P1 DIVERSITY AND LIFE CYCLES

Key Notes

Classification

Algae are classified as plants or protists and consist of several unicellular divisions and three main multicellular divisions: brown algae, red algae and green algae. There are two divisions of land plants, the bryophytes (mosses and liverworts) and the tracheophytes or vascular plants, including spore bearing groups such as ferns, and the seed plants.

Life cycles

All plants have alternating diploid and haploid generations. Diploid sporophytes produce haploid spores. These germinate to produce gametophytes. Gametes from these fuse to form a diploid cell that can grow into a new sporophyte. There is great variation among the algae with different groups showing reduction of either the sporophyte or the gametophyte. In bryophytes the gametophyte is the main plant. In the tracheophytes the sporophyte is dominant, with gametophytes free-living in most ferns, horsetails and some clubmosses, but much reduced in other vascular plants, the female gametophytes being retained on the sporophyte.

Related topics

The algae (P2)
The bryophytes (P3)
Early evolution of vascular plants (Q1)

Classification

A basic classification of plants is given in *Table 1*. The dividing line between plants and protists is arbitrary (Section A) and the **algae** are considered in either kingdom. The algae contain chlorophyll and are the main primary producers in the sea. They have some other features in common with other plants. Three groups contain large multicellular species, though they are probably not closely related to each other. They and the major unicellular and colonial divisions are considered briefly. The two main divisions among the land plants, bryophytes and tracheophytes, may have arisen independently from marine algae related to the present-day Chlorophyta (green algae), the bryophytes possibly more than once, although DNA evidence suggests one origin of land plants.

Life cycles

Fundamental to the life cycle of all plants and most plant-like algae is an **alternation** between a **sporophyte** generation and a **gametophyte** generation (*Fig. 1*). The sporophyte is **diploid**. To reproduce, cells of the sporophyte divide by meiosis to produce **haploid spores**. The spores germinate without any fertilization to form a haploid generation, the gametophyte. This produces gametes by mitosis. Male and female gametes fuse to form a diploid cell that can germinate and grow into a new sporophyte. In most multicellular groups the sporophyte is the main plant, but in some it is small and dependent on the gametophyte. The gametophyte may be multicellular and free-living, or much reduced and dependent on the sporophyte. The gametophytes can be **hermaphrodite**, producing gametes of both sexes, or **dioecious**, producing either only female or only male

Table 1. Classification of plants into their main divisions and subdivisions

- Algae
- Several unicellular groups
- Division Phaeophyta – Brown algae
- Division Rhodophyta – Red algae
- Division Chlorophyta – Green algae

- Division Bryophyta – Mosses and liverworts
  - Bryopsida (Musci); Mosses
  - Marchantiopsida (Hepaticae); Liverworts
  - Anthocerotopsida; Hornworts
- Division Tracheophyta – Vascular plants
  - Subdivision Pteridophytina – Spore-bearing vascular plants
    - +Rhyniopsida
    - +Zosterophyllopsida } Fossil groups of early land plants
    - +Trimerophytopsida
    - Lycopsida; Clubmosses and fossil groups
    - Equisetopsida (Sphenopsida); Horsetails and fossil groups
    - Polypodiopsida; Ferns
    - + Progymnospermopsida; Fossil group
  - Subdivision Spermatophytina – Seed-bearing vascular plants
    - + Lyginopteridopsida (Pteridospermopsida); Seed ferns or pteridosperms
    - + some other fossil groups of uncertain status
    - Cycadales or Cycadopsida; Cycads
    - Ginkgoales or Ginkgoopsida; Maidenhair tree
    - Pinopsida; Conifers
    - Gnetales or Gnetopsida; *Gnetum*, *Ephedra*, *Welwitschia*
    - Angiospermopsida (Magnoliopsida); Flowering plants, divided into:
      - Primitive dicotyledons
      - Eudicotyledons
      - Monocotyledons

Those marked + are known only as fossils.

gametes. Divisions in plant classification are based on whether the sporophyte or gametophyte is the main plant, the degree of reduction of the subsidiary stage and the structures involved with reproduction. In algae, fundamental differences in pigment structure and storage compounds are also used.

Among multicellular algae, most green algae (Chlorophyta) have the gametophyte as the main plant, the sporophyte being represented by a single resting spore or zygote, although some have two multicellular generations looking

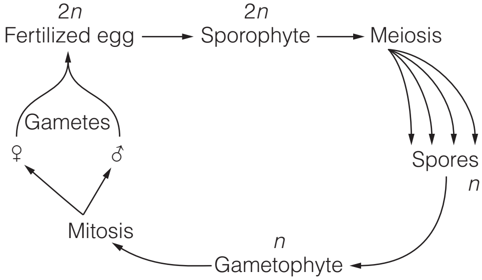

Fig. 1. Life cycle of plants, showing the alternation between diploid sporophyte and haploid gametophyte generations.

alike. In the brown algae (Phaeophyta), the sporophyte is the dominant generation and the gametophyte much reduced in size. In a few, such as *Fucus* species (the wracks), the gametophyte is reduced to a gamete, so reproduction resembles that of a vertebrate. The red algae (Rhodophyta) are variable.

