SEM II: BOTANY

C4T: Archegoniate

Unit 2: Bryophytes
General characteristics; Adaptations to land habit; Classification; Range of thallus organization.

What is bryophyte?

Bryophyta (Gr. Bryon = mass; phyton = plant), a division of kingdom Plantae comprises of Liverworts, Hornworts and mosses. They are groups of green plants which occupy a position between the thallophytes (Algae) and the vascular cryptogams (Pteridophytes).
Bryophytes produce embryos but lack seeds and vascular tissues. They are the most simple and primitive group of Embryophyta. They are said to be the first land plants or non-vascular land plants (Atracheata). Presence of swimming antherozoids is an evidence of their aquatic ancestory.

Where from Bryophytes originated?

Nothing definite is known about the origin of Bryophytes because of the very little fossil record. There are two views regarding the origin of Bryophytes.
These are:
(i) Algal hypothesis of the origin of Bryophytes.
(ii) Pteridophytean hypothesis of the origin of Bryophytes.
(i) Algal Hypothesis of Origin:
There is no fossil evidence of origin of Bryophytes from algae but Bryophytes resemble with algae in characters like-amphibious nature, presence of flagellated antherozoids and necessity of water for fertilization.
This hypothesis was supported by Lignier (1903), Bower (1908), Fritsch (1945) and Smith (1955) etc. According to Fritsch (1945) and Smith (1955) Bryophytes have been originated from the heterotrichous green algae belonging to the order Chaetophorales for e.g., *Fritschiella*,
(ii) Pteridophytean Hypothesis of Origin:
According to this hypothesis Bryophytes are descendent of Pteridophytes. They are evolved from Pteridophytes by progressive simplification or reduction.
This hypothesis is based on certain characters like-presence of type of stomata on the sporogonium of *Anthoceros* and apophysis of mosses similar to the vascular land plants, similarly in the sporophytes of some Bryophytes (e.g., *Anthoceros*, *Sphagnum*, *Andreaea*) with some members of Psilophytales of Pteridophytes (e.g., *Rhynia*, *Hormophyton* etc.)
This hypothesis was supported by Scot (1911), Kashyap (1919), Kidston and Lang (1917-21), Haskell (1914) Christensen (1954), Proskaner (1961), Mehra (1968) etc.

Distribution of Bryophytes?

Bryophytes are represented by 960 genera and 24,000 species. They are cosmopolitan in distribution and are found growing both in the temperate and tropical regions of the world at an altitude of 4000-8000 feet.

In India, Bryophytes are quite abundant in both Nilgiri hills and Himalayas; Kullu, Manali, Shimla, Darjeeling, Dalhousie and Garhwal are some of the hilly regions which also have a luxuriant growth of Bryophytes. Eastern Himalayas have the richest in bryophytic flora. A few species of *Riccia, Marchantia* and *Funaria* occur in the plains of U.P., M.P. Rajasthan, Gujarat and South India.

In hills they grow during the summer or rainy season. Winter is the rest period. In the plains the rest period is summer, whereas active growth takes place during the winter and the rainy season.

Some Bryophytes have also been recorded from different geological eras e.g., *Muscites yallourensis* (Coenozoic era), *Intia vermicularies, Marchantia* spp. (Palaeozoic era) etc.

Habitat of Bryophytes:

Bryophytes grow densely in moist and shady places and form thick carpets or mats on damp soils, rocks, bark of trees especially during rainy season.

Majority of the species are terrestrial but a few species grow in fresh water (aquatic) e.g., *Riccia fluitans, Ricciocarpos natans, Riella* etc. Bryophytes are not found in sea but some mosses are found growing in the crevices of rocks and are being regularly bathed by sea water e.g., Grimmia maritima.

Some Bryophytes also grow in diverse habitats e.g., *Sphagnum*-grows in bogs, *Dendroceros*-epiphytic, *Radula protensa*. *Crossomitrium* -epiphyllous, *Polytrichum juniperinum*-xerophytic, *Tortula muralis*-on old walls. *Tortula desertorum* in deserts, *Porella platyphylla*-on dry rocks, *Buxbaumia aphylla* (moss), *Cryptothallus mirabilis* (liverwort) are saprophytic.

