Series on Diversity of Microbes and Cryptogams

BRYOPHYTA

About the Author

O P Sharma, with his 36 research articles published in national and international journals, 33 books written for university students, and 40 years of teaching experience, is an able researcher, established Indian author, and an experienced teacher. His areas of research include pollen morphology, angiosperm's anatomy and mycology, with special focus on Indian Cyperaceae (with particular interest on *Cyperus*). Over a dozen of Dr Sharma's books have been published through internationally known publishers. He has also revised *Economic Botany*, an internationally renowned text by the late Professor Albert F Hill (Harvard University, USA), a publication of McGraw-Hill, New York.

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Recently, Dr O P Sharma revised some of his widely circulated books published through McGraw Hill Education, which include *Plant Taxonomy* (released first in 1993 and reprinted 19 times); *Textbook of Algae* (released first in 1986 and reprinted 20 times), now titled *Algae*; and *Textbook of Fungi* (released first in 1989 and reprinted 17 times), now titled *Fungi and Allied Microbes*. His latest published books through McGraw Hill Education are *Pteridophyta* (published in 2012) and the present one titled *Bryophyta* (being published in 2013).

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BRYOPHYTA

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Dedicated with deep sense of respect to

Late (Dr) G Gopalkrishna

who taught me ***Bryophyta*** *at the postgraduate level in 1965–1966, and from whom I learnt the art of teaching Botany in the classroom, which later became the means of earning my bread and butter.*

O P SHARMA

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Preface

Bryophyta is the next and last of the ***Series on Diversity of Microbes and Cryptogams***, and my *main aim* of writing this book is to fill a gap which exists between the full, straightforward treatment of the morphology of bryophytes and research literature in all its details and diversity of topics. My hope is that it will enable the university students to see morphological and other related bryological facts from a new angle and at the same time have their interest directed to other branches of botany.

Another major aim of writing a book on Bryophyta is evidenced by Appendix-IV of this book (Globally Published Books on Bryophyta), which mentions a list of approximately 120 books. Out of this list, only three books are available in the Indian market which suit, to some extent, the syllabi requirements of UG and PG students of Indian universities, but none of these three has been revised during the last 10 to 15 years. This, in itself, provides sufficient ground for writing and publishing a new book on **Bryophyta**, which discusses and explains the subject matter in the light of recent developments in bryology. This is not only a *need* of the students but also their *right* to study the subject in the light of recent global developments. The contents of this book were prepared to fulfill this requirement of the students of Indian universities and of the Indian subcontinent, and the book in its present form is the result.

Furthermore, Bryophyta is a syllabi requirement of botany students as a compulsory full paper at the postgraduate level and half of a paper at the undergraduate level in all universities of the country. Due to this too, a new book of such nature is a 'must' and a 'need of the hour' for Indian students.

Chapter Organisation

The present book on Bryophyta includes 32 chapters.

The initial two chapters deal with the basics of Bryophyta and a glimpse of their classification, followed by eight chapters (3 to 10) discussing the major aspects and life-history details of almost all major genera of all the three bryophytic groups (i.e. Hepaticopsida, Anthoceropsida and Bryopsida). They are followed by the remaining 22 chapters (11 to 32) discussing almost all important general topics of Bryophyta.

Four appendices are given at the end of the book. Appendix I provides "answers to all short-answer questions" of all the chapters of the book. Appendix II compares different aspects of all major and commonly available bryophytic genera in the form of some comparative tables. Appendix III explains

the meanings/definitions of 233 bryological terms in simple language, and Appendix IV gives a list of about 120 globally published books and theses on Bryophyta. Details of research publications have been intentionally avoided, with the feeling that the book should not look too cumbersome to young students.

Salient Features

Some *major highlights* of the book are as follows:

- **Complete coverage to general aspects of all groups of Bryophyta:**
  - Hepaticopsida (including Takakiales, Calobryales, Jungermanniales, Sphaerocarpales, Monocleales and Marchantiales)
  - Anthoceropsida
  - Bryopsida
- **Complete coverage to all important topics in Bryophyta:** Classification, Physiology, Reproduction, Regeneration, Constituents, Origin and Evolution, Ecology, Economic Importance
- **Detailed life-histories of:**
  - 13 liverworts, 2 hornworts and 8 mosses
  - Specific life-history details of over a dozen genera included in the syllabi for postgraduate students (*Takakia, Calobryum, Haplomitrium, Frullania, Riccardia, Fossombronia, Sphaerocarpos, Riella, Monoclea, Notothylas, Andreaea, Buxbaumia, Tetraphis* and *Archidium*)
- **Complete chapter-wise coverage of all important general topics in bryology:**
  - Gametophytes of bryophytes
  - Sporophytes of bryophytes
  - Alternation of generations
  - Vegetative reproduction in bryophytes
  - Origin and fate of archesporium in bryophytes
  - Apospory and apogamy in bryophytes
  - Physiology of bryophytes
  - Evolution of gametophyte in bryophytes
  - Evolution of sporophyte in bryophytes
  - Ecology of bryophytes
  - Origin of bryophytes and their fossil history
- **Six independent chapters on *new and modern topics*, not available in most Indian books on bryology:**
  - Sexuality in Bryophytes
  - Phylogeny of Bryophytes: Role of Genosystematics
  - Chemical Constituents of Bryophytes
  - Bryophytes as Indicators of Environmental Conditions and Pollution
  - Biologically Active Compounds from Bryophytes
  - Conduction in Bryophytes
- **Five *application-based chapters:***
  - Economic Importance of Bryophytes
  - Morphogenesis

- Cytogenetics and Cytotaxonomy of Bryophytes
- Role of Bryophytes in Carbon and Nitrogen Cycling
- Classification of Bryophytes

- **Rich pedagogy:**
  - Profusely illustrated with more than 200 well-labelled diagrams
- ***Examination preparation tools*** **to help students:**
  - More than 500 chapter-end questions, patterned on university questions, with answers to select questions in Appendix I
  - 18 comparative tables spread across the text and at the end of the book in Appendix II
  - Glossary of over 230 bryological terms explained in Appendix III
  - List of 120 globally published books on Bryophyta in Appendix IV
  - Pictorial life-cycles of dozens of genera

In view of the above-mentioned highlights, I can confidently say that the present book caters to all needs of readers, particularly undergraduate and postgraduate students of botany as well as agriculture of all universities the world over, in general, and of Indian universities, in particular. It should also prove useful to students preparing for AIPMT, CPMT, IAS, IFS, PCS, NET, SLET and several other major competitive examinations of the country.

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At this stage, I also wish to express my special thanks to Professor M U Charaya of CCS University, Meerut, for the desired help in searching and supplying me some valuable literature from the library and the Internet; my wife, Dr (Mrs) Kanti D Sharma, PhD, for her unfailing assistance and patience; and my lovely and dearest grandchildren (Kuhu and Karan) for allowing me time that was due only to them.

Last, but not the least, I wish to put on record my most sincere thanks to the entire editorial and production teams of McGraw Hill Education (India). Without their support, my this *ninth book from McGraw Hill Education (India)* under their Higher Education Programme, would have not seen the light of day. I express my gratitude to all of them.

Feedback

Comments and suggestions for the improvement of this book may be sent to the publisher's email, given below, or directly to me.

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Publisher's Note

Do you have any further request or a suggestion? We are always open to new ideas (the best ones come from you!). You may send your comments to ***tmh.sciencemathsfeedback@gmail.com***

1
Introduction

WHAT ARE BRYOPHYTES? 1.1

Bryophytes (Greek—*bryon*—moss; *phyton*—plant) include liverworts, hornworts and mosses, and occupy a position in the plant kingdom in between *thallophytes* and *pteridophytes*. These are land-inhabiting plants, restricted mostly to moist, shady places, and totally dependent on external water for completing their life-cycle. Because of these characters, bryophytes are also called "*amphibians of the plant kingdom*". The name '*bryophyta*' was first introduced by Braun(1864). Recently, Crum(2001) in his ***Structural Diversity of Bryophytes*** stated that " in the 1600's, Jung considered mosses to be aborted plant foetuses! Today, they occupy a position within the plant kingdom and may even be considered to have their own subkingdom".

Engler (1886) opined that all the plants above the level of Thallophyta (i.e. algae, fungi and lichens) should be grouped under the subkingdom *Embryophyta*. The Embryophyta (or *Embryobionta*) comprises all those plants in which a multicellular embryo develops from the zygote while the zygote is still attached to the parent. The Embryophyta includes Bryophyta, Pteridophyta and Spermatophyta. The Pteridophyta and Spermatophyta (i.e. gymnosperms and angiosperms) possess vascular tissues and are often grouped together under *Tracheophyta*. Bryophytes do not possess vascular tissues. Bryophytes may, therefore, be defined as "the embryophytes that do not possess vascular tissue."

Bryophytes are photosynthetic, nonvascular plants which show clear heteromorphic alternation of generations. Gametophytic generation is dominant, well-developed and independent. Gametophytes are either thalloid or foliose, i.e. bear leaflike structures. The sporophyte is never independent. It is always dependent on the gametophyte. All bryophytes require water for the process of fertilization. No vascular tissue is present in either generation. True roots, stems and leaves are absent in either generation in all bryophytes. Cuticle and stomata are absent in the leaflike structures of mosses.

Bryophytes have also been described variously by different workers as under:

As defined in the 1989 edition of the ***Chambers Biology Dictionary*** of Cambridge University Press, **Bryophyta** is a "division of the plant kingdom containing about 25,000 species of small, rootless, thalloid or leafy nonvascular plants; includes the **liverworts** (**Hepaticopsida**), the **hornworts** (**Anthoceropsida**) and the **mosses (Bryopsida)**, having alternation of generations in which the

gametophyte is the dominant generation, the sex organs are archegonia and antheridia and the sporophyte is more or less parasitic on the gametophyte".

In the ***Penguin Dictionary of Botany***, Bryophyta has been described as "a division of nonvascular plants, mainly terrestrial in habitat." It comprises three classes—Hepaticae (liverworts), Musci (mosses) and Anthocerotae (hornworts). Bryophyta are generally small, low-growing plants, in most cases susceptible to desiccation and hence limited to damp or humid environments. Their life-cycle shows a heteromorphic alternation of generations with the haploid gametophyte, which may be homo- or heterothallic, the dominant generation. The ephemeral sporophyte is partly or completely parasitic on gametophyte ...." Close resemblances between some bryophytes (e.g. mosses) and algae, especially between moss protonema and algal filaments "suggest that bryophytes evolved from algae, most probably green algae", since both of them "share similar photosynthetic pigments, food reserves and cell-wall constituents". Bryophytes, however, show more "morphological differentiation than the algae and differ also in producing aerial spores and having enclosed sex organs". They also lack roots, and water is required by them for the dispersal of their male gametes and also for the fertilization process.

Bryophytes depend on water for their process of fertilization. Their ciliate antherozoids have to swim in water drops to effect fertilization. Due to these characteristics, bryophytes are also called "amphibians of the plant kingdom." Recently, Daniel Norris (2003), in an interesting article in ***Fremontia***, defines bryophytes as "green plants without flowers and fruits, and lacking a well-defined system of vascular tissue for transporting plant fluids throughout the plant. They reproduce, not by seeds, but by single-celled spores. Mosses and most liverworts have clearly recognisable leaves on clearly recognisable stems but they totally lack a root system. All hornworts and some liverworts lack even a leaf–stem differentiation but instead grow as ribbonlike **thalli**." Dan Norris of University of California has the **largest collection of bryophytes in the world**, which includes over 1,06,000 specimens.

1.1.1 Are all Mosses Bryophytes?

No, all "mosses" are not bryophytes. In bryophyta, all mosses belong to the class Musci or Bryopsida, which includes more than 600 genera and more than 15,000 species. They have a leafy (not thalloid) gametophyte, multicellular rhizoids, and a majority of them have a capsule with both a columella and a lid or operculum. *Chondrus crispus,* an alga, is commonly called Irish moss while *Cladonia rangifera* (a lichen) is commonly called Reindeer moss and *Lycopodium* (a pteridophyte) is commonly called club-moss, and Spanish moss (*Tillandsia usneoides*) is a flowering plant.

1.1.2 What are Liverworts?

The word *liverwort* is a misnomer, and in bryophytes it is used for members of a class (Hepaticae or Hepaticopsida). Liverworts are both thalloid as well as leafy. Some thalloid members of Hepaticopsida resemble the liver, and hence the name "liverwort" is given. There is, however, no evidence that these liverworts are of medicinal value. In **thalloid liverworts**, the gametophyte is a flat, more or less undifferentiated thallus, whereas in **leafy liverworts**, the gametophyte has a simple stem, growing from the apex and bearing small leaves in the rows along it. About 80% of the liverwort species are leafy, while only about 20% of liverwort species are thalloid.

HOW DO RECENT SYSTEMATISTS TREAT THE TERMS "BRYOPHYTA", "BRYOPHYTES" AND "BRYOBIOTINA"? 1.2

On the basis of recent genetic information, available molecular data between 2001 and 2010, and the current concepts of phylogeny and classification, systematists have started treating these terms quite differently from their existing explanations.

1. The **hornworts**, sharing their small size and independent, dominant gametophyte and dependent sporophyte with the mosses and liverworts, have been considered by most systematists and recent bryologists now to be in a separate phylum, the ANTHOCEROTOPHYTA.
2. A majority of the recent bryologists now also agree that the **liverworts** should occupy an independent phylum, the MARCHANTIOPHYTA (also known variously as **Hepatophyta**, **Hepaticophyta**, **Hepaticopsida** and **Hepaticae**).
3. Only **mosses** (included earlier under the class Musci) are now treated as the only members of the phylum BRYOPHYTA.
4. All mosses, liverworts and hornworts together are still considered by bryologists under the English name BRYOPHYTES, a term having no taxonomic status, and some bryologists have suggested the rank of a subkingdom under the name BRYOBIOTINA.

All bryophytes are, therefore, now treated by recent bryologists (Crum, 2001; Norris, 2003; Shaw and Renzaglia, 2004; Zander, 2006; and Troitsky et al., 2007) under the subkingdom BRYOBIOTINA, which are classified into three phyla, viz. **Marchantiophyta** (= liverworts), **Bryophyta** (= mosses) and **Anthocerotophyta** (= hornworts). The characters, which all bryophytes share with tracheophytes, are:

1. Development of an embryo within a **multicellular reproductive organ**
2. Presence of a covering of **sporopollenin** on their spores
3. Presence of **flavonoids**.

The characters in which all bryophytes differ from tracheophytes are the following:

1. Bryophytes have a dominant gametophyte supporting a parasitic sporophyte.
2. They lack meristematic tissue, lignin, tracheids and sieve cells.

Only due to the characters, like lack of lignin, and lack of tracheids and vessels, bryophytes have a very small stature and are also termed **nontracheophytes**.

WHY ARE BRYOPHYTES ALWAYS SMALL-SIZED AND LACK TRUE LEAVES? 1.3

Bryophytes are small-sized plants, and a majority of them attain a length or height of only up to a few centimetres. According to Hebant (1977), "one contribution to their small size is their lack of **lignin**, limiting their size to that which their unlignified tissues can support." However, there are conflicting reports about the presence or absence of lignin in bryophytes. Downey and Basile (1989) reported lignin in the sporophytes of *Pellia epiphylla*, and Crum (2001) reported lignin-like compounds in peristomes of some bryophytes. However, the presence of lignin in gametophytes of bryophytes has still not been conclusively evidenced. A lignin-like substance in the cell walls of *Rhacocarpus purpurascens*, a moss, has been reported by Edelmann et al. (1998). Some phenolic compounds, similar to lignin, have certainly been reported in many bryophytes.

The characteristic of "being without lignin" imposes some other limits on the plants. Due to absence of lignin, bryophytic plants have no tracheids or vessels, hence they lack the type of the conducting system, which is present in tracheophytes or vascular plants. This implies that the bryophytes lack **true vessels**, and are also, therefore, called **nontracheophytes**.

Instead of tracheids or vessels, many bryophytes possess **hydroids** that confer much the same function as xylem. Many others possess **leptoids**, the moss version of phloem. Many moss stems possess a **central strand**, with or without hydroids, but with elongate cells. It functions in conduction. Because of the greater density of smaller cells in the conducting strand, it also provides support to the plant.

WHY DO BRYOPHYTES POSSESS RHIZOIDS INSTEAD OF ROOTS? 1.4

Bryophytes lack tracheids and vessels and also, therefore, a sophisticated tracheid conducting system. This limits or slows the movement of water within the plant, and, therefore, the **roots** are absent in bryophytes. This lack of roots is substituted in most bryophytes by the nonvascular thread-like structures, called **rhizoids**.

Rhizoids in bryophytes help in obtaining nutrients from a larger soil volume. They also help in slowing the process of desiccation. Due to this characteristic, many bryophytes are **desiccation tolerant**.

NUMBER OF SPECIES AND GENE-BANK DATABASE 1.5

As mentioned in some more detail in Chapter 2, in **modern classifications**, bryophytes are divided into three groups having the "rank or divisions: Bryophyta, Marchantiophyta and Anthocerotophyta, or even superdivisions" (Kenrick and Crane, 1997; Troitsky et al. 2007). And according to estimates of Ignatov (2007), modern bryophytes—hornworts (= Anthocerotophyta), liverworts (= Marchantiophyta) and mosses (= Bryophyta)—"include about 100, 5,000 and 10,000 species, respectively".

According to Troitsky et al. (2007), "As of September 2007, there are 337 entries for hornworts, 5517 for liverworts, and 17412 for mosses in the **GeneBank database**." The current state of the problem with the number of bryophyte species and their GeneBank database is reflected in ***Molecular Systematics of Bryophytes*** by Goffinet et al. (2004) and in an article of Renzaglia et al. (2007) in the journal ***Bryologist***.

AGE OF BRYOPHYTES 1.6

As detailed in a review entitled "Contribution of Genosystematics to Current Concepts of Phylogeny and Classification of Bryophytes", Troitsky et al. (2007) stated that "The time of origin of bryophytes and their phyla is not well determined from paleontological data. The cause is a bad preservation of these plants in sediments and rarity of findings of sporophytes, on which the modern systematics is greatly based. Most of such well-identified forms are <60 million years old. However, the age of fossil spores, which can be classified as bryophytes, is 440–450 million years, which is in good agreement

with the most reliable molecular-genetic chronology of the origin of land plants (425–490 million years ago)."

OCCURRENCE AND DISTRIBUTION 1.7

Represented by approximately 960 genera and over 15,000 (Gradstein et al., 2001) to 25,000 species (Crum, 2001), bryophytes are of widespread occurrence in almost all parts of the world. They grow in almost all habitats but are mainly amphibious in nature. A majority of the bryophytes are moisture-loving terrestrial plants growing in shaded grounds, on moist rocks, trunks of trees and other similar moist places. They usually grow in tufts and cushions, and are responsible for providing the green colour to the grounds, forests and mountains, especially during the rainy season. Bryophytes grow luxuriantly in humid climates of both tropical and temperate regions. Liverworts grow commonly in humid tropics but are rare in arctic environments. Mosses, however, survive in arctic and alpine regions. Only a few bryophytes are aquatic, e.g. *Riccia fluitans, Ricciocarpos natans*, *Riella* sp. and *Fontinalis antipyretica*. A few members (e.g. *Leucobryum glaucum*, *Calypogeia fissa* and *Sphagnum* sp.) grow in bogs, i.e. wet and soft grounds, while some are found in xeric conditions, e.g. *Torula muralis* and *Polytrichum juniperinum*. *Buxbaumia* and *Cryptothallus mirabilis* are saprophytic bryophytes.

Though bryophytes are not found in the sea, some mosses (e.g. *Grimmia maritima* and *Eurhynchium praeolongum*) grow in crevices of rocks regularly bathed by sea water. Bryophytes usually occur on the mountains at an altitude of 4000-8000 feet but a few mosses (e.g. *Aongstroemia julacea*) have also been reported from an altitude of even 20,000 feet.

GAMETOPHYTE (PLANT BODY) 1.8

The plant body is gametophytic, and the gametophyte is independent and autotrophic in bryophytes. It is either **thalloid** (i.e. thallus-like, and not differentiated into roots, stem and leaves; (Fig 1.1a) or **foliose** (i.e. containing a definite rootless "leafy" shoot; Fig 1.1b). The gametophytic phase is, therefore, the dominant and longer-lived phase of the life-cycle as compared with the sporophytic phase. According to Renzagalia et al. (2000), the "bryophyte gametophytes are amongst the most elaborate of any phylum of plants".

The plant body of most bryophytes is small-sized, reaching only up to a few centimetres in length. However, some species of the Australasian genus *Dawsonia* reach up to a height of 40–70 cm. *Fontinalis antipyretica*, a moss, attains a length of 50–70 cm, while Martin (1951) recorded a remarkable example of a stem of *Polytrichum commune* attaining a length of over 180 cm. Crum (2001) mentioned that some mosses (e.g. *Ephemeropsis* and *Viridivellus pulchellum*) are only a few millimetres tall and have only a few leaves. The liverwort thallus of *Monocarpus* is only 0.5–2 mm in diameter, and some *Fontinalis* species can be 2 m in length.

True roots, stems and leaves, as found in vascular plants, are completely absent in the plant body of bryophytes. The "stem" and "leaflike" structures of foliose bryophytes have been termed "axis" and "phylloid" by Koch (1956). Vascular tissues (xylem and phloem) are completely absent in all bryophytes and, therefore, Tippo (1942) suggested the name *Atracheata* to them. Cuticle and stomata are also absent.

