and transport on the northward rafting India for the entry of several lineages into Laurasia. Long-distance dispersal from Africa to South America and the other way around also played a role (cf. the case of *Annona glabra* cited in Thorne 1973 and S. S. Renner). Paradoxically, even though Myristicaceae show a similar branching pattern in relation to biogeography and is coeval with Annonaceae, estimates based on molecular branch lengths suggest a much younger age of divergence among extant taxa (crown group) and implausibly imply numerous long-distance dispersal events involving large zoochorous seeds. The long branch between the stem and crown groups in Myristaceae and the inability of fossils to calibrate any intermediate date raise the possibility that the rate of molecular evolution suddenly slowed at some unknown time over the past 17–82 m.yr. This is a fundamental problem with no obvious solution, and it has radical implications for the evolutionary timetable of Myristicaceae.

F. Rutschmann et al. explore the possible role of “beached Viking funeral ships” (McKenna 1973)—that is, rafting of India and other elements of the Deccan plate from Africa into Asia—for the evolution of Crypteroniaceae and their allies in the Myrtales. Their calibration of a three-gene cpDNA phylogeny implies a slightly more complex scenario than hitherto envisaged, with short-distance dispersal from Africa-Madagascar as the Deccan plate rafted past, followed by disembarkation after the collision with Asia. Calibration using different fossils and different nodes results in different age estimates, but if the fossils considered most suspect on independent grounds are ignored, then the estimates are in excellent accord with each other.

K. J. Sytsma et al. provide an incisively complex picture of the historical biogeography of another portion of the ancient order Myrtales, focusing on the clade composed of the amphi-Atlantic Vochysiaceae, South African Heteropyxidaceae,

Mascarene Islands Psiloxylaceae, and pantropical+Mediterranean Myrtaceae. Vochysiaceae diverged from the other three families at ca. 93 Ma, with African *Erismadelphus* arising from this otherwise South American family 28 m.yr. ago, long after the tropical Atlantic had rifted. This implies an origin via long-distance dispersal, most likely via water, given the occurrence of floating seeds with corky coats in at least one South American species of *Erisma*. *Heteropyxis*-*Psiloxylon* from South Africa and the Mascarene Islands separated from Australasian-originated Myrtaceae at ca. 85 Ma, too late to reflect the rifting of West and East Gondwana at ca. 180–150 Ma and probably involving short over-water dispersal and/or indirect rafting via the Deccan Plate. *Psiloxylon*, which we note has fleshy fruits—unlike its sister taxon Vochysiaceae or basal Myrtaceae—most likely dispersed over water to the Mascarene Islands sometime during the past 40 m.yr. (when *Psiloxylon* and *Heteropyxis* diverged); the oldest island in the Mascarene hotspot chain, Mauritius, is less than 8 m.yr. old, but the *Psiloxylon* lineage may have arrived on an older, now submersed, island (see Givnish et al. 1995 for Hawaiian lobeliads; Berry et al. 2004 for Polynesian *Fuchsia*). The crown lineage of Myrtaceae is clearly Australasian, but it is not clear whether the family arose there as well, given the nearly contemporaneous appearance of fossils in Africa, South America, and Asia in the Upper Cretaceous. Paraphyletic Leptospermoideae at the base of the family are capsular fruited and occupy extremely infertile substrates today, where fleshy fruits would probably not be favored due to a lack of an insect protein (caterpillar) subsidy for avian frugivores due to selection for heavily defended leaves (Givnish 1998). Subsequently, however, fleshy fruits evolved numerous times independently, apparently associated with colonization of the Mediterranean (*Myrtus*), Africa (*Eugenia*, *Syzygium*), and possibly South America (Myrtoideae), although colonization of the latter area may also have occurred overland, given that crown radiation of the American myrtoids appears to have happened 48–56 m.yr. ago when a warm, temperate connection still linked Australia, Antarctica, and South America. Recent long-distance dispersal also appears to have occurred in dust-seeded, wind-dispersed *Metrosideros* in islands across the Pacific (Wright et al. 2000) and in “*Metrosideros*” *angustifolia* in Africa.

C. C. Davis et al. discuss the infrequently invoked scenario that some tropical disjunctions may have arisen via boreotropical migration (but see Lavin and Luckow 1993; Chanderbali et al. 2001; Renner and Meyer 2001)—that is, via high-latitude land connections during the Tertiary, when northern areas supported tropical forests. Fossils and phylogenetic analyses indicate that the family Malpighiaceae arose in South America 68 m.yr. ago and that six amphiatlantic disjunctions occurred at ca. 60, 34–31, and 21–17 Ma. Paleoclimate, previous land configurations, and malpighiaceae fossils at high latitudes suggest that overland, high-latitude migrations could easily have occurred via the North Atlantic Land Bridge in four of six instances and that such migrations might have occurred across the North Atlantic during the last two events in the early Miocene warming. Detailed studies of fossil Malpighiaceae will be required to test these ideas further.

