MEXICAN MOSSES: A FLORA OF TRANSITION IN THE AMERICAS

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Resumen. La flora de musgos mexicanos contiene alrededor de 967 especies y variedades; aunque es esencialmente neotropical, contiene numerosos taxa de afinidad boreal, austral y de amplia distribución. Su distribución local y mundial sugiere que México es el sitio de convergencia de floras tropicales y templadas que se segregan altitudinalmente a lo largo de las montañas y están separadas latitudinalmente por el Eje Neovolcánico. La flora de la porción sur del país está formada principalmente por taxa tropicales cuya distribución septentrional puede extenderse más allá de los 20°N siguiendo los planos costeros.

Palabras clave: musgos, fitogeografía, México, flora neotropical.

Abstract. The Mexican moss flora, with about 967 species and varieties, is essentially neotropical in character, but it also contains numerous boreal, southern and widely distributed taxa; their world and local ranges suggest that Mexico is the site of convergence of tropical and temperate floras that segregate altitudinally along the mountains and are separated latitudinally by the Neovolcanic Belt. The southern part of the country contains mostly tropical taxa whose distribution may extend northward beyond 20°N along the coastal plains.

Key words: mosses, phytogeography, Mexico, neotropical flora.

With the publication of Sharp, Crum and Eckel's Moss Flora of Mexico (1994), first-hand taxonomic and floristic information became available for the American tropics. This was followed by four other publications which, in time, will permit a detailed analysis of the distribution of species in Mexico and tropical America, namely, Allen's (1994) Moss Flora of Central America, Churchill and Linares' (1995) *Prodromus Bryologiae Novo-Granatensis*; Delgadillo, Bello and Cárdenas (1995) *LATMOSS*, A catalogue of Neotropical mosses; and Flora of Suriname (Görts 1996), a recently published fascicle prepared by Florschütz-de Waard and collaborators. Equally important is the appearance of the Index of Mosses (Crosby, Magill & Bauer 1992; Crosby & Magill 1994) and the availability through the Internet of TROPICOS, both produced by the Missouri Botanical Garden.

Parallel to the publication of the above mentioned works, our own research has been contributing data

on the distribution of Mexican mosses. The systematic arrangement of this information will eventually lead to a point by point analysis of floristic patterns through a database now in preparation at MEXU.

Research in the last 25 years has substantiated the phytogeographical significance of the Neovolcanic Belt of Mexico. This is considered as a key feature of the Mexican geography which, by virtue of its position, high elevation, history and climatic influence, has determined moss distribution to and from North, Central and northern South America. Our hypotheses propose that its connections with other continental mountain systems have favored the floristic interchange at high elevations (Delgadillo 1985); and that, in conjunction with the northern Andes, the Neovolcanic Belt has reduced floristic flow at lower elevations between the area delimited by them and other latitudes (Delgadillo 1992). Because of limited information, large scale floristic comparisons involving Mex-

ico and other continental areas have not been undertaken. However, with current publications and available herbarium records, a preliminary discussion may be offered on aspects of the distribution of the Mexican moss flora as affected by the Neovolcanic Belt.

Method

A catalogue of moss species was compiled from herbarium and literature sources, especially from Sharp *et al.* (1994) and from my own research. The information was organized in a database that included distribution in Mexico and in the world for each taxon; the latter corresponds with that listed in LATMOSS (Delgadillo *et al.* 1995). The phytogeographical elements resulted from consideration of the world ranges; the number of species for each major division of Mexico was obtained from the literature and from herbarium records contained in a database currently in preparation at MEXU following a model designed by CONABIO, The Mexican Biodiversity Commission.

The elements

By current counts, the moss flora of Mexico consists of about 967 species and varieties. These may be divided into seven basic phytogeographical elements that are regular constituents of the moss flora in various parts of the country. Their ranges have been discussed in several contributions (Delgadillo 1971, 1979, 1987a & b) and in other regional studies. Briefly, the Northern element, as represented by *Heterocladium macounii*, *Jaffueliobryum wrightii* and *Tayloria splachnoides*, is distributed in North America and other areas of the northern hemisphere; in the New World its range may show southward extensions along the western mountains and in eastern North America, thus its conspicuous presence in Mexico.

A small group of species, the Chihuahuan element, is distributed in northern Mexico and southwestern United States within the Chihuahuan-Sonoran desert area; *Pseudoleskeella arizonae*, *Tortula californica* and *Weissia andersoniana* follow this pattern which corresponds in part with the so-called Mexican element recognized by Delgadillo and Cárdenas (1987) in a previous study.