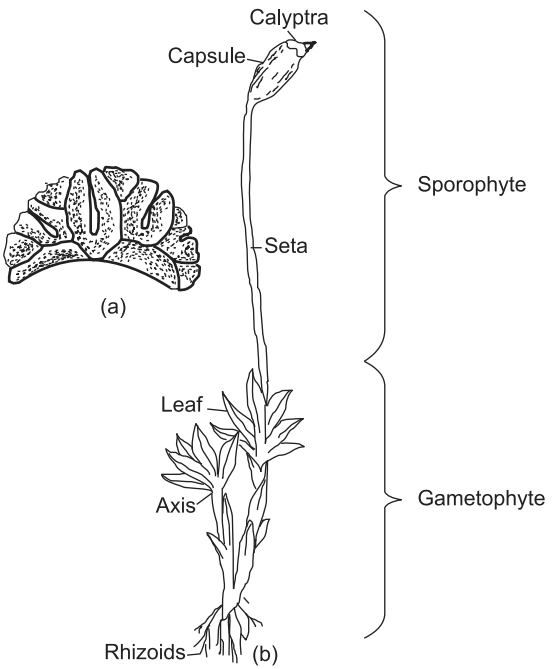


Fig. 1.1 *(a)* Thalloid plant body of *Riccia (b)* Foliose plant body of *Funaria*

The plant bodies of thalloid members (e.g. *Riccia*, *Marchantia*, *Anthoceros*) grow prostrate on the ground and remain attached to the substratum with the help of several fine, delicate, hairlike, unicellular organs called **rhizoids**. Along with the rhizoids, several scales may also be present in several genera (*Riccia*, *Marchantia*) on the ventral surface of the thalloid plant body. Sex organs, i.e. antheridia and archegonia, are present on the dorsal surface of thalloid genera.

The plant body of foliose members (i.e. leafy Hepaticopsida and mosses) usually grows erect and remains differentiated into rhizoids, axis (comparable to stem) and leaflike structures called **phylloids** or **phyllids**. The rhizoids develop from the basal older parts of the axis and are usually well-branched and multicellular.

Developing on the gametophyte, and dependent on it for nutrition and physical support, is the **sporophyte**. It is usually differentiated into foot, seta and capsule (Fig. 1.1b). The **foot** is usually embedded within the gametophyte and functions for anchorage and absorption. **Seta** is a long stalk-like structure and helps in projecting the **capsule**, which is a spore-producing body of the sporophyte. The sporophyte has no connection with the soil and is completely dependent on the gametophyte for its water and mineral nutrition supply.

VEGETATIVE REPRODUCTION 1.9

Vegetative reproduction is the most prevalent and efficient method of reproduction in most bryophytes. It takes place by a variety of ways, described briefly as under:

1. **Fragmentation,** due to the progressive death and decay of older parts, as in majority of Hepaticopsida and Anthocerotopsida.
2. **Adventitious branches**, often developing from the underside of the midrib, as in *Riccia fluitans, Marchantia, Corsinia, Reboulia, Dumortiera* and *Anthoceros.*
3. **Innovations**, which are the axillary branches, growing vigorously in some plants, such as *Sphagnum* and several acrogynous Jungermanniales.
4. **Phylloid cladia**, which are small detachable branches, originating from the individual cells of the 'leaf' or phylloid, as in *Bryopteris* and *Frullania.*
5. **Axis cladia,** which originate in the axis in some foliose genera and occupy the same position as the sexual branches, as in *Leptolejeunea*.
6. **Tubers**, which develop in the form of swollen tips of the underground branches during drought and other unfavourable conditions, are formed in several species of *Riccia, Anthoceros, Fossombronia, Asterella, Conocephalum,* etc. Food reserves, such as starch grains and oil globules, remain packed in tubers.
7. **Gemmae**, the propogative organs of definite form, are formed in several genera of Hepaticopsida, Anthoceropsida and Bryopsida. Gemmae are large, stalked and multicellular in *Marchantia* and *Lunularia*; small, multicellular and discoid in *Radula*; bicelled, endogenous bodies in *Riccardia multifida;* discoid and platelike in *Metzgeria*; filamentous, microscopic and multicellular in *Torula papillosa* and, globular and multicellular in *Bryum rubens.*
8. **Primary protonema**, which develop by the germination of spores, as in *Funaria.*
9. **Secondary protonema**, which develop from the methods other than the germinating spores, as in *Sphagnum* and *Funaria.*
10. **Apospory** which is the production of diploid gametophyte from the vegetative cells of sporophyte, i.e. without the production of spores, as in *Anthoceros* and several mosses.

Vegetative reproduction in bryophytes has been discussed in detail in Chapter 18.

SEXUAL REPRODUCTION  1.10

Without exception, the sexual reproduction in all bryophytes is of highly *oogamous* type, i.e. takes place by motile male gametes (**antherozoids**) and a large nonmotile female gamete (**egg**). The gametes are produced within the multicellular sex organs, which are provided with an outer sterile layer of jacket. Such an outer layer of sterile jacket is absent in the sex organs of algae. The male sex organ is called **antheridium** while the female sex organ is called **archegonium**.

Antheridium (Fig. 1.2) is a multicellular, ellipsoidal or club-shaped, short-stalked body consisting of a mass of **androcytes** or **antherozoid mother cells** surrounded by a single layer of protective sterile jacket cells. Each androcyte produces a single biflagellate motile male gamete called **antherozoid**. Usually, the antherozoids are spirally coiled bodies, each possessing two whiplash-type flagella. In most bryophytes, the antheridium, on dehiscence, discharges the androcytes in a mass.

The **archegonium** (Fig. 1.3) is also a multicellular but flask-shaped body with a basal swollen portion called **venter** and an upper elongated portion called **neck**. Each archegonium consists of an axial row of cells surrounded by a sterile jacket. The axial row of archegonium contains usually 4–6 or more **neck canal cells**, a **venter canal cell** and a single large basal cell called **egg** or **oosphere**. Nourishment and protection to the egg and the developing embryo are provided by the archegonium.

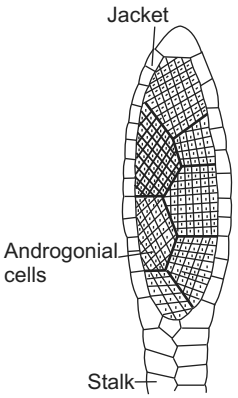


Fig. 1.2 A mature antheridium of *Riccia*

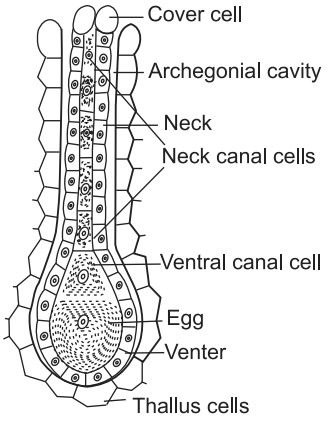


Fig. 1.3 A mature archegonium of *Riccia*

Fertilization takes place only in the presence of water. At the time of fertilization, the axial row of neck canal cells and venter canal cell of the archegonium disintegrate and disorganise (Fig. 1.4), forming a mucilaginous liquid. Only the egg remains inside the cavity of the venter. The liberated, flagellated, antherozoids swim in a thin film of water and reach up to the neck of the archegonium. The mouth or the tip of the archegonium also opens at this stage. Several antherozoids pass through the neck canal to the venter, where a single antherozoid fertilizes the egg, and a diploid **zygote** is resulted.

Gametes (antherozoids and egg) are the last structures of the gametophytic generation, while the zygote is the first cell of the sporophytic generation.

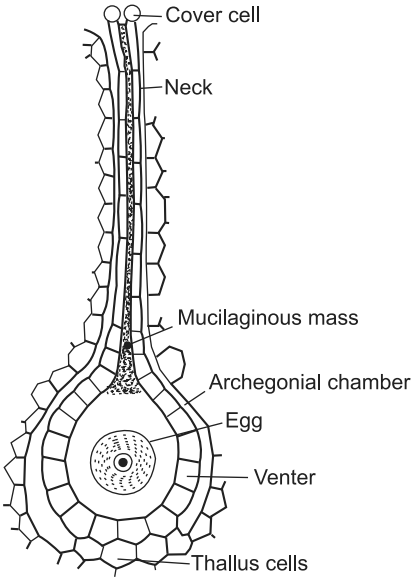


Fig. 1.4 An archegonium of *Riccia* just before fertilization

SPOROPHYTE 1.11

The diploid zygote is the starting point of the sporophytic generation. The zygote, without any resting period, begins to grow at once, divides and redivides, and forms a multicellular **embryo**. The embryo develops into a **sporophyte** or **sporogonium**. The sporophyte in bryophytes is never an independent body. It is always dependent on the parent gametophytic plant. The wall of the venter enlarges with the developing embryo to form a protective covering called **calyptra**. The multicellular **embryo** obtains its nourishment directly from the gametophytic thallus, to which it is attached. The young embryo is an undifferentiated mass of cells. But it soon gets segmented and differentiated into well-developed sporophyte.

The **sporophyte** is usually differentiated into three parts, viz. **foot**, **seta** and **capsule** (e.g. *Marchantia*, *Porella*, Fig. 1.5). In certain cases, the seta is absent (e.g. *Corsinia*), and in certain others, both seta and foot are absent (e.g. *Riccia*). The **foot** is basal and usually a bulbous structure, embedded in the tissue of the gametophyte. Its function is absorption. The **seta** is present in between the foot and the capsule. Its main function is elongation. It also conducts the food absorbed by the foot to the capsule. The **capsule** is the terminal part of the sporophyte and its function is spore production. Inside the capsule are present some sterile **elater mother cells** and fertile **spore mother cells**. Elater mother cells change into long, slender **elaters**, which are hygroscopic in nature. The **spore mother cells** are diploid and represent the last stage of sporophytic generation. They divide reductionally to form **spore tetrads**, which soon separate into **haploid spores** or **meiospores**. Each spore develops into a young haploid gametophyte.

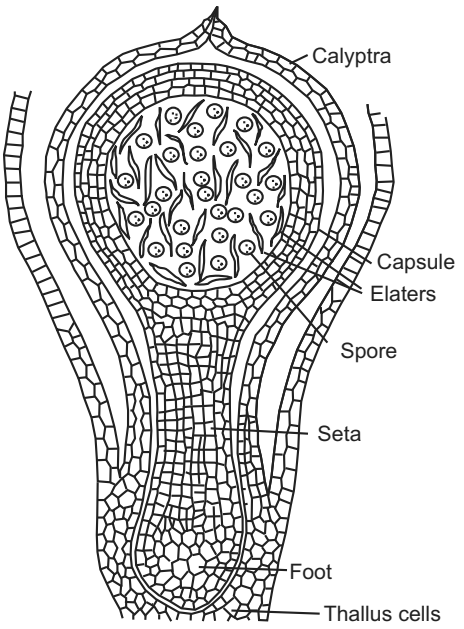


Fig. 1.5 A mature sporophyte of *Porella*

YOUNG GAMETOPHYTE 1.12

The spore is the initial stage of the gametophytic plant body. The spores are usually morphologically similar in shape, size and structure, i.e. they are **homosporous** in bryophytes. Each spore is unicellular and haploid, and germinates into a young gametophytic plant (e.g. *Riccia*, *Marchantia*). In *Funaria* and several other mosses, the spore first germinates into a filamentous **protonema**, from which the buds are produced to give rise to young gametophytic plants.

LIFE CYCLE (ALTERNATION OF GENERATIONS) 1.13

Bryophytes are peculiar in that their life-cycle is completed by a regular alternation between two generations: a gamete-producing generation (gametophyte) and a spore-producing generation (sporophyte). Because both of them are quite distinct from each other and also are quite dissimilar in their sizes, they show **heteromorphic alternation of generations**.

In the life-cycle of these plants, there exist two distinct phases. One is the **haploid** (**X**) or **gametophytic phase**, with one complete set of chromosomes in the cells. This phase is represented by thalloid (e.g. liverworts) or foliose (e.g. mosses) gametophytic plant body, which is the dominant and independent phase of the life-cycle. The gametophytic plant body is haploid and bears the sex organs, i.e. antheridia and archegonia. Haploid gametes are produced in these sex organs, i.e. antherozoids in the antheridium and egg in the archegonium. (The green individual plant is called 'gametophyte' since it bears the gametes). The haploid or gametophytic generation is also called **sexual generation**, as it bears the sex organs. Two different gametes fuse under the process of fertilization and form a diploid **zygote**. The zygote is the starting point of the next phase of the life-cycle, i.e. **diploid** (**2X**) or **sporophytic phase**.

On germination, the **zygote** does not produce the gametophytic plant. It divides and redivides to form a multicellular **embryo**, which, by further segmentation, is differentiated into the second diploid adult of the life-cycle called **sporophyte**. In the capsular region of the sporophyte are present the diploid **spore mother cells**, which undergo **meiosis** and form haploid **spores** called **meiospores**. The zygote, embryo, sporogonium and spore mother cells together constitute the **sporophytic generation**. This is called 'sporophytic generation' because it is concerned with the production of spores. Since two sets of chromosomes exist in the cells of all stages of this phase, it is also called **diploid phase** (**2X**). It is also called **non-sexual generation** because it ends in the production of asexual spores. The sporophytic generation is dependent, usually completely or sometimes partially, on the gametophytic generation for its nutrition. The haploid spores, produced at the end of this diploid phase, are the starting point of the haploid gametophytic plant body. Each spore germinates and produces a gameteophytic plant body. Each spore germinates and produces a gametophytic plant, which again bears the sex organs (antheridia and archegonia). And in this way, the life-cycle goes on. Since the sex organs, i.e. antheridia and archegonia, are not exposed, these plants are described as **cryptogams** (Greek—*kruptos*, hidden; *gamos*, wedded). Because the two generations (gametophytic and sporophytic) appear alternately in the life-cycle, these plants show **alternation of generations**. Since the two 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 generations**.

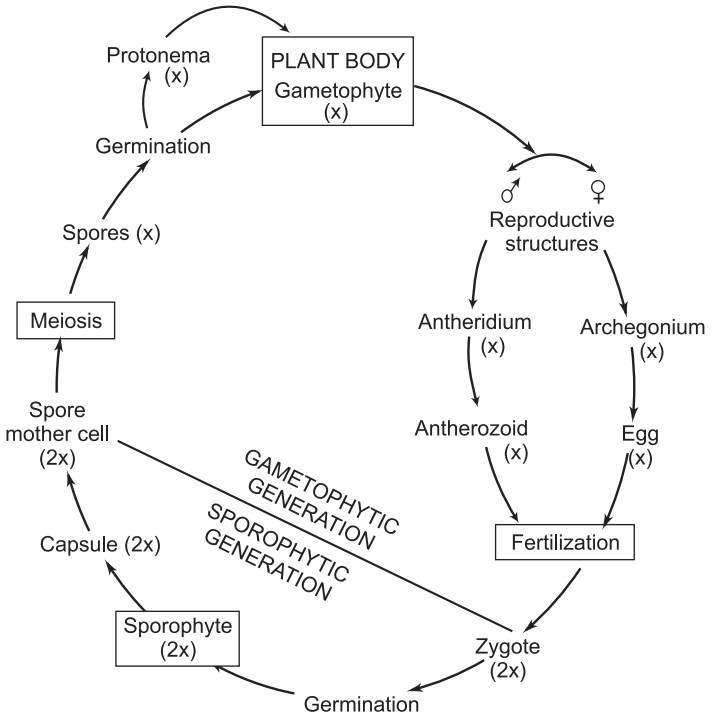


Fig 1.6 Diagrammatic representation of the life cycle in bryophytes

A NOTE ON REGENERATION IN BRYOPHYTES 1.14

Bryophytes have exceptional capacity of **regeneration**. In the dry conditions, the gametophytic plant body of these plants becomes brittle and its isolated fragments readily regenerate to form entire plants. Regeneration is also shown by the cells of the sporophyte. These cells regenerate to develop into a protonema, and soon the gametophytes appear on these protonemal bodies. Such a regeneration of gametophytes from the sporophytic cells, without the formation of spores, is called **apospory**. On the contrary, in some bryophytes there is seen the regeneration of a sporophyte from a gametophyte, without the formation of gametes, and this phenomenon is called **apogamy**. **Gemmae** (cluster of cells on the gametophyte, which, on separation from the parent plant, give rise to a new gametophytic plant) are also the effective means of regeneration in several bryophytes, e.g. *Marchantia*. In bryophytes, however, the phenomena of apospory and apogamy are not of common occurrence.

SALIENT FEATURES OF BRYOPHYTES: AT A GLANCE 1.15

1. Bryophytes live in wet, shady habitats and include liverworts, hornworts and mosses.
2. Their vegetative plant body is completely adapted to the land habit. For their sexual reproduction, however, they rely upon water because their swimming habit is retained by their male gametes or antherozoids.

3. Their plant body is gametophytic, which is independent.
4. The plant body lacks true roots, stem and leaves.
5. It is either thalloid or foliose.
6. Most bryophytes have very little or no vascular system. The characteristic vascular tissue (xylem and phloem) of higher plants is absent.
7. Thalloid bryophytes (e.g. *Riccia, Marchantia*) grow prostrate on the ground and remain attached to the substratum by several delicate, unbranched, unicellular, hairlike structures called rhizoids.
8. Foliose bryophytes (e.g. *Funaria*) have an erect plant body possessing a central axis bearing many leaflike expansions. They remain attached to the substratum by many branched, multicellular rhizoids.
9. Gametophyte is concerned with the sexual reproduction, which is invariably highly oogamous.
10. Differing from algae, the sex organs in bryophytes are jacketed and multicellular.
11. The **antheridium** is club-shaped and multicellular, and bears many biflagellate antherozoids, of which both the flagella are of whiplash type.
12. The **archegonium** is the female sex organ. It is a flask-shaped body, containing a globular venter and long neck. The female gamete is in the form of an egg.
13. Fertilization takes place only in the presence of water.
14. The fertilized egg or **zygote** is retained within the venter of the archegonium and divides only there. It never becomes independent, i.e. it always remains within the parent gametophyte.
15. Repeated divisions of the zygote results into the formation of a multicellular **embryo**.
16. The first division of zygote is transverse, and the apex of the embryo develops from the outer cell. The embryogeny is thus **exoscopic**, a characteristic feature of bryophytes.
17. The venter of the archegonium develops into a protective, multicellular structure called **calyptra**.
18. Embryo, in the later stages, differentiates into a spore-producing structure called **sporophyte** or **sporogonium**.
19. The sporophyte in bryophytes is never differentiated into structures like roots, stem and leaves. It is always dependent, partially or completely on the gametophyte, and usually contains structures like foot, seta and capsule.
20. Diploid spore mother cells of the sporogonium divide reductionally to form **haploid spores** or **meiospores**.
21. Meiospores of one species are morphologically similar. Bryophytes are, therefore, **homosporous**.
22. Each spore germinates into a **haploid gametophytic plant**.
23. All bryophytes show **heteromorphic alternation of generations**.

AFFINITIES OF BRYOPHYTES 1.16

Bryophyta are a group of amphibian plants occupying a position in between algae (being aquatic) and pteridophytes (being terrestrial). They, thus, have some affinities with both algae and pteridophytes, discussed briefly as follows:

1.16.1 Affinities of Bryophytes with Algae

1. *Resemblances of Bryophytes with Algae*

(a) Both bryophytes and algae have thallus-like bodies.
(b) Both lack vascular tissue, i.e. xylem and phloem.
(c) Roots are absent in both.
(d) Visible plant body in all bryophytes and most algae is gametophytic.
(e) Members of both groups possess chlorophyll and are thus autotrophic.
(f) Chlorophyll *a* and *b*, xanthophyll and carotene are present in both bryophytes and in green algae (Chlorophyta).
(g) Antherozoids of both groups have a swimming habit.
(h) Antherozoids of both groups have whiplash flagella.
(i) Filamentous thalli of many green algae show striking similarities with the early developmental stages of gametophytes of many bryophytes.
(j) In both bryophytes and green algae, the carbohydrate food is a true starch, containing a mixture of two kinds of glucose macromolecules, amylose and amylopectin.
(k) In both bryophytes and green algae, the structure and composition of cell walls show many resemblances. They possess cellulose cell walls.
(l) Presence of pyrenoids in green algae and Anthocerotales (e.g. *Anthoceros*) is also a striking similarity between them.

The resemblances mentioned above support the theory of the evolution of bryophytes from algae, especially from the green algae (Chlorophyceae).

2. Differences between Bryophytes and Algae

Some of the striking differences between algae and bryophytes are listed in Table 1.1.

1.16.2 Affinities of Bryophytes with Pteridophytes

1. Resemblances of Bryophytes with Pteridophytes

(a) Terrestrial habit is usually shown by both groups.
(b) Asexual spores (mitospores) are absent in the life-cycle of members of both groups.
(c) Oogamous sexual reproduction is shown by members of both groups.
(d) Plants are archegoniate in both groups, and structure of archegonium in both groups is almost similar.
(e) A layer of sterile jacket cells surrounds the antheridium in both.
(f) Male gametes are flagellated in members of both groups.
(g) Water is essential for fertilization in both.
(h) All members of both the groups show development of zygote into an embryo.
(i) In both groups, the embryo develops within the archegonium protected by multicellular maternal tissue.
(j) A well-marked heteromorphic alternation of generations is shown by members of both groups.