Among land plants the two groups differ in which is the dominant generation. In the bryophytes it is the haploid gametophyte, the sporophyte being a multicellular stalk and capsule that remains attached to the living gametophyte and dependent on it. In the tracheophytes (vascular plants) the diploid sporophyte forms the main plant body. The gametophyte of most ferns, horsetails and some clubmosses, is up to 1 cm across, multicellular and separated from the parent sporophyte but short-lived. It is normally hermaphrodite. In the other vascular plants the gametophyte is always dioecious and is reduced to a few cells retained within the spore wall. In seed plants the male gametophyte is reduced to the three nuclei of the pollen grain and the female gametophyte to an embryo sac, normally of eight cells, retained on the parent sporophyte (Topics D2 and D3).

P2 THE ALGAE

Key Notes

The variety of algae	Algae are classified using differences in reproductive structures, cell wall structure and storage products. There are many groups with no clear affinities. Unicellular groups include the planktonic diatoms and dinoflagellates responsible for most photosynthesis in the seas. Most are haploid and reproduce mainly asexually.
Rhodophyta, the red algae	They are mainly multicellular and characteristic of deep inshore waters with low light. Unicellular and filamentous forms occur. Reproduction involves a gametophyte and two different sporophyte generations. One or more of these generations can be reduced. The gametes are non-motile.
Phaeophyta, the brown algae	These are the largest and most complex seaweeds, dominating many intertidal regions. All are multicellular, some with holdfast, stipe and lamina. Reproduction involves a gametophyte and sporophyte, with both generations looking similar or the gametophyte reduced, in some to a gamete. Vegetative fragmentation is important in *Sargassum* and others.
Chlorophyta, the green algae	This is a highly diverse group, sharing features with the land plants. There are unicellular and multicellular forms. Sexual reproduction normally involves an alternation of similar generations or with either the sporophyte or the gametophyte much reduced. Members of the most complex group, the stoneworts, have a well differentiated body and elaborate sex organs.
Related topics	Introduction (A1) Diversity and life cycles (P1)

The variety of algae

There is a large variety of unicellular photosynthetic algae and each group has undergone an independent evolution (*Table 1*). Classification of the algae is based mainly on their reproduction and the type of chlorophyll, cell wall and storage products in the cells. The affinities of many groups are not clear. All groups are capable of asexual reproduction either by binary fission or by producing spores by mitosis.

Unicellular diatoms and dinoflagellates (*Fig. 1*) are the main members of the plankton in seas and fresh water, and are responsible for much of the photosynthesis of the oceans, and therefore of the world. Diatoms are enclosed in a silica cell wall consisting of two halves fitting together like a petri dish; these walls have the most intricately sculpted patterns. They form numerous fossils. Dinoflagellate species are responsible for toxic 'red tides' and for phosphorescence in the sea. Euglenas (*Fig. 1*) occur mainly in high nutrient environments in freshwater and are commonly demonstrated in biological laboratories. Some of the unicellular and colonial groups can occur as heterotrophic organisms without chloroplasts and may have affinities with other protists not considered

Table 1. Some major divisions of algae

Division	Vegetative structure	Reproduction	Pigments
Euglenophyta (euglenas)	Unicellular or a few colonial; flagellate, no cell wall	Asexual only	Chlorophyll *a*, *b*
Bacillariophyta (diatoms)	Unicellular or colonial; silica cell wall forming a box	Asexual; sexual by cells dividing by meiosis to form gametes	Chlorophyll *a*, *c*; brown pigments
Pyrrophyta or Dinophyta (dinoflagellates)	Unicellular or filamentous; cellulose cell wall	Asexual; sexual occasional	Chlorophyll *a*, *c* or none (heterotrophic)
Rhodophyta (red algae)	Multicellular (a few unicellular); cellulose cell wall	Asexual and sexual, some involving three generations	chlorophyll *a*; red and purple pigments; unusual storage products
Phaeophyta (brown algae)	Multicellular; cellulose cell wall	Asexual and sexual, involving alternation of generations	chlorophyll *a*, *c*; brown pigments; unusual storage products
Chlorophyta (green algae)	Unicellular and multicellular; some large and complex; cellulose cell wall; a few flagellate; huge and variable group	Asexual and sexual; zygote usually dividing by meiosis after fertilization	chlorophyll *a*, *b*; many other pigments and storage products like those of land plants

as algae. It is possible that some of these have developed chloroplasts independently, perhaps through engulfing a photosynthetic cell and using the chloroplast (e.g. euglenas, dinoflagellates).

Most unicellular algae are haploid but the diatoms and a few dinoflagellates are diploid. Sexual reproduction involves flagellated sperm cells and the fertilized egg often lies dormant, meiosis taking place when it germinates.

