

## 1

## Evolutionary significance of bryophytes

Vascular plants, particularly seed plants, dominate vegetation throughout much of the world today, from the lush rainforests of the tropics harbouring a vast diversity of angiosperms, to the boreal forests of coniferous trees, draping the northern latitudes of the globe. This dominance in the landscape is the result of a long evolutionary history of plants conquering land.

Evolution is the result of a suite of incessant attempts to improve fitness and take advantage of opportunities, such as escaping competition and occupying a new habitat. Pilgrims, fleeing the biotic interactions in the aquatic habitat, faced severe abiotic selection forces on land. How many attempts were made to conquer land is not known, but at least one of them led to the successful establishment of a colony. At least one population of one species had acquired a suite of traits that allowed it to complete its life cycle and persist on land. The ancestor to land plants was born. It may have taken another 100 million years for plants to overcome major hurdles, but by the Devonian Period (approximately 400 mya), a diversity of plants adapted to the terrestrial environment and able to absorb water and nutrients, and transport and distribute them throughout their aerial shoots, occupied at least some portions of the land masses. Soon thereafter, plants were freed from the necessity of water for sexual reproduction, by transporting their sperm cells in pollen grains carried by wind or insects to the female sex organs, and seeds protected the newly formed embryo. Angiosperms, with their elaborate flowers and seeds packed with a reserve-filled endosperm, are the last major product of land plant evolution. Their origin dates back to approximately 150 mya, at most. Today, scientists estimate the diversity of flowering plants at about 250–300 000 species, distributed throughout the globe, in virtually all habitats. This evolutionary success story has its roots in the Ordovician Period, with the initial transition to land and the diversification of the earliest land plants.

Bryophytes, which evolved during a pivotal moment in the history of life on earth and have persisted for hundreds of millions years (Renzaglia *et al.* 2007), are considered the closest modern relatives of the ancestors to the earliest terrestrial plants. Furthermore, the ancestor to the vascular plants is thought to have shared many features with bryophytes. These diminutive and often overlooked members of our green world hold the key part in the evolutionary history of land plants: bryophytes mark the transition to land and the origin of vascular plants, and hence, link the seed and vascular plants to their algal ancestors.

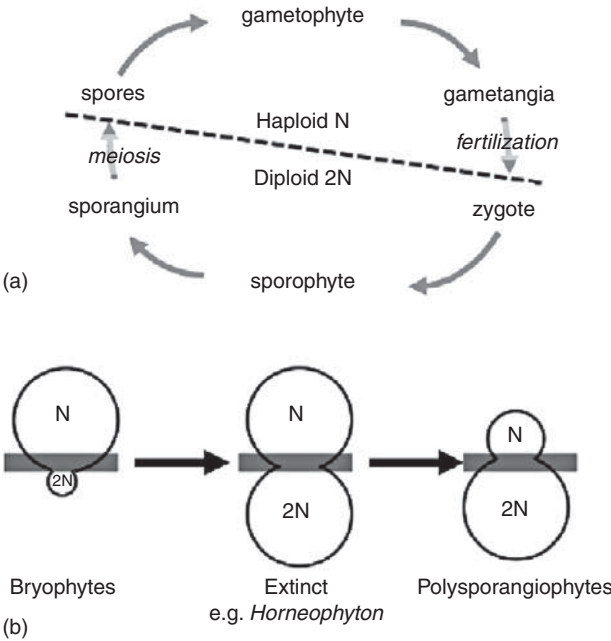
In this chapter, we outline the characteristics of bryophytes, contrast them to those of other early land plants and summarize our current understanding of the significance of bryophytes in land plant evolution. The phylogeny of land plants also serves to implicitly reconstruct the transformations of critical morphological or life history features. Several physiological and morphological adaptations provided the fundamental requirements for the colonization of and diversification on land. One such critical innovation may have been the ability to establish close interactions with micro-organisms, such as bacteria and fungi, to ensure access to limited and scattered nutrients. Today, bryophytes are vital at the ecosystem level, from playing an essential role in global biogeochemical cycles by sequestering large quantities of carbon as peat in *Sphagnum* bogs, controlling water and nutrient flow in tropical montane forests where they form luxuriant epiphytic vegetation, to providing shelter for a diversity of micro-organisms (see Chapter 2).

