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Review / Revisión

Fifty years of Bryology in Mexico
Cincuenta años de Briología en México

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Abstract
Background: Mexican botanists were not involved in bryophyte research fifty years ago; only four small floristic contributions were published between 1942-1958.
Questions: What has been learned in the last fifty years? How many bryophytes are there in Mexico? What are the contributions by Mexican scientists?
Studied species: Bryophyte flora.
Study site and dates: Mexico, between 1942-2021.
Methods: Bibliographic compilations were used to revise the status of bryophyte research in Mexico. Data for the last fifty years cited there and in an updated version of Latmoss served to determine the current knowledge of Mexican bryophytes as contributed by Mexican scientists. No thesis research was considered unless published in a scientific journal.
Results: There are 16 species of Anthocerotophyta, ca. 600 of Marchantiophyta, and 997 Bryophyta in Mexico. At least seven phytogeographic elements are represented: Northern, Meso-American, Caribbean, Southern, Wide distribution, and Endemic. Highlights of Mexican research include the discovery of *Hypnodontopsis* sp., a Miocene amber fossil from Chiapas, identification of heavy metals deposits in urban mosses in Mexico City and Toluca, determination of chloroplast and mitochondrial genomes of *Pseudocrossidium replicatum*, and the potential use of recombinant proteins from *Physcomitrella patens*.
Conclusions: Taxonomic and floristic studies should be continued along with the bryological exploration of the country. Conservation is urgent, but studies of drought tolerance, air pollution, climate change, and potential uses in medicine require support and collaboration from other scientists.
Keywords: Amber bryophytes, Mexican flora, phytogeographic elements, recombinant proteins, uses.

Resumen
Antecedentes: Hace cincuenta años los botánicos mexicanos no estaban involucrados en investigación briológica; publicaron cuatro pequeñas contribuciones entre 1942-1958.
Preguntas: ¿Qué aprendimos en los últimos cincuenta años? ¿Cuántas briofitas hay en México? ¿Cuál es la contribución mexicana?
Especies de estudio: Flora de briofitas.
Sitio y años de estudio: México, 1942-2021.
Métodos: Con varias recopilaciones bibliográficas se revisó la situación de la briología mexicana. Los datos de los últimos cincuenta años, incluyendo los de la versión actualizada de Latmoss, sirvieron para determinar la contribución nacional a la briología de México. La información en tesis no fue considerada, a menos que fuera publicada en revistas científicas.
Resultados: En México hay 16 especies de Anthocerotophyta, ca. 600 de Marchantiophyta y 997 Bryophyta. Al menos siete elementos geográficos están representados en su flora: Boreal, Mesoamericano, Caribeño, Austral, Amplia distribución y Endémico. Destacan el descubrimiento de *Hypnodontopsis* sp., en ámbar fósil del Mioceno de Chiapas; la deposición de metales pesados en musgos urbanos de la Ciudad de México y de Toluca, la determinación del genoma del cloroplasto y mitocondrial de *Pseudocrossidium replicatum*, y el uso potencial deproteínas recombinantes de *Physcomitrella patens*.
Conclusiones: Los estudios taxonómicos y florísticos deben continuar durante la exploración briológica del país. La conservación es urgente, pero estudios sobre tolerancia a la sequía, contaminación atmosférica, cambio climático y usos potenciales en medicina son prioritarios en colaboración con otros científicos.
Palabras clave: Ámbar, elementos fitogeográficos, flora mexicana, proteínas recombinantes, usos.