Rhodophyta, the red algae

Red algae occur in fresh and sea water and as unicellular and multicellular organisms, but most are multicellular seaweeds occurring in deep offshore waters in dim light. A few are used either as foodstuffs (*Porphyra*, laverbread) or as the source of agar (mainly *Gelidium*), a food additive and laboratory gelling agent,

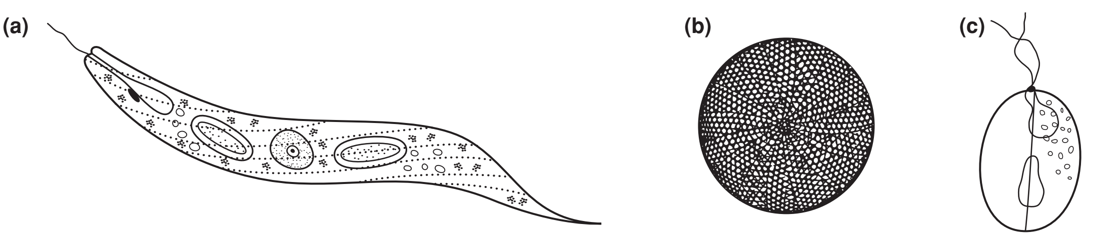

Fig. 1. Unicellular algae. (a) Euglena; *(b)* Coscinodiscus *(a diatom); (c)* Exuviaella *(a dinoflagellate).*

made from mucilage in the cell walls. The red or purple pigments absorb most of the available light in the deep waters where they grow, although in strong light this pigment may disappear and the plants appear green. A few secrete a calcium-rich exoskeleton which contributes to the formation of coral reefs.

The life cycle and reproduction of red algae is variable and more complicated than that of any other algal group, typically involving one gametophyte and two sporophyte generations (*Fig. 2*). The first sporophyte is small and normally remains attached and dependent on the gametophyte, producing diploid spores which disperse to grow into a second sporophyte generation. The gametophyte or the second sporophyte or both may form the main plant. In some species one sporophyte is missing from the life cycle. Uniquely among algae the sperms are non-motile, relying entirely on passive drift to reach the eggs.

Phaeophyta, the brown algae

These are the largest and most complex algae. They include the great kelps, *Macrocystis* and *Nereocystis*, of the Pacific which can grow up to 1 m day^{-1} and reach 70 m in length. Brown algae are usually the most abundant seaweeds on sea shores; *Sargassum* forms the basis of life in the mid-Atlantic Sargasso Sea; *Laminaria* may be hung up by children to detect humidity, while alginates can be extracted to be used as emulsifiers in ice creams and other food stuffs. They also are used occasionally as fodder for domestic animals (e.g. on Irish islands) and as fertilizer. They are flexible but extremely strong to withstand the buffeting of the sea in intertidal zones. Some have a simple filamentous structure, but most are differentiated into a holdfast with no absorptive function, a stipe and a lamina. The lamina of some wrack species, *Fucus*, includes air bladders, though at times with a rather different gas combination from normal air (high in carbon monoxide). They may secrete toxic polyphenols inhibiting bacterial growth.

Sexual reproduction involves the typical alternation of diploid and haploid generations. These may or may not be alike in morphology, but both large and

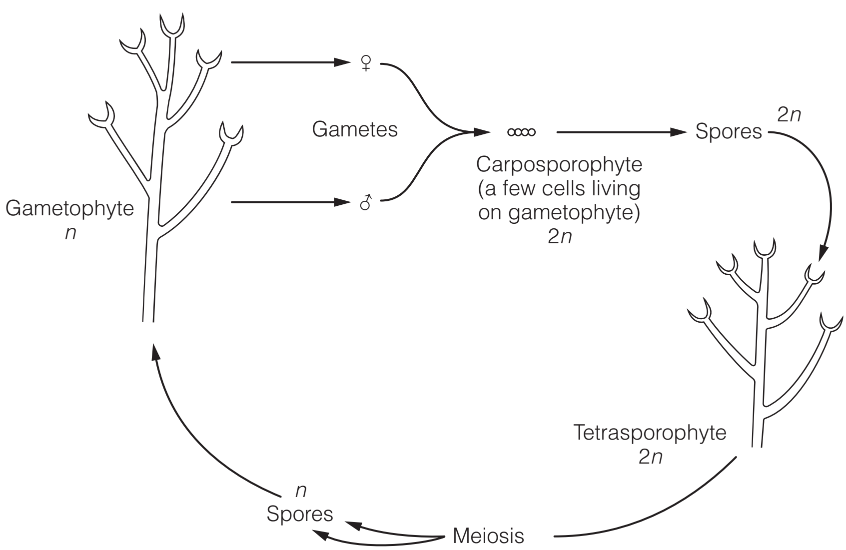

*Fig. 2. Life cycle of a red alga (*Ceramium *sp.).*

complex, or the gametophyte much reduced. In the wracks the gametophyte is reduced to gametes only, so there appears to be no alternation of generations and reproduction resembles that of vertebrates. Some brown algae can spread vegetatively by fragmentation, notably in *Sargassum*, which only reproduces in other ways when attached to the sea bed around coasts.