General Characters of Bryophytes:

1. Bryophytes grow in damp and shady places.
2. They follow heterologous haplodiplobiontic type of life cycle.
3. The dominant plant body is gametophyte on which sporophyte is semiparasitic for its nutrition.
4. The thalloid gametophyte differentiated in to rhizoids, axis (stem) and leaves.
5. Vascular tissues (xylem and phloem) absent.
6. The gametophyte bears multi-cellular and jacketed sex organs (antheridia and archegonia).
7. Sexual reproduction is oogamous type.
8. Multi-cellular embryo develops inside archegonium.
9. Sporophyte differentiated into foot, seta and capsule.
10. Capsule produces haploid meiospores of similar types (homosporous).
11. Spore germinates into juvenile gametophyte called protonema.
12. Progressive sterilization of sporogenous tissue noticed from lower to higher bryophytes.
13. Bryophytes are classified under three classes: Hepaticae (Liverworts), Anthocerotae (Hornworts) and Musci (Mosses).

Classification of Bryophytes:

According to the latest recommendations of ICBN (International Code of Botanical Nomenclature), bryophytes have been divided into three classes.

1. Hepaticae (Hepaticopsida = Liverworts)
2. Anthocerotae (Anthocertopsida= Hornworts)
3. Musci (Bryopsida= Mosses)

Class 1. Hepaticae or Hepaticopsida:

1. Gametophytic plant body is either thalloid or foliose. If foliose, the lateral appendages (leaves) are without mid-rib. Always dorsiventral.
2. Rhizoids without septa.
3. Each cell in the thallus contains many chloroplasts; the chloroplasts are without pyrenoid.
4. Sex organs are embedded in the dorsal surface.
5. Sporophyte may be simple (e.g., *Riccia*) having only a capsule, or differentiated into root, seta and capsule (e.g., *Marchantia, Pallia and Porella* etc.)
6. Capsule lacks columella.
7. It has 4 orders:

(i) Calobryales
(ii) Jungermanniales
(iii) Spherocarpales
(iv) Marchantiales.

Table 22.1 Bryophyte Taxonomy

Common Name	Traditional Taxonomic Name
Hornworts	Anthocerotophyta (=Anthocerophyta)
Liverworts	Marchantiophyta (=Hepaticophyta or Hepatophyta)
	Jungermanniopsida
Leafy liverworts	Jungermanniidae
	Porellales
	Porella
	Radulales
	Pleuroziales
	Lepicoleales
	Jungermanniales
Simple thalloids	Metzgeriidae
	Metzgeriales
	Haplomitriales
	Blasiales
	Treubiales
	Fossombroniales
Complex thalloids	Marchantiopsida
	Marchantiales
	Marchantia
	Sphaerocarpales
	Monocleales
	Ricciales
	Riccia
Mosses	Bryophyta
Granite mosses	Andreaeopsida
Peat mosses	Sphagnopsida
	Sphagnum
True mosses	Bryopsida
	Dawsonia, Ptychomnion, Bryum
	Takak Jungermanniidae iopsida

Class 2. Anthocerotae or Anthocerotopsid:

1. Gametophytic plant body is simple, thalloid; thallus dorsiventral without air chambers, shows no internal differentiation of tissues.
2. Scales are absent in the thallus.
3. Each cell of the thallus possesses a single large chloroplast with a pyrenoid.
4. Sporophyte is cylindrical only partly dependent upon gametophyte for its nourishment. It is differentiated into bulbous foot and cylindrical capsule. Seta is meristematic.
5. Endothecium forms the sterile central column (i.e., columella) in the capsule (i.e. columella is present).
6. It has only one order-Anthocerotales.

Class 3. Musci or Bryopsida:

1. Gametophyte is differentiated into prostrate protonema and an erect gametophores
2. Gametophore is foliose, differentiated into an axis (=stem) and lateral appendages like leaves but without midrib.
3. Rhizoids multi-cellular with oblique septa.
4. Elaters are absent in the capsule of sporangium.
5. The sex organs are produced in separate branches immersed in a group of leaves.
6. It has only three orders:

(i) Bryales,

(ii) Andriales
(iii) Sphagnales.

Bryophytes are not a natural group

Bryophyte is a common name applied to three distinct lineages of plants that lack lignified vascular tissue. Bryophytes do not form a monophyletic group, because vascular plants are descended from them. This chapter considers them as three lineages (Table 22.1).