Bryophytes from Mexico have been investigated since mid-nineteen century. Müller (1849-1851), Gottsche (1863), and Bescherelle (1872) described and compiled floristic and taxonomic data from early bryological exploration of the country. Bescherelle's publication listed 375 moss species, but by the first quarter of the twentieth century, Thériot (1931) estimated that the moss flora comprised around 700 species. Twenty years later Crum (1951) raised that number to 836 species and varieties. Sharp *et al.* (1994; Figure 1) cited about 842, and Delgadillo recorded 997 species and varieties in an updated digital version of LATMOSS (Delgadillo *et al.* 1995). For the liverworts, those enumerated by Gottsche (1863), and others cited in various publications or listed by Fulford & Sharp (1990) add up to about 592 species and varieties (Delgadillo-Moya & Juárez-Martínez 2014). The Anthocerotophyta remain as the smaller and least known bryophyte group; for Mexico only nine species were recognized (Delgadillo-Moya & Juárez-Martínez 2014), but recent work toward an introductory manual considers at least 16 species, three of them endemic to the country.

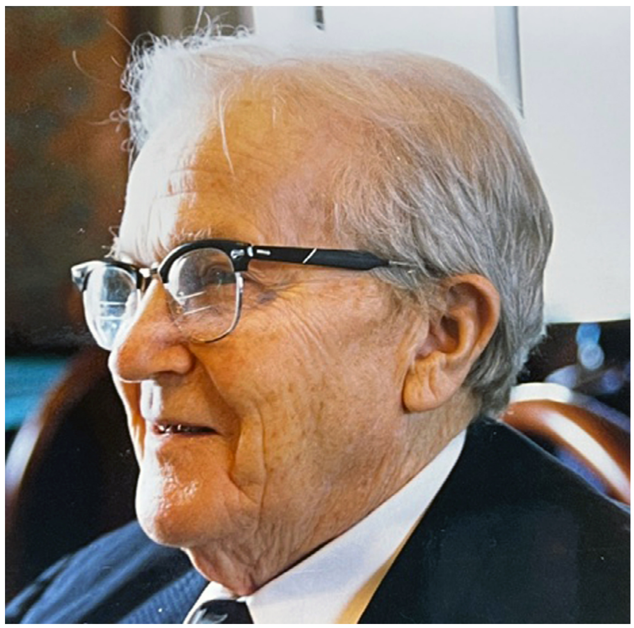

Figure 1. Aaron J. Sharp, a key figure in the publication and co-editor of *The Moss Flora of Mexico.* Photo by Kenneth D. McFarland, courtesy of William R. Buck.

Mexican botanists did not become involved in the study of bryophytes until mid-twentieth century. Ruiz (1942), Ruiz and Herrera (1948), Ortega (1953), and Sánchez (1958) published small contributions on liverworts and mosses. In 1973, a research position at Instituto de Biología was offered, for the first time in Mexican botany, to establish a bryological program and a supporting bryophyte collection at the National University of Mexico. For the last 50 years advances in our knowledge of Mexican bryophytes have included active participation by resident scientists. This contribution highlights bryological research conducted by Mexican scientists and identifies trends and progress toward the next 50 years.

Materials and methods

This evaluation is based on literature compiled since 1969. No attempt has been made to list every contribution by Mexican bryologists during the last fifty years, although those that represent noteworthy progress in various fields of research are pointed out. Historically, information on Mexican bryophytes may be found in two literature lists covering all aspects of bryology (Delgadillo 1969, 1975). Delgadillo & Equihua (1990) updated those lists and discussed more than 600 references. For mosses, Sharp *et al.* (1994) listed floristic and taxonomic references. Except for three references cited in the introduction, the literature covering 1969 to date was obtained from an updated electronic version of Latmoss (Delgadillo *et al.* 1995) and the revision of bryological journals. No student theses were considered unless they were published in scientific journals.