M. Gottschling et al. calibrate divergence in ITS sequences among species in three woody groups (Ehretiaceae, Cordia-

ceae, Heliotropiaceae) often considered as subfamilies of Boraginaceae. These groups display striking disjunctions in tropical (and sometimes subtropical and temperate) latitudes. Calibrated dates of divergence generally exclude continental drift as a mechanism—across either the tropical Atlantic or the ancient Tethys Sea—and point toward dispersal as the more likely mechanism. This conclusion also accords with the widespread occurrence of animal-dispersed fleshy drupes and water-dispersed corky or inflated propagules.

Fossils and molecular data are essential, complementary tools for the reconstruction of the biogeographic history of major clades. The greater the number of fossils used for calibrating nodes and constraining chronologies in molecular phylogenies, and the more accurately assigned those fossils are to lineage and chronological horizon, the more likely that an accurate history of a group can be recovered. Similarly, the greater the number of characters and their range of genomic origin, the greater the statistically supported resolution of individual nodes, and the fewer the long branches along which evolutionary rates might have changed in unverifiable ways (see above). Such solidly sampled taxon and genome data sets likely increase the accuracy of historical reconstructions (e.g., see Sanderson 2003). Although these principles may seem obvious, it is vital to keep them in mind. For example, Wikström et al. (2001) used three genes and nonparametric rate smoothing to estimate the ages of several hundred branching events in the evolution of the flowering plants as a whole. One of the dates they obtained—for the origin of the Dipterocarpaceae, with a disjunct, seemingly Gondwanan distribution in South America, Africa, Madagascar, Sri Lanka, India, Southeast Asia, and Malesia—was 14 to 28 m.yr., precluding continental drift as an explanation for the observed distribution. Yet traditional taxonomic and biogeographic treatments, as well as other DNA-based analyses, support Gondwanan vicariance as playing a role in the history of dipterocarps (Ashton and Gunatilleke 1987; Ducousso et al. 2004). When we realize, however, that these dates are based on calibration against but a single fossil date (in Fagales, far removed from Dipterocarpaceae in Malvales) and include only one dipterocarp, the headache recedes. Given the striking disjunctions seen in Dipterocarpaceae and the likelihood that they cannot be explained by recent long-distance dispersal, more detailed investigations of the historical biogeography of this family should be a high priority.

Finally, whatever inferences we draw from molecular phylogenies—by whatever models, be they parsimony, maximum likelihood, or Bayesian—they remain inferences and, as such, must be tested and extended, wherever possible, with additional paleobotanical and ecological data. No clearer illustration exists than that provided by the southern pines of the family Araucariaceae. These gymnosperms are well represented in the fossil record since at least the Jurassic; possess heavy, disintegrating cones and large, mostly wind- or gravity-dispersed seeds; and today inhabit a strikingly disjunct, mainly subtropical range including Australia, New Zealand, Norfolk Island, Fiji, New Caledonia, New Guinea, Malesia, and South America (Kershaw and Wagstaff 2001). An *rbcl* phylogeny (Setoguchi et al. 1998) places monotypic *Wollemia*, now restricted to a few remote gorges in southern Australia, sister to *Agathis* (13 spp.) and *Araucaria* (19 spp.). If we overlay

distributions and conduct a formal parsimony reconstruction of biogeographic history using the phylogenetic and biogeographic data provided by Setoguchi et al. (1998), then we infer an Australian origin with subsequent expansions into the other six biogeographic regions, including at least two colonizations of New Caledonia by *Agathis* and *Araucaria* (fig. 1).

Without further information or formal tree calibration, one might infer that most or all of these disjunctions resulted from ancient continental drift, given the origin of the family 205–250 m.yr. ago and the existence of links between Australia, New Guinea, New Zealand, Antarctica, and South America until 70–80 m.yr. ago (Wilford and Brown 1994). However, the fossil record shows that *Araucaria* sect. *Eutacta* was widespread in the Northern and Southern Hemispheres during the Mesozoic, so that long-distance dispersal or overland transport may also have been an important process (Setoguchi et al. 1998; Kershaw and Wagstaff 2001). Nevertheless, our inference that continental drift accounts for the invasion of South America from Australia is likely to prove valid, given that (1) section *Eutacta* today is restricted to Australia–New Guinea (connected overland during glacial periods) and the continental rafts of Norfolk Island and New Caledonia; (2) the earliest and most widespread araucarian fossils are from Australia (Kershaw and Wagstaff 2001); (3)

Araucaria sect. *Araucaria*—now the only two endemic species in South America—also occurred in Australia during the early Cretaceous (Hill and Brodribb 1999); and (4) the basal scolytine beetles that inhabit the bark of *Araucaria* appear, based on calibrated molecular data, to have shared a common ancestor 78 m.yr. ago (Sequeira and Farrell 2001). The occurrence of *Agathis* in Malesia appears likely to represent at least short-distance dispersal between the Sahul and Sunda shelves; its occurrence on Fiji, to be a result of continental drift; and its occurrence on Vanuatu (New Hebrides), to be a result of drift, dispersal, or indirect *in situ* dispersal on pieces of the Australian Plate as it moves toward and is subducted below the Pacific Plate near Vanuatu. Although differential extinctions do not appear to have distorted the biogeographic history recovered from parsimony analysis, in other systems they could easily have done so, with a resulting tendency to identify areas with low extinction rates as ancestral. Manos (1997), Hill (2001), and Swenson et al. (2001) have previously shown, using *Nothofagus*, how including extinct taxa can eliminate discordance between tectonic history and biogeographic inferences based on phylogeny.