Mosses are familiar to everyone as a green mat in shady, moist places or lining the cracks in rocks and walls (Fig. 22.2b). Although less familiar, the liverworts also are quite common and can be found in many places if you know what to look for (Fig. 22.2d). The hornworts are the least familiar, because they often are rare and inconspicuous (Fig. 22.2e). Because they lack lignified stiffening and vascular tissues, bryophytes remain small. Mosses and liverworts, however, seldom grow alone. Colonies can cover large areas of ground and represent substantial biomass in certain communities. Some bryophytes have flat, ribbon-like bodies called thalli (singular, thallus) that often bifurcate as they grow, whereas others have a more familiar upright form with tiny leaves born on short stems.

Bryophytes frequently also possess minute projections composed of single or multiple cells that anchor the plants to the soil and thus resemble roots. In some species, they may even serve to conduct water and minerals from the substrate. However, because these structures are quite different from true roots in development, form, and function, they are called rhizoids (Fig. 22.3).

All of the traits discussed in this section are ancestral in the land plant lineage--that is, they were inherited from a common ancestor. Because only derived traits can reveal the exact path of evolution, we must examine differences among bryophyte lineages to determine how their body forms and life histories changed over time in their great leap onto the land.

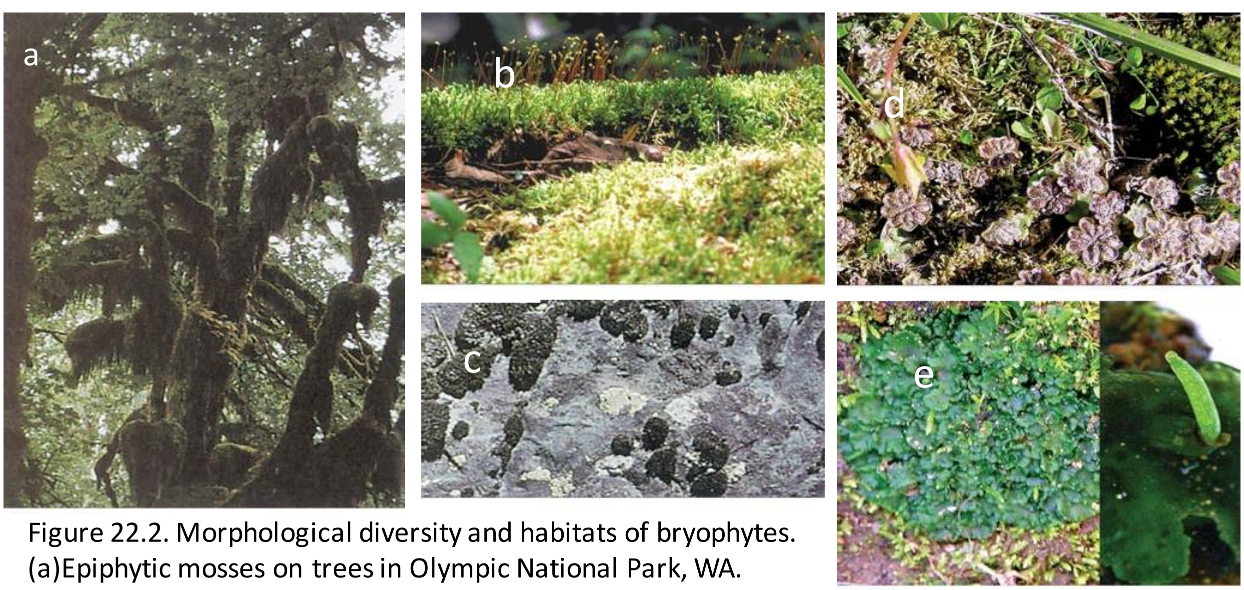


Figure 22.2. Morphological diversity and habitats of bryophytes. (a)Epiphytic mosses on trees in Olympic National Park, WA. (b)Moss. (c) Granite moss *Grimmea* growing on bare rock outcrop in the Appalachian Mountains. (d) Liverwort. (e) Hornwort

Why Bryophytes called Amphibians of Plant Kingdom?