**1.1 What do we call a bryophyte?**

The term ‘bryophyte’ has its origin in the Greek language, referring to plants that swell upon hydration (see Section 8.1). ‘Bryophytes’ is a generic name for plants characterized by a life cycle featuring alternating haploid and diploid generations with a dominant gametophyte (Box 1.1). In fact, bryophytes are the only land plants with a dominant, branched gametophyte, which exhibits a diversity of morphologies unparalleled in tracheophytes (Crum 2001). This feature was long considered indicative of a unique shared ancestry, but the notion of the monophyly of bryophytes has now been strongly challenged. Extant bryophytes belong to either liverworts (Marchantiophyta), mosses (Bryophyta in the strict sense) or hornworts (Anthocerotophyta). These lineages share several characters, some of which have been retained by all other land plants (e.g. an embryo which gives land plants their name ‘embryophytes’), and others that are unique (e.g. an unbranched sporophyte, with a single spore producing tissue, or sporangium). As in other extant land plants, the gametophyte lacks stomata. The three major bryophyte lineages

Box 1.1  
The bryophyte life cycle

The life cycle of all land plants is characterized by an alternation of generations, in which a haploid phase gives rise, following fertilization, to a diploid phase that eventually undergoes meiosis to regenerate haploid cells. The transition from haploid to diploid generation is characterized by fusion of gametes, yielding a zygote. The reverse transition is marked by meiosis, resulting in spore formation. The gametophyte bears the sex organs and the sporophyte holds the sporangium. In all land plants, sex organs are specialized for producing male or female gametes (the sex cells; Box 1.1 Fig. 1a).

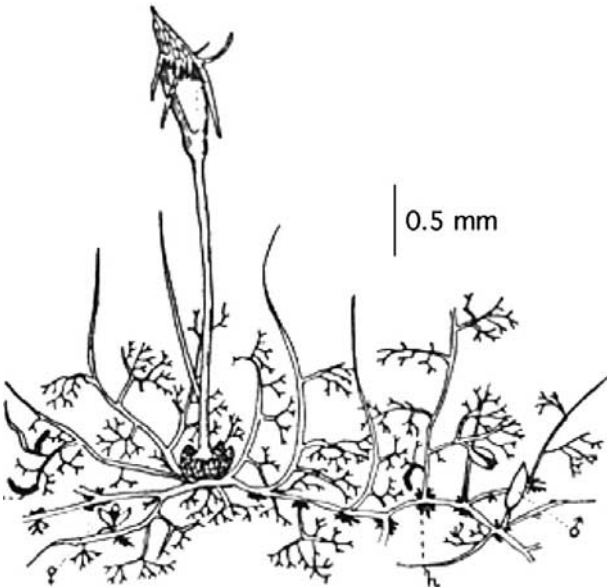


Box 1.1 Fig. 1. The bryophyte life cycle. See text for details.

Bryophytes are the only extant land plants in which the gametophyte is the dominant generation in the life cycle. The sporophyte is unbranched and permanently attached to the maternal (gametophyte) plant. This sporophyte yields a single sporangium. The first multicellular stage following the germination of the spore is termed a sporeling that develops into a gametophyte. In mosses, the sporeling lasts somewhat longer than in liverworts and hornworts and develops into a thallus or a filamentous network termed protonema, which is able to produce several gametophytes. The latter may be branched or unbranched. In all other extant land plants, the balance of dominance is reversed (Box 1.1 Fig. 1b): the sporophyte is branched and independent and the

Box 1.1 (cont.)

gametophyte is reduced. In seed plants, the female gametophyte is enclosed in the ovule and the male cells remain protected by the spore wall (or pollen grain). In some, now extinct, land plants the two generations were very similar, and each was probably independent at maturity.



Box 1.1 Fig. 2. The Southeast Asian moss *Ephemeropestis tibodensis*, wherein both male and female gametangia as well as sporophytes are directly produced on a persisting protonema. Such a case of neoteny is interpreted as a short-cut in the life cycle, allowing for rapid maturation and reproduction in unstable, temporary habitats such as the twigs and living leaves on which the species grows (reproduced from Goebel 1887).

Because the sperm and egg cells of bryophytes are produced in two distinct organs, and even on two different plants in the case of dioicous species, the sperm must reach the egg for fertilization to occur. Typically, the flagellated sperm cells swim to reach the egg, which must be in close proximity for the fusion to occur. Raindrops crashing onto male sex organs arranged in cups formed by tight whorls of leaves may, upon fragmentation, catapult sperm cells inside tiny droplets over greater distances. Sperm dispersal may also be enhanced by arthropods that are recruited as vectors (Cronberg *et al.* 2006a).

In bryophytes, both generations are usually conspicuous, but reduction of one or the other, or both, is not rare. Loss of complexity characterizes the sporophyte of various lineages of bryophytes, often as an adaptation to dry habitats

Box 1.1 (cont.)

