

Neotropical moss floras: Species common to North and South America.

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Abstract. North and South America share about 675 species that show two basic patterns, namely, those with a continuous range and those with a disjunct distribution. Both may have resulted from step-by-step migration, but the latter, including 118 species, may be due to break up of previous distributions by post-Tertiary tectonic and climatic changes or by long-distance dispersal.

The distribution of vascular plants includes many genera common to North and South America (Johnston 1940, Miranda 1959). Some of them have widespread ranges while others exhibit disjunct distributions between both land masses (Good 1964, Rzedowski 1978). While long-range dispersal has been proposed as an explanation (Raven 1963), it is often assumed that the shared taxa resulted from past plant migrations even though certain such patterns as the bicentric distributions are difficult to explain because the herbaceous and woody species seem to represent different periods of floristic interchange (Johnston 1940).

Modern studies have proposed origins, times and routes of migration for vascular plants. It is said, for instance, that the high altitude South American flora is largely derived from north temperate sources (Gentry 1982) and that many

shared families of flowering plants could be referred to Gondwanan or Laurasian origins (Raven & Axelrod 1974). Gentry (1982), in discussing the floristic richness of the neotropics, pointed out that with the closure of the Central American isthmus many South American taxa moved north to completely dominate the Central American lowlands and that most of this invasion is so recent that there has been little differentiation at the species level. In the upper elevations of Costa Rica the vascular flora shows distinct links with northern Central America and Mexico, and with the Andes; at the generic level, 95% of the flora is shared with the Andean region (Cleef & Chaverri 1992). This seems to reflect dispersal trends that occurred in the area. Hammen and Cleef (1983) proposed that the floristic interchange between North and South America increased little by little since the Miocene through "Mesoamerican" islands and the Antilles; by the

Pliocene, with the elevation of mountains and the full closure of the Central American Isthmus, the interchange also included holarctic taxa that migrated to the Andean region.

The similarities between the moss floras of North and South America are well known. Because at the species level mosses follow patterns of distribution similar to those observed in the vascular plants, the hypotheses to account for their present ranges are essentially the same. The high degree of community between the North and South America has already been explained in terms of migration through both Central America and the West Indies (Delgadillo 1992, 1993). However, the number of moss species participating in the interchange or the degree of community between both land masses had not been determined accurately because of the lack of complete floristic catalogues for the neotropical area; the number of disjunct species had also remained undetermined.

We have recently compiled a data bank for neotropical mosses (LATMOSS) and have initiated a wider comparison of the North and South American moss floras. The coverage and characteristics of LATMOSS was described elsewhere (Delgadillo 1992), but in this contribution its information is used to review the subject of the floristic relationship between North and South America with emphasis on the origin of the North-South American moss disjunction.

LATMOSS includes about 675 species and varieties of neotropical mosses that are shared between North and South America. These can be placed into two groups according to their continental distribution, namely, those with a continuous range in the neotropics and the disjunct taxa (Table 1). The group of taxa with a continuous range is the most important; it comprises 514 species widely represented in North, Central, South America and the West Indies. Included is a group of 159 taxa that are known from Central America, but not from the West Indies; among the 393 taxa represented in the West Indies there are 38 unknown from Central America. The presence of species distributed in Central America and the West Indies has been regarded as indicative of the intense biotic ex-

Table 1. Neotropical mosses common to North and South America

Range	No. taxa
CONTINUOUS	
Central America (CA)	514
CA, not in WI	162
West Indies (WI)	393
WI, not in CA	38
CA & WI	355
DISCONTINUOUS	
Disjunct	118
TOTAL	675
Percent from total flora (675/4050) 16.7	

change that has taken place between North and South America through these routes; the subject was discussed by Delgadillo (1992, 1993) and Schuster (1983) for bryophytes, and by contributors in Stehli and Webb (1985), for other organisms.

The second group is of great phytogeographical interest for it comprises 118 disjunct moss taxa, *i.e.* species known from stations in North and South America, but not from intermediate areas in Central America or the West Indies. This pattern is well documented in the plant kingdom and has received ample consideration (*e.g.*, Bray 1898, Campbell 1944, Raven 1963), although there is still controversy as to its mode of origin (Daubenmire 1978); examples among vascular plants include species of *Clarkia* (Raven & Lewis 1959), *Prosopis* (Good 1964) *Larrea* (Bray 1898), and many others (*cf.* Constance 1963, Raven 1963). However, for mosses, it has received little consideration except to say that they may have become widespread in the Pleistocene by mountain "hopping", but disappeared from Central America afterwards.