Bryophytes are also known as amphibians of plant kingdom because water is needed to complete the life cycle. In animal kingdom class Amphibia (Gr. Amphi = two or both; bios = life) includes those vertebrates which are amphibians in nature i.e., they can live on land as well as in water. Similarly, majority of the bryophytes are terrestrial but they are incompletely adapted to the land conditions.

They are unable to grow during dry season and require sufficient amount of water; for their vegetative growth. Water is absolutely essential for the maturity of sex organs ar. fertilization. Without water they are unable to complete their life cycle. On account of their complex dependence on external water for completing their life cycle, Bryophytes along with Pteridophyte are regarded as amphibians of plant kingdom.

Alternation of Generation in Bryophytes

Bryophytes show a distinct and sharply defined heteromorphic alternation of generation. In the life cycle of these plants, there exist two distinct phases. One is haploid (X) or gametophytic phase (produces gametes). It is the dominant and independent phase of the life cycle. It produces the male and female sex organs i.e., antheridia and archegonia respectively.

Haploid gametes i.e. antherozoids and eggs are produced inside the sex organs. Antherozoids are produced in antheridia and eggs are produced in archegonia. The gametes fuse to form a diploid (2x) zygote. The zygote is the starting point of the next phase of the life cycle.

On germination the zygote forms the second diploid adult of the life cycle called sporophyte or sporogonium. Sporogonium produces spore mother cells in the capsule region, which undergo meiosis and form the haploid spores called meiospores. The zygote, embryo, sporogonium and spore mother cells together constitute the sporophytic generation.

This generation is dependent completely or partially on the gametophytic generation for its nutrition. Each meiospore germinates and produces a gametophytic plant which again bears the sex organs. In this way the life cycle goes on. Because the two generations (gametophytic and sporophytic) appear alternately in the life cycles, Bryophytes show alternation of generation.

Since the generations differ completely in their morphology i.e., gametophyte is either thalloid or foliose, and the sporophyte usually consists of foot, seta and capsule, it is called heteromorphic alternation of generation.

What is Apogamy and Apospory in Bryophytes

Bryophytes are endowed with a remarkable regeneration capacity. Parts of the plant or any living cell of the thallus are capable of regenerating the entire plant. The sporophytic cells regenerate to form a protonema on which appear gametophytes. This regeneration of diploid gametophyte from a sporophyte without the formation of spores is called apospory.

Conversely a gametophyte may form a mass of cells which may regenerate a sporophyte. This regeneration of a diploid sporophyte from a gametophyte, without the formation of gametes is called apogamy. Aposory and apogamy are rarely found in life cycle of Bryophytes.

Rhizoids and Scales in Bryophytes:

Rhizoids:

In Bryophytes roots are absent and the functions of the root i.e., anchorage and absorption is performed by the filamentous structures known as rhizoids.

Rhizoids may be unicellular, un-branched (Fig. 3B-D) in thallose forms of Hepaticopsida and Anthocerotopsida (e.g., *Riccia, Marchantia, Anthoceros*) or multicellular and branched in foliose forms of Bryopsida (Fig. 3 E) (e.g., *Funaria, Polytrichum*) Multicellular rhizoids possess oblique cross walls.

Unicellular rhizoids are of two types smooth-walled and tuberculated (Fig. 3 B-D). The members of order Marchantiales (e.g., *Riccia, Marchantia*) possess both types of rhizoids while Anthocerotales (e.g., *Anthoceros*) possess only smooth walled rhizoids.

In thalloid forms rhizoids are borne on the ventral surface (Fig. 3 A) along the mid rib, however, in foliose forms rhizoids arise from the base of the 'stem'. In aquatic Bryophytes (e.g., *Riccia fluitans, Ricciocarpus natans*) rhizoids are absent.

Scales:

Scales are present only in the members of order Marchantiales and absent in all Bryophytes. The scales are multicellular, violet coloured and single cell thick. They are violet in colour due to the presence of the pigment anthocyanin. Scales develop on the ventral surface of the thallus (Fig 3A).

They may be arranged in one row (e.g., young thallus of *Riccia*) or in two rows on each side of the mid rib (e.g., *Targionia*) or in two to four rows on each side of the mid rib (e.g., *Marchantia*) or irregularly distributed over the entire ventral surface (e.g., *Corsinia*).