Results and discussion

Floristics and Phytogeography. A research project initiated in 1967 proposed that the Neovolcanic Belt was both a pathway and a barrier for migration of bryophytes in central Mexico. The highest peaks were regarded as stepping-stones for plant distribution, a condition that was supported by results of the exploration of alpine areas in Nevado de Toluca, Popocatépetl, Iztccíhuatl, La Malinche, Pico de Orizaba (Delgadillo 1971), and Nevado de Colima (Delgadillo 1987, De Luna 1985). While mosses were not entirely restricted to the highest peaks, it was shown that there was a distinct alpine flora extending from the western to the eastern coasts across central Mexico. Furthermore, field work showed that many species were absent from either side of the Neovolcanic Belt, *i.e*., the high elevations of this mountain range prevented crossing from northern to southern localities and vice versa. Floristic comparison between the drylands of Zacatecas in the north with those of the Tehuacán Valley on the southern slopes of the Belt (Delgadillo & Zander 1984, Delgadillo & Cárdenas 1987) showed few species in common. However, at about 2,700 m and below, the barrier effect was not complete as shown by species occupying paths or discontinuities (corridors) along the Belt (Delgadillo 1988, 1992a, 1998, 2009). Seven such inland floristic corridors were identified, with the eastern one as an essentially continuous lowland pathway along the Gulf coast (Delgadillo 2011). Because there are no important topographic barriers in the coastal area, mosses show a broad latitudinal distribution there.

Exploration in the highlands and other parts of Mexico indicate that the Mexican flora contains at least seven basic floristic elements, *viz*., Northern, Chihuahuan, Meso-American, Caribbean, Southern, Wide distribution, and Endemic (Delgadillo 1987, 2003). Further exploration may resolve the limits and definition of these elements as, for instance, whether the northern element may include species with western or eastern American patterns of distribution. The wide-distribution element may be broken to separate cosmopolitan, bicentric, tricentric or other disjunct taxa with diverse history and origin. In any event, the patterns of distribution and the similarity in species composition suggest that the Mexican moss flora is a complex array of lineages that arrived and dispersed at various times in response to climatic and geologic events. This is complexity is especially evident at points of contact of physiographic provinces in the Neovolcanic Belt (Herrera-Paniagua *et al*. 2008) and in hot spots where high numbers of mosses co-exist with some vascular plants (Villaseñor *et al.* 2006). At high elevations, in the alpine and subalpine areas, some lineages produced endemic taxa that represent a high percentage of the alpine flora (Delgadillo 1971, 1987). In areas with extreme environments endemism is not high because the newly formed taxa have dispersed or else, the floristic knowledge is still incomplete (Delgadillo 1994, Delgadillo *et al*. 2003, Degadillo-Moya 2019).

Despite foreign involvement, bryological exploration in Mexico has been uneven and haphazard. Early collectors visited high mountains, areas near or around cities, or where railroad lines facilitated access. The southern states (Veracruz, Oaxaca, and Chiapas) received ample attention, but most other states were ignored, except for incidental visits, *e.g*., Nayarit (Bartram 1928, Norris 1969) and Tabasco (Delgadillo & Zamudio 1988). In terms of liverworts and hornworts, the entire country needs exploration, but mosses are perhaps the best-known bryophytes in Mexico, even though many areas remain under-collected or were studied only in recent years. In connection with the Neovolcanic Belt project, mosses from Aguascalientes, Guanajuato, Querétaro, and Zacatecas were collected, along with miscellaneous collections from Hidalgo. Even with current studies, the moss flora of the central states is far from well-known, and, in fact, a thorough sampling may be required for an adequate panorama of species richness per state. The same may be said of the northwestern states, which are still poorly known, and of Tamaulipas in the northeast, whose deciduous forests have been visited by foreign and national botanists, but still have many potential bryological areas. Baja California and its islands are poorly represented in bryological collections; the Yucatán Peninsula has a comparatively small bryophyte flora, but its southeastern portion and coastal areas adjacent to Belize deserve intense bryological exploration as there seem to be no collections from that area.