The Southern element is comparatively small and is represented by such species as *Hedwigidium integrifolium*, *Leptodontium capituligerum* and *Rigodium toxarion* that are distributed from Mexico to southern South America and other southern continents. The Mesoamerican element—as illustrated by *Holomitrium pulchellum*, *Leucodon curvirostris* and *Pterobryopsis mexicana*—, and the Caribbean element (*e.g.*, *Breutelia jamaicensis*, *Cyrtolophium sharpii* and *Lepidopilum scabrisetum*) are distributed in Central America and northern South America. The latter element is also found in the Caribbean islands; some species have narrower distributions and may be restricted to the northern part of the range.

The endemic element is comparatively small; several taxa (*e.g.*, *Bryoxiphium norvegicum* var. *mexicanum*, *Grimmia pulla* and *Morinia stenotheca*) are known from several states, but many are species with narrow ranges that were described in the last two decades. The alpine area of the Neovolcanic Belt is particularly rich in endemic taxa (ca. 19%); high altitude, strong diurnal temperature fluctuation, high UV radiation, a substrate poor in potassium, phosphorus and organic nitrogen, account for the environmental factors that may have induced speciation there. This set of selective pressures are not present elsewhere in Mexico or the results of speciation have had ample opportunity to spread to other countries. The significance of endemism in the neotropical moss flora was reviewed by Delgadillo (1994).

It has long been known that Mexico is the meeting ground of elements of diverse affinities (Rzedowski 1962, 1972, 1991). Many taxa that are widely distributed in the world occur there, including species with continuous and disjunct ranges. The former pattern is illustrated by mosses with cosmopolitan or subcosmopolitan ranges (*e.g.*, *Bryum argenteum* and *B. caespitium*) while the latter comprises species shared with Africa, or Africa and Asia, showing distinct bi- and tricentric patterns (*Aongstroemia julacea* and *Levierella perserrata*; table 1).

The transitional nature of the flora

As a whole, the Mexican moss flora is essentially neotropical. Besides the Mesoamerican and the Caribbean elements that account for 43 percent of the entire

Table 1. Phytogeographical elements in the moss flora of Mexico

Elements	Species	%
Northern	147	15.2
Chihuahuan	18	2.0
Meso-American	181	18.7
Caribbean	237	24.5
Southern	54	5.6
Wide distribution	233	24.0
Endemic	97	10.0
Total	967	100.0

Table 2. Number of species per element in northern and southern Mexico and in the Neovolcanic Belt

Element/Area	NE ¹	NW ²	Belt	South ³
Northern	58	70	64	52
Chihuahuan	2	17	4	2
Meso-American	44	33	110	116
Caribbean	102	32	121	186
Southern	17	18	44	29
Wide Distribution	119	102	146	146
Endemic	19	10	42	26
TOTAL	361	282	531	557

¹Includes Nuevo León, Tamaulipas and San Luis Potosí; ²Baja California, Baja California Sur, Sonora, Chihuahua and Sinaloa; ³Chiapas and Oaxaca.

Table 3. Elements in the moss flora of northern and southern Mexico and in the Neovolcanic Belt, expressed as percentages of each local flora

Element/Area	NE ¹	NW ²	Belt	South ³
Northern	16.1	24.8	12.0	9.3
Chihuahuan	0.5	6.1	0.8	0.4
Meso-American	12.2	11.7	20.7	20.8
Caribbean	28.2	11.3	22.8	33.4
Southern	4.7	6.4	8.3	5.2
Wide Distribution	33.0	36.2	27.5	26.2
Endemic	5.3	3.5	7.9	4.7

¹Includes Nuevo León, Tamaulipas and San Luis Potosí; ²Baja California, Baja California Sur, Sonora, Chihuahua and Sinaloa; ³Chiapas and Oaxaca.

flora, the Endemic element further emphasizes its neotropical character (Table 1). However, the flora also contains taxa that may be identified as of temperate affinity; these are primarily the species included in the Northern and Southern elements. The proportion of tropical and temperate elements varies with latitude or altitude, but both are usually present in any given area intermixed with taxa of wide distribution. Mexico may therefore be seen as a zone of floristic transition between the Holarctic and the Neotropical floristic realms. The limits between them are not sharply defined, but correspond with a broad altitudinal and latitudinal area where, in terms of moss distribution, the neotropical elements are generally dominant. Because of insufficient floristic data, the width of this transition area has not been established either for mosses or for vascular plants. Rzedowski (1978, 1993) suggests that most of Mexico lies within the Neotropical floristic realm and that most mountain areas, except those in northern Baja California, represent zones of transition between realms (Rzedowski 1978: 100).

Table 2 shows a preliminary analysis of the distribution of mosses in four major areas in Mexico. The number of species recorded for each subdivision reflects literature as well as herbarium information which, expressed as percentages of the local flora, appear in table 3. From these, it seems that the north-western area is dominated by the north temperate element and is, in fact, an extension of the western North American flora though the neotropical elements are sparsely represented there. In the northeast, the Caribbean element is larger than the Northern so that this area may still be considered within the transitional area. As expected, while the neotropical elements

increase, the Northern element decreases southwards (table 3); the Caribbean element attains its highest proportion in southern Mexico.