Table 1.1 *Differences between algae and bryophytes*

S. No.	Algae	Bryophytes
1	Most algae are aquatic.	Chiefly terrestrial, occurring in moist shady places.
2.	Plant body is either unicellular or multicellular, filamentous or pseudoparenchymatous.	Plant body is multicellular and thalloid or foliose (differentiated into rhizoids, axis and leaflike structures).
3.	Filaments are unbranched or branched, showing irregular branching.	Thalloid plant body is usually dichotomously branched.
4.	Rhizoids are usually absent except in some heterotrichous forms.	Rhizoids are present in all bryophytes.
5.	Almost all cells of the plant body are capable of divisions.	Divisions are restricted only to certain apical cells.
6.	Asexual reproduction by formation of mitospores, e.g. zoospores.	Mitospores, like zoospores, are completely absent.
7.	Sexual reproduction is isogamous, anisogamous or oogamous.	Sexual reproduction is always oogamous.
8.	Sex organs do not possess a covering of sterile cells.	Sex organs are always covered by a single sterile layer of jacket.
9.	The female sex organ is usually a unicellular oogonium.	Female sex organ is always a multicellular archegonium.
10.	The diploid zygote is usually liberated from the female sex organ and only then it starts dividing.	The zygote is never liberated. It starts dividing into a sporogonium inside the gametophytic plant body only.
11.	Prior to germination, the zygote requires a resting period.	The zygote does not require a resting period. It starts dividing immediately after its formation.
12.	There is no embryo formation after gametic union.	All bryophytes show development of zygote into an embryo.
13.	The diploid sporophytic phase is in the form of a zygote which is an independent body.	The diploid sporophytic phase is never an independent body. It is always dependent on the gametophyte.
14.	Alternation of generations, if present, is of homologous type.	All bryophytes exhibit alternation of generations, and it is always of heteromorphic type.
15.	Gametophytes and sporophytes are both independent bodies.	Sporophyte in all bryophytes is always dependent on gametophyte, either wholly or partially.

2. Differences between Bryophytes and Pteridophytes

The major differences between bryophytes and pteridophytes are listed in Table 1.2.

Table 1.2 *Differences between bryophytes and pteridophytes*

S. No.	Bryophytes	Pteridophytes
1.	Dominant phase in the life-cycle is gametophytic.	Dominant phase in the life-cycle is sporophytic.
2.	Plant body is either thalloid or foliose. It is never differentiated into roots, stem and leaves.	Plant body is always differentiated into roots, stem and leaves.
3.	Vascular tissue (xylem and phloem) is absent.	Vascular tissue in the form of xylem and phloem is always present.
4.	Sporophyte is dependent on the gametophyte.	Sporophyte is independent. It is never dependent on the gametophyte.
5.	All bryophytes are homosporous.	Pteridophytes are both homosporous as well as heterosporous.

ORIGIN OF BRYOPHYTES 1.17

Discussed in detail in Chapter 31.

TEST YOUR UNDERSTANDING

1. Who was the first to introduce the word “bryophyta”?
2. Bryophyta includes liverworts, hornworts and _____.
3. The name “amphibians of the plant kingdom” is often given to _____.
4. What are bryophytes? Explain in about 100 words.
5. Embryophyta includes _____, pteridophyta and spermatophyta.
6. Are all “mosses” bryophytes?
7. Differentiate between the terms “liverworts” and “hornworts”.
8. Discuss briefly how the modern systematists treat the terms (a) Bryophyta, (b) Bryophytes, and (3) Bryobiotina?
9. Write at least 10 salient features of bryophytes.
10. Is vascular tissue completely absent in bryophytes?
11. Explain in brief various methods of the vegetative reproduction in bryophytes.
12. Antheridia of bryophytes are club-shaped while their archegonia are _____ shaped.
13. Bryophytes are always small-sized and lack true leaves. Why?
14. How will you differentiate between the sex organs of algae and bryophytes?
15. Why do bryophytes possess rhizoids and not roots?
16. Write a brief note on the sporophyte in bryophytes.
17. Explain alternation of generations in bryophytes.
18. Discuss affinities of bryophytes in detail.

2
Classification

CLASSIFICATION 2.1

Braun (1864), who introduced the term "*Bryophyta*", included all algae, lichens and mosses under bryophytes. The rank of the division to the Bryophyta was first given by Schimper (1879).

Eichler (1883) was the first to divide Bryophyta into two classes, viz. **Hepaticae** and **Musci**. Engler (1892) also followed Eichler but divided the class Hepaticae into the following three orders:

1. Marchantiales
2. Jungermanniales
3. Anthocerotales

The abovementioned same system of classification of Bryophyta and *Hepaticae* has also been followed by some eminent botanists including Fritsch (1929), Bower (1935), Evans (1939) and also in ***Syllabus der Pflanzenfamilien*** by Engler, Melchior and Werdermann (1954).

Underwood (1894) and Gayet (1897) studied in greater detail the evolution of Hepaticae, and suggested that there exist several fundamental differences between Anthocerotales and the remaining members of Hepaticae. On the basis of such differences, several later workers (Smith, 1938, 1955; Takhtajan, 1953; Wardlaw, 1955; and Schuster, 1958) divided Bryophyta into following three classes:

1. Hepaticae
2. Anthocerotae
3. Musci

Howe (1899) was actually the first to provide a separate 'class' status to Anthocerotales and has named the class '**Anthocerotes**'.

International Code of Botanical Nomenclature suggested in 1956 that the suffix —'opsida' should be used for the classes, and all subclasses should end with the suffix- "idae". And, such usage had already been proposed by Rothmaler (1951) for the classes of Bryophyta. He suggested that the names **Hepaticopsida**, **Anthoceropsida** and **Bryopsida** should be used instead of the older names, i.e. ***Hepaticae, Anthocerotae*** and ***Musci*** for the classes of Bryophyta.

Proskauer (1957) suggested that the class name **Anthoceropsida** should be changed to **Anthocerotopsida**. Proskauer's classification, followed by Parihar (1965), Holmes (1986) and most other bryologists has been followed in this book. It divides Bryophyta into three classes:

1. Hepaticopsida
2. Anthocerotopsida
3. Bryopsida

An outline of the classification of the division Bryophyta, suggested by Sandra Holmes (1986) in her book ***Outline of Plant Classification***, is mentioned below:

Division BRYOPHYTA

Class 1 Bryopsida (Musci, mosses)

Subclass 1. *Sphagnidae (*peat or bog mosses)
Order—Sphagnales

Subclass 2. *Andreaeidae* (granite mosses)
Order—Andreaeales

Subclass 3. *Bryidae* (true mosses)

Cohort 1. Eubryidae
Orders—1. Archidiales 2. Dicranales 3. Fissidentales 4. Encalyptales 5. Pottiales 6. Grimmiales 7. Funariales 8.Eubryales (Bryales) 9. Orthotrichales 10. Isobryales 11. Hookeriales 12. Hypnobryales 13. Thuidiales 14. Schistostegales 15. Tetraphidales

Cohort 2. Buxbaumiidae
Orders—1. Buxbaumiales 2. Diphysciales

Cohort 3. Polytrichiidae
Orders—1. Polytrichales 2. Dawsoniales

Class 2. Hepaticopsida (true liverworts)

Subclass 1. *Jungermanniae*
Orders—1. Takakiales 2. Calobryales 3. Jungermanniales 4. Metzgeriales

Subclass 2. *Marchantiae*
Orders—1. Sphaerocarpales 2. Monocleales 3. Marchantiales

Class 3. *Anthocerotopsida* (horned liverworts or hornworts)

Order—Anthocerotales.

MAJOR DIFFERENCES BETWEEN CLASSES OF BRYOPHYTA 2.2

Some basic differences between the three classes (Hepaticopsida, Anthoceropsida and Bryopsida) of Bryophyta are given in Table 2.1:

Table 2.1 *Basic differences between three classes of Bryophyta*

S. No.	Hepaticopsida	Anthoceropsida	Bryopsida
1.	Spores are usually tetrahedral.	Same as in Hepaticopsida.	Spores are usually spherical.
2.	Protonema is either absent or not sharply differentiated from gametophyte.	Almost same as in Hepaticopsida.	Protonema is well-developed. It is sharply differentiated from gametophytic plant body.
3.	Gametophytic plant body is either thalloid or foliose and strongly dorsiventral.	Gametophytic plant body is thalloid but in *Dendroceros* it becomes slightly foliose.	Plant body is gametophytic and never thalloid. It is foliose.
4.	Leaf-like structures are present only in foliose members. They are never spirally arranged. If present, the leaves are always made of a single cell-thick plate of cells. A midrib is absent.	Leaflike structures are usually absent.	Leaflike structures always present. They are always spirally arranged on the axis. A midrib is always present, except in some species of *Andreaea* and *Sphagnum.*
5.	Rhizoids are thread-like unbranched, unicellular, and of two types, i.e. smooth-walled and tuberculate.	Rhizoids are threadlike, unbranched, unicellular and only smoothwalled.	Rhizoids are well-branched, multicellular. They usually contain oblique septa.
6.	Scales are present in many members, e.g. *Riccia, Marchantia.*	Scales absent.	Scales absent.
7.	Antheridia are cylindrical or spherical with no association of any hairs or paraphysis-like structures.	Almost same as in Hepaticopsida.	Antheridia are club-shaped, with a massive stalk, and are always associated with many hairlike, multicellular paraphyses.
8.	Archegonia are usually sessile or shortly-stalked, with a short neck; jacket made up of 4–6 vertical rows of cells; without any paraphyses.	Archegonia are completely sunk in the gametophytic tissue; jacket of neck is made up of 6 vertical rows of cells; paraphyses absent.	Archegonia have a distinct stalk or pedicel; neck is very long, twisted and composed of 6 vertical rows of cells; several paraphyses present amongst the archegonia.
9.	A four-celled lid or cover cells are present at the top of each archegonium.	Same as in Hepaticopsida.	Cover cell functions as an apical cell for a long time and contributes to the wall of the neck and the neck canal cells.
10.	Sporogonium is a simple structure, represented by only capsule (e.g. *Riccia*) or divisible into foot, seta and capsule (e.g. *Marchantia*).	Sporogonium is not a simple structure. A meristematic zone is present in between a bulbous foot and spore-producing capsule.	Sporogonium is most complex amongst bryophytes, divisible into foot, seta and capsule, it shows a high degree of internal differentiation of tissues.
11.	Sporogonium growth is fixed and determinate.	Sporogonium growth is continuous and indeterminate due to the presence of meristematic zone in between foot and capsule.	Sporogonium growth is indeterminate; seta is meristematic in nature.
12.	Columella is absent.	Columella is usually present.	Columella is mostly present.
13.	Some genera bear elaterophore (e.g. *Pellia*).	Elaterophore absent.	Elaterophore absent.

(*Contd.*)

Table 2.1 (*Contd.*)

S. No.	*Hepaticopsida*	*Anthoceropsida*	*Bryopsida*
14.	Archesporium or sporogenous tissue is usually *endothecial* in origin.	Archesporium is usually *amphithecial* in orgin, with a few exceptions as in some species of *Notothylas*.	Archesporium develops mostly from the outermost layer of endothecium, except in a few cases as in some species of *Sphagnum*.
15	*Elaters* (sterile filaments or cells mixed with spores) are present in the capsules of many genera.	*Pseudoelaters* are present instead of elaters.	Elaters or pseudoelaters are absent.
16.	Capsule *dehisces* either irregularly or by transverse or longitudinal slits.	Capsule dehiscence is simple and takes place by 2 to 4 longitudinal slits.	Capsule dehiscence is usually brought about by operculum and annulus, and it is the *peristome* which controls dispersal of spores.

LATEST POSITION OF CLASSIFICATION OF BRYOPHYTES 2.3

On the basis of the current state of morphology, available data of molecular studies, genosystematics, phylogeny, diversification and classification of bryophytes, almost all modern bryologists (including Clarke and Duckett, 1979; Smith, 1982; Schuster, 1984; Rykovskii, 1987; Newton et al., 2000; Shaw and Goffinet, 2000; Crum, 2001; Norris, 2003; Shaw and Renzaglia, 2004; Zander, 2006; and Troitsky et al., 2007)now agree that all bryophytes should be treated under an independent subkingdom (BRYOBIOTINA), divisible further into the following three phyla:

1. Marchantiophyta (= Liverworts or Hepatophyta, Hepaticophyta, Hepaticae, or Hepaticopsida)
2. Bryophyta (= Mosses or Musci or Bryopsida)
3. Anthocerotophyta (= Hornworts or Anthoceropsida or Anthocerotae)

The phylum Bryophyta now, therefore, includes only "mosses" in the modern classifications.

Crum (2001), on the basis of morphological evidence, coupled with some biochemical evidence, suggested the creation of a fourth phylum *Sphagnophyta* (including *Sphagnum*) under the subkingdom Bryobiotina. However, several other workers (Rykovskii, 1987; Newton et al., 2000) supported the concept of monophyletic origin for the bryophytes, including *Sphagnum*, when they studied data from morphological, developmental, anatomical, ultrastructural and nucleotide sequence characters together.

2.3.1 Marchantiophyta (= Liverworts)

On the basis of available molecular data and studies of genosystematics, a completely new system of classification of liverworts has been proposed by HeNygren et al. (2006). As detailed in the journal ***Cladistics***, an outline of this system is mentioned here as under:

Phylum Marchantiophyta

Class 1 Treubiopsida

Subclass: Treubiidae
Order—Treubiales

Subclass: Haplomitriidae
Order—Haplomitriales

Class 2 Marchantiopsida

Subclass: Blastidae
Order—Blastiales

Subclass: Marchantiidae
Orders—Sphaerocarpales, Marchantiales

Class 3 Jungermanniopsida

Subclass: Pelliidae
Orders—Pelliales, Fossombroniales

Subclass: Metzgeriidae
Order—Metzgeriales

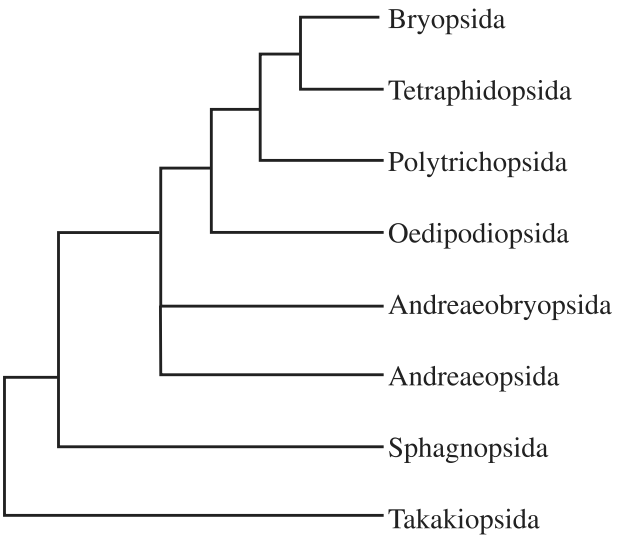
Subclass: Jungermanniidae
Orders—Pleuroziales, Porellales, Jungermanniales

2.3.2 Bryophyta (= Mosses)

The latest system, which has assimilated the genosystematics data, has been proposed by Goffinet and Buck (2004) in ***Molecular Systematics of Bryophytes***. It divides mosses into eight classes as under:

1. Takakiopsida
2. Sphagnopsida
3. Andreaeopsida
4. Andreaeobryopsida
5. Oedipodiopsida
6. Polytrichopsida
7. Tetraphidopsida
8. Bryopsida (*largest class of mosses*)

Troitsky et al. (2007) studied the phylogenetic relationships between basal groups of mosses on the basis of molecular data and shown them as under:



2.3.3 Anthocerotophyta (= Hornworts)

On the basis of methods of molecular phylogenetics, Duff et al. (2004, 2007) divided Anthocerotophyta into the following two subclasses:

1. Anthocerotidae
2. Notothylatidae

TEST YOUR UNDERSTANDING

1. All the bryophytes are traditionally divided into three classes. Name them.
2. Who was the first to use the suffix - "opsida" for the classes of Bryophyta?
3. Proskauer's classification of Bryophyta has been followed by most of the later workers, including Parihar (1965) and Holmes (1986). Give an outline classification of Bryophyta used by Parihar.
4. Write any seven major differences between Hepaticopsida, Anthoceropsida and Bryopsida.
5. How do modern bryologists classify bryophytes, now in the 21st century?

3

Hepaticopsida: Takakiales and Calobryales

WHAT ARE HEPATICOPSIDA (= LIVERWORTS)? 3.1

Formerly known as *Hepaticae* or "*liverworts*", Rothmaler (1951) suggested the name "*Hepaticopsida*" to the class taxon of bryophytes. The names ("Hepaticopsida" for Hepaticae, "*Anthoceropsida*" for Anthocerotae and "*Bryopsida*" for Musci) have also been recognised by ICBN. Recently, some taxonomists have started calling Hepaticopsida as "*Marchantiopsida*".

In ***The Penguin Dictionary of Botany,*** Hepaticopsida or Hepaticae (Marchantiopsida) is "a class of Bryophyta containing the thallose and leafy liverworts, which number about 10,050 species in about 295 genera". They "differ from the Musci (mosses) in showing marked dorsiventrality in the gametophyte. The antheridia and archegonia may be borne on the surface of the thallus or on fleshy stalks (gametangiophore). The capsule of the sporophyte, which contains sterile elaters as well as fertile spores, matures before the seta lengthens, while in mosses the reverse occurs. The capsule does not contain a central pillar of the sterile cells (columella) as is found in Musci and Anthocerotae."

In the ***Chambers Biology Dictionary***, Hepaticopsida is described as a class of Bryophyta, in which "the gametophyte is thalloid or leafy with unicellular rhizoids and the capsule (sporophyte) without a columella".

WHY ARE THEY CALLED LIVERWORTS OR HEPATICOPSIDA? 3.2

In earlier times, it was believed that plants resembling the shape of the liver were good for liver ailments. Since many bryophytes were thalloid or liverlike in their external morphology, the name Hepaticae or Hepaticopsida was given to them, because the Latin word for liver was *hepatica.* Only because of this, the common name "*liverworts*" was given to these plants. It is, however, not correct that all liverworts are good for liver ailments.

GENERAL CHARACTERISTICS 3.3

1. The vegetative plant body is gametophytic and the gametophyte is dorsiventral and either thalloid (i.e. thallus like) or foliose (i.e. bearing a leafy axis).
2. In foliose members, the leaves are arranged on the axis either in two or three rows.
3. A well-marked midrib is almost absent in the leaves.
4. Photosynthetic cells of the gametophyte contain numerous chloroplasts, which lack pyrenoids.
5. One to many refractive oil bodies are usually present in all the chlorophyll-containing cells.
6. The sex organs are in the form of well-developed antheridia and archegonia.
7. Each sex organ develops from a single initial cell.
8. Fertilization results in the formation of a sporogonium.
9. The sporogonium is usually devoid of chlorophyll-containing cells.
10. Stomata are also absent in sporogonium.
11. The sporogonium is either simple (e.g. *Riccia)*, or differentiated into foot, seta and capsule (e.g., *Marchantia*). In some members, it is made of only foot and capsule with no seta.
12. The *archesporium* (the tissue that gives rise to the spore mother cells) is endothecial in origin.
13. The sporogenous tissue of the capsule gives rise to fertile spore mother cells and sterile elaters (e.g. *Marchantia*). In a few genera, the elaters are absent (e.g. *Riccia).*
14. In most of the genera, the elaters are unicellular structures with spiral thickenings in their walls.
15. Columella is absent in the capsule of the sporogonium.
16. The capsule generally remains covered by a well-developed jacket. On being dry, the jacket ruptures releasing the spores.

CLASSIFICATION OF HEPATICOPSIDA 3.4

Tracing history of the classification of Hepaticopsida, Engler (1892) included only two orders, namely Marchantiales and Jungermanniales in this class.

Due to the presence of a special envelope around sex organs in members of the family Sphaerocarpaceae of order Jungermanniales, this family has been elevated to the rank of an order Sphaerocarpales by Cavers (1910). Class Hepaticopsida has thus been divided into three orders—Marchantiales, Jungermanniales and Sphaerocarpales (Cavers,1910). Division of this class into the same three orders has also been favoured by bryologists like Evans (1939), and Engler, Melchior and Werdermann (1954).

Campbell (1936) separated the family Calobryaceae from the order Jungermanniales and proposed to elevate it as a separate order Calobryales on the basis of peculiar characters like

1. Somewhat erect stems, bearing three rows of similar leaves, and
2. One-celled-thick jacket of the capsule. Four orders are thus recognised in Hepaticopsida: (i) Marchantiales, (ii) Jungermanniales, (iii) Sphaerocarpales, and (iv) Calobryales.

Instead of Hepaticopsida, Schuster (1953, 1958) preferred to call this class as Hepaticae and divided it into two subclasses: (i) Jungermanniae, including three orders, namely Calobryales, Jungermanniales

and Metzgeriales, and (ii) Marchantiae, including two orders, namely Sphaerocarpales and Marchantiales. Schuster, on the basis of his detailed study of a large number of Hepaticae from USA, New Zealand and Tasmania, thus divided this class into five orders, viz. (i) Calobryales, (ii) Jungermanniales, (iii) Metzgeriales, (iv) Sphaerocarpales, and (v) Marchantiales.

The unigeneric family Monocleaceae shows characters of both Marchantiales and Jungermanniales and has been placed by some bryologists amongst Marchantiales, and by others amongst Jungermanniales. *Monoclea,* however, shows *Calobryum*-type of archegonial development, thus showing its closeness with Calobryales. On the basis of his detailed studies of antipodal Hepaticae, Schuster (1963) suggested it to be placed in a separate order Monocleales, including a single family Monocleaceae and a single genus *Monoclea.* Schuster (1963), thus later recognised six orders amongst Hepaticae, viz. (i) Calobryales, (ii) Jungermanniales, (iii) Metzgeriales, (iv) Sphaerocarpales, (v) Marchantiales, and (vi) Monocleales.

Takakia lepidozioides, a new bryophytic genus discovered from Japan and Canada around the sixties of the last century has been placed in a new order Takakiales with a single unigeneric family Takakiaceae by Hattori and Inoue (1958) on the basis of some unique characters like (i) absence of rhizoids, (ii) very low chromosome number ($n = 4$), and (iii) each leaf unit bearing two solidly parenchymatous structures. Class Hepaticopsida thus includes seven orders: (i) Takakiales, (ii) Calobryales, (iii) Jungermanniales, (iv) Metzgeriales, (v) Sphaerocarpales, (vi) Monocleales, and (vii) Marchantiales. Sandra Holmes (1986) also divided the class Hepaticopsida into the same seven orders. An outline of her proposed classification of Bryophyta is given in Article 2.1 of Chapter 2.