Research on the Neovolcanic Belt, the publication of a Mexican moss flora (Sharp *et al.* 1994), field work in southern states, and extant literature for the country do supply taxonomic and floristic data for a general picture of species richness and distribution of mosses. These, along with published floristic lists, manuals, monographs, and taxonomic revisions, were then used to compile LATMOSS, a catalogue of mosses for the Neotropical region (Delgadillo *et al.* 1995). The original database is continuously updated from information in taxonomic revisions and monographs - it is the basis to identify and propose explanations for the patterns and relationships of floras in the American tropics. Through Latmoss, an important African-American element has been resolved and the close relationships seen between the Antilles and Central America now indicate the existence of two alternate pathways of floristic interchange between Mexico and northern South America. Comparison of the numbers of lowland species shared with Central America versus northern South America suggests floristic discontinuities attributed to the presence of the northern Andes (Delgadillo 1992b).

Collections and Taxonomic Studies. The Bryophyte Collection at MEXU (Figure 2) is a by-product of fieldwork from the Neovolcanic Belt, the Valley of Mexico, and with other floristic projects carried out since 1967, and including exchange materials received from herbaria in the United States, Europe and Australia, the number of specimens now exceeds 52,000 specimens. Most of the specimens are mosses, but hornworts and liverworts are also represented. A database has been produced that includes all geographical and environmental information for each specimen (Portal de Datos Abiertos UNAM, Colecciones Biológicas: DGRU 2021).

Figure 2. Bryophyte Collection at MEXU. Specimens are preserved in metal cabinets.

Other institutional collections are being established in various states, *e.g*., in Chihuahua (HUACJ), Michoacán (EBUM), Querétaro (QMEX), and Veracruz (XAL). ENCB has a small collection from the Valley of Mexico, supplementary to that kept at MEXU.

Herbarium specimens (with loans from the international community) have aided local taxonomic studies, such as the revision of the liverwort family Stephaniellaceae (Juárez-Martínez & Delgadillo-Moya 2017) and the Neotropical genus *Grimmia* (Delgadillo 2015); conversely, specimen loans to foreign institutions have assisted the preparation of numerous taxonomic publications that refer to our holdings.

Reports of taxa new to the country and the description of species new to science are worthy bryological contributions. An example of the former, is the report of 11 cleistocarpic species, seven of them new to Mexico, listed from the Valley of Mexico (Cárdenas 1988). Their small stature, seasonal immersed sporophytes, and geographical concentration make their finding an outstanding contribution. New species include *Astomiopsis x altivallis* Delgad., a presumed hybrid between *A. amblyocalyx* Müll. Hal. and *A. exserta* (E. B. Bartram) Snider (Delgadillo 1989); *Bruchia paricutinensis* Delgad. & Cárde. (Delgadillo & Cárdenas 1991), *Neosharpiella aztecorum* H. Rob. & Delgad. (Robinson & Delgadillo 1973), and *Pleuridium aurantiacum* Snider & Delgad. (Snider & Delgadillo 1988) from the central highlands.

Continued work on the Hedwigiaceae by De Luna (1995) has produced various contributions that clarify the status of species and genera and offer critical evaluation of characters and character states. Thus, *Braunia secunda* (Hook.) Bruch & Schimp. is re-examined and its geographical distribution updated (De Luna 2016); *Hedwigidium* is not synonymous with *Braunia* on the basis of statistical tests of seta length in numerous specimens (De Luna 2021).

Fossil Bryophytes. It is usually acknowledged that bryophyte fossils are uncommon around the world (Tomescu *et al.* 2018). There have been several incidental discoveries made by foreign bryologists that are worth citing because they are little known records for Mexico; they include four leafy liverworts *Ceratolejeunea antiqua* Heinrichs & Schäf.-Verw., *C. palaeomexicana* (Grolle) G.E. Lee, Schäf.-Verw., A.R. Schmidt & Heinrichs, *C. sublaetefusca* Heinrichs, Pócs & Schäf.-Verw., and *Mastigolejeunea extinta* Heinrichs, Sass-Gyarmati & Schäf.-Verw. (Heinrichs *et al*. 2014, 2015). These were recovered from Miocene amber deposits. A moss specimen identified as *Hypnodontopsis* sp. (Estrada-Ruíz & Riquelme 2017) was also recovered from a Miocene amber deposit in the Simojovel area in Chiapas.