Chlorophyta, the green algae

This large and highly variable group includes unicellular and colonial flagellate forms, such as *Volvox* (*Fig. 3*) used in laboratory demonstrations, filamentous forms such as *Spirogyra* and complex multicellular organisms such as the stoneworts, *Chara* (*Fig. 3*). They occur in a wide range of mainly aquatic environments and some are planktonic. They have many features similar to those of land plants. In multicellular Chlorophyta, alternation of generations may involve both generations looking similar, a reduction of the sporophyte to a single cell or the reduction of the gametophyte to a single cell. The gametes (and sometimes the zygotes) are motile and flagellate; all require an aquatic medium for reproduction and their colonization of land is confined to damp places. Many can also reproduce asexually by diploid spores, again flagellate, sometimes with multiple flagella.

The most complex green algae are the stoneworts, Charales, characteristic of lime-rich fresh water. They can reach 10 cm or more in length and have rhizoid-like cells (Topic Q2) that attach the plant to soft substrates, This means that *Chara* strongly resembles some aquatic flowering plants. Specialized male and female reproductive organs are produced by the branch whorls and are large enough to be visible to the naked eye. The fertilized zygote may undergo meiosis before regenerating the plant body but this is not confirmed and it is not clear whether the main plant is diploid or haploid. The name stonewort derives from secretions of calcium carbonate on the outside of the branches.

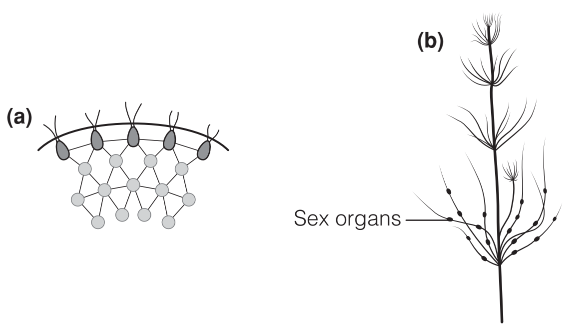

Fig. 3. Green algae. (a) Volvox *(colonial, flagellate); (b)* Chara *(multicellular).*

P3 THE BRYOPHYTES

Key Notes

Description

Three groups of bryophytes are known: mosses, liverworts and hornworts. The gametophyte is the dominant plant with the sporophyte growing attached to it. Fossil bryophytes occur in Carboniferous rocks, the liverworts perhaps occurring earlier. They may have originated independently from tracheophytes.

Vegetative structure of liverworts

Liverworts are highly variable with leafy and thallose forms. Leafy liverworts usually have three ranks of leaves, all one cell thick, one rank usually reduced in size, of many different shapes and arrangements used to distinguish species. Thallose forms have thicker structures which may have cavities and pores.

Vegetative structure of hornworts

Hornworts produce a simple thallus similar to some thallose liverworts but, in most, cells have a single chloroplast.

Vegetative structure of mosses

The first growth from the germinating spore is a filamentous protonema from which the main plant grows. Mosses have spirally inserted tapering leaves, mostly one cell thick, but are highly variable in growth form and in details of leaf structure and cell shape. Many have a midrib and *Polytrichum* has lamellae. *Sphagnum* has large dead hyaline cells that retain water.

Water relations

Most bryophytes rely on surface water and capillary action, often enhanced by leaf arrangement. This limits their size. In *Polytrichum* and some other large mosses there is a rudimentary conducting system, resembling a simple form of that found in the true vascular plants.

Ecology

They occur in all habitats, particularly in wet places and deep shade. They dominate some sub-polar regions and bogs where they form peat. They are abundant on the floor of wet woods, by streams and as epiphytes. Some can tolerate desiccation and occur on rocks where no other plants can grow.

Interactions of bryophytes

Pioneer communities may lead to succession. Different growth forms occur and interactions between species may be competitive or beneficial. Only a few specialist invertebrates eat bryophytes; fungi can infect bryophytes and are the main decay organisms. Nitrogen-fixing cyanobacteria can colonize.

Human uses

Bryophytes have been used for bedding and as filling in buildings and have a small role as ornamentals. *Sphagnum* has been an important wound dressing. Peat, based on *Sphagnum*, is an important fuel. Scientifically they have been useful as genetic tools and for monitoring pollution. Peat has preserved numerous biological and archaeological remains used for reconstructing history.

Related topics

Diversity and life cycles (P1) Reproduction in bryophytes (P4)

Description

The bryophytes, subkingdom Bryophyta, comprise two large groups: the **mosses**, Bryopsida or Musci, and the **liverworts**, Marchantiopsida or Hepaticae; and the small group of **hornworts**, Anthocerotopsida. They are almost entirely land plants, with a few in fresh water. They are complex, multicellular plants, but all are small, often less than 2 cm high, with the largest reaching up to 1 m above the substrate. The three groups of bryophytes share many features but also differ markedly.

Bryophytes show a typical alternation of generations (Topic P1), the main plant body being the haploid **gametophyte**. The **sporophyte** consists solely of a basal foot with a stalk and capsule and remains attached to the gametophyte throughout its life. The sporophyte lives for only a few days in most liverworts, and up to a few months in mosses and hornworts, in contrast to the perennial gametophyte. Meiosis in the capsule leads to spore production and dispersal. Vegetative fragmentation is an important mode of propagation in many species and some produce specialized asexual **gemmae** (rounded groups of cells that disperse to form new plants).