Setoguchi et al. (1998) proposed that the species of *Agathis* and *Araucaria* sect. *Eutacta* on New Caledonia, the current center of diversity for both genera, represent the product of recent radiations following long-distance dispersal, based on the very small amount of genetic divergence among extant species in each clade and the fact that the ultramafic substrates they occupy are thought to have been exposed only for the last 13 m.yr. This inference appears to conflict with ecology, based on the large seeds of Araucariaceae and the fact that large *Araucaria* cones often fall to the ground intact. But, in fact, it calls for more ecological research. Although most *Araucaria* and all *Agathis* have winged seeds adapted for wind dispersal, a few *Araucaria* (*A. bidwillii* in Australia and *A. araucana* and *A. angustifolia* in South America) lack seed wings, and at least *A. angustifolia* appears to be dispersed by birds such as the azure jay (*Cyanocorax caerulea*) and vinaceous parrot (*Amazona vinacea*) (http://www.misiones.gov.ar/ecologia/TODO/Planes_de_Manejo/pp%20ccaballero/PlanCCaballeroCap5.htm). If the bunya (*A. bidwillii*) ever had such a seed disperser, it has gone extinct; perhaps not coincidentally, the bunya now has a tiny range. Setoguchi et al. (1998) also showed that the fossil record alone—even if it is as superb as that for *Araucaria*—does not always speak for itself and can generate misleading inferences if unaccompanied by molecular phylogenetic analyses. Based on *rbcL* sequences, *Wollemia* clearly diverged from *Agathis* and *Araucaria* before they diverged from each other (fig. 1). Yet *Wollemia* is the youngest genus in the “fossil record” based on the current ability of paleobotanists to recognize macro- and microfossils (Kershaw and Wagstaff 2001). And *Wollemia* vanished entirely from the “fossil record” 2 m.yr. ago, only to be rediscovered 10 yr ago by David Noble when he stumbled across it in a remote gorge in New South Wales (Jones et al. 1995)! Finally, given the topology of the molecular phylogeny and the distribution of present-day taxa, it is impossible to infer whether *Agathis* arose in Australia, Malesia, New Caledonia, or in any combination of these regions (fig. 1). Additional detailed paleobotanical data from Malesia and New Caledonia will be needed to resolve this

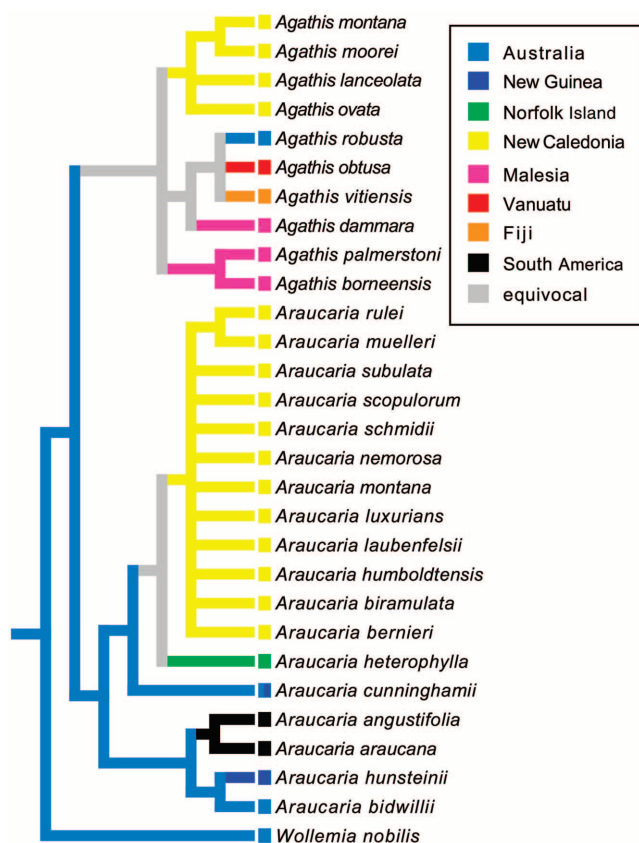


Fig. 1 Parsimony reconstruction of ancestral geographic distributions in the conifer family Araucariaceae, based on the *rbcL* phylogeny presented by Setoguchi et al. (1998) and distributions of present-day taxa and implemented using MacClade 4.03 (Maddison and Maddison 2001).

issue. The moral of the story in this case, as for most studies of disjunct plant distributions, is that conclusions require the

judicious use of complementary data on phylogeny, biogeography, ecology, and paleodistributions in time and space.

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