On the basis of their detailed study of sex organs and sporophytes of *Takakia*, Smith and Davidson (1993) have shown the need to transfer *Takakia* from liverworts to mosses. Rashid (1998) has also shown "the need to reclassify this genus to mosses". However, some detailed studies are still needed and till then this new unigeneric order created by Hattori and Inoue (1958), and Hattori and Mizutani(1958) has been discussed here in this text as an order of the class Hepaticopsida.

Recent studies of molecular biology, genosystematics, phylogeny, diversification and classification of bryophytes (Newton et al., 2000; Norris, 2003; Shaw and Renzaglia, 2004; Zander, 2006; He-Nygren et al., 2006; and Troitskey et al., 2007) treat all bryophytes under an independent subkingdom (*Bryobiotina)* and divided it further into three phyla, of which one is *Marchantiophyta* (= Liverworts or Hepaticopsida or Hepaticae). For details, see Article 2.3.1, Chapter 2.

TAKAKIALES 3.5

3.5.1 What is Takakiales?

Takakiales is an interesting monogeneric order represented by only one genus, *Takakia.* It resembles Calobryales of Hepaticopsida on one hand and mosses (Bryopsida) on the other hand. Smith and Davidson (1993) studied the structure of its capsule and sex organs and suggested it to belong to mosses, whereas in general, the organisation of its body structure and low haploid number of its chromosome ($n = 4$) suggest that it belongs to Hepaticopsida. Detailed studies are, however, still needed to finally decide about its inclusion either in Hepaticopsida or in mosses.

3.5.2 General Characteristics

Some of the general characteristics of Takakiales are listed below:

1. Rhizoids are absent, and the function of absorption is taken up by the underground rhizomatous stem.
2. A number of multicellular, usually unbranched, flask-shaped, mucilage-producing cells are present on the underground rhizome.
3. Several thick, fleshy, green, cylindrical structures are present on the aerial portion of the plant. These are called **phyllids**.
4. Phyllids are morphologically uniform and present in three rows. These are 3–5 cells thick structures, each attaining a length of about 1 mm.
5. Plants apparently lack dorsiventrality.
6. Asexual reproduction is not well-known.
7. The gametophytes are heterothallic. The male plants have not been clearly reported.
8. The archegonia occur either singly or in groups of two or three on the female plants.
9. A small massive neck is made of six rows of neck cells. A fleshy venter is also present in the archegonium.
10. The haploid chromosome number is $n = 4$.

3.5.3 Classification

Takakiales includes a single family (Takakiaceae) represented by only a single genus, *Takakia.*

Some required details of *Takakia* are discussed below.

TAKAKIA  3.6

3.6.1 Distribution and Habitat

Takakia, the only genus of the family Takakiaceae of the order Takakiales, is represented by only two species, viz. *T. lepidozioides* and *T. ceratophylla.* The name has been given after Takakia, a Japanese botanist.

Takakia lepidozioides was discovered first by Hattori and Inoue in 1958 from the alpine zones of Japan at an altitude of 2400–2800 metres. Later, it was also reported from British Columbia, Canada and North Borneo at an altitude of about 3000 metres. Its gametophytes prefer to grow in moist shady places on rocks, crevices and humus.

Takakia ceratophylla has been reported by Grolle (1963) from Sikkim in the eastern Himalayas in India at an altitude of about 3800 metres. Later on, Hattori *et al.* reported this species from Aleutian Islands of British Columbia in 1968. It grows on moist soil, ditches and also on the banks of streams.

3.6.2 Plant Body

The plant body is differentiated into a leafy shoot or gametophore and rhizome. The leafy shoot is an aerial, erect, radially symmetrical structure attaining a length of about 1 cm. The rhizome is a subterranean, branched and cylindrical structure (Fig. 3.1A,B). Rhizoids are absent. A large number of mucilage hairs are present on both the leafy shoot as the well as on the rhizome.

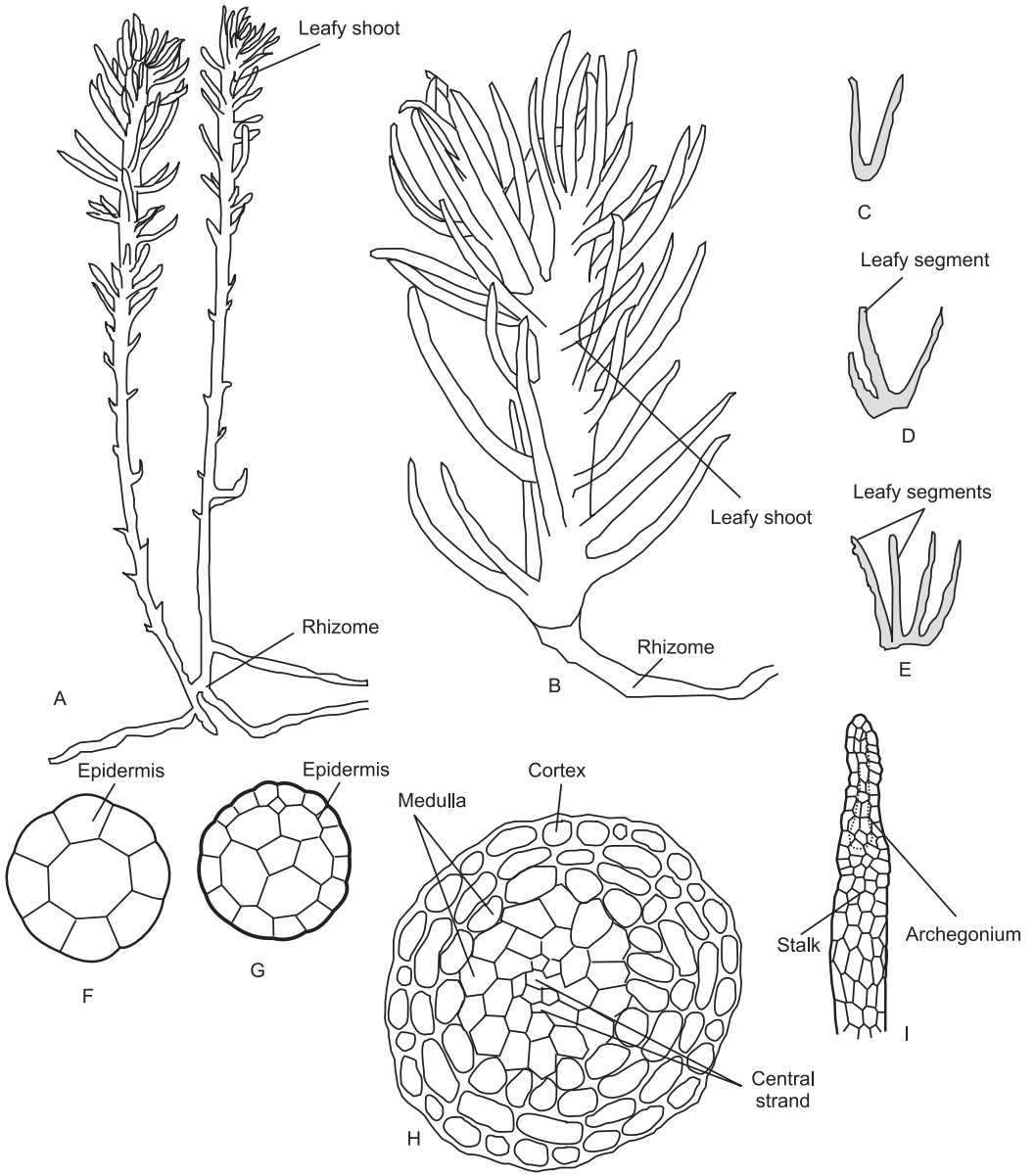


Fig. 3.1 A-I, *Takakia.* A, Gametophores of *T. lepidozioides;* B, Gametophore of *T. ceratophylla;* C-E, Two, three and four leafy segments of phyllids; F, A phyllid in cross section; G, A phyllid of complex construction in cross section; H, TS aerial shoot; I, Stalked archegonium.

Mucilage hairs are of two types. These are filamentous "closed" type and beaked "open" type (Proskauer, 1962). The **filamentous closed type** of mucilage hairs are found on leafy shoots. These are unbranched filaments, of which the terminal cell secretes mucilage through the unruptured cell wall. The **beaked open-type** of mucilage hairs are found on both leafy shoots as well as on rhizomes. These

are usually branched and occur in clusters. Their terminal cell becomes beak-shaped and their tip bursts and secretes mucilage.

Rhizome is almost colourless. It generally grows downwards and possesses no leafy structures. There are no root caps. In dry conditions, the rhizome gets covered by mucilage. Rhizome has been termed "stolon" by Schuster (1966), "caulid" by Hattori and Mizutani (1958), "rhizome" by Berrie (1962) and also "root" by Grubb (1970).

Phyllids are the deep cylindrical structures present on the gametophores. They are isophyllous, i.e. all alike and attain a length of about 1 mm. They are arranged triseriately on all sides of the leafy shoot. Each phyllid is either bifid, trifid or quadrifid i.e. divided into two, three or four segments.

3.6.3 Anatomy

Anatomically, each leaf segment is divided into two parenchymatous cylindrical structures, each made of a central row (Fig 3.1 F) or several rows (Fig 3.1G) of cells surrounded by a layer of epidermal cells.

In a cross section, the aerial shoot (Fig 3.1H) is a somewhat elliptical structure and exhibits no evidence of any dorsiventrality. Its cortex consists of one or two layers of thick-walled cells surrounding a few centrally located thin-walled cells. The cells of the central strand, when mature, have no protoplasmic content. Their end walls are perforated by many small pores. Hebant (1972) confirmed the conducting role of this strand.

3.6.4 Apical Growth

The apical growth takes place by a single tetrahedral apical cell with three cutting faces. In this aspect, *Takakia* resembles Calobryales and almost all Bryopsida.

3.6.5 Reproduction

Asexual reproduction has not been reported in *Takakia.* With reference to sexual reproduction, *Takakia* is a dioecious or heterothallic plant. However, male plants have also not been clearly reported so far in this genus. Female plants bear archegonia. Either a single archegonium is produced at the apex of the main shoot or two or three archegonia occur in groups.

The archegonium (Fig. 3.1 I) does not possess any protective structures around it, and it is thus naked. It is a large, flask-shaped body mounted on a stalk. The large and massive nature of archegonium shows its resemblance more with mosses than with Hepaticopsida. The neck is made up of six rows of neck cells (Inoue, 1961). But, according to Hattori and Mizutani (1958), it consists of only four vertical rows of cells. The venter is fleshy in nature. The jacket of the venter is usually two-layered.

Sporophytes have been discovered in *Takakia* by Smith and Davidson (1993). According to them, the available details of the structure of sex organs and capsule bring *Takakia* close to mosses.

3.6.6 Affinities and Phylogenetic Importance of *Takakia*

Takakia possesses several primitive features of phylogenetic significance, and on the basis of such features, this genus is considered nearest to the ancestors of Hepaticopsida. Some such primitive features are listed below:

1. Lowest haploid chromosome number in Hepaticopsida ($n = 4$).
2. Radial organisation of the plant axis with no differentiation into typical type of leaves.

3. Isophyllus, uniseriate to triseriate phyllids.
4. Mucilage hairs present on both rhizome and axis.
5. Presence of some thin-walled, water-conducting cells in the axis.
6. Complete absence of rhizoids.
7. Presence of slime papillae.
8. Presence of well-developed, massive archegonia having a primitive type of structure.
9. Particular lack of drought resistance.

All the above-mentioned features indicate that *Takakia* is a highly primitive genus and nearest or quite close to the ancestral stock of liverworts. Presence of low haploid chromosome number (n = 4) suggests that *Takakia* represents relics of a race that appears to have died out. Only due to such primitive features, Mehra (1969) opined that "*Takakia* is a **living fossil in Hepaticae**".

Takakia resembles Calobryales in several characteristics including

1. Lack of rhizoids
2. Function of absorption taken up by underground rhizomatous stem
3. Presence of cluster of multicellular, mucilage-producing, flask-shaped cells on the rhizome
4. Isomorphous phyllids present in three rows
5. Radially organised shoots
6. Massive and primitive type of archegonial structure
7. Apparent lack of dorsiventrality

3.6.7 Is *Takakia* a Moss?

Smith and Davidson (1993) discovered sporophytes in *Takakia.* On the basis of their detailed studies of its capsule and sex organs, they have proposed to reclassify *Takakia* along with mosses. They have strongly pleaded that *Takakia* should be transferred from liverworts (Hepaticopsida) to mosses.

3.6.8 *Takakia* and Evolution of Liverworts

Schuster (1966) opined that the low chromosome number (n = 4) in the gametophyte of *Takakia* shows its resemblance with the lowest basic chromosome number of Chlorophyceae (green algae), as in *Ulothrix.* In over 75% of all the liverwort species investigated so far, the basic haploid number, however, is n = 9. This throws some light on the evolution of liverworts from algae.

3.6.9 *Takakia*: A Landmark in the History of Bryology

RM Schuster (1958), a noted American bryologist, worked on the relationships of *Takakia* with other bryophytes. He may be quoted as "I am still not sure, but I suspect that a class parallel with Musci, Hepaticae and Anthocerotae is at hand". EV Watson (1964) elaborated it further that "If this were so, the discovery of *Takakia* would be a landmark in the history of bryology".

CALOBRYALES 3.7

3.7.1 What is Calobryales?

Calobryales is a small order of Hepaticopsida represented by only two genera, viz. *Calobryum* and *Haplomitrium.* Its members are commonly described as "mosslike hepatics" because their radially

symmetrical gametophytes are erect leafy structures, in which the leaflike bodies are almost all alike and remain arranged in three vertical rows. *Calobryum* is **acrogynous** because its apical cell develops into an archegonium. *Haplomitrium* is, however, anacrogynous because there is no involvement of apical cell in the development of archegonia. Schuster (1963) opined that separation of these two genera on the basis of acrogynous or anacrogynous characteristics is unwarranted, and he thus united and treated them as one single genus, namely *Haplomitrium.* A majority of bryologists, however, treat them as two independent genera.

3.7.2 General Characteristics

1. A branched, creeping, rhizome-like underground stem is present at the basal part of the gametophytic plant body.
2. Erect leafy shoots develop from the underground rhizome-like stem.
3. Rhizoids are absent.
4. The leaflike structures are flat, unlobed, simple and entire.
5. The leaves are almost all-alike in shape and size. Out of three ranks of leaves, one is smaller than the other two. This smaller one has been equated with the amphigastria of the order Jungermanniales.
6. Plants are dioecious.
7. Female plants are acrogynous.
8. Arrangement of antheridia on the gametophore is different in both the genera of Calobryales. In *Haplomitrium,* the antheridia arise in the axils of leaves while in *Calobryum* they are present in groups on a terminal receptacle. Enlarged leaves form a cuplike structure around the terminal receptacle.
9. Mode of development of sex organs is of the most primitive type than any other group of bryophytes.
10. A massive calyptra, present in the sporophyte, is a peculiarity.

3.7.3 Classification

Calobryales includes only one family, Calobryaceae, having only two genera, viz. *Calobryum* and *Haplomitrium.*

Calobryum, along with a few details of *Haplomitrium*, is discussed here in some detail.

CALOBRYUM AND *HAPLOMITRIUM* 3.8

3.8.1 Distribution and Habitat

Eight species of *Calobryum* have been reported so far while *Haplomitrium* is represented by only one species (*H. hookeri*). Of the eight species of *Calobryum,* three have been reported from India. These are *C.blumii* from Jawaii (Assam), *C. indica* from Darjeeling (West Bengal) and *C. denundatum* from Himalayan regions. The remaining five species are *C. adinum* from Peru (Equador), *C. gibboiae* from New Zealand, *C. giganteum* from Philippines, *C. intermedium* from Australia and *C.mnioides* from Japan. Ram Udar, a noted Indian bryologist, reported *Haplomitrium hookeri* from Jawail (Assam)

and Vyas Shikhar (Western Himalayas). *Haplomitrium* also occurs in northern Europe and USA. *Calobryum* chiefly occurs in tropical regions.

Both the genera of Calobryales occur in mesophytic conditions on forest floors, steepy clay banks and other such surroundings in extremely shady and wet conditions.

3.8.2 Plant Body

Plant body of both *Calobryum* and *Haplomitrium* (Fig. 3.2 A,B) is gametophytic, and the gametophytes contain a prostrate part and an erect succulent system. The prostrate underground part represents a rhizomatous system from which develop erect and bright green leafy branches.

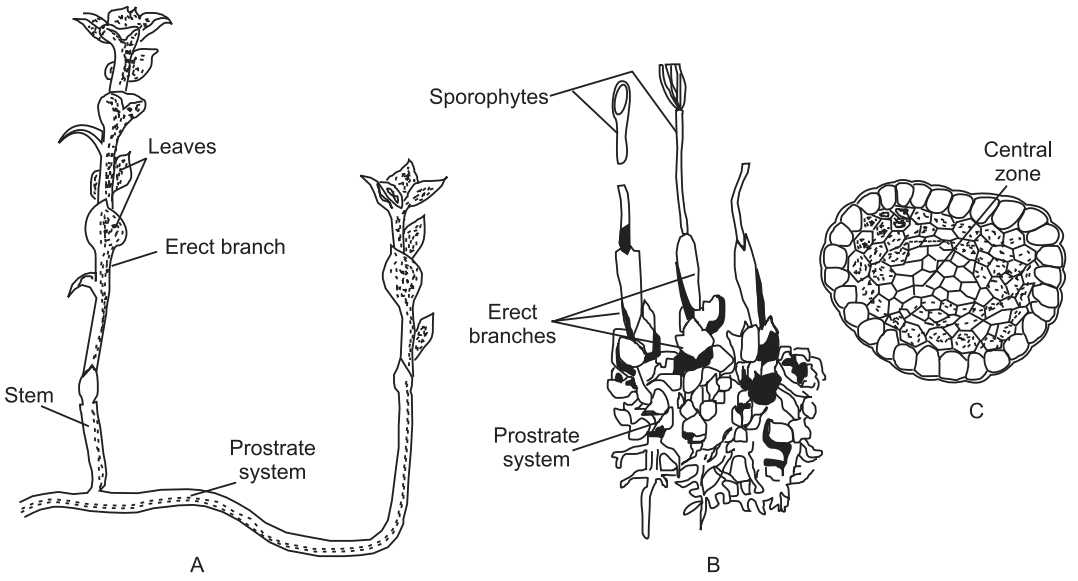


Fig. 3.2 A, Male gametophyte of *Calobrium blumei;* B, Sporophyte-bearing gametophyte of *Haplomitrium;* C, TS stem

The leaves are arranged in three vertical rows on the stem. They possess almost the same shape and size. Sometimes the leaves of one row are slightly smaller than those of two other rows. The leaves are elliptical, contain the entire margin and attain a width of 2 to 5 mm. Sometimes they reach up to 10 mm in *Haplomitrium.* Usually, the leaves are unistratose.

The underground part of the gametophytes is branched, extends downward and lacks leaves. Both prostrate as well as erect systems lack rhizoids.

Anatomically, the stem (Fig 3.2C) contains enlarged cells in the outer zone. The cells of this zone possess a few chloroplasts and many oil droplets. Narrow cells are present in the central zone. Its cells are devoid of chloroplasts and contain only a few oil droplets. The cells of the central zone function as a conduction system and resemble the hydroids of mosses.

Apical growth takes place by a pyramidal apical cell with three cutting faces.

3.8.3 Reproduction

Sex organs in both *Calobryum* and *Haplomitrium* develop at the tip of the leafy branches, and both are dioecious. Antheridia in male plants are surrounded by large-sized, rosette-forming leaves, giving an appearance of mosses.

At the time of the development of **antheridium**, the antheridial initial divides transversely to form a basal cell and an outer cell. The basal cell remains embedded in the gametophytic tissue while the outer cell projects out and divides to form a primary stalk cell and primary antheridial cell. The primary antheridial cell divides by three successive vertical divisions forming three jacket initials, surrounding a single primary androgonial cell. Transverse and longitudinal divisions take place in the androgonial cell and thus androcyte mother cells are resulted. These divide and form spermatozoids. The stalk cell divides to form a stalk of the antheridium made up of several superimposed tiers, each made up of four cells. A **mature antheridium**, thus developed, is a spherical body with a prominent stalk. Many such antheridia surrounded by leaves are present near the shoot apex (Fig. 3.3A). The leaves form a cuplike rosette. The antheridia are lateral and axillary in position.

Calobryum is **acrogynous** (in which terminal growth of the plants comes to an end due to utilization of the apical cell in the formation of an archegonium), while *Haplomitrium* is **anacrogynous** (in which archegonia are formed without the utilization of the apical cell). In *Calobryum,* the apical cell cuts off segments to form about six or more archegonia, and ultimately the apical cell starts functioning as an archegonial intital. Similar to antheridia, the archegonia are also lateral and axillary in position.

At the time of the development of **archegonium**, the primary archegonial initial forms a primary axial cell surrounded by three jacket intitals. The primary axial cell functions directly as a central cell without forming a primary cover cell. The archegonial neck is made up of only four rows of cells because amongst the jacket cells only one divides. A **mature archegonium** contains a long neck surrounding a vertical row of 16–20 neck canal cells. The venter has a breadth like that of a neck, and at maturity it is only two cells thick. Usually, only one archegonium gets fertilised on an erect shoot.

3.8.4 Post-Fertilization Changes

The diploid zygote divides by irregular divisions to form a multicellular embryo. Its lower or hypobasal part develops into a haustorium and the upper or epibasal part develops into foot, seta, and the capsule. Elaterophore is absent. The sporogenous tissue of the capsule is differentiated into **elaters** and **spore mother cells**. Several spore tetrads are seen in the early stages. The developing sporophyte remains surrounded by a massive calyptra.