The proportion of certain elements may be used as a criterion to estimate the position of the borderline between floristic realms; the site where the relative importance of the tropical and temperate elements is reversed may be considered as the limit between the Holarctic and Neotropical realms. Even with our present knowledge, there are still insufficient field data to draw this line as it applies to Mexican mosses; from fragmentary records, it is clear that the higher elevations along the coasts have temperate affinities while the lowlands may be predominantly tropical. The proportion of floristic elements in the Mexican Plateau should be revised in detail because the number of species shared with the Great Plains area of the United States does not facilitate the identification of realm limits there.

Despite insufficient information, the transitional nature of the Mexican moss flora is unquestionable; this is perhaps due to an effective mixture of elements induced by such factors as variable topography and climate, important northern and southern land connections, and a complex geological history. The presence of Northern and Southern elements may be explained by the broadly distributed taxa that reached Mexico through the higher elevations; their actual ranges are frequently associated with the cordilleras in eastern, western or southern Mexico. In addition, the orogenic events of the Tertiary that gave rise to these mountains, and the Pleistocene climatic changes are responsible, through migration, of the advent and spread of temperate elements and of the products of speciation. The latitudinal spread of the migrants is dependent upon the breadth of the mountain rang-

es so that it is not surprising to encounter high proportions of temperate elements in parts of southern Mexico; their altitudinal distribution seems to reflect lower vegetational belts in glacial times. It may be concluded that, in addition to topography, the climatically induced displacement of the vegetation and the broad ecological tolerance exhibited by certain mosses explain the presence of temperate taxa at comparatively lower elevations in southern Mexico.

In addition to latitudinal overlap, Mexico is the site of altitudinal overlap of tropical and temperate mosses. The zone of altitudinal overlap includes areas of the Neovolcanic Belt where the neotropical Mesoamerican and Caribbean elements, are in high numbers. In southern Mexico these last elements exhibit a broad zone of overlap which extends to the intermediate elevations of the Neovolcanic Belt where the Caribbean element has its northern limit. Delgadillo (in press) has shown that in the state of Michoacán in western Mexico, some tropical mosses reach 2 200 m in elevation and may grow intermixed with temperate species from the higher elevations. Species of *Cyrtophyllum*, *Daltonia* and *Ectropothecium* grow in the same altitudinal story as *Grimmia* and *Rhynchostegium*.

The proportion of tropical and temperate (northern or southern) elements undergoes gradual latitudinal changes in Mexico. Endemism, is important in the Neovolcanic Belt, perhaps for the large number of unique taxa in the higher peaks; it is variously represented elsewhere as are other elements and contributes to make the flora of any part of Mexico a mosaic of taxa of diverse affinities. All these facts clearly mark that country as a territory of floristic transition in the Americas.

The role of the Neovolcanic Belt

Table 4 shows the number of species in each of four major areas and their shared distribution in Mexico. With respect to the Neovolcanic Belt, table 4 indicates that a) there is a large number of taxa (109 species, or 20.5% of the local flora) distributed around this

mountain range; b) there are strong floristic connections with southern Mexico as indicated by the 114 taxa (21.5%) shared with the southern area; and c) a small temperate component represented by 60 taxa (11.3%) is shared with northern localities only. The taxa of wide local distribution, 248 (46.7%), are known from northern and southern localities in Mexico.

The features cited above illustrate the floristic importance of the Belt. It may be considered as a point of contact between floras or a major continental barrier separating the tropical from the temperate elements. The latter explanation is suggested by the numerous species common with southern Mexico, and in the absence of other distributional data, this would mean that the Belt is indeed the geographical landmark that separates the Holarctic and the Neotropical realms. This issue, however, is still unresolved because, among other things, the presumed barrier effect of the Belt is not complete; many tropical and temperate species surpass it along the coastal plains or elsewhere across the mountain range. Furthermore, herbarium data indicate that the range of temperate mosses from the higher elevations overlaps with that of neotropical taxa from lower altitudes. This would make the Belt part of the transitional area between realms, but not the true limit. In search of a better circumscription of the floristic units in Mexico, additional field and herbarium records should complete our database information. It is doubtful whether moss distribution will alter dramatically previous phytogeographic interpretations based on vascular plant data, but may actually confirm and refine those findings.

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Table 4. Number of species shared among major areas in Mexico

	South	+Belt- NW	+Belt- -NE	+Belt- NW- NE	Belt	+NW- NE	NW	NE	TOTAL
South	139	33	103	112	114	9	13	34	557
Belt					109	18	26	16	531
NW							60	11	282
NE								58	361

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