In Riccia the scales are ligulate (Fig. 3G) while in Marchantia the scales are of two types-ligulate and appendiculate (divided by a narrow constriction into two parts—body and appendage, Fig. 3F). Scales protect the growing point by covering their delicate cells and secreting slime to keep them moist. The scales are absent in some aquatic members of order Marchantiales e.g., *Riccia fluitans*

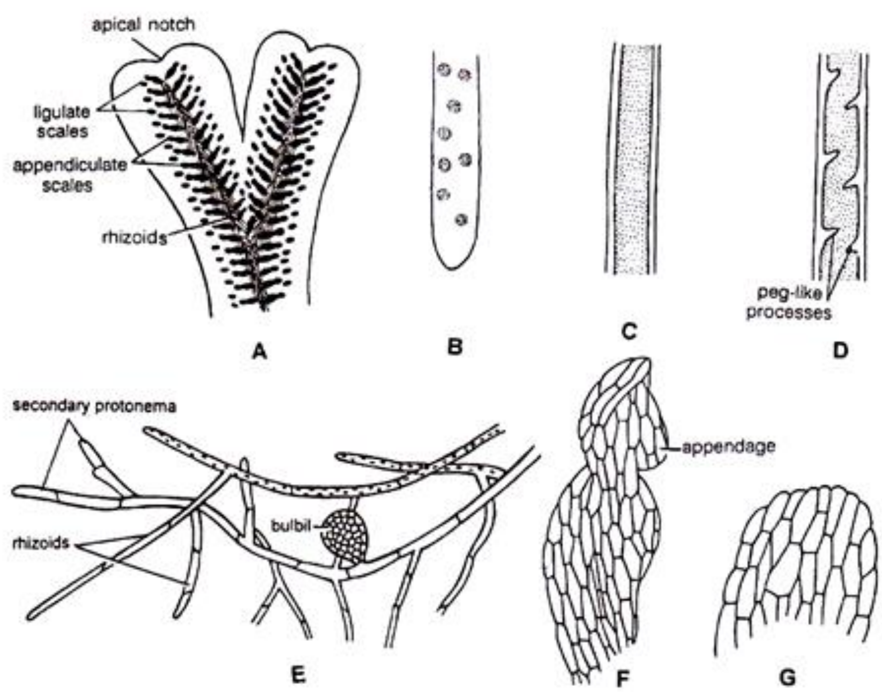


Fig. 3. (A–G) *Marchantia*. Scales and rhizoids. (A) *Marchantia* thallus : Ventral surface showing rhizoids and scales, (B) Tuberculated rhizoid (surface view), (C) Smooth walled rhizoid (surface view), (D) Tuberculate rhizoid (internal view), (E) Multicellular rhizoids, (F) Appendiculate scale, (G) Ligulate scale.

Affinities of Bryophytes:

From evolutionary point of view Bryophytes occupy an intermediate position between the Algae and the Pteridophytes. They show affinities with both Algae and Pteridophytes.

Resemblance of Bryophytes with Algae:

1. Plant body simple, thalloid and gametophytic.
2. Autotrophic.
3. Gametophytic phase is dominant.
4. Roots are absent.
5. Cell wall is made up of cellulose.
6. Pigments (chlorophyll a, chlorophyll b, α and β carotene, Lutin, Violaxanthes and Xeoxanthin) are similar in chloroplast.
7. Vascular tissue is absent.
8. Antherozoids are motile (bi-flagellated).
9. Flagella are whiplash type.
10. Water is essential for fertilization.
11. A filamentous protonema is produced by Bryophytes (juvenile stage in mosses) which resembles with the filamentous green algae.
12. In order Anthocerotales of Bryophytes, plastids are with pyrenoid which is a characteristic of Chlorophyceae (Green algae).

Resemblance of Bryophytes with Pteridophytes:

1. Plants are terrestrial.
2. Primitive simple leafless and rootless sporophytes of Pteridophytes (members of order Psilophytales) can be compared with the sporophytes of Bryophytes.
3. Sexual reproduction is oogamous.
4. Androcytes are enclosed by sterile jacket layer.
5. Antherozoids are flagellated.
6. Water is essential for fertilization.
7. Permanent retention of zygote within the archegonium.
8. Zygote forms the embryo.
9. Moss capsule is similar to terminal sporangium and columella of Psilophytales.
10. Both Bryophytes and Pteridophytes are characterised by heteromorphic alternation, of generation.