A **mature sporophyte** (Fig. 3.3 B-D) bears an acuminate foot, long seta and a well-developed capsule. Spore tetrads and several long elaters, tapering at both ends (Fig. 3.3 E), are present in the capsule. Elaters bear helical thickenings. The capsule wall is one-celled thick throughout, except in the apical regions (Fig. 3.3D). The jacket of the capsule possesses ornamentation showing unique longitudinal bands, perpendicular to the capsular surface.

Seta becomes very long (8–30 mm) before dehiscence of capsule. The capsule comes out of the calyptra. It dries, shrinks in length and dehisces, thus releasing the spores and elaters. Seta disintegrates and collapses in the dehisced capsule. Spores are unicellular, green and possess chlorophyll. Each spore germinates by forming a globose mass of cells. From the latter, the reclining branches come out to form the primary rhizomatous system. Erect branches develop from this rhizomatous system. Thus develops a young gametophyte bearing leaves on the erect branches.

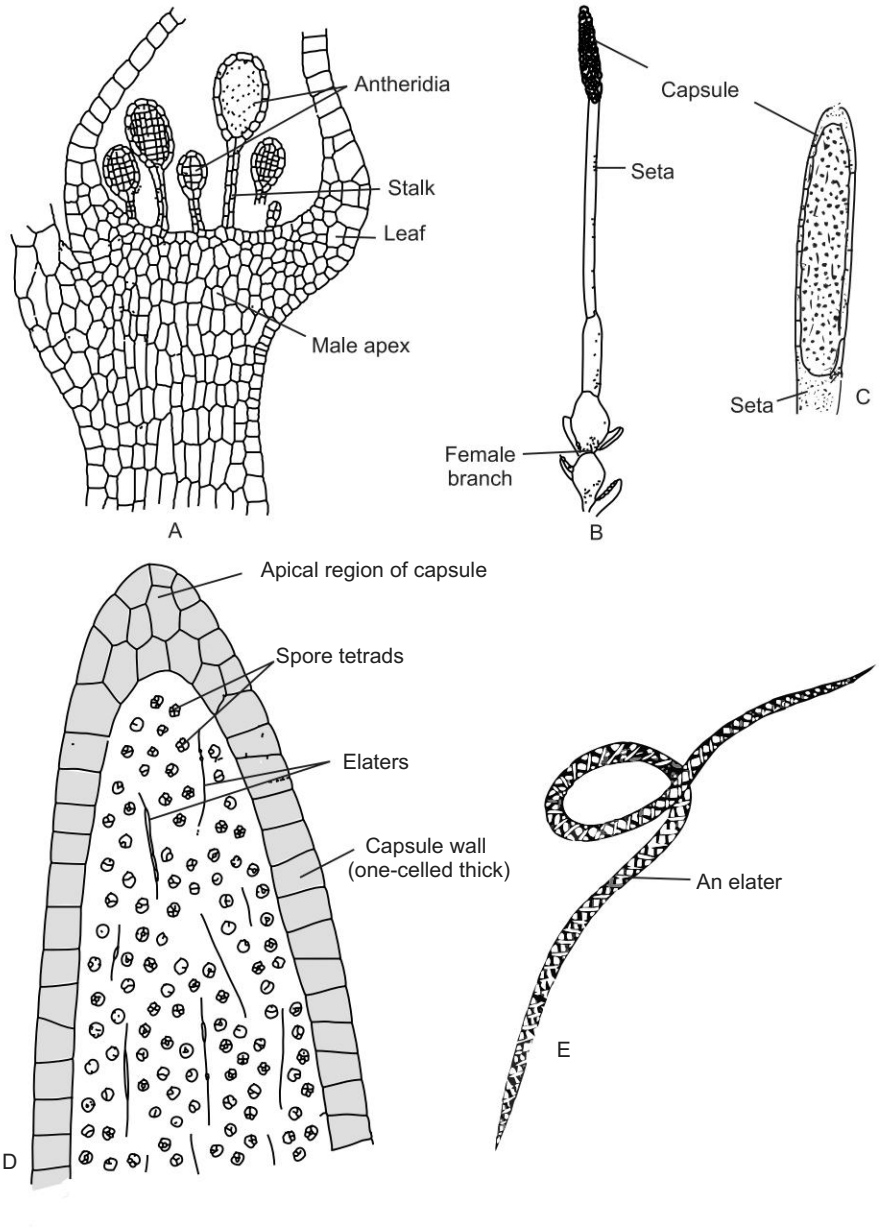


Fig. 3.3 A, Vertical section through the male apex of *Calobryum blumei;* B, Female plant with a mature sporophyte; C-D, Capsule and its upper part enlarged showing spore tetrads, elaters and capsular wall; E, An elater.

TEST YOUR UNDERSTANDING

1. What are Hepaticopsida commonly called?
2. What are Hepaticopsida? Describe in about 50 words.
3. In recent years, some taxonomists have started calling Hepaticopsida as _____.
4. Why do the members of Hepaticopsida commonly called liverworts?
5. Enumerate at least 10 characteristic points of Hepaticopsida.
6. Write a scientific note on the classification of Hepaticopsida in about 250 words.
7. What are Takakiales?
8. How many genera do Takakiales include?
9. Write any five distinguishing points of Takakiales.
10. Give an illustrated account of some details of the life history of *Takakia* in about 500 words.
11. Where is *Takakia* found in India?
12. Describe affinities and phylogenetic importance of *Takakia.*
13. Is *Takakia* a moss? Comment.
14. "*Takakia* is a landmark in the history of bryology". Describe in about 50 words..
15. What are Calobryales? Write at least five of their characteristic features.
16. Calobryales is represented by only two genera, viz. *Calobryum* and _____ .
17. Describe the distribution of Calobryales in about 50 words.
18. Write an account of some life-history details of *Calobryum* and *Haplomitrium.*

4

Hepaticopsida (Jungermanniales)

GENERAL CHARACTERISTICS 4.1

Represented by about 250 genera and more than 9000 species, Jungermanniales represent the largest order of Hepaticopsida. They are worldwide in their distribution and show the following general characteristic features:

1. Plant body is gametophytic, and gametophytes are either thalloid or foliose.
2. Thalloid members contain a simple thallus while the foliose members have a leafy axis with least differentiation of histological tissues.
3. Plant body is attached to any suitable substratum by rhizoids, which are always smooth-walled.
4. Scales are generally absent.
5. Sex organs are represented by antheridia and archegonia, and plants are both monoecious (e.g. *Pellia epiphylla*) as well as dioecious (e.g. *Pellia neesiana)*. The monoecious species are generally protandrous.
6. The antheridia are globose or subglobose.
7. In the process of antheridium development, "the primary antheridial cell does not undergo two centric vertical divisions at right angles to each other, with the result that a quadrant of four daughter cells is not formed" (Parihar, 1987).
8. Archegonial neck is almost as broad as the venter.
9. Archegonial jacket is generally made up of five vertical rows of cells.
10. The sporogonium is divisible into foot, seta and capsule.
11. Foot is somewhat bulbous, seta is highly elongated, and the capsule is globose or round and bears spores and elaters.
12. The capsule is multistratose, i.e. its jacket is made up of two or more layers of cells in thickness.
13. Prior to the first nuclear division, the spore mother cells generally become deeply four-lobed, indicating the position of four spores in each of them.
14. The archesporium ultimately develops into fertile spores and sterile elaters.
15. The capsule generally dehisces by four valves on maturity.

CLASSIFICATION 4.2

Classification of Jungermanniales is still in a very controversial stage, and different bryologists include very different families and different number of genera in this taxa. Verdoorn (1932) divided Jungermanniales in two artificial groups and treated them as two independent orders as under:

1. Jungermanniales Anacrogynae
2. Jungermanniales Acrogynae

Anacrogynae members are those in which archegonia develop on the dorsal surface of the prostrate shoot, and there is no involvement of the apical cells in the formation of archegonia. On the other hand, *Acrogynae* members are those in which archegonia develop at the apex of the shoot, and apical cell is utilised in the formation of the archegonium.

Evans (1939) divided all members of the order Jungermanniales into three sub-orders as under:

1. Haplomitrineae
2. Metzgerineae
3. Jungermannineae

Sub-order Metzgerineae is equivalent to *Jungermanniales Anacrogynae* while the sub-order Jungermannineae is equivalent to *Jungermanniales Acrogynae* of Verdoorn. Campbell (1936), another well-known bryologist, opined that the sub-order Haplomitrineae of Evans has no resemblance with Jungermanniales and should be treated under the order Calobryales.

Parihar (1987) followed Campbell (1936) and treated all members of the order Jungermanniales in two sub-orders as under:

Sub-order 1: Jungermannineae (Jungermanniales Acrogynae)

Sub-order 2: Metzgerineae (Jungermanniales Anacrogynae)

The same classification has been followed in this text.

SUB-ORDER JUNGERMANNINEAE (JUNGERMANNIALES ACROGYNAE) 4.3

General Characteristics

More than 75% of the members of Hepaticopsida belong to the sub-order Jungermannineae of the order Jungermanniales. There are about 220 genera and more than 8500 species in this sub-order. Its members show the following general characteristics:

1. The gametophytic plant body is usually differentiated into stem and leaves, and plants remain attached to the substratum by a large number of rhizoids.
2. A very definite type of segmentation process is initiated by an apical cell, which is pyramidal with three cutting faces.
3. Three rows of leaves are usually present on the stem or axis. Of these three rows, two rows of leaves are laterally placed and made up of leaves of normal size while the third row of leaves is present on the lower side, are smaller-sized and called *amphigastria.* In some genera, the amphigastria are either highly reduced or even absent.
4. Dichotomous branching of the axis is never present.
5. The antheridia develop, either singly or in small groups, in the axils of modified leaves.

6. The archegonia develop at the apices of the stem or branches.
7. The apical cell is utilised in the formation of the last-formed archegonium. Due to this, the vegetative growth of the axis or a branch stops after the formation of the last archegonium.
8. Fertilization usually takes place through the agency of water, present in the capillary spaces existing between the plants and overlapping leaf surfaces.
9. The sporogonia are terminal on the branches or axis. A mature sporogonium usually consists of an indistinct foot, short seta and a globose capsule.

The sub-order Jungermannineae contains 17 families, of which only two (Porellaceae and Frullaniaceae) are briefly discussed here with some life-history details of *Porella* of Porellaceae and *Frullania* of Frullaniaceae.

PORELLACEAE 4.4

Porellaceae is also known by the name **Madothecaceae**. It shows the following major features:

1. The rhizoids form tufts at the bases of the amphigastria.
2. The leaves show *incubous arrangement*, i.e. if seen from the above, the forward edge of each leaf overlaps the hind edge of the leaf immediately next above to it on the same side.
3. The lobule or postical lobe of the leaf is quite distinct.
4. The amphigastria or underleaves are large-sized.
5. The postical lobes or lobules are replaced by lateral branches.
6. The perianth is bilabiate, well-developed, inflated, and contains almost compressed mouth.
7. At the time of dehiscence, the valves split about halfway down the capsule.

The life history of *Porella* is discussed here.

PORELLA 4.5

4.5.1 Systematic Position

Division—Bryophyta
Class—Hepaticopsida
Subclass—Jungermanniae
Order—Jungermanniales
Sub-order—Jungermannineae (Jungermanniales acrogynae)
Family—Porellaceae (=Madothecaceae)
Genus—*Porella L.* (=*Madotheca* Dum.)

4.5.2 Distribution and Habitat

Over 180 species of *Porella* have so far been reported, of which most occur in tropical regions and only a few species are found in temperate regions of the world. About 35 species have been reported from India, mostly in the Himalayan regions and a few also in south India. Plants grow on moist shady rocks, stones and also on the bark of the trees. A few species grow on moist soil. *P. platyphylla*, a robust liverwort (Watson, 1967), occurring commonly in limestone regions of Europe, North America and several Asian countries, is the most widely distributed species.

Some of the common Indian species along with the regions of their common occurrence are *Porella gollani* (Mussoorie, Garhwal), *P. plumosa* (Mussoorie, Chamba, Dalhousie), *P. variabilis* (Mussoorie), *P. macroloba* (Kumaon, Kullu valley), *P. angusta* (Simla, Kashmir), *P. hastata* (Mussoorie), *P. densiramea* (Chamba), *P. densifolia* (Kumaon) and *P. boreilli* (Kashmir).

GAMETOPHYTIC PHASE

4.5.3 External Morphology of Gametophyte

The plant body is gametophytic, and the gametophytes are large, flat, compact, dorsiventral, well-branched and foliose structures, divisible into rhizoids, axis and leaves (Fig. 4.1 A-C). The plants reach up to 15 cm or more in length.

The axis or stem is prostrate, dorsiventrally flattened and bi- or tri-pinnately branched. Each branch of the axis remains covered by three rows of leaves, of which two rows of larger leaves are present on the dorsal side, while the third row of smaller leaves is present on the ventral side of the axis. The smaller leaves are called **amphigastria**. The larger leaves of the dorsal side of the axis are bilobed, and the lobes are unequal-sized. The upper, oval-shaped lobe of each larger leaf is large and called the **antical lobe**, while the lower smaller lobe is called the **postical lobe**. The postical lobe contains

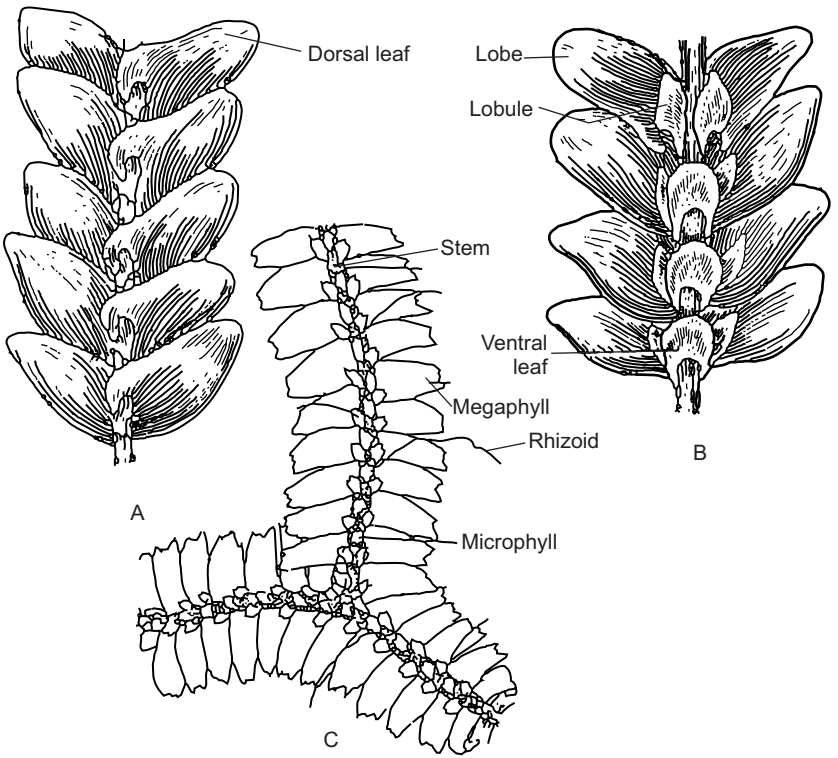


Fig. 4.1 A-C, External features of the gametophyte of *Porella*. A, Dorsal view of a branch of *P. platycarpa*; B, Ventral view of a branch of *P. platycarpa*; C, A part of the gametophytic plant body of *P. gollani*

an acute apex and appears like a separate leaf. The posterior margin of the leaf underlines the anterior margin of the older leaf and this arrangement is called **incubous type**. The amphigastria resemble the postical lobes of the larger leaves.

A large number of the smooth-walled rhizoids arise on the lower side of the stem. The plants remain closely pressed to the moist substratum, and the absorption of water takes place directly through the cells of stem and leaves. The main function of rhizoids is thus the anchorage of the plants to the substratum.

4.5.4 Anatomy of Axis

There is little or no differentiation of tissues in the young axis. Old stems show some differentiation of outer cortical cells and central medullary cells. Usually the cells of the cortex are small and thick-walled while that of the medulla are large and thin-walled. Almost all cells are parenchymatous.

4.5.5 Anatomy of Leaf

Internally, the leaves are very simple in structure, consisting of a single layer of isodiametric, polygonal cells, each containing abundant chloroplasts. There is no midrib. Each cell in *P. acutifolia* contains 7–19 oil bodies (Udar, 1971).

4.5.6 Apical Growth

It takes place by the activity of a tetrahedral apical cell with three cutting faces. The apical cell is pyramidal in shape, and it regularly cuts three sets of segments, of which two sets are dorsal and lateral while the third set is ventral. Each segment develops into a leaf and a part of the stem.

4.5.7 Vegetative Reproduction

Plants have been reported to reproduce vegetatively by *fragmentation*, especially when they grow under humid conditions. Schiffner described the presence of discoid *gemmae* as the means of vegetative reproduction in *Porella rotundifolia* growing in Brazil, but this report has been denied by Degenkolbe (1938). No other authentic report of vegetative reproduction is available in *Porella*.

4.5.8 Sexual Reproduction

The sexual reproduction is oogamous. *Porella* is dioecious. The male plants are smaller in size than the females. The antheridial branches arise more or less at right angles to the main axis (Fig. 4.2). Usually, the female plants are larger and bear the archegonial branches which are shorter than that of antheridial branches.

4.5.9 The Male or Antheridial Branch

Usually, the antheridial branches arise at right angles to the main axis and have more compactly arranged leaves than the vegetative branches. The leaves of the antheridial branches are closely imbricated and called **'bracts**'. A single antheridium develops in the axil of each bract of the male branch.

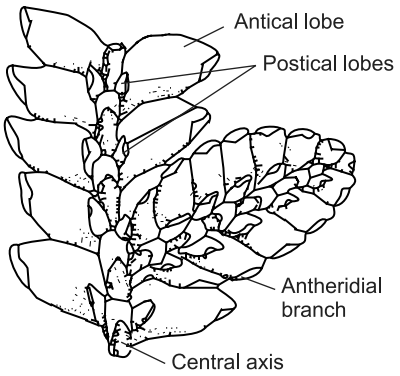


Fig. 4.2 A part of the leafy shoot of *Porella platycarpa* having one antheridial branch in vertical view

1. Development of Antheridium

The development of antheridium in *Porella* resembles with *Pellia* and other members of Jungermanniales, and a general account of the same is given below:

A superficial dorsal cell starts to function as an ***antheridial initial***. It becomes papillate and divides by a transverse wall into an **outer cell** and a **basal cell** (Fig. 4.3 A,B). The outer cell remains protruded above the general surface of the thallus while the basal cell usually remains embedded in the thallus tissue. The outer cell divides transversely into an upper primary **antheridial cell** and a lower **primary stalk cell** (Fig. 4.3C).

The stalk of the antheridium develops from the primary stalk cell. The primary antheridial cell divides by a median vertical division (Fig. 4.3D) to form two equal-sized daughter cells. Each of these daughter cells divides by a somewhat periclinal division forming two unequal cells (Fig. 4.3F). The smaller of these two unequal cells represents the **first-jacket initial** while the larger one divides by another periclinal division to form an outer **second-jacket initial** and an inner **primary androgonial cell** (Fig. 4.3E). Two triangular, centrally-located primary androgonial cells surrounded by four jacket initials are seen in the cross section of the young antheridium at this stage (Fig. 4.3G). Both the primary androgonial cells divide by repeated transverse and vertical divisions to form a large number to **androgonial cells** (Fig. 4.3 H-J), of which the last generation is of the **androcyte mother cells**. Repeated anticlinal divisions in the jacket initials give rise to a single-layered sterile **jacket**. Each androcyte mother cell divides diagonally to form two androcytes, of which each metamorphoses into a uninucleate and biflagellate **antherozoid**.

2. Mature Antheridium

The mature antheridium has a globular body and a long stalk (Fig. 4.4). The stalk consists of two rows of cells while the body remains surrounded by a sterile jacket. The jacket is single-layered in the upper part while it is bi- to tri-layered at the base. The jacket encloses the androcytes, which soon metamorphose into biflagellate and coiled antherozoids.

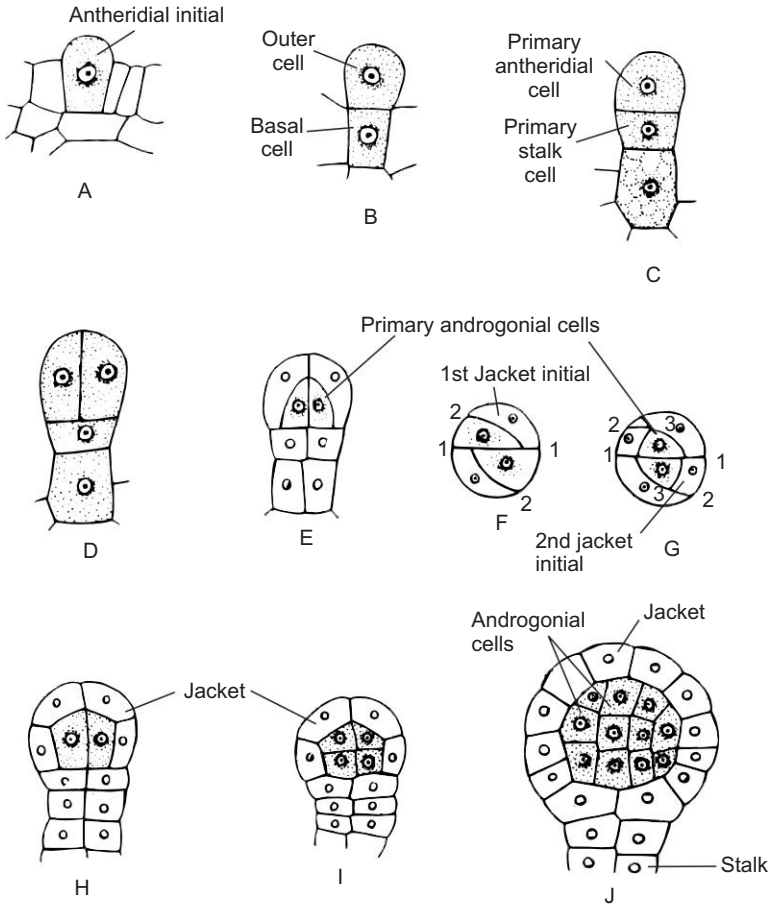


Fig. 4.3 A-J Development of antheridium in *Porella* and other Jungermanniales

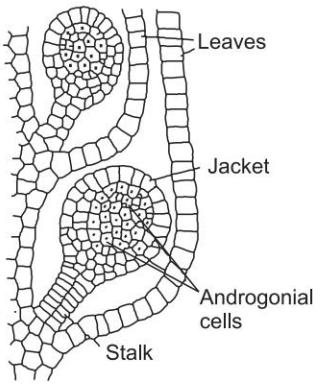


Fig. 4.4 A part of an antheridial branch of *Porella* bearing antheridia in the axil of leaves

3. Dehiscence of Antheridium

One-celled-thick distal region of the jacket of the antheridium is thinner, and when it is near to the water, it bursts open into a number of irregular lobes. These lobes curl back strongly. Because of this, the entire mass of androcytes is forced out into the water. This mass of androcytes along with several antherozoids soon ruptures, and thus the antherozoids are liberated.