Although not strictly a fossil, as single plant of *Fissidens crispus* Mont. was recovered in a core from Salazar Lake in central Mexico (Castañeda-Bernal & Delgadillo 1998). Radiocarbon analysis indicated that it had been in the area for more than 2,400 years and suggested that other subfossils might be found in additional cores.

Pollution. Bryophytes are indicators of different forms of pollution. Air pollution in Mexico City is a major concern for its effect on humans and other living organisms. Field surveys and the general response of epiphytic mosses to air pollution were made in the urban area of Mexico City (Durán *et al.* 1992). Air quality, heat, and other human activities seem to affect moss development, especially in the downtown area with a gradient toward peripheric and forested areas of the city. Gómez-Arroyo *et al.* (2021) have used *Hypnum amabile* (Mitt.) Hampe samples as a bioaccumulator of atmospheric pollutants and biomonitor of the genotoxic effect in Mexico City. Analyses detected bioaccumulation of 14 heavy metals, 22 polycyclic aromatic hydrocarbons, and DNA damage. Studies of this nature stress the value of mosses exposed to the atmosphere of Mexico City.

Recently, Zepeda-Gómez *et al*. (2014) have shown decrease in bryophyte diversity and abundance in the metropolitan area of Toluca, an area with heavy metal deposition attributed to the intense vehicular traffic and fossil fuel combustion (Zarazúa-Ortega *et al.* 2013). Mosses, according to these authors "…have proved to be a powerful tool for determining the deposition of heavy metals coming from diverse point sources of pollution". The sources and risk areas due to heavy metal (Cr, Cu, Pb, Zn) exposure have been identified in the metropolitan area of Toluca using the mosses *Fabronia ciliaris* (Brid.) Brid. and *Leskea angustata* Taylor (Figure 3) as biomonitors (Ávila-Pérez *et al.* 2018, 2019, Macedo-Miranda *et al*. 2016).

Current and Potential Uses. For a long time, botanists thought that bryophytes had little or no economic value, except for mosses employed as part of the so called "nacimientos". With respect to these, Gómez-Peralta & Wolf (2001) and Anastacio-Martínez *et al.* (2017) described extraction procedures and economic gain by the commercial exploitation of mosses during Christmas celebrations. However, because of the ecological damage caused by the widespread use of mosses in "nacimientos", it has been suggested that other materials be employed for their preparation (*e.g.,* Gómez-Peralta & Ortega 2019).

Besides Christmas celebrations, the use of mosses in horticultural practices has been depicted elsewhere, and recent work in Sierra Juárez in Oaxaca mentions the role of *Dendropogonella rufescens* (Schimp.) E. Britton in construction, ornamental, social, political, and religious events (Hernández-Rodríguez & Delgadillo-Moya 2021).

Technological advances have made possible other uses of bryophytes. Gregorio *et al*. (2016) noted that mosses have several advantages to produce recombinant proteins that are important for therapeutic uses. Three recombinant proteins produced in *Physcomitrella patens* (Hedw.) Bruch & Schimp. are being tested against several diseases. A study by Gómez-Arroyo *et al.* (2021) that demonstrated heavy metal bioaccumulation and the presence of aromatic hydrocarbons in samples of *Hypnum amabile* was mentioned above.

Figure 3. *Leskea angustata*. Portion of a fertile stem.

Ecological Studies. Two ecological studies have been attempted by Mexican bryologists. Spore liberation, the first step toward colonization and establishment of bryophytes, was explored by Delgadillo & Pérez-Bandín (1982). They proposed that shape and structure of the moss plants regulated the rate of spore liberation and that such features as stem height, seta length, urn shape, peristome type, etc. could be tested in wind tunnel experiments. Gemmae-cups, on the other hand, were tested for dissemination of asexual structures that unlike spores, had shorter dispersal distances (maximum 120 cm) in *Marchantia polymorpha* (Equihua 1987).