(Vitt 1981). By contrast, some mosses and liverworts exhibit highly reduced gametophytic phases. Some species have the ability to reproduce sexually in the juvenile state. In such neotenic species, the sporophyte develops directly onto the sporeling or protonema (Box 1.1 Fig. 2) (Gradstein & Wilson 2008).

differ from one another in a variety of attributes, most conspicuously in the architecture of the vegetative (gametophyte) body and the sporophyte, to the extent that they are easily distinguished in the field. In essence, the following combinations of morphological and anatomical characters are diagnostic for each of these three lineages:

- ***Marchantiophyta*** (liverworts; see Chapter 3 and Crandall-Stotler *et al.* 2009 for a more detailed account). The vegetative gametophyte is either thalloid (i.e. ribbon-like plants; Fig. 1.1a) or composed of a leafy stem, with leaves arranged in two or three parallel rows (Fig. 1.1b). Specialized water conducting cells account for endohydric transport in the gametophytes of some taxa (Edwards *et al.* 2003), but are always lacking in the sporophyte. The sporophyte produces a single sporangium elevated, at maturity, on a seta that grows primarily by cell elongation rather than extensive cell divisions. The mode of dehiscence of the sporangium varies but typically, the capsule wall splits along four vertical lines. Stomata are always lacking in the sporangial wall. The capsule holds spores and elaters, elongated cells with spiral wall thickenings that are thought to promote spore release. An axial columella is lacking in the sporangium. Spores typically develop into a single, branched gametophyte.
- ***Bryophyta*** (in the strictest sense, the division ‘Bryophyta’ includes only mosses; see Chapter 4 and Goffinet *et al.* 2009 for a more detailed account). The vegetative body is always composed of a stem bearing leaves, typically arranged in spiral rows (Fig. 1.2). Axial water conducting strands occur in both generations of many taxa. The activity of an intercalary meristem, located immediately below the presumptive capsule, gives rise to the seta, which completes its development prior to sporogenesis. This stalk is almost never branched, although in very rare cases two capsules may be found on the same seta (Leitgeb 1876). The sporangium is always terminal. In the majority of mosses, the capsule sheds an operculum (Fig. 1.2). Stomata may occur in the capsule wall, but are always lacking on the seta. The columella typically extends beyond the sporogenous layer. In most taxa, the spore sac surrounds an axial columella, rarely does it also arch over it. Cells of the sporogenous tissue never divide to form elaters. Spore germination results in a filamentous or, in some basal lineages including *Sphagnum* and *Oedipodium*, a thalloid sporeling called a protonema, which subsequently develops into one to several gametophytes.



Fig. 1.1a. The complex thalloid *Marchantia berteroana*, dorsal view, showing hexagonal outlines of the air chambers. Note also the conical gemmae cups (photo R. Rozzi). See plate section for colour version.

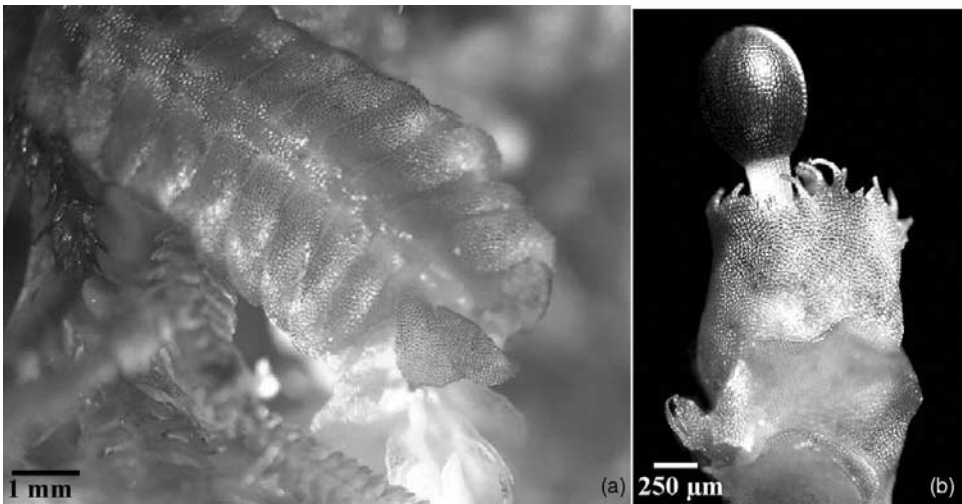


Fig. 1.1b. Dorsal view of the leafy liverwort *Leptoscyphus australis* (a), showing lateral leaves organized in two rows. The seta is hyaline and the capsule globose (b) (photo D. Glenn and B. Malcolm). See plate section for colour version.



1.1 What do we call a bryophyte?

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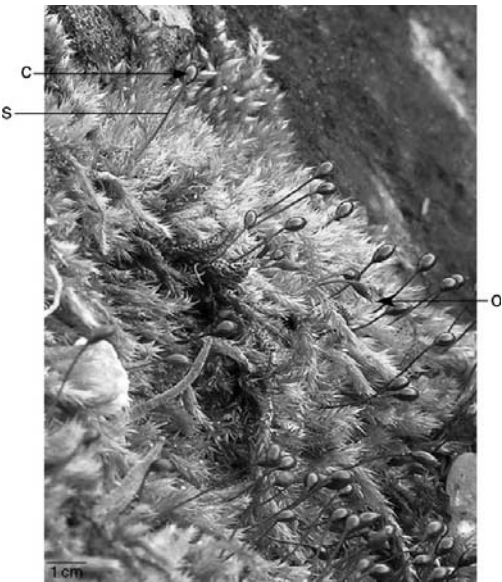


Fig. 1.2. The moss *Sciurohypnum plumosum* with a chlorophyllous seta, S, and capsule, C, closed by a rostrate operculum, O. Note the spiral insertion of the leaves around the stem (photo P. Degroot). See plate section for colour version.

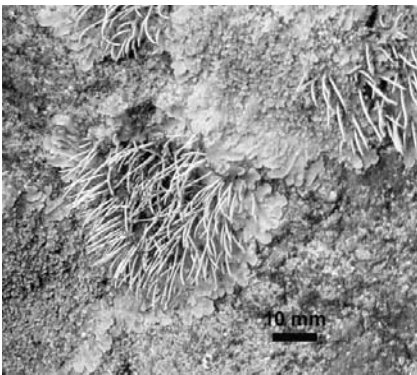


Fig. 1.3. The hornwort *Leiosporoceros dussii*. Note the thalloid gametophyte and the elongate, chlorophyllous sporophyte (photo J.C. Villarreal). See plate section for colour version.

- *Anthocerotophyta* (hornworts; see Chapter 5 and Renzaglia *et al.* 2009 for a more detailed account). The vegetative gametophyte is always thalloid. The thallus may be dissected but never bears leaves (Fig. 1.3). Water conducting cells are lacking in both generations of the life cycle. The sporophyte is linear and composed, except for the foot, of the long sporangium. A seta is thus completely

lacking. A basal meristem adds new cells to the base of the sporangium, which consequently matures basipetally. Dehiscence follows two longitudinal lines, extending downward much like a zipper, gradually exposing a spore mass surrounding an axial columella. Pseudo-elaters facilitate the dispersal of spores. Stomata are present on the sporangial walls of some taxa. All hornworts harbour endosymbiotic colonies of *Nostoc*, which form globular or channelled clusters throughout the thallus.

## 1.2 Bryophytes are embryophytes

The conspicuous morphological disparity between bryophyte and vascular lineages may, at first, obscure their shared evolutionary history. Their common ancestry is revealed, however, by fundamental attributes that these lineages share, as first highlighted by Parenti (1980) and Mishler and Churchill (1984) based on morphology, and subsequently demonstrated repeatedly with DNA sequence data. Land plants clearly share a suite of characteristics, which were all inherited from a single common ancestor, rather than acquired independently by multiple lineages. Morphological features that bryophytes share with other embryophytes (also called land plants) include multicellular sex organs, a cuticle and the retention of the zygote, which undergoes mitotic divisions within the confines of the archegonium. In fact, if the zygote undergoes meiosis (as in most algae), only four spores can be produced. Delaying meiosis, which results in the production of a multicellular body through mitotic divisions, offers the opportunity for more cells to divide meiotically, each meiotic division resulting in four spores. Hence, more spores are produced per zygote, and more spores are dispersed per sexual reproductive event. As more spores are produced, the number of newly established gametophytes is likely to rise. In organisms with unisexual gametophytes, higher population densities may reduce the distance between male and female plants and thereby favour sexual reproduction. Developing a multicellular diploid generation (the sporophyte) with a proliferation of cells undergoing meiosis undoubtedly provides advantages which, over evolutionary time, must have outweighed the cost of resources invested in the production of the sporophyte and spores.

A multicellular sporophyte, however, introduces a weak link in the life cycle: the embryo. Selection on embryo survival must have been so strong that only plants adopting maternal care for the offspring persisted. Indeed, no land plant, whether extant or now extinct, is known to disperse its zygote or its embryo. The zygote develops within the female sex organ. The growing embryo of all land plants is physically attached and physiologically dependent



on the female gametophyte (a situation known as matrotrophy), if only during the earliest ontogenetic stages.

Matrotrophy is apparent in bryophytes, as the sporophyte remains physically dependent on the maternal gametophyte from which it receives water, mineral nutrients and various organic compounds. At the junction between the gametophyte and sporophyte, transfer cells forming the placenta enhance the movement of inorganic and organic compounds through the infolded cell wall and membrane, offering a vast surface for exchanges between the two generations (Ligrone *et al.* 1993). A physical connection between the maternal plant and the embryo is required for matrotrophy, hence the zygote, and thus the egg, must remain enclosed in the archegonium. Physical and physiological constraints on matrotrophy may be such that only plants carrying a single egg in their archegonium provide such care. In bryophytes, the maternal plant initiates, upon fertilization, a protective sheath derived from the gametangium and adjacent vegetative tissues around the nascent embryo. The archegonium thus plays a dual role of protecting the egg, and later, the embryo. In liverworts, the sporophyte may complete its development protected by various gametophytic tissues from the archegonium, leaves, or stem (Section 3.1.1). By contrast, the sporophyte of hornworts emerges quickly from the basal sheath, which encloses only the portion of the sporangium undergoing meiosis. In mosses, the modified archegonium or epigonium typically ruptures near its base and the hood (the calyptra) covers the apex of the sporophyte until meiosis is completed. Protection of the young sporophyte seems essential to ensure sporogenesis and thus maximize the chance of producing viable spores. Further evolutionary modifications and improvements eventually led to the ultimate maternal care, as seen in flowering plants. Here, the embryo, along with nutrient reserves and the remainder of the whole female gametophyte, is enclosed within a seed.

Matrotrophy may have been a key innovation acquired early in the evolution of embryophytes, a trait conferring a significant advantage and promoting diversification (Graham & Wilcox 2000). A single lineage with plants nurturing the developing multicellular sporophyte was successful. This lineage gave rise to the land plants as we know them today.

### 1.3 Bryophytes and land plant evolution

Elucidating the phylogenetic relationships among major lineages of embryophytes, and in particular the relationships among the three main lineages of bryophytes, is essential to reconstructing the origin of critical morphological, anatomical and physiological innovations of plants to conquer land, and

thereby to understanding the selection forces that shaped the evolution of plants following the transition to land. Three sources of evidence are available to establish the relationships among early land plants: comparative morphology and anatomy of extant and fossil plants and, more recently, analysis of DNA sequence data.

### ***1.3.1 Bryophytes and the transition to land: evidence from fossils***

Fossilization is an extremely rare event. One just has to look around today to appreciate that few of the individuals living at any particular time will ever be preserved in sediments. The quality of the plant material preserved in geological strata varies, particularly with the mode of fossilization and the time elapsed since the burial. Most Paleozoic Era plant remains occur as compression or impression fossils. Plants were rapidly covered by sediments and, under the growing pressure, were dehydrated and flattened, in some cases reduced to only a thin carbonaceous film, or some cuticular fragments. If all organic material was degraded, a mere imprint of the plant part remains. In aquatic environments, water rich in minerals may have infiltrated the tissues, filled the cells, precipitated and cemented the cell walls. Such permineralized fossils typically retain their three-dimensional architecture, as well as microscopic features of the cell, and therefore offer the most complete picture of early land plant body structure.

Silurian Period (443–416 mya) and younger deposits hold increasingly intact plant remains (megafossils), whereas the Ordovician Period (488–443 mya) and older sediments yield only cellular debris and spores (microfossils; Edwards 2000, Wellman & Gray 2000) (Fig. 1.4). The oldest fragments consist of tubes, tracheids and cuticle. The presence of such decay resistant materials is thought indicative of land plants or their immediate precursors. How these fragments are connected to modern or even extinct lineages that are defined primarily by reproductive features is difficult to establish. Some of the tubular microfossils resemble remains obtained from extant mosses treated with high temperature acid hydrolysis (Kodner & Graham 2001). Similar treatments on several extant bryophytes further revealed a similarity between the fragments resisting the treatment and those recovered from early- and mid-Paleozoic sediments (Graham *et al.* 2004). Spores retaining their tetrahedral arrangement inside an envelope have been recovered from the Ordovician Period (Edwards *et al.* 1995) (Fig. 1.4), and these too find a counterpart among extant liverwort lineages. The microfossil record thus suggests that bryophytes, and in particular liverworts, were integral parts of the earliest plant