4.5.10 The Female or Archegonial Branch

The archegonial branches are smaller than the antheridial branches, and are hence much less distinct. At the tip of these female branches are present the archegonia. The first two or three leaves in each archegonial branch are sterile and do not bear archegonia. When young, the first few archegonia develop in strict acropetal succession. However, ultimately the apical cell of the archegonial branch starts to function as an archegonial initial. Any further growth of the archegonial branch is thus stopped.

1. Development of Archegonium

In the development of the archegonia also, *Porella* shows strict resemblance with *Pellia* and other Jungermanniales, and a general account of the same is given below:

The development of archegonium starts from a single superficial cell, which soon becomes papillate and starts to function as an **archegonial initial** (Fig. 4.5A). It first divides transversely into a lower basal cell and an upper outer cell (Fig. 4.5B). The basal cell divides transversely into a stalk initial and a **basal cell** (Fig. 4.5C). The outer cell divides by three intersecting vertical divisions, resulting ultimately into a central **primary axial cell** surrounded by three peripheral initials (Fig. 4.5 D-F and D_1-F_1). One of these three peripheral initials is small and does not divide by any vertical division while the remaining two peripheral initials divide by vertical divisions. This results in the formation of five **jacket initials** (Fig. 4.5 G_1).

Each jacket initial divides transversely to form the lower **venter initial** and upper **neck initial** (Fig. 4.5G). The neck initials divide only transversely and form a neck consisting of five vertical rows of cells. The venter initials divide several times to form the globular **venter** of the archegonium.

The primary axial cell (Fig. 4.5 E) divides by a transverse division to form an upper **primary cover cell** and a lower **central cell** (Fig. 4.5F). Yet another transverse division in the central cell divides it into an upper **primary neck canal cell** and a **lower primary ventral cell**. The primary neck canal cell divides, redivides transversely and gives rise to 6–8 **neck canal cells**, while the primary ventral cell divides transversely only once and gives rise to an upper **ventral canal cell** and a lower **egg** (Fig. 4.5 I).

The primary cover cell (Fig. 4.5F) divides by two vertical divisions at right angles to one another to form four cover cells (Fig. 4.5 G).

2. Mature Archegonium

The mature archegonium (Fig. 4.5I) contains a long neck and a slightly globular venter. The neck consists of five vertical rows of cells and encloses 6 to 8 neck canal cells. The wall of the venter is bi-layered and encloses a ventral canal cell and an egg.

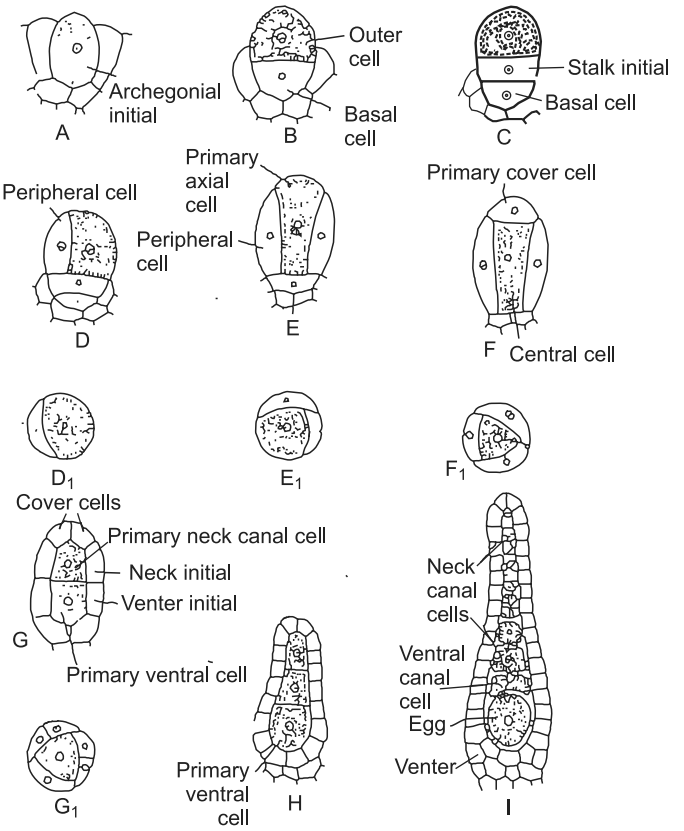


Fig. 4.5 A-I Generalized process of archegonium development in *Porella* and other Jungermanniales (Note D1-G1, which are the cross sections)

4.5.11 Fertilization

The fertilization takes place with the help of water, present usually in the fine spaces existing between the closely growing male and female plants or in between the overlapping leaf surfaces of two plants. Male and female plants in *Porella* grow in very dense, compact patches. The antherozoids from the antheridia reach up to the archegonia of female plants with the help of water. The two gametes fuse and form a diploid zygote.

SPOROPHYTIC PHASE

4.5.12 Development of the Sporogonium

The zygote starts to increase in size and almost fills the entire cavity of the venter. Soon, it divides transversely into an upper **epibasal cell** and a lower **hypobasal cell** (Fig. 4.6 A,B). One more transverse division in the epibasal cell makes the three-celled stage of the young embryo (Fig. 4.6 C). There is no further division in the hypobasal cell and it functions as a **suspensor** (Fig. 4.6D, E) or **haustorium**. The

derivatives of the epibasal cell are responsible for the formation of the whole sporogonium. The upper two cells of the three-celled embryo divide first by transverse and then by vertical divisions (Fig. 4.6D, E) to form a multicellular structure, in which it is very difficult to draw a demarcation line between the capsule and the seta.

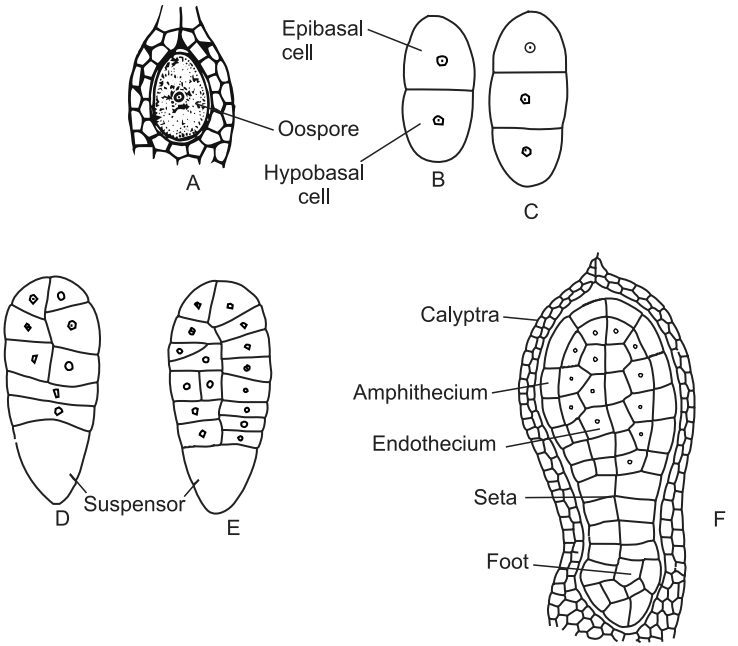


Fig. 4.6 A-F Development of the sporogonium in *Porella* bolanderi

The terminal segments of this multicellular embryo divide by a periclinal division to form an outer layer of **amphithecium** and an inner tissue of **endothecium** (Fig. 4.6F). The amphithecium divides by a few periclinal divisions to form a 3- to 4-layered jacket of the capsule. The archesporium is endothecial in origin in *Porella*. The cells of the sporogenous tissue get arranged in distinct rows radiating from the base of the capsule. Some of the sporogenous cells show no further division and start to function as young spore mother cells, while other sporogenous cells elongate and develop into young elaters. Soon, the spore mother cells become four-lobed. Their diploid nucleus divides reductionally to form four haploid nuclei, of which one enters into each lobe of the spore mother cell. The infolding of the walls of the four-lobed spore mother cell takes place and four haploid spores are formed from a spore mother cell. The **elaters** are short, have tapering ends, and each contains one or two spiral thickenings (Fig. 4.8 A).

The **seta** is present in between the capsule and the foot. It is short and gradually merges into the basal part of the capsule.

The **foot** is present at the base of the young sporogonium. It is bulbous and grows downward into the tissue of the female branch. A short tubelike structure, formed from the outer tissue of the stem of the female branch, encloses the foot as well as the seta.

Three definite coverings or envelopes surround the sporogonium when it is young. These are **calyptra**, **perianth** and **involucre**. The calyptra is multilayered and surrounds the capsule completely

in its young stages. The perianth develops by the fusion of two uppermost bracts. The enlarged bracts, covering the base of the perianth, form the involucre.

4.5.13 Mature Sporogonium

The mature sporogonium (Fig. 4.7) consists of foot, seta and capsule. The foot is less conspicuous, globular or oval and remains embedded in the tissue of the stem of the archegonial branch. The seta is short and present in between the foot and the capsule. The capsule is surrounded by a 3- to 4-celled thick wall, which encloses fertile spores and sterile elaters (Fig. 4.8). Three definite envelopes (calyptra, perianth and involucre) also surround the sporogonium.

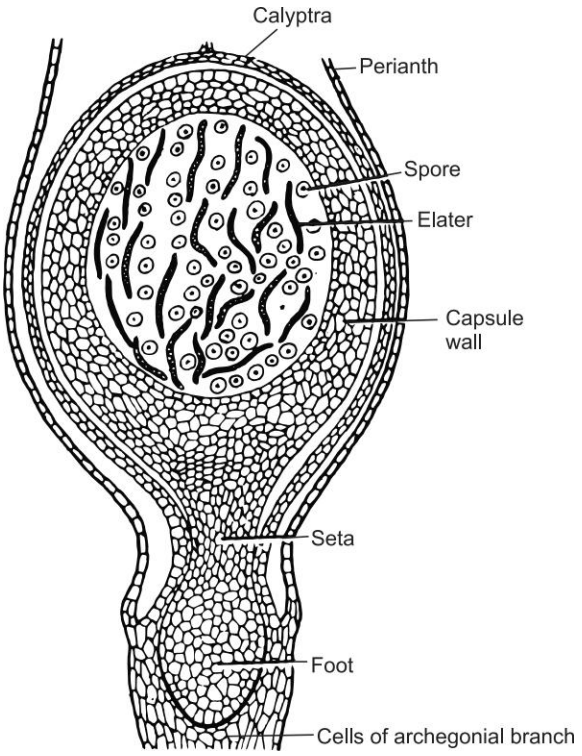


Fig. 4.7 L.S. of a mature sporogonium of *Porella* spp.

4.5.14 Dehiscence of Capsule and Dispersal of Spores

In mature sporogonium, the seta elongates, and because of this elongation, the capsule pushes and ruptures the outer protective coverings of calyptra, perianth and involucre. The capsule opens by four valves, and through this opening the spores are dispersed.

YOUNG GAMETOPHYTE

4.5.15 Spores

The spores are round, spherical or globular bodies varying from 0.03 to 0.05 mm in diameter. The wall of each spore is bilayered, of which the outer layer is smooth, papillose or echinate and called **exospore**, while the inner layer is smooth and called **endospore**. Sometimes, the remnants from the old spore mother cells also get deposited on the exospore in the form of a third layer called **outer exospore** or **perinium**. The spores are uninucleate.

4.5.16 Development of Young Gametophyte

The spores start dividing while they are still inside the undehisced capsule. Some of them become multicellular even within the capsule wall. With the help of some transverse and vertical divisions in the spore, a multicellular protonema is resulted (Fig. 4.8 B-F). Soon, an apical cell of the shoot becomes differentiated in this multicellular protonema. A few rhizoids also develop at a slightly later stage.

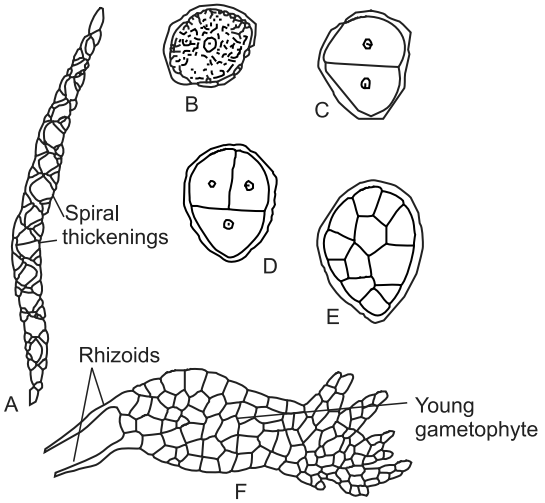


Fig. 4.8 A-F, *Porella platyphylla*. A, An elater; B-E, Showing germination of spore; F, Multicellular thalloid structure which develops into new gametophyte

FRULLANIACEAE 4.6

General Characteristics

Frullaniaceae includes only three genera (*Frullania, Jubula* and *Neohattoria),* and some of the general characteristics of this family are listed below:

1. Plants are usually large-sized and predominantly reddish brown or deep green in colour. Sometimes they are purplish brown in colour.

2. The stem is usually prostrate and pinnately or bipinnately branched.
3. Three rows of leaves are present on the stem, of which two rows are of lateral leaves and one row of underleaves called *amphigastria*.
4. Characteristic *Frullania*-type of branches are present in the majority of members. In this type, a "branch develops from the ventral half of the lateral segment replacing the lobule of the leaf. The lateral leaves are complicate-bilobed and each leaf is divided into a flat antical lobe and a cylindrical saccate or postical lobe (lobule)" (Parihar, 1987).
5. Usually, the lobule or postical lobe of the leaf is divided into two parts, viz. *stylus* and lobule proper.
6. The amphigastria or underleaves, are usually bilobed.
7. The tuft of rhizoids is present usually at the base or middle of the amphigastria.
8. Archegonia vary from 2 to 12 in a group.

Some life-history details of only *Frullania* are discussed here.

FRULLANIA 4.7

Predominantly a tropical genus, *Frullania* is represented by more than 700 species. Many of these species also occur luxuriantly in subtropical regions of the world. More than 40 species of *Frullania* have been reported from India. It grows commonly on wet grounds and generally on moist rocks as a lithophyte. Plants are found to form extensive mats on tree trunks, rocks, etc.

Plant body (Fig. 4.9A) is gametophytic, and the gametophytes are reddish-brown or blackish in colour. Each plant is differentiated into a well-branched prostrate, stemlike central axis possessing many leaves. The axis is pinnately or bipinnately branched. Many smooth-walled, unicellular and unbranched rhizoids are present in tufts at the base of the axis or middle of amphigastria (underleaves). Rhizoids keep the thallus attached to the substratum. The leaves are attached on the axis or stem in three rows i.e. two rows of lateral leaves and one row of amphigastria or underleaves. Each leaf contains a large antical lobe and a small postical lobe or lobule. The antical lobe of the lateral leaf is the well-expanded part. It is sub-orbicular or obliquely ovate. Its margin is entire. The postical lobe or lobule is cucculate, galeate or saccate, and either remains open or forms a water sac. *Stylus* a short subulate process, is present on the postical lobe. It is actually situated between the stem and the postical lobe. The amphigastria or underleaves are round, notched or deeply-lobed and smaller than that of the lateral leaves. The amphigastria, together with stylus, form capillary spaces which retain water. In the female plants or branches, the archegonial group is surrounded by 2 to 5 pairs of perichaetial bracts, of which the uppermost bracts are laterally fused to form the perianth. The small lobe of the leaves forms a water sac or pitcher. The function of the water sacs is to hold a part of the rainwater, which would otherwise be lost. The stylus, underleaves and lateral leaves also form capillary spaces which retain water.

The **anatomy of the stem** (Fig. 4.9D) exhibits very little cell specialisation or tissue differentiation. It is circular in outline. The epidermis is not well-defined and the cortical and central medullary zones can be recognised. The cortical region is peripherally located and its cells are smaller than that of the centrally-located medullary zone. Cortical-region cells are pigmented in the older portion of the axis. The medullary region cells are thin, colourless and quite large. Conducting tissue is absent.

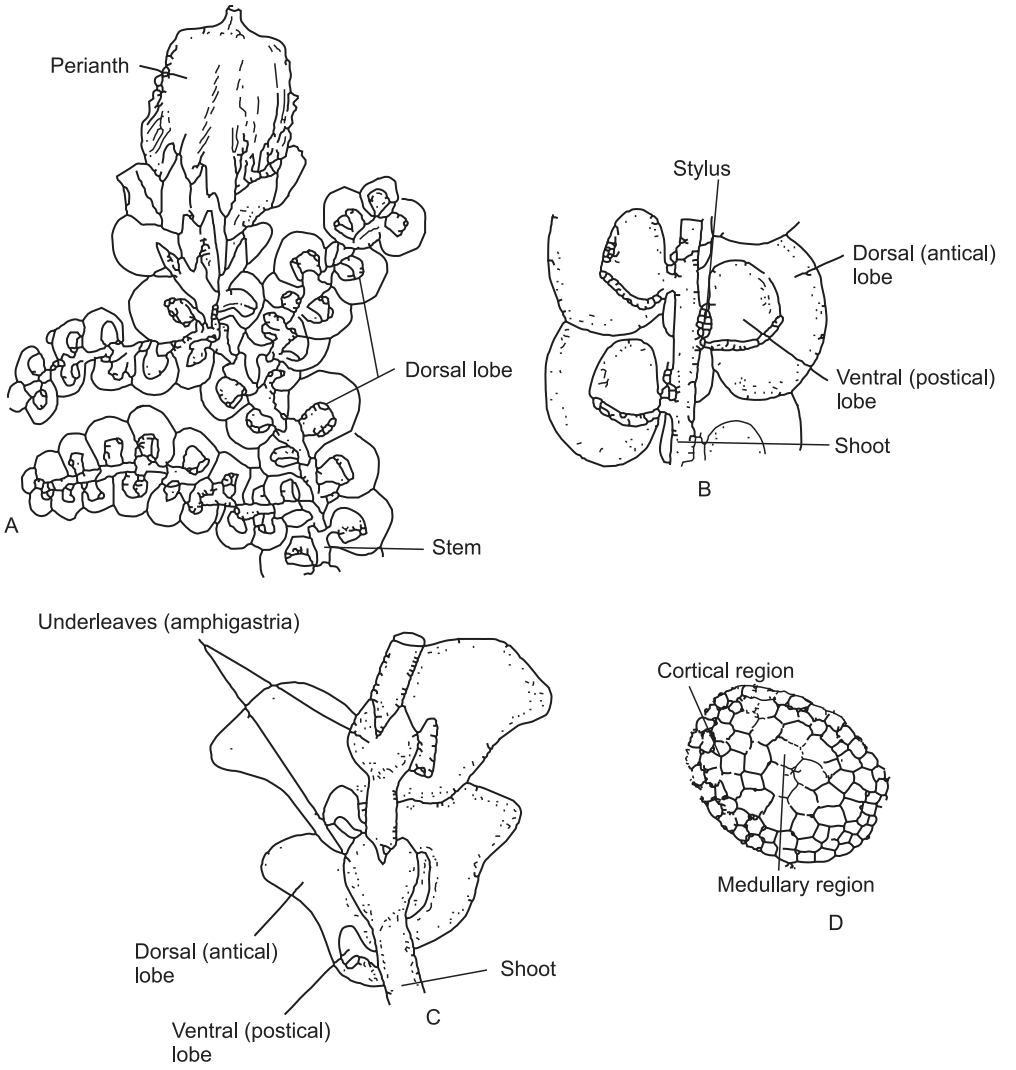


Fig. 4.9 *Frullania dilatata.* A, A part of female gametophyte showing perianth; B, Ventral view of the shoot with underleaves removed; C, A part of the shoot from below (*F.squarrosa*); D, Cross section of axis

Apical growth takes place by a tetrahedral apical cell with three cutting faces. Three sets of segments are cut off from this apical cell, of which two sets are dorsolateral while the third set is ventral. From each of these sets develop a leaf and a portion of stem subtending it. The young primordium of each dorsolateral leaf divides into two parts. The upper part of this young leaf primordium develops faster, bends over the growing point and forms the leaf lobe. The lower smaller half develops into a hollow structure which matures or develops into a pitcher or water sac.

Vegetative reproduction takes place by (i) death and decay of the older parts, leaving the ordinary branches to develop into new plants; and (ii) gemmae, which are the multicellular, nodular outgrowths, which are discoid to irregular in outline and develop into new plants on being detached.