Desiccation tolerance in bryophytes has been a subject of interest among bryologists (see Proctor *et al.* 2007). Bryophytes exhibit complex molecular, biochemical, and physiological mechanisms in response to drought; their immediate metabolic activity upon rehydration has attracted the attention of some Mexican scientists. They intend to identify and isolate genes linked to dehydration in Mexican mosses (Martínez-Zavala *et al.* 2009) with potential for agricultural application. Some results of their investigations are cited elsewhere in the text.

Research has been initiated on moss taxa that are taxonomically and floristically better understood in Mexico. Collecting records of *Grimmia* offer a tool to examine the potential distribution of species; field validation may further support to current hypotheses on the history of plant occupation of highland areas in central and southern Mexico (Delgadillo *et al*. 2012, Delgadillo-Moya & Peña-Retes 2019). Also, identification of the sexual condition in Mexican mosses (Peña-Retes & Delgadillo-Moya 2018, 2020) is an opportunity to further investigate their ecological and evolutionary behavior. Although a slightly higher percent of our species are dioicous, nothing is known of the effect of their condition in the history and distribution of species and floras.

The interaction of bryophytes with animals has been identified in zoological studies in Mexico. Hoffmann & Riverón (1992), Mojica-Guzmán & Johansen (1990), Pérez-Pech *et al*. (2017) and others have identified mites, thrips, and tardigrades living on mosses. Specific epithets for bryophytes are usually missing.

DNA Research. Various publications have contributed data on subjects requiring DNA analysis. García-Avila *et al.* (2009), for instance, used two chloroplast codifier genes and an intergenic spacer to study the phylogenetic relationships of Thuidiaceae and Leskeaceae. The analyses sampled representatives of presumed related families such as Amblystegiaceae and Anomodontaceae, as well as Rigodiaceae, Pterigynandraceae, and others. Although the relationships of the Thuidiaceae were not adequately resolved, it was concluded that they are not monophyletic, as currently defined, whereas the Leskeaceae are polyphyletic.

Cevallos *et al.* (2019) grew a desiccation tolerant *Pseudocrossidium replicatum* moss (Figure 4) from Mexican material; its peculiar leaf margins are spirally inrolled and contain abundant chlorophyll. Its complete chloroplast genome consists of 123,512 bp and the phylogenetic analysis indicated that it is closely related to *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr. Similar analyses were made to obtain the mitochondrial genome of *P. replicatum* which was found to consist of 105,495 bp from which several genes have been lost in several linages during evolution (Cevallos *et al*. 2020).

Figure 4. *Pseudocrossidium replicatum*. The dry leaves are spirally contorted around the stem.

Research on the effect of osmotic stress by glucose and sorbitol on *Physcomitrella patens* protonema indicates that there are more than 100 enzyme-coding genes associated with metabolic pathways important in stress tolerance (Orbe Sosa *et al.* 2020).

A final note. Projects underway at different institutions attest to the quality of the research material represented by bryophytes. Few Mexican scientists would call themselves bryologists, but their involvement and utilization of these plants have contributed greatly to advancements in this field of study. Such studies did not occur fifty years ago.

Bryology in Mexico is a young discipline. National and local inventories are a prerequisite to learning about numbers of species and distribution of diversity in our territory; for mosses, these are incomplete or non-existent for large regions, especially in the northwestern states. For hornworts and liverworts, the whole country needs to be explored. Development of regional bryophyte collections would offer a better understanding of their distribution and history in the country. Many bryophyte groups are poorly understood and require systematic studies. Molecular analyses would assist in the solutions of problems in phylogeny, medicine, and agriculture. Scientists would be able to answer questions about ecosystem services, climatic change, and air, soil, and water pollution by using bryophytes as model organisms. Conservation should not be postponed in view of environmental degradation, and student training in bryology is also important if work opportunities are made available.

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