The fossil record of bryophytes is patchy but fossil mosses occur from Carboniferous rocks, while the liverworts may go back to the Silurian and were probably the earliest land plants. They may have originated independently from tracheophytes (Topic Q1) and are likely to be derived from green algae. The three groups of bryophytes may have arisen separately; they certainly diverged early in their evolution.

Vegetative structure of liverworts

Liverwort gametophytes are highly variable in structure, ranging from leafy shoots with leaves one cell thick to flat thalli many cells thick and of indeterminate growth (*Fig. 1*). The **leafy liverworts** usually lie prostrate or nearly so in damp places or as **epiphytes** and normally grow up to a few centimeters in length. They consist of a simple stem, leaves and often **rhizoids**, single cells forming a hair-like projection into the substrate. Most have three lines of simple, toothed or lobed leaves but, in many, one of these is much reduced in size to form '**underleaves**' on the ventral side, or is lost. All the leaves are a single cell thick. The classification of leafy liverworts is mainly based on the shape and arrangement of the leaves.

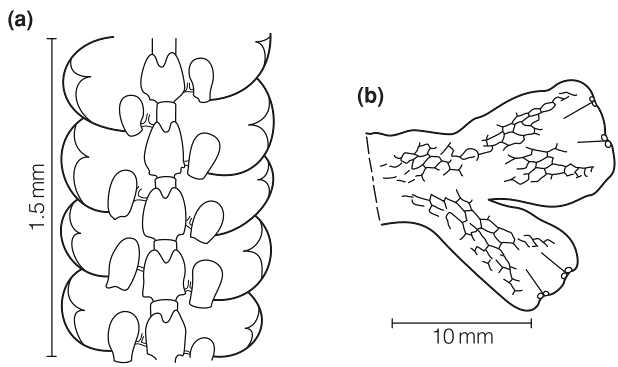

Fig. 1. Vegetative shoots of liverworts. (a) Leafy liverwort, Frullania, *showing small under-leaves and helmet-shaped lobes of main leaves; (b) thallose liverwort,* Conocephalum.

Thallose liverworts have a simple thallus (*Fig. 1*) several cells thick that branches dichotomously. Some consist of little more than this but, in the more complex forms, there is a thickening of the central part into a midrib, pores in the upper surface and rhizoids anchoring them to the substrate. Some species produce gemmae. Most liverworts contain oil bodies in their cells and sometimes these are fragrant when the plant is crushed, e.g. *Conocephalum*. They also produce antibacterial products but the potential of these for human use has not been examined.

Vegetative structure of hornworts

The gametophyte of the hornworts resembles that of a simple thallose liverwort, with no midrib and with no dichotomous branching. They differ in having cavities, often with a symbiotic nitrogen-fixing cyanobacterium in them, and, in most, by having cells containing a single chloroplast, a feature otherwise unknown in land plants but occurring in the algae. They are separated by differences in the sporophyte.

Vegetative structure of mosses

The mosses are the most abundant and important of the three groups and a few grow to 1 m above the ground. After germination, a spore produces filaments of undifferentiated cells known as the **protonema**, resembling filamentous algae, which spread over the substrate. These normally grow for only a few days in this way before growing into the main gametophyte, though they persist in a few species. Mosses have simple stems with no specialized cells. Most are branched and the shoots may grow upright often forming a tight clump or mat, or trail along the substrate. Rhizoids grow into the substrate, anchoring the plant but with no special adaptations for absorption, and some mosses grow similar hair-like structures along their stems. Mosses normally have spirally arranged leaves, tapered, often to a point, so in general not closely resembling those of leafy liverworts (*Fig. 2*). One genus, *Fissidens*, has two ranks of leaves. A few mosses produce gemmae.

The majority of mosses have leaves one cell thick (*Fig. 2*) but there is frequently a line of narrow thick-walled cells forming a midrib or nerve and some have another line around the edge. The nerve can extend beyond the end of the lamina as a hair point. ***Polytrichum*** and its relatives have lamellae of cells along the leaf (*Fig. 2*), making the leaves fully opaque and much tougher than

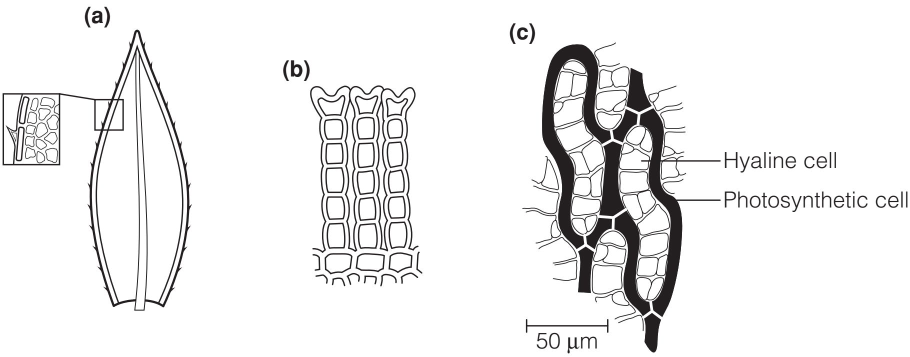

Fig. 2. Leaves of mosses. (a) Mnium, *showing midrib and border; (b) cross-section of* Polytrichum *leaf showing lamellae; (c) leaf cells of* Sphagnum, *showing photosynthetic cells and hyaline cells.*

those of other mosses. The leaves of the bog mosses (***Sphagnum***) have normal photosynthetic cells interspersed with much larger dead cells, known as **hyaline** cells, with prominent spiral thickening and pores (*Fig. 2*). The hyaline cells act as a water reservoir giving the mosses their sponge-like character and allowing them to be particularly effective as bog builders. The details of leaf and leaf cell structure and their arrangement are some of the main features distinguishing moss species.

Water relations

All bryophytes except *Polytrichum* and its relatives have no internal conducting system and are dependent on surface rain water and capillary action across their surfaces. The leaves frequently form sheaths along the stem enhancing water flow. Many are able to dry out and remain dormant in a place free from competition such as a wall top. The leaves usually distort in the dry state (often twisted) and some can remain dormant for months, but they absorb water and resume growth within minutes of rain starting. The cushion form of many mosses will slow water loss.

Polytrichum and its relatives are the tallest of bryophytes and do possess a rudimentary conducting system in the stems that conducts water and solutes effectively around the plant. The long vertically arranged water-conducting cells lose their contents and connect by pores, like tracheids of xylem tissue, and solute conducting cells have pores, oblique walls and degenerating nuclei and are associated with cells with high metabolic rates, resembling phloem sieve elements and companion cells (Topic C3). Other large mosses may have a similar system in a less well-developed form.

Ecology

Bryophytes tend to occupy places that other plants cannot grow in and frequently fit in spaces between other plants. They occur throughout the world and in almost every habitat, living mainly in wet places and places with dim light, e.g. under dense woodland, or in places with little or no soil, as epiphytes or growing on rocks. They dominate some plant communities in polar and subpolar regions, where extensive areas are covered with moss carpets, sometimes with very few or no other plants (though lichens, a symbiosis of fungus and alga, frequently occur too). In acid cold conditions, such as peat bogs, bog mosses (*Sphagnum*) dominate. They are able to store water and secrete acid from their cells inhibiting other plants and creating conditions of limited decay. The result is that few other plants can grow on the *Sphagnum* cushions. *Sphagnum* moss is the basis of much of the world's **peat**, partially decayed, waterlogged, compressed plant matter that gradually accumulates in boggy ground.

Extensive bryophyte communities occur on the floor of wet woods and by streams. Numerous bryophytes occur as epiphytes throughout the world and they can smother tree branches, particularly on tropical mountains. In temperate regions they are often the only epiphytic plants. In tropical rainforests some species grow on leaves, when they are known as **epiphylls**. Smaller bryophyte species may be some of the only plants growing on walls and as epiphytes on tree trunks in drier woods; growth is slow and interspersed with frequent dormant periods, but they are often the only visible life form growing there except for the even more resistant lichens. In almost all situations mosses are more common than liverworts, which tend to fit around the mosses. A few mosses have specialized ecology such as species in flowing fresh water and those that grow on mobile sand dunes. A few species have colonized deserts and rely on dew for water, and some live by hot springs.

Interactions of bryophytes

Bryophytes (mainly mosses) may follow an ecological succession similar to that of flowering plants (Topic K2), e.g. colonizing bare rock, although change is often slow. In cold and waterlogged climates where mosses predominate, moss hummocks persist for decades or even centuries with little change. Pioneer species are usually low-growing but retain some water and allow other species to colonize. There may be competition between species, but frequently the presence of one bryophyte stimulates others to grow and the role of competition and beneficial interactions are not well understood.

A few invertebrates, mainly fly larvae, are specialist moss feeders but bryophytes are nutrient-poor and are not eaten by animals to a great extent. Many microscopic animals live in moss cushions and birds use them as nesting material. Fungi can infect mosses, particularly in the high latitudes, and other fungi are responsible for decay. Nitrogen-fixing cyanobacteria (Topic M2) can associate with certain species and enhance their growth.

Human uses

Mosses have been used for centuries as bedding material owing to their soft quality. They were also used as padding for building, e.g. between timbers, and blocking air vents in chimneys, etc. The wiry stems of *Polytrichum* have been used for baskets. *Sphagnum* can be used as an absorbent anti-bacterial wound dressing and to retain water in window boxes or plant nurseries. Mosses have occasionally been used as ornamentals, particularly in Japan. Peat derived from *Sphagnum* has been an important domestic fuel when dried out, e.g. in Ireland where there are few trees, and several power generating stations use peat. Peat is also used in the horticultural trade as a soil conditioner, but many peat bogs have been destroyed through over-extraction and its use is not favored by conservationists.

In science bryophytes have several uses. They are haploid and have been useful in genetic studies since geneticists can look directly at gene expression (although many are polyploid). Some species are sensitive to pollution, particularly by sulfur dioxide, and their presence, along with that of lichens, has been used to monitor pollution levels. Peat accumulation has led to the preservation of numerous remains of plants, animals and human artifacts. Reconstruction of vegetative and human history over the past tens of thousands of years has been possible through examination of these remains.

P4 Reproduction in bryophytes

Key Notes

Sexual reproduction	All bryophytes have antheridia with sperm and archegonia with eggs. Antheridia are spherical to oblong bags of sperm and archegonia cylindrical with a bulbous base containing the egg. They may be scattered along stems or clumped at the stem tips. Sperms are motile and require water. Some have sterile hairs interspersed with the sex organs and a few have explosive dispersal of the sperms.
The sporophyte of liverworts	This is short-lived and consists of a foot embedded in the gametophyte, a colorless stalk and a roundish capsule, usually black. Almost all nutrients come from the gametophyte. The capsule splits into four valves at maturity and usually has sterile hairs (elaters) that aid spore dispersal. Some have reduced sporophytes.
The sporophyte of hornworts	This consists of a long-lived foot and capsule only. The capsule is green and photosynthetic, cylindrical to 4 cm, with a central column and elaters. Spores disperse when it splits from the tip.
The sporophyte of mosses	Typical mosses have a foot, a strong stalk and capsule. A protective calyptra from the gametophyte may persist until maturity. The tip of the capsule has peristome teeth that open and close with different humidity dispersing the spores. Details of capsule structure distinguish species. Bog mosses and rock mosses have a capsule borne on an outgrowth from the gametophyte. In bog mosses spores disperse explosively; in rock mosses, the capsule splits.

Related topics Diversity and life cycles (P1) The bryophytes (P3)

Sexual reproduction

All bryophytes have **antheridia** which produce motile sperm and **archegonia** containing eggs. The structure of these organs is fairly uniform across the three groups of bryophytes and more elaborate than in other plant groups. The antheridia (*Fig. 1*) are near-spherical to ovoid sacs on short stalks with a wall one cell thick enclosing sperm mother cells and eventually the sperms. The sperms themselves have two flagella and can only swim a very short distance, but in some species the sperm mother cells are dispersed passively in water first. The archegonia (*Fig. 2*) are cylindrical with an inflated base. A jacket of sterile cells encloses the egg in the inflated basal part and approximately 10 **canal** cells in the neck above, that degenerate at maturity. Archegonia are usually on short stalks. These sex organs range in size from about 0.1 mm long in most species up to about 1.5 mm for a few archegonia.

In most liverworts and some mosses the sex organs are scattered along the stems, but in others they are clustered at the branch tips in 'inflorescences'

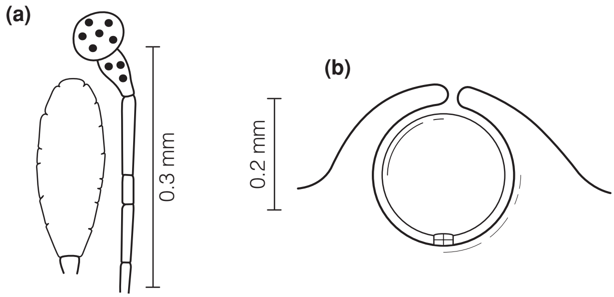

Fig. 1. *Antheridium of (a) a moss, with sterile hair, (b) a thallose liverwort sunk in the thallus.*

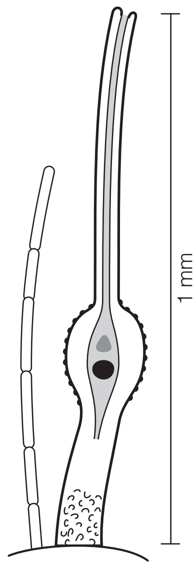

Fig. 2. *Archegonium of a typical moss, with sterile hairs.*

which may be surrounded by a cup-like cluster of leaves making them conspicuous. Sterile hairs may be associated with clusters of either sex organ and these help retain water and perhaps aid dispersal. In some thallose liverworts and hornworts, antheridia are sunk in pits and sperms are discharged explosively. Hornworts also have small sunken archegonia. The most striking sexual reproductive structure is the archegonial stem in some thallose liverworts. This is approximately 2 cm long and looks like a small parasol with the archegonia on the underside; antheridia are produced on the upper side of a similar but smaller structure.

Some bryophytes are monoecious, bearing male and female organs and, in these, capsules are often abundant. In dioecious bryophytes, each plant bearing only male or female organs, sporophyte formation is often rare.