Key concepts

1. Bryophytes are land plants that differ from all other plants lacking lignified vascular tissue by having the gametophyte generation dominant and having unbranched sporophytes that produce a single sporangium.
2. Modern bryophytes almost certainly evolved from a single common ancestor, and they likely represent several lineages along the evolutionary path to vascular plants. Recent fossil discoveries push back the earliest appearance of bryophytes to 475 million years ago. Existing bryophytes preserve a suite of ancestral characteristics that give us insight into the origin of land plants. Bryophyte relationships remain uncertain; however, existing bryophytes fall into three lineages: liverworts (Marchantiophyta), hornworts (Anthocerotophyta), and mosses (Bryophyta).

Traditionally, liverworts have been considered the earliest evolving lineage of bryophytes, but recent evidence suggests that hornworts may be the earliest. Mosses are likely the closest sister group to vascular plants.

3. Key innovations of the bryophyte radiation, not present in their algal ancestors, include multicellular gametangia (antheridia and archegonia) that protect and insulate gametes from the environment; a multicellular sporophyte that develops from an embryo embedded within and nutritionally dependent on the gametophyte; and the presence of a waxy coating on the shoots (cuticle) and the spores (sporopollenin). The most complex bryophyte sporophytes also contain novel structures such as stomata and water- and sugar-conducting tissue (unlignified vascular tissue). Bryophyte gametophytes are not able to control their water balance, and they dry out rapidly in the absence of free water. The desiccated plants are still alive and can become active within minutes of being rewetted.

4. Mosses are important in many ecosystems. They provide most of the biomass in boreal vegetation such as tundra, they dominate the understory of cool-temperate forests, and they are common in damp microenvironments. Some species are aquatic and most require humid conditions, but some can colonize dry, exposed habitats such as rock outcrops and desert soil surfaces.

Adaptation to Land Habitat

Bryophytes are first land plants. Evidences support that Bryophytes are evolved from Algae. During the process of origin they developed to certain adaptations to land habit.

These are:

1. Formation of a compact multi cellular plant body which helped in the conservation of water by reducing cell surface area exposed to dry land condition. Presence of cuticle further reduces loss of water by evaporation. i.e, Development of compact plant body covered with epidermis.
2. Development of special organs for attachment and absorption of water e.g., rhizoids.
3. Development of photosynthetic tissues into special chambers for the absorption of carbon dioxide without losing much water and exposure to light. i.e, Absorption of carbon dioxide from atmosphere for photosynthesis. e.g, airpores.
4. Gametes are produced and protected by the special multi cellular organs (antheridia and archegonia).
5. Protection of reproductive cells from drying and mechanical injury i.e., jacketed sex organs. Heterogamy (production of two types of gametes) is evolved, forming non motile egg containing stored food and motile sperms.
6. Multi-cellular embryo is formed which is retained and protected inside the female reproductive body during its development, i.e, Retention of zygote within the archegonium.
7. Alternation of spore-producing generation (sporophyte) with gamete producing generation gametophyte enabled the plant to produce and test the best genetic combinations for adapting to the versatile terrestrial conditions.

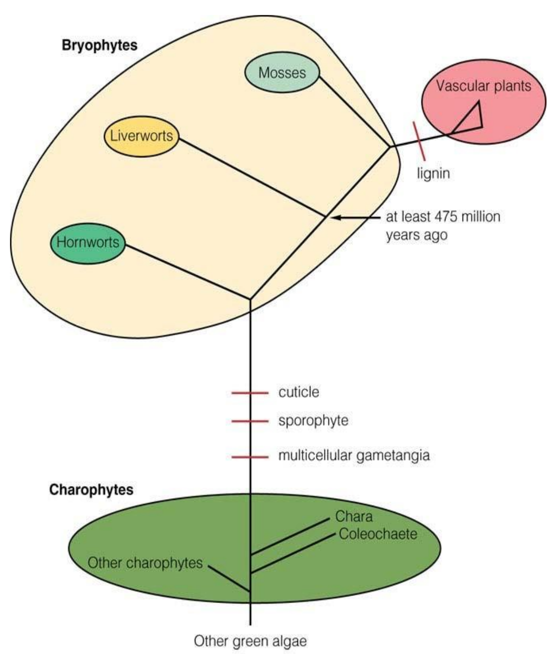


Figure 22.1. A cladogram of relationships between the bryophytes and vascular plants. Hornworts are the basal-most lineage of land plants, although other hypotheses place liverworts in that position. Mosses are almost certainly the sister group to vascular plants.

8. Production of large number of thick walled spores.
9. Dissemination of spores by wind.

The leap onto land

Despite being common almost everywhere, bryophytes often are ignored because of their small stature, lack of familiar features, and the fact that in many environments they are dormant for much of the year. Yet bryophytes are exceptionally diverse, with nearly 25,000 named species. Among land plants, only flowering plants and ferns have more species. Bryophytes also are extremely widespread, being present on all continents, including Antarctica. They have a long evolutionary history, and some bryophytes are a sister group to vascular plants (Fig. 22.1).

The great diversity of bryophyte species reflects a stunning diversity of habitats, from barren arctic and alpine ground to hot deserts, from the bottom of lakes to the canopy of tropical rain forests. Peat mosses grow submerged in the acidic waters of bogs, whereas various liverworts grow as epiphytes on the leaves of trees. Some mosses grow on rocks exposed to ocean salt spray or intense heat and sunlight.

Others tolerate very dim light and grow in the understory of dense forests or inside caves and burrows (Fig. 22.2). These adaptable plants can be found nearly everywhere that plant life is possible. But despite being so adaptable, all bryophytes have one major limitation. They require free water, not just soil moisture, in their environment. Without it, they cannot reproduce sexually.

As you might expect from the diverse environments inhabited by bryophytes, they have a corresponding diversity of body forms, from the giant moss *Dawsonia superba*, which can reach a height of 70 cm and resembles a pine tree seedling, to *Ptychomnion aciculare*, in which "dwarf" male plants grow attached to the leaves of the female plants.

These relatively inconspicuous and overlooked plants warrant more careful study for a number of reasons. Bryophytes can be important ecologically, by altering pH, absorbing carbon, and regulating nutrient cycling, colonizing barren surfaces, creating soils, and reducing erosion. They often are important elements in the local water cycle, absorbing and holding moisture so that other plants benefit. They are also useful to environmental scientists because the majority of bryophytes, despite their amazing resilience, are intolerant of pollution and often disappear from contaminated areas. This sensitivity makes them good indicators of air and water quality. Bryophytes also possess many physiological adaptations that interest scientists. For example, some bryophytes can survive extended periods (more than20 years) of desiccation and then when rewetted revive in a matter of minutes to resume normal growth.

Bryophytes Faced Many Problems When They Moved onto the Land

Bryophytes retain many of the characteristics of their algal ancestors, including a nutritionally independent (photosynthetic) and complex gametophyte; the photosynthetic pigments chlorophyll a and b, carotenoids, and xanthophylls; sperm that swim by means of two asymmetrically attached flagella; chloroplasts with conspicuous grana, which store food as starch; and cell walls composed primarily of cellulose and pectin. Bryophytes also engage in a particular type of cell division that is present in charophytes but absent in other green algae: the nuclear envelope breaks down and microtubules oriented perpendicular to the plane of division form a cell plate that grows from the center to the outer portion of the cell.

Faced with the great difficulties of a terrestrial life, bryophytes also evolved many new and highly successful adaptations. The primary problems of life on land were preventing death by drying out, dispersing spores through the air, and avoiding damage from weather and intense solar radiation. The responses to these problems, which bryophytes pioneered, were subsequently passed on to all their descendents and have become the fundamental innovations that define land plants.

Economic importance of Bryophytes:

1. Protection from soil erosion:

Bryophytes, especially mosses, form dense mats over the soil and prevent soil erosion by running water.

2. Soil formation:

Mosses are an important link in plant succession on rocky areas. They take part in binding soil in rock crevices formed by lichens. Growth of *Sphagnum* ultimately fills ponds and lakes with soil.

3. Water retention:

Sphagnum can retain 18-26 times more water than its weight. Hence, used by gardeners to protect desiccation of the seedling during transportation and used as nursery beds.

4. Peat:

It is a dark spongy fossilized matter of *Sphagnum*. Peat is dried and cut as cakes for use as fuel. Peat used as good manure. It overcomes soil alkalinity and increases its water retention as well as aeration. On distillation and fermentation yield many chemicals.

5. As food:

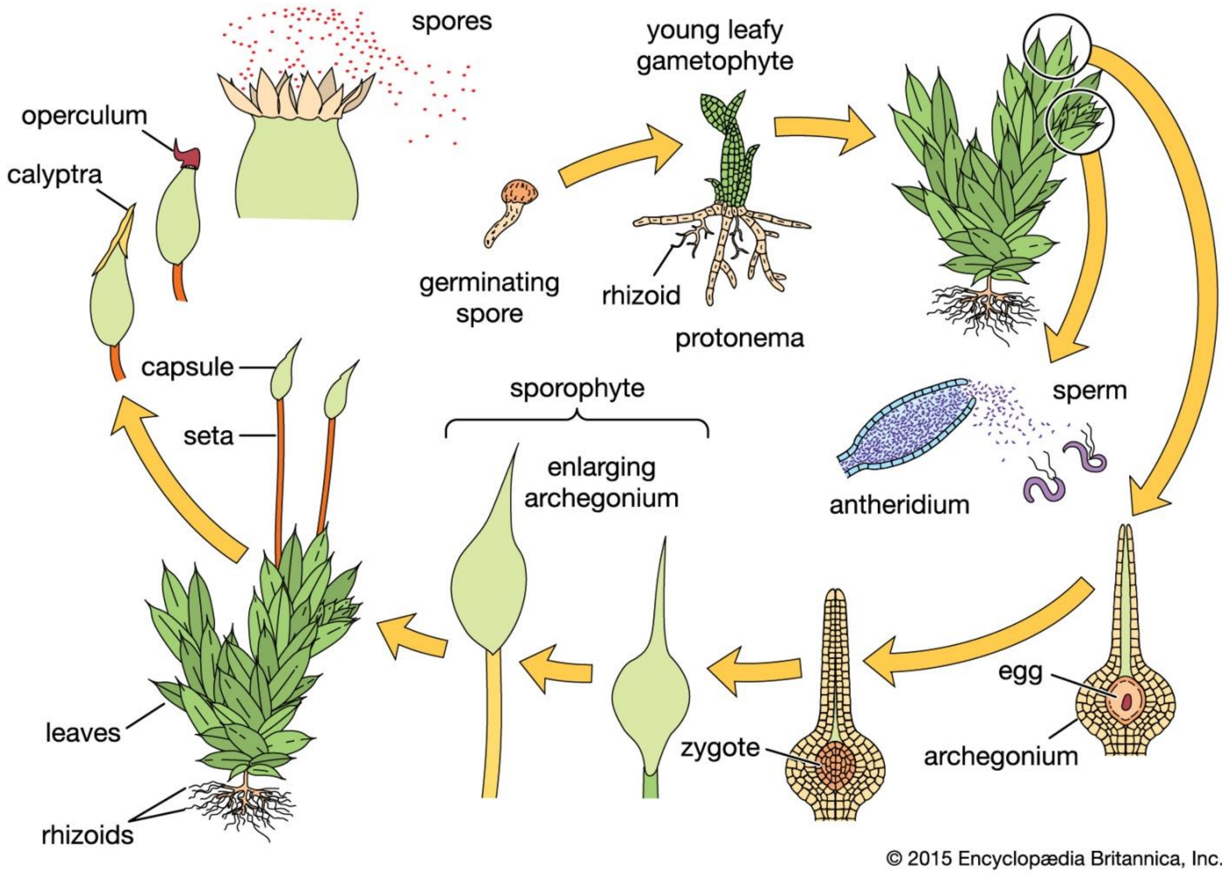
Mosses are good source of animal food in rocky and snow-clad areas.

6. Medicinal uses:

Decoction of *Polytrichum commune* is used to remove kidney and gall bladder stones. Decoction prepared by boiling Sphagnum in water for treatment of eye diseases. *Marchantia polymorpha* has been used to cure pulmonary tuberculosis.

7. Other uses:

Bryophytes arc used as packing material for fragile goods, glass wares etc. Some bryophytes act as indicator plants. For example, *Tortell tortusa* grow well on soil rich in lime.



Life cycle of Moss