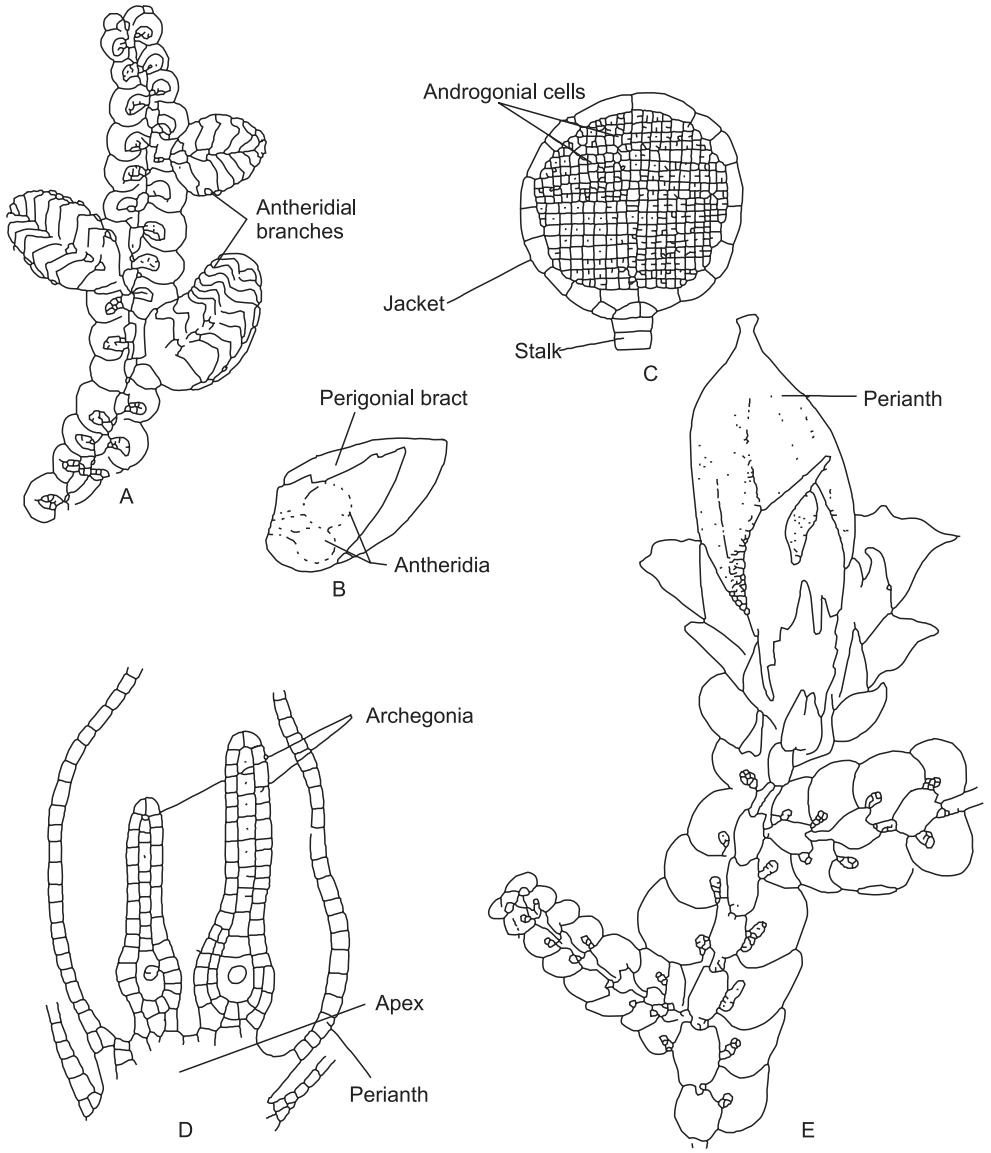


Fig. 4.10 *Frullania dilatata* A-B, Male plant bearing antheridial branches (A) and a male branch bearing antheridia (B); C, A mature antheridium; D, LS perianth showing two archegonia; E, Part of the plant showing perianth.

Sexual reproduction is oogamous. Both dioecious as well as monoecious species are present in *Frullania.* Antheridia and archegonia develop on different branches in monoecious species.

Antheridia (Fig. 4.10 A-B) develop in the axils of perigonial bracts of which two or more pairs develop on short lateral branches. These bracts are arranged in a densely intricate manner. Usually, two antheridia develop in the axis of each bract.

The **development of the antheridium** follows the same pattern as that of *Porella* (Fig. 4.3 A-J) and Jungermanniales and has been described in detail under Article 4.5.9(1). The *mature antheridium* is a globose or spherical body (Fig. 4.10 C) with a slender stalk of two rows of cells. The globose body of the antheridium is differentiated into a centrally-located mass of androgonial cells surrounded by a sterile layer of jacket. Each androgonial cell divides diagonally into two androcytes. The protoplast of each androcyte metamorphoses into a typically biflagellate antherozoid.

Clusters of *archegonia* (Fig. 4.10 D-E) occur at the apices of short lateral branches of the female branch in monoecious species and female plant in dioecious species of *Frullania.* Each cluster contains two to four archegonia (Fig. 4.10 D). The leaves associated with archegonia on the female branch are called perichaetial bracts. Two to five pairs of perichaetial bracts surround each cluster of archegonia. Each perichaetial bract is bilobed or dentate and larger than the foliage leaves. The bracts situated in the upper part of the female branch are laterally fused and form the perianth (Fig. 4.10E). The perianth is inversely heart-shaped. It remains contracted to form a tubular mouth. The development of archegonium (Fig. 4.5 A-I) follows the same pattern as that of *Porella* and other Jungermanniales and has been described in detail under Article 4.5.10(1). The mature archegonium is a flask-shaped body containing a basal swollen venter and long narrow neck . A small egg cell and a ventral canal cell are present in the region of the venter. Five vertical rows of neck cells form the neck. They surround an axial row of as much as eight neck canal cells.

Fertilization takes place as usual with the help of water and follows the same pattern as described for *Porella* (Article 4.5.11). The two gametes fuse and form a diploid zygote.

The diploid zygote divides and redivides to form a sporophyte. First, it divides by a transverse wall forming an epibasal and a hypobasal cell (Fig. 4.11A). The epibasal cell divides by a transverse wall and the hypobasal cell by a vertical wall to form a four-celled stage (Fig. 4.11B). Thus formed two upper cells divide by two vertical walls at right angles to one another. Two lower cells (hypobasal cells) divide by another vertical division at right angles to the first one. The so-formed young embryo now consists of three tiers, each tier made up of four cells. Of these three tiers the upper tier develops into capsule, the middle tier into seta, and the lowermost tier develops into the foot of the mature sporophyte. Repeated irregular divisions (Fig. 4.11 C-E) take place in the lowermost tier which ultimately develops into an absorptive organ called foot (Fig. 4.11E). Its cells grow into papillae. The cells of the middle tier divide by longitudinal divisions to form seta. The cells of the uppermost tier are responsible for the formation of capsule. They divide by periclinal division to form four outer or peripheral cells representing amphithecium and four central or axial cells representing the endothecium.

The archesporium (Fig. 4.11 E,F) is endothecial in origin. The endothecium cells divide only longitudinally to form as many as two hundred or more cells forming a mass of cells. These cells differentiate into fertile sporocyte-producing cells and sterile elater-producing cells (Fig. 4.11H). Sporocyte-producing cells form spore mother cells (Fig. 4.11I) by repeated transverse divisions. The elater-producing cells remain undivided and grow into long and narrow elaters with a single broad spiral band. Round or cubical spore mother cells and long elaters are thus present in regular alternate bands (Fig. 4.11I) The capsule wall contains two layers which develop from the amphithecium. The archegonial venter develops into calyptra which surrounds the young sporogonium. The perianth also encloses the sporogonium along with the calyptra (Fig. 4.12A).

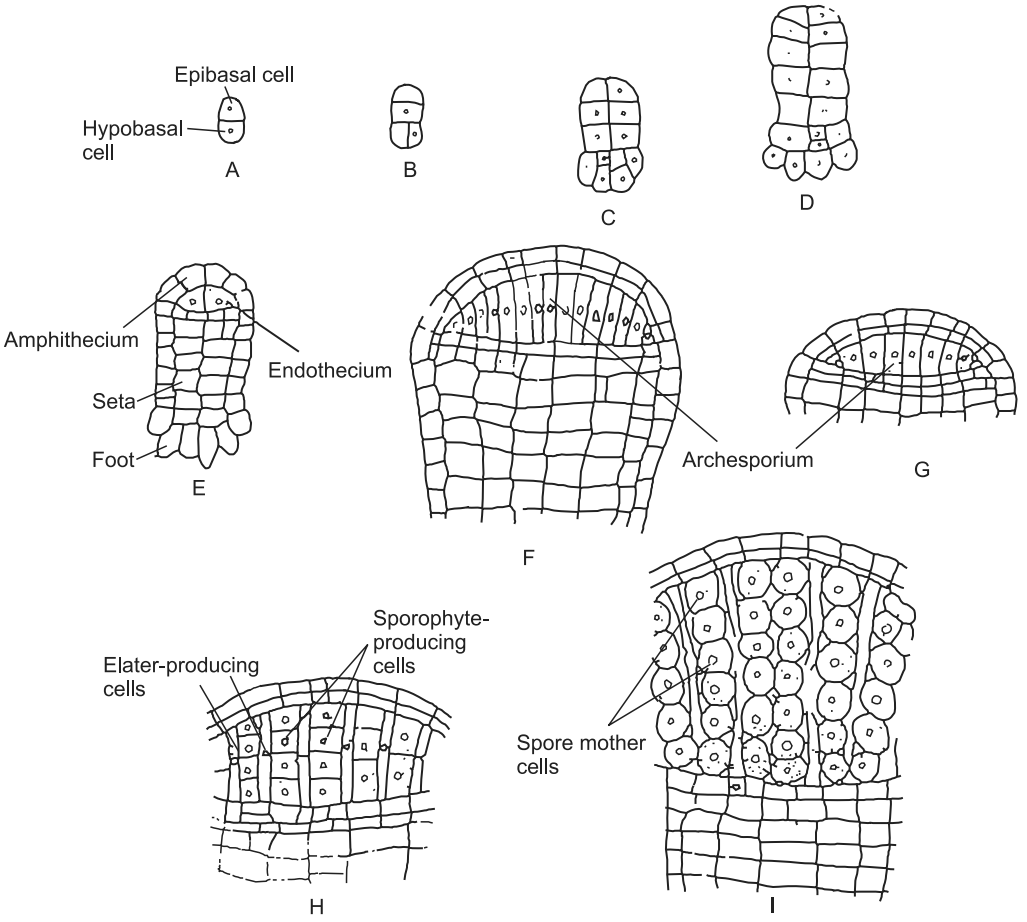


Fig. 4.11 A-I Showing stages of embryogeny and development of young sporophyte in *Frullania dilatata*.

Mature sporophyte *of Frullania* consists of a blunt foot, short seta and a globose capsule. The foot remains embedded in the tissues of the female branch and functions as an absorbing organ. The seta is very short and attains a length of only about 1mm. The mature seta is about 8 to 9-cells thick and supports the capsule at its distal end. The capsule is globose and remains surrounded by a two-layered wall. Their walls are sclerified. The cells of the outer layer contain rodlike fibres, particularly at the corners of their lateral wall. The walls of the cells of the inner layer of capsule possess irregular network of thickening fibres. The capsule wall encloses many spores and elaters. The elaters extend from roof to the floor of the globular capsule. The elaters are flattened, nonspiral and each possesses a trumpet-shaped lower end. The spores are round or oblong in shape. Each spore is uninucleate and remains surrounded by a two-layered wall, of which the outer layer is rough or tuberculate and the inner layer is generally smooth. Many chloroplasts are also present in the spore.

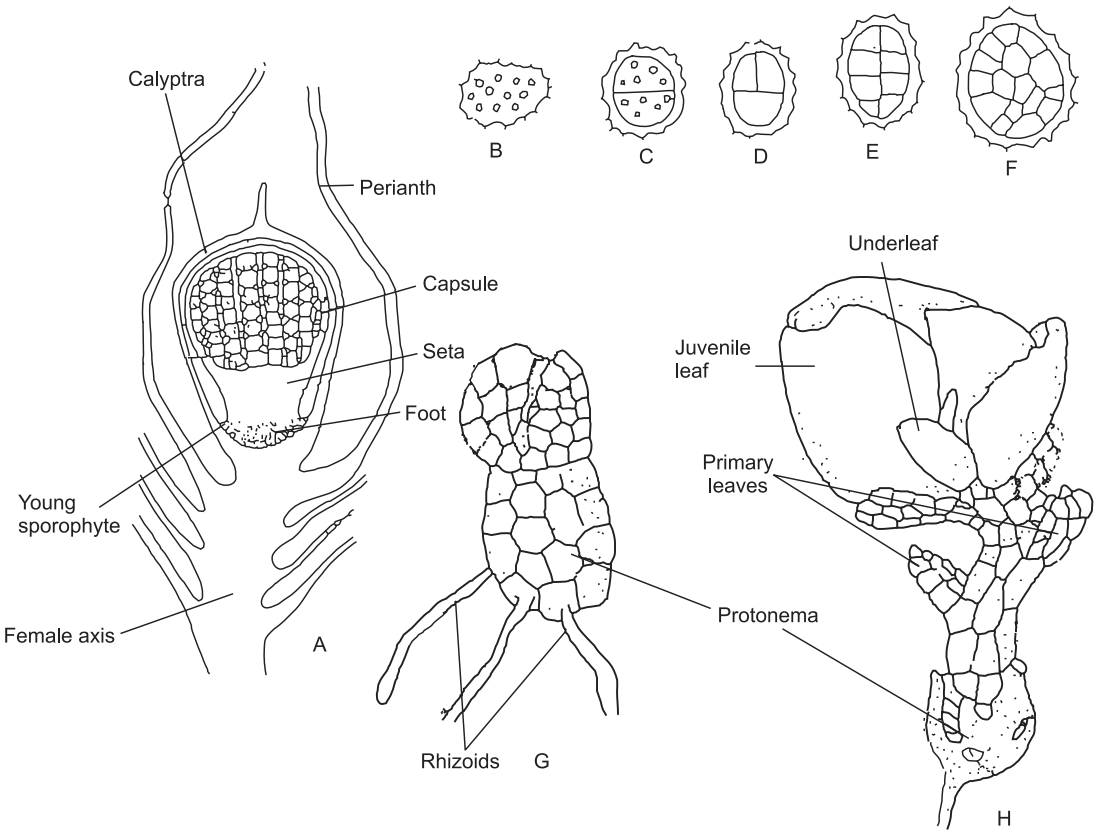


Fig. 4.12 *Frullania dilatata.* A, Young sporophyte; B-H, Various stages of the development of gametophyte.

At the time of **dehiscence**, the capsule wall splits suddenly into four valves. Spores are flicked away in the air by the sudden movements of the contracting elaters.

Each spore germinates into a young gametophyte. Germination of spore starts while it is still inside the capsule. The first division of the spore is transverse (Fig. 4.12 B-C) forming two cells, of which the upper cell now divides by a vertical division (Fig. 4.12 D). Divisions in all the three planes now take place, resulting into a young globose protonema of 50–60 cells (Fig. 4.12 E-F). Few rhizoids now develop from the young multicellular sporeling (Fig. 4.12 G). Primary leaves followed by the development of juvenile leaf and underleaf now start developing from the young gametophyte (Fig. 4.12 H).

SUB-ORDER METZGERINEAE (JUNGERMANNIALES ANACROGYNAE) 4.8

4.8.1 General Characteristics

About 25 genera and more than 600 species constitute the sub-order Metzgerineae. Its members show the following general characteristics:

1. Gametophytic plant body is usually thalloid, and rarely is differentiated into stem and leaves.
2. Usually, the gametophtes are dorsiventral and prostrate.
3. Being basically thalloid, with some also having leafy thalli, and rarely differentiated into stem and leaves, members of Metzgerineae are commonly named ***multiform-thallose-hepatics.***
4. Sex organs remain scattered on the dorsal surface of the thalloid plant body. But they are also sometimes present on highly reduced specialised branches.
5. Apical cell cuts off young segments which develop into archegonia. Differing from Jungermannineae, the apical cell in these members is not utilised in the formation of an archegonium.
6. The fully developed sporophyte is dorsal in position, and it is located some distance behind the apex of the plant body.
7. The wall of the capsule is not strictly two-layered. It is 2-5 layers thick.

4.8.2 Classification

Parihar (1987) followed Evans (1939) and mentioned that the sub-order Metzgerineae includes eight families, viz. Treubiaceae, Fossombroniaceae, Pelliaceae, Blasiaceae, Pallaviniaceae, Metzgeriaceae, Riccardiaceae and Monocleaceae. But, Rashid (1998) mentioned that Metzgeriales (multiple thallose hepatics) include as many as 12 recognised families.

Only three genera, namely *Pellia* of Pelliaceae, *Riccardia* of Riccardiaceae and *Fossombronia* of Fossombroniaceae are described in this text.

PELLIACEAE 4.9

Some characteristics of Pelliaceae are listed below:

1. Plant body is thalloid, often with lobed or sinuous margins.
2. Sex organs (antheridia and archegonia) remain scattered on the dorsal surface of the thalloid plant body.
3. Capsule is a globular or oval body.
4. A basal elaterophore is present in the capsule.

PELLIA 4.10

4.10.1 Systematic Position

Division—Bryophyta
Class—Hepaticopsida
Order—Jungermanniales

Sub-order—Metzgerineae (Jungermanniales Anacrogynae)
Family—Pelliaceae
Genus—*Pellia*

4.10.2 Distribution and Habitat

Pellia is a thalloid liverwort spread widely in north temperate regions of the world. It is represented by four species, namely *P. epiphylla, P. endiviaefolia, P. neesiana* and *P . columbiana.* Jones (1958) recognised a fifth species, *P. borealis.* Three of its species occur widely in the Himalayas, including *P. epiphylla* and *P. endiviaefolia* according to Kashyap (1929). *P. epiphylla* is quite common in Sikkim, Darjeeling and eastern Himalayas while *P. endiviaefolia* occurs commonly in western Himalayas and Kumaon regions.

Parihar (1987) mentioned that it was Raddi who formed this genus and named it *Pellia* "in honour of Leopoldo Pelli-Fabbroni, a lawyer of Florence, Italy, and a friend of Raddi".

Pellia loves to grow in moist shady places, particularly by the sides of moist rocks, ditches, streams and other similar surroundings. It also sometimes grows submerged under flowing water.

4.10.3 External Morphology of Gametophyte

Plant body is gametophytic, thalloid, prostrate, thin, dorsiventral and appears to be dichotomously branched. Margins of thallus are sinuous (Fig. 4.13 A-C). A well-defined midrib is present on the

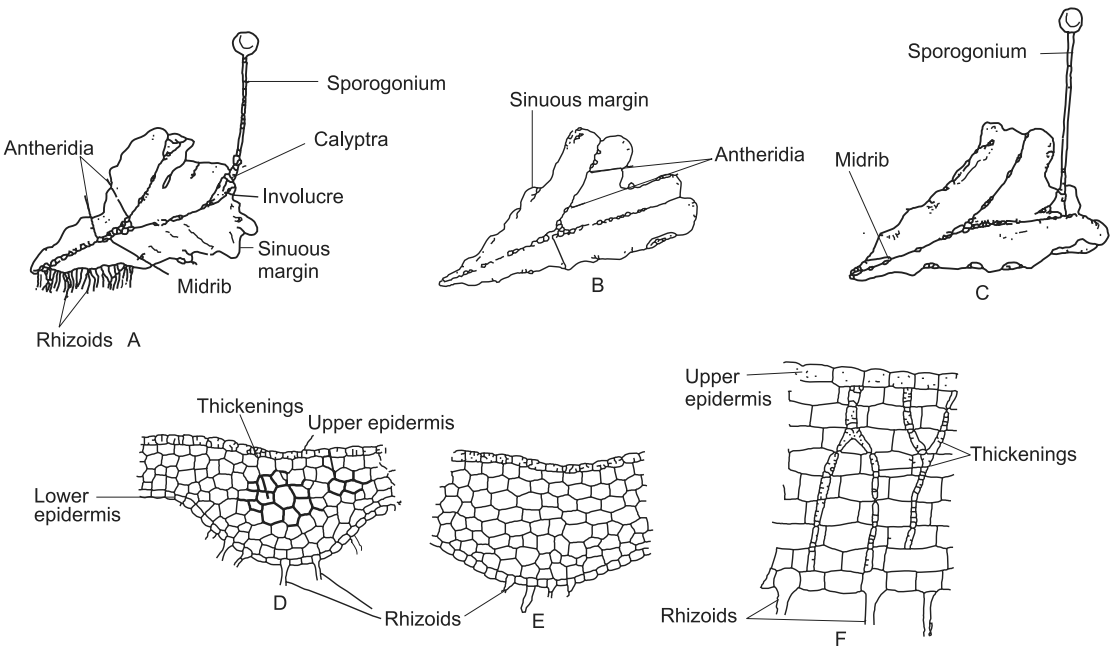


Fig. 4.13. A, Thallus of *Pellia epiphylla*; B, A male thallus; C, A female thallus; D-E, TS thallus; F, Part of longitudinal section of thallus

dorsal surface of the thallus. The growing point is situated in a notch at the anterior end of each branch of the thallus. Thousands of smooth-walled, unicellular rhizoids are present in the midrib region on the ventral surface of the thallus. Tuberculate rhizoids and scales are absent.

The thallus becomes long, narrow, ribbonlike, thin and delicate, when growing either in the water or in highly moist and shady places. In such conditions, the thallus also contains very thin margins and a distinct midrib. The plant body becomes broader, robust and elongated on damp grounds. It becomes shorter, thicker, stouter and stunted with no clear midrib when growing on dry sandy soil.