The sporophyte of liverworts

There are three parts to the typical liverwort sporophyte: a **foot** embedded in the gametophyte; a colorless **stalk** up to about 2 cm long; and a **capsule**, 0.5–2 mm across and usually glossy black, at the tip (*Fig. 3*). It is short-lived, normally lasting only a few days. The foot is embedded in the gametophyte and draws

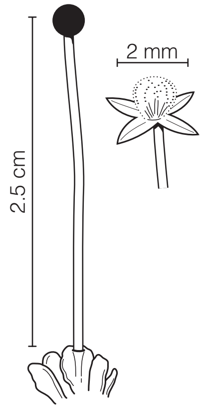

Fig. 3. *Sporophyte of liverwort.*

nutrients from it throughout the life of the sporophyte. When the spores are mature the capsule wall splits into four valves. Spores are mixed with sterile hairs, known as **elaters**, that assist in spore dispersal as they have spiral thickening and respond to drying out by jerky contracting movements. In humid conditions they lengthen and fewer spores are dispersed. Details of the form of the sporophyte can be used as reliable, if microscopic, characters to distinguish liverwort groups and particular species.

In a few liverworts the sporophyte is smaller and in the small thallose liverwort *Riccia*, there is just a sac of spores which remains embedded in the gametophyte until the gametophyte itself decays around it. The sporophyte generation has all but disappeared in this liverwort.

The sporophyte of hornworts

This has a large foot, no stalk but a cylindrical capsule 2–4 cm long directly on the foot (*Fig. 4*). They last for several weeks, unlike that of liverworts, growing from the base and can outlive the gametophyte. The capsule is green and photosynthetic with stomata on the outside, so does not rely solely on the gametophyte for its growth. There is a column of non-reproductive cells with attached elaters in the middle. Spores mature in the hollow part around the column and are dispersed when the capsule wall splits in two starting at the tip. The capsule wall, the central column and the elaters all twist and aid dispersal. Frequently, the capsule continues growing from the base when spores are being dispersed from the tip.

The sporophyte of mosses

There are three different groups of mosses, typical mosses, bog mosses, and rock mosses, and they differ mainly in the structure of the sporophyte. The typical mosses (the great majority) have a sporophyte that lasts for several weeks (*Fig. 5*). There is an anchoring foot embedded in the gametophyte, a tough stalk that elongates early in the sporophyte's life and persists, and a capsule. As the sporophyte grows there is often a cup-like piece of the gametophyte derived from the archegonium, known as the **calyptra**, attached to the capsule. This protects the developing sporophyte and may fall only when the capsule is fully mature. The capsule is usually photosynthetic and has stomata and a central column of sterile tissue. There is a lid at the tip of the capsule that is thrown off when the capsule is mature. Inside this most have one or two

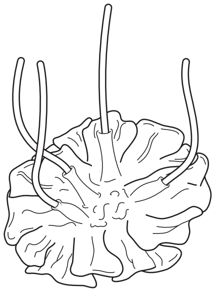

Fig. 4. Sporophyte of hornwort.

layers of teeth, the **peristome**, the number and arrangement distinguishing different genera. They respond to humidity with movements that open the capsule for spore dispersal in dry weather and close it in wet weather, or by a twisting movement, or active throwing out of the spores by a combination of outer and inner teeth sticking together.

One unusual family of typical mosses, the Splachnaceae, lives mainly on dung and its spores are dispersed by flies. Their extraordinary sporophytes have long stalks up to 10 cm long, and a swollen base of the capsule which can be up to 2 cm across and brightly colored resembling a toadstool. These produce an odor that attracts flies which carry off the sticky spores to another dung heap.

In bog mosses (*Sphagnum*) and rock mosses (*Andreaea*; a group of small almost black mosses that grow encrusted on mountain rocks), the capsule has no stalk but is raised on an outgrowth of the gametophyte (*Fig. 5*). In *Sphagnum* the capsule is a brown spherical structure about 2 mm across, in which air pressure builds up as it dries until the tip is explosively blown off and the spores are discharged. In *Andreaea* the capsules are tiny, some only about 0.5 mm across, and they split into four sections except at the base and the tip. The cracks gape in dry weather to disperse the spores.

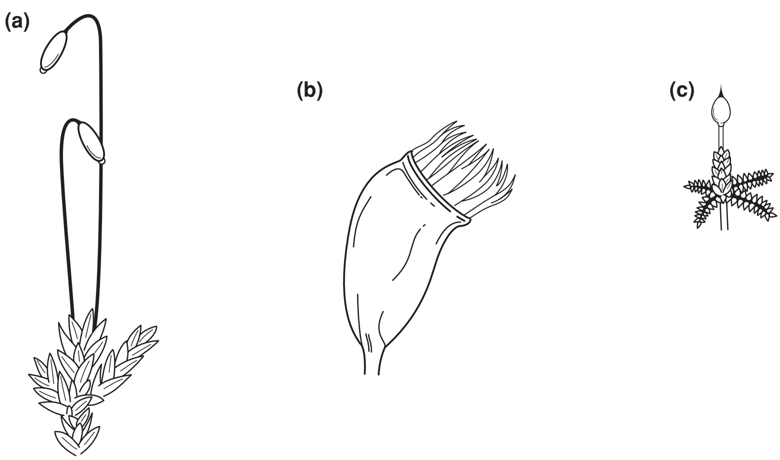

Fig. 5. Sporophytes of mosses. (a) Typical moss; (b) capsule of typical moss with peristome teeth; (c) Sphagnum.