LATMOSS lacks altitudinal information

for some mosses, but the remaining disjuncts generally have broad altitudinal ranges or are distributed from above 1,000 m up to about 5,000 m in elevation. This altitudinal distribution and their present ranges in South America suggest that the disjunct taxa became widespread after the uplift of the Andes in the Pliocene and that further upward and downward shifts during the Pleistocene increased floristic interchange with the displacement of vegetational belts. However, climatic fluctuation may have also eliminated certain taxa from the Central American flora.

According to Janssens and Zander (1980), the disjunctive patterns in North America may have resulted from mid-Tertiary ranges that broke up following tectonic and climatological changes. *Leptodontium flexifolium* -known today from Mexico, Central and South America, and from stations in Arizona, New Mexico and North Carolina-, had a range that extended to the Yukon area in the Quaternary, as shown by subfossil samples collected in Canada (Janssens & Zander 1980). Subfossil material attributable to present-day North-South American disjuncts has been reported from the Quaternary of North America (cf. Janssens 1980, 1983; Miller 1980). Although fossil evidence is scanty, the distribution in Africa of many disjunct mosses suggests ancient links with pre-Tertiary floras and wider ranges in periods of warm and equable climate during the Tertiary. Zanten (1978) seems to think that because of the downward shift of vegetational belts, it may have been easier for cool-temperate taxa to migrate though Central America in glacial times. Thus, whether Tertiary or Pleistocene in age, it is theoretically possible that the disjunct distribution of mosses in North and South America is the by-product of broken-up ranges, as may be the case of 28 species and varieties with populations presently known from subtropical and temperate latitudes of North America (Table 2). Schuster (1983, p. 546-7), in reference to the distribution of certain liverworts, suggested massive extinctions during the Pleistocene.

Range dissection or species disappearance from ample sectors of the original area of distribution is a viable explanation for the disjunct range of many neotropical mosses. Orogeny

is certainly responsible for the present distribution of mosses because of its direct or indirect influence on continental climates in the neotropics; in Mexico, the elevation of the eastern sierras favored the drier climates in the Mexican Plateau thus restricting the advance of tropical lowland mosses into continental areas of northern Mexico. Rain shadows, easily observed in the state of Puebla and elsewhere along the Neovolcanic Belt of Mexico, developed with the uplift of mountain ranges. The drier climates of western Central America and northern South America combined with the late uplift of the southern Central American mountains may have modified moss ranges producing disjunct patterns of many species. However, while this contention may be acceptable for Central America, it does not account for the absence of other moss species in the West Indies.

I have stated elsewhere (Delgadillo 1993a) that the archipelago condition of the Antilles, the late elevation of the mountains and the climatic changes of the Pleistocene must have depleted the extant moss flora. It is likely that this loss resulted in disjunct ranges for species that were unable to reenter the islands while, at the same time, produced a high degree of floristic similarity between islands and continent as floristic replenishment could only come from continental sources.

Although most neotropical mosses exhibiting the North-South American disjunction are mainly distributed along the Andes, there are several species whose continental distribution includes North America and Brazil, only. Among them, *Eccremidium floridanum* Crum and *Mnium cylindricum* Hornsch., are apparently restricted to these two areas and their distribution is not easily explained by the range dissection hypothesis; according to Stoneburner *et al.* (1993), the former species is a synonym of *E. exiguum* and its range includes Africa and Australia.

Long distance dispersal is an alternate explanation for discontinuous distributions between North and South America. According to Zanten (1983) and Zanten and Pócs (1981), moss dispersal from one climatic zone to another or

Table 2. Subtropical and temperate North American taxa disjunct with South America. Age of fossil and subfossil samples are cited from the literature.

Taxon	Age	Reference
<i>Bryum atrovirens</i> Vill. ex Brid.		
<i>Dicranoweisia crispula</i> (Hedw.) Mild.		
<i>Dicranum montanum</i> Hedw.		
<i>Eccremidium floridanum</i> Crum		
<i>Entodon concinnus</i> (De Not.) Par.	6 200	Janssens 1983
<i>Fissidens adianthoides</i> Hedw.		
<i>Fontinalis duriaei</i> Schimp.		
<i>Funaria calcarea</i> Wahlenb.		
<i>Funaria microstoma</i> Bruch		
<i>Heterocladium dimorphum</i> (Brid.) B.S.G.		
<i>Hymenostylium recurvirostrum</i> (Hedw.) Dix. var. <i>insigne</i> (Dix.) Bartr.		
<i>Hypnum circinale</i> Hook.	6 600	Miller 1980
<i>Leucodon sciuroides</i> (Hedw.) Schwaegr.		
<i>Pohlia camptotrachela</i> (Ren. & Card.) Broth.		
<i>P. longicollis</i> (Hedw.) Lindb.		
<i>P. ludwigii</i> (Schwaegr.) Broth.		
<i>Racomitrium lanuginosum</i> (Hedw.) Brid.	>32 000	Miller 1980
<i>Schlotheimia fusco-viridis</i> Hornsch.		
<i>Scorpidium scorpioides</i> (Hedw.) Limpr.	1 800 000-700 000	Janssens 1983
<i>S. turgescens</i> (Jens.) Loeske	>38 000	Miller 1980
<i>Sphagnum balticum</i> (Russ.) Jens.	2 330	Miller 1980
<i>S. capillifolium</i> (Ehrh.) Hedw.	670	Miller 1980
<i>S. lindbergii</i> Schimp. ex Lindb.		
<i>S. molle</i> Sull.		
<i>S. pulchricoma</i> C. Muell.		
<i>Tortula muralis</i> Hedw.		
<i>Trichostomum linealifolium</i> C. Muell.		
<i>Voitia nivalis</i> Hornsch.		

across the equator is difficult or does not occur. Nevertheless, Zanten (1978) states that the transequatorial transport of spores between the northern and southern hemispheres may be achieved by the Hadley circulation or by eddies in the upper troposphere for tropical and temperate species, respectively. Since the spores may experience desiccation, UV radiation or freezing conditions when in the upper atmosphere (cf. Zanten 1976), their viability may be greatly reduced as are their chances for successful establishment.

Because long-range dispersal is a remote possibility unless long periods of time are considered and because the number of mosses exhibiting the North-South American disjunction is rather large, the range disruption hypothesis is perhaps more credible. Furthermore, since most disjunct taxa are high-altitude inhabitants, they may be considered as recent introductions that reached either subcontinent after the formation of the mountains in Pliocene-Pleistocene times. However, other explanations may be required for such patterns as that of species whose South

American range includes one single country. Many of these have wider distributions in the world and represent old lineages that reached either North or South America through other routes (*cf.* Delgadillo 1993b).

The lack of an adequate collecting record and different taxonomic concepts are sources of scientific bias regarding the North-South American moss disjunction. Despite recent work in the area (Allen 1994), there are still few collections from several Central American countries and it is probable that some taxa may still be listed among those with disjunct patterns. It is surprising that species of *Didymodon*, *Grimmia*, *Polytrichum*, *Racomitrium*, *Rhodobryum*, *Tortula* and *Zygodon* have not yet appeared in Central American collections while they are repeatedly collected in North or South America. Species of *Aloina*, *Astomum*, *Eccremidium*, *Erpodium* and *Lorentziella* are small or ephemeral and occupy peculiar habitats that may require detailed exploration before it is established whether they are part of the Central American flora.

Unresolved taxonomic difficulties involving species currently recognized by different epithets in North or South America may increase the number of disjunct species or produce a better-known ranges. *Funaria calcarea* Wahlenb., for instance, as recognized here is a distinct species, but Lawton (1971) lists it under the synonymy of *F. muhlenbergii* Hedw.; if *Ditrichum rufescens* (Hampe) Hampe is conspecific with *D. difficile* (Duby) Fleisch. (*cf.* Allen 1994), the name should be deleted from the list of disjunct taxa.

There is no evidence that man has induced North-South American moss disjunctions. It is feasible, however, that transportation of mosses in various forms, herbarium specimens included, may eventually lead to broader distributions.

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