4.10.4 Anatomy of Thallus

Anatomically, the thallus is very simple with least differentiation of tissues and mainly consists of parenchymatous cells (Fig. 4.13 D, E). The midrib region is many-layered, thick and remains projected towards the lower side. Marginal sides or wings of the thallus are thin and only single-layered. Abundant chloroplasts are present in the cells of the wings and upper layers of the midrib region. Cells of the lower regions of the midrib contain only a few chloroplasts or are completely devoid of chloroplasts. Most of the cells of the thallus contain starch grains. The thallus also contains some oil-filled cells. Some yellow or brown interlacing thickenings form a network of bands in the cells of the median region in species such as *Pellia neesiana* and *Pellia epiphylla.* These bands run vertically as well as transversely, and are seen clearly in mature thalli of *P. epiphylla (*Fig. 4.13 F). These thickenings are, however, absent in *Pellia endiviaefolia.* The thallus is bounded on both the sides by a layer of epidermis. Smooth-walled rhizoids develop from some cells of the lower epidermis in the midrib region.

4.10.5 Apical Growth

In *Pellia*, the growth takes place by an apical cell, situated in the notch. In *P. endiviaefolia,* the apical cell is cuneate or wedge-shaped with four cutting faces (Fig. 4.14 A), of which two are lateral, one dorsal and one ventral. But in *Pellia epiphylla,* it (Fig. 4.14 B) is lenticular and has a posteriorly convex and two lateral cutting faces. Mucilage-secreting glandular hairs are also present in the regions of the growing points of the thallus. In *P. epiphylla,* the cells cut off from the posterior face, divide repeatedly and form the midrib of the thallus, while the lateral segments divide repeatedly and form the wings.

4.10.6 Vegetative Reproduction

Pellia reproduces vegetatively by (i) adventitious shoots, which may develop from the margins of the dorsal surface of the thallus, and (ii) death and decay of the older portions of the thallus, as in many other thalloid bryophytes.

4.10.7 Sexual Reproduction

Plants may be monoecious (*Pellia epiphylla)* or dioecious (*P neesiana, P. endiviaefolia).* Antheridia develop first in monoecious species, i.e. they are protandrous, as *P. epiphylla.*

4.10.8 Antheridia and Their Development

The antheridia develop in two to four rows on the dorsal surface of the thallus along the midrib (Fig. 4.13B). They appear as wartlike outgrowths along the midrib of the thallus. Each such outgrowth is

actually the antheridial cavity containing a single antheridium. Each antheridial cavity opens by an opening on the dorsal surface.

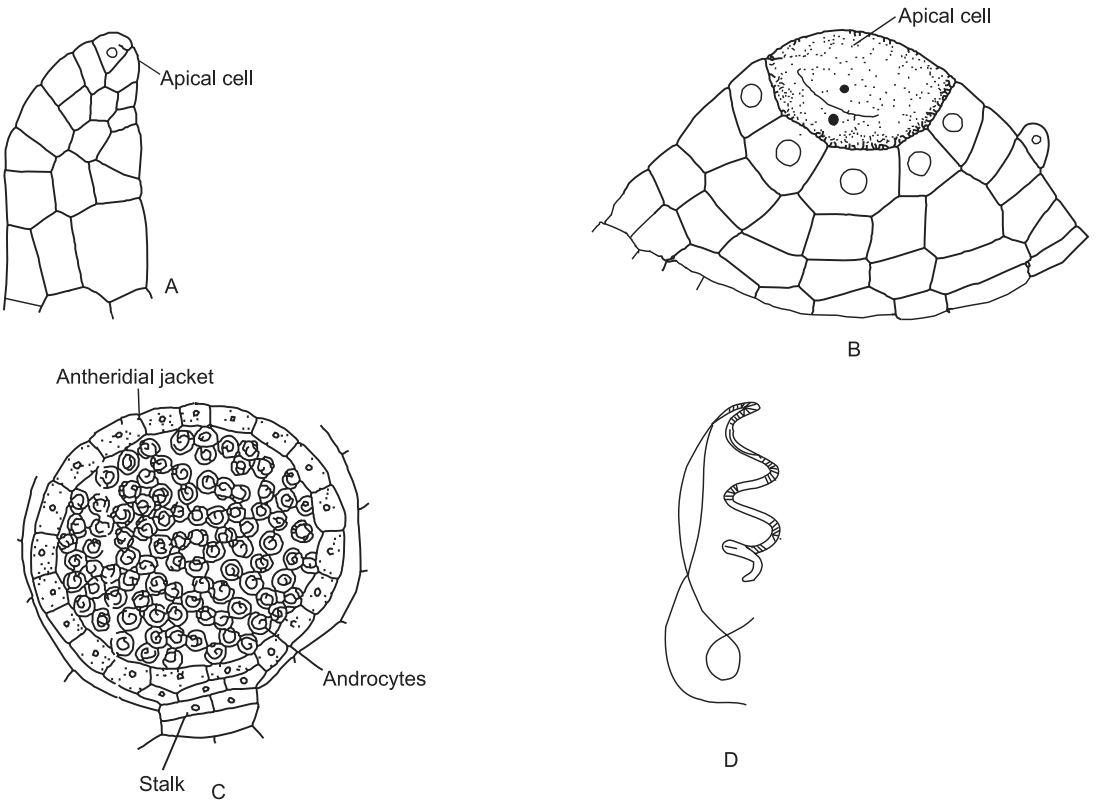


Fig. 4.14 Apical cell and its segmentation in *Pellia endiviaefolia* (A) and *P. epiphylla* (B); C, A much enlarged mature antheridium of *Pellia epiphylla*; D, A free antherozoid of *P. epiphylla*

Development of antheridium follows almost the same pattern as that of other Jungermanniales, and has been described in detail for *Porella* under Article 4.5.9(1), Fig. 4.3 A-J.

The mature antheridium is almost a spherical structure borne in an antheridial chamber opening outside by a small pore. It remains attached to the thallus by a short multicellular stalk, and its main body remains surrounded by a single-layered antheridial jacket (Fig. 4.14 C), which encloses numerous androcytes. Each androcyte produces a single antherozoid (Fig. 4.1D), which possesses a spirally coiled body containing a nucleus. Two long flagella are attached at the anterior narrow end of the antherozoids.

The antheridium dehisces when water finds its way into the antheridial chamber. The antheridial apex ruptures, releasing the mucilaginous mass of cells. The released mass of cells spreads over the water as a thin film, and thus dehiscence is completed. Spreading of the mass of cells over the water surface in *Pellia* and other bryophytes is probably due to lowering of the surface tension. Androcytes are thus carried up to the archegonial involucre. Walton (1943) opined that "androcytes reach the archegonial involucre in 15 seconds in *Pellia epiphylla"*.

4.10.9 Archegonia and Their Development

Groups of 4 to 12 archegonia develop at the anterior end (Fig. 4.15A) of the thallus near the growing point. A flaplike (*Pellia epiphylla)* or tubular (*P. endiviaefolia)* or cylindrical (*P. neesiana)* involucre protects the group of archegonia. The involucre develops from the cells of the thallus behind the archegonial group. Short mucilaginous hairs accompany the archegonial group.

Development of archegonium follows almost the same pattern, as discussed earlier along with *Porella* in Article 4.5.10(1) and depicted in Figure 4.5 A-I.

The mature archegonium (Fig. 4.15 B) is a shortly-stalked multicellular body with a dilated venter and a long neck. Six to eight neck canal cells are enclosed in the neck which remains surrounded by a jacket made up of five vertical rows of cells. The venter and lower part of the neck may become bilayered prior to fertilization.

The process of fertilization and syngamy is similar to that of *Riccia* and discussed in detail under Article 7.6.9. The ultimate result is the formation of a diploid zygote.

4.10.10 Sporophyte

The zygote increases in size and secretes a wall around itself. Cells of the venter grow actively and form a well-developed calyptra, which keeps enclosing the young developing sporogonium for quite some time.

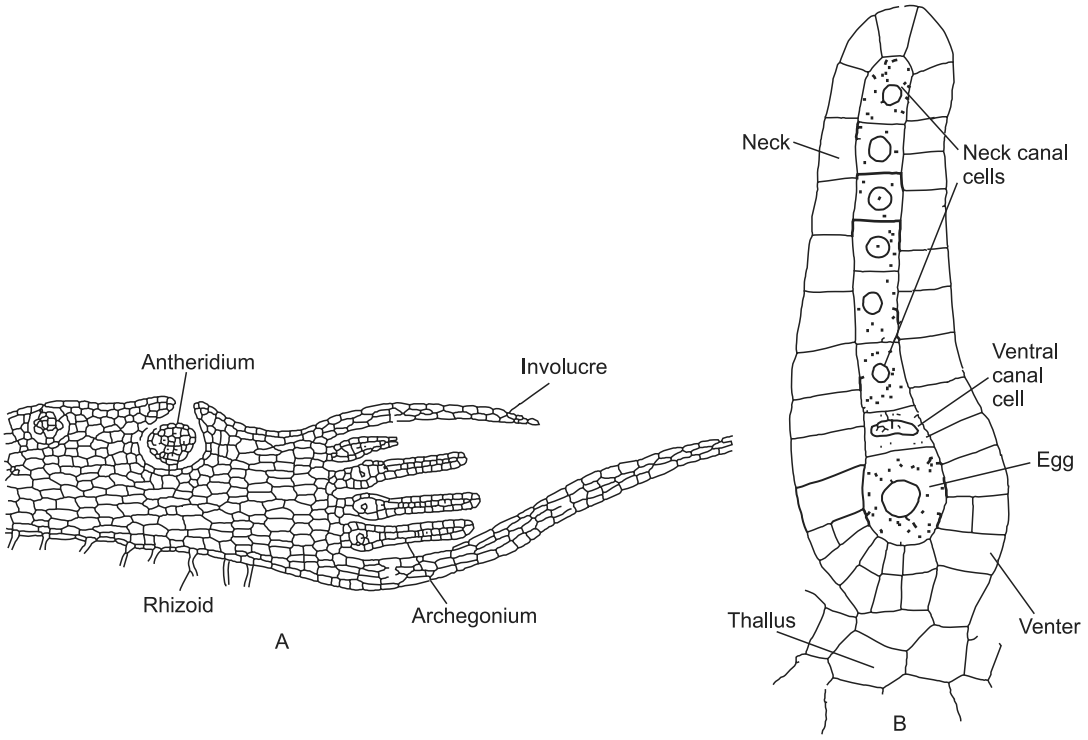


Fig. 4.15 A, LS of thallus of *Pellia epiphylla* showing sex organs; B, A mature archegonium

Development of sporogonium starts first by a transverse division forming an upper epibasal and a lower hypobasal cell (Fig. 4.16 A, B). There is no role of the hypobasal cell in the formation of proper embryo. It simply forms a suspensor which functions as a haustorium. All major parts of the mature sporogonium (such as foot, seta and capsule) are thus formed by the upper epibasal cell.

The epibasal cell divides first by a vertical wall followed by transverse division at right angles to the first division, thus forming four cells. All these four cells now divide by vertical divisions, thus forming two tiers of four cells each. The lower tier of four cells now divide and redivide to form the foot and seta. The foot is well-developed and attains a conical shape. Its projecting edges grow upwards, overlap the basal part of the seta and appear like a collar. The upper tier of four cells of the young embryo divide periclinally to form the central endothecium and outer or peripheral amphithecium (Fig. 4.16 C, D). The archesporium is endothecial in origin. The cells of the endothecium divide and redivide irregularly and form sporogenous cells. Large-sized sterile cells get differentiated at the base of the capsular region of the sporogonium. Spiral thickenings develop on the walls of these sterile cells, and this entire structure represents an *elaterophore* (Fig. 4.16). Some of the elaters remain attached also on the elaterophore. The remaining sporogenous cells develop into fertile spore mother cells and sterile elaters. Spiral thickenings develop on the walls of the elaters.

At the time of sporogenesis, each spore mother cell becomes a 4-lobed body. Its dipoid nucleus divides meiotically to form four daughter nuclei, of which one each enters into each lobe (Fig. 4.16 H) of the spore mother cell. Ultimately each uninucleate lobe develops into a haploid spore. In a majority of the species, including *Pellia epiphylla,* the number of chromosomes in the gametophyte is nine ($n = 9$).

Anticlinal divisions followed by periclinal divisions in the jacket initials form a jacket layer of two or more cells thick. A sheath, called **calyptra** develops above the young sporogonium.

Seta remains short for quite some time. But soon it elongates rapidly. In some species (e.g. *Pellia epiphylla),* the seta sometimes elongates so rapidly that from 1 mm it becomes as large as 80 mm within a week's time.

The mature sporogonium (Fig. 4.16 F) is made up of foot, seta and capsule. The foot consists of parenchymatous cells. It is conical in shape with edges like a collar around the basal part of the seta. The ***seta*** is made up of regular longitudinal rows of cells, which contain starch when young. The cells of seta in the mature sporogonium are quite elongated and are devoid of starch grains. Capsule is a globular or spherical structure surrounded by a jacket of two or more layer of cells. The outer wall layer usually contains brown radial thickening bands while the cells of the inner wall layer contain many semi-annular thickening bands in most of the species. An elaterophore is present in the lower end of the base of the capsule. It consists of a bundle of stout fixed elaters, which are 20 to 100 in number. Elaters are long, spindle-shaped bodies, each with 2 to 3 spiral thickened bands (Fig. 4.16 G). Thousands of haploid spores are present in the capsule, along with elaters (Fig. 4.16F).

Dehiscence of capsule starts by an extraordinary elongation of the cells of the seta. They elongate as much as 40 to 50 times. During this process of elongation, the starch of the seta cells converts into sugar with the simultaneous rapid absorption of water. All this pushes the capsule through the calyptra. The capsule dehisces by splitting in four valves (Fig. 4.16 I,J) along the lines of dehiscence. During this process of dehiscence, the elaterophore comes out and gets exposed (Fig. 4.16J). The process of spore dispersal is promoted by hygroscopic movement of elaters and elaterophore.

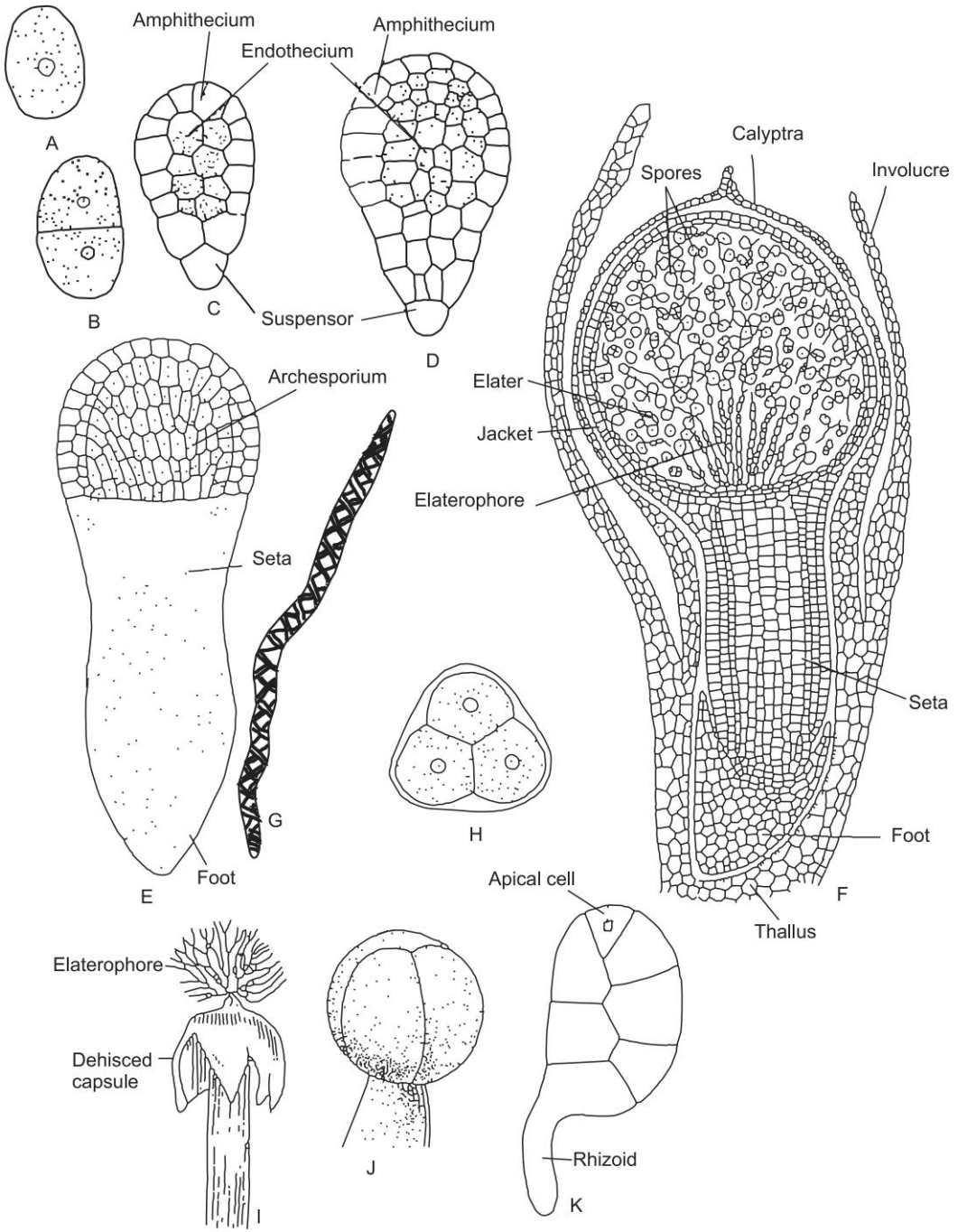


Fig. 4.16 A-E, Stages of the development of sporogonium in *Pellia epiphylla*; F, A mature sporogonium in longitudinal section; G, An elater; H, A spore tetrad; I, A capsule showing dehiscence and exposed elaters; J, A capsule showing lines of dehiscence; K, Germination of multicellular spore

Dispersed spores are multicellular, 4- to 9-celled, oval bodies (Fig. 4.16 K). Its basal portion extends into a rhizoid. An apical cell gets differentiated in the apical region, and ultimately a new thallus of *Pellia* is resulted.

A semi-diagrammatic depiction of the life cycle is shown in Fig. 4.17 (A-M).

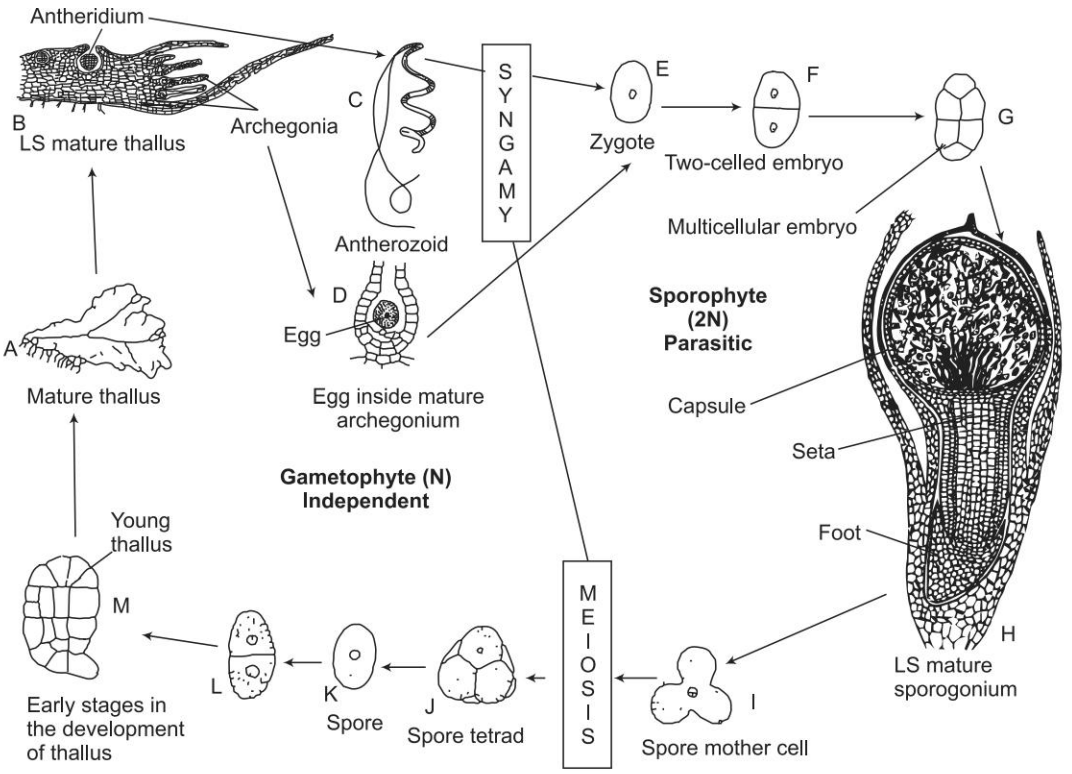


Fig. 4.17 A-M. Semi-diagrammatic representation of the life cycle of *Pellia*

RICCARDIACEAE 4.11

Evans (1939) included only two genera under the family Riccardiaceae, These are *Riccardia* and *Cryptothallus*. Some of the major characteristic features of Riccardiaceae are listed below.

1. Plant body is thalloid, and cells of the thallus contain prominent finely segmented oil bodies.
2. Sex organs are present on the dorsal side on short lateral branches.
3. The capsule is ovoid to cylindrical and remains surrounded by calyptra.
4. The calyptra is thick, fleshy, large and quite prominent.
5. The involucre is absent.
6. Elaterophore is present but it is distal in position. It is made up of long prosenchymatous cells, marginal ones of which have a free tip.
7. Few, fixed elater-like cells also grow from the surface of elaterophore.
8. The capsule dehisces longitudinally into four valves, extending towards its base.

Some details of the life history of *Riccardia* are discussed below.

RICCARDIA 4.12

Riccardia is represented by about 300 species, distributed throughout the world, but mainly in tropics and subtropical regions. *R. multifida* and *R. pinguis* are almost cosmopolitan in their distