

BRYOPHYTE SYSTEMATICS

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Summary

The bryophytes are land plants characterized by a heteromorphic life cycle in which the haploid green phase, the gametophyte, is the dominant thalloid or foliose plant. The diploid generation, the unbranched sporophyte, remains attached to the gametophyte and is photosynthetic for a short time. Molecular data indicate that the three groups traditionally included in the bryophytes do not constitute a natural monophyletic group, and the classification of the higher categories has thus been modified to reflect their relationship as they are understood at present.

According to the current classification, the Division Marchantiophyta (hepaticae or liverworts) represents the basal lineage of all land plants, while the Division Antocerotophyta (hornworts) and the Division Bryophyta (musci or mosses) are more closely related to each other than to the liverworts. The mosses are the sister group to other land plants, the tracheophytes. The hypotheses behind this classification have not received universal support and additional morphologic information, molecular data, and cladistic analyses are required to determine the phylogenetic relationships of these plants.

1. Introduction

The bryophytes constitute a group of green land plants characterized by a gametophyte-dominated heteromorphic life cycle. The gametophyte is a haploid, thalloid, or foliose structure that grows by means of an apical meristematic cell and originates from a ribbon-like or filamentous phase called the protonema. The sporophyte is an unbranched diploid structure consisting of a foot, a pedicel or seta that bears a single terminal capsule, the sporogonium. It is at least partly dependent on the gametophyte for nutrients and becomes attached to it after the fertilization of the female cell, the oosphere, as the zygote continues to grow within the female sexual organ, the archegonium. Both the dispersal and fertilization by antherozoids require liquid water. While bryologists agree that the subdivisions of the bryophytes are closer to each other than to other extant groups of plants, there is no consensus as to the degree of relationship or how this should be expressed in a classification system. The Anthocerotae, the Hepaticae and the Musci were considered as classes of the division Bryophyta in the past, but recent trends rank each at the division level.

The term Bryophyta was coined by Braun 1864 to include the algae, fungi, lichens, and mosses. Recent research appears to indicate that bryophytes do not have a common origin, so that the system of classification needs to be altered.

There are about 100 species of hornworts, 6500 to 7000 liverworts, and about 12 800 mosses. Their morphological and ecological diversity, and their evolutionary history make them a cornerstone for understanding the evolution of all land plants.

2. Morphology

2.3 Anthocerotae (Hornworts)

The gametophyte in the hornworts is a thalloid, multi-layered lobed body that may be smooth on the dorsal surface (Figure 1).

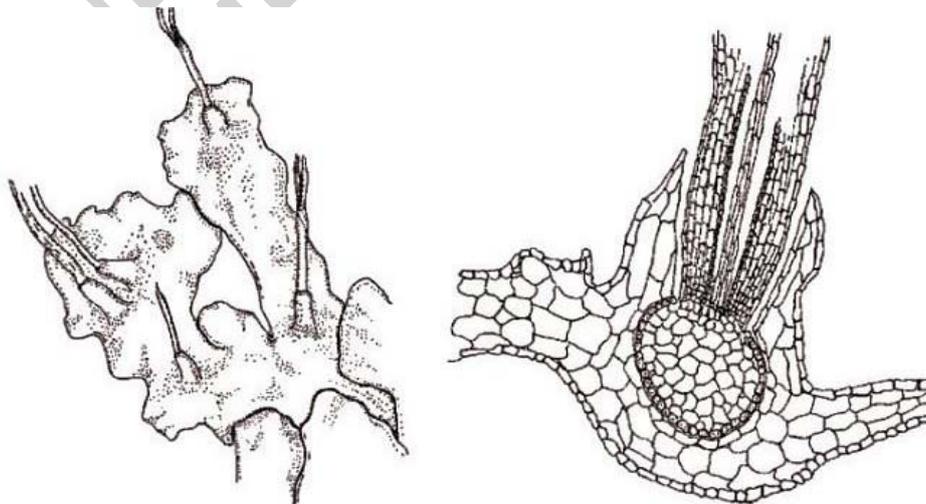


Figure 1. *Anthoceros* sp. Left: portion of a thallus with sporophytes. Right: section through the gametophyte and sporophyte.

Each gametophytic cell contains, as a rule, a single lenticular chloroplast, but there may be up to 12 chloroplasts in *Megaceros*. The central part of the chloroplast contains a single pyrenoid. Growth occurs by an apical cell located in the notch of the thallus. On the ventral surface there are numerous smooth-walled rhizoids and pores that communicate with mucilage chambers frequently filled with *Nostoc*, a nitrogen-fixing alga. The pores are sometimes interpreted as stomata that are remnants of an ancestor with radial symmetry. The sex organs develop from surface cells; the antheridia are found in dorsal chambers with openings toward the dorsal surface while the archegonia have the neck canal cells and the oosphere surrounded by undifferentiated gametophytic cells. Following the fertilization, the first division of the zygote is longitudinal resulting in a bilateral sporophyte.

While the gametophyte may be thought of as primitive and quite simple, the sporophyte has a comparatively complex structure. The capsule wall is a multistratose jacket enclosing the sporogenous tissue that gives rise to spores and pseudoelaters, and the columella (Figure 1). The outer layer of the jacket contains stomata. Dehiscence occurs by one, two, or four longitudinal lines and maturation proceeds from the tip downwards. The indeterminate growth of the sporophyte is due to an intercalary meristem located between the foot and the capsule; because of this meristem, the sporophyte may produce spores for an indefinite period of time. Dispersal is aided by the drying usually multicellular pseudoelaters and capsule walls that coil and twist and release the spores.

2.4 Hepaticae (Liverworts)

The gametophyte in the liverworts (gametophore) is either a thalloid ribbon-like body (Figure 2) or a foliose structure (Figure 3). The thalloid liverworts are usually prostrate, dorsiventral, dichotomously branched, with a distinct midrib, and numerous unicellular rhizoids on the ventral surface. Internal differentiation is variable, from very simple and consisting of a few layers of cells to comparatively complex, with an epidermal layer, air chambers and pores, a well-developed photosynthetic tissue, and several layers of storage cells. Under the light microscope, the epidermis or the leaf cells frequently show certain organelles called oil bodies that contain terpenoids and vary in number, color, and distribution. The sex organs are formed either on the dorsal surface of the thallus within a median longitudinal furrow or on specialized branches that elevate them into the air. Asexual reproduction occurs by progressive death and decay of the older parts of the thallus and the separation of the surviving branches, or by gemmae produced in branches or in special receptacles called gemma cups.

The foliose liverworts have stems with unicellular rhizoids and three rows of leaves: two dorsal rows of large, bilobed leaves inserted diagonally on the stem; and the ventral row formed by smaller leaves that may become reduced or wanting and are inserted transversely on the stem. There are, however, some isophyllous taxa where all three rows of leaves are present and transversely inserted on the stem. Both the dorsal and ventral leaves are variously dissected, usually consisting of a unistratose lamina and sometimes a band of several long thick-walled cells at mid leaf, the vitta. The stem shows little internal differentiation, with an outer cortical layer that may be made of smaller cells than those of the inner medullar area. The archegonia are terminal on stems or branches while the antheridia are borne singly or in groups in leaf axils.

In the liverworts, the sporophyte has a small seta that elongates when the spores are mature and the capsule wall consists of one to several layers of cells with no stomata. The capsule wall opens by four valves that expose the mature capsules and elaters to the wind. The sporogenous tissue gives rise to spores and elaters. The latter have hygroscopic movements, due to the combined action of one or several spiral wall thickenings and changes in water tension that aid in the dispersal of spores.



Figure 2. *Pterobryon densum* illustrates the dendroid habit of many neotropical mosses.



Figure 3. *Dumortiera hirsuta*, a thalloid liverwort growing on basaltic rock.

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Biographical Sketch

Claudio Delgadillo-Moya, born on February 18, 1945, is a research scientist at the National University of Mexico where he works on taxonomy and phytogeography of mosses, with emphasis on the Mexican and neotropical species. He received an undergraduate diploma from the National University of Mexico, a Master of Science degree from the University of Tennessee, and a Ph. D. from Duke University, the latter two in the United States. He is member of several professional societies, author of about 85 scientific

articles, 4 books, and about 20 popular articles; has served on the editorial board of such scientific journals as *Flora Neotropica* and *Tropical Bryology*, and is past editor of *Flora de México* and of *Briolatina*, the newsletter of *Sociedad Latinoamericana de Briología*. He is currently responsible for the Bryophyte Collection of the National Herbarium (MEXU) at the National University of Mexico. He has received various research grants from CONACYT, CONABIO, The Society of the Sigma Xi, and The National Geographic Society; he earned a National Researcher status since 1984, a distinction from the federal government in Mexico.

Claudio Delgadillo is married to Maria Teresa Chavez and lives in Mexico City with their daughter and son (Claudia 26 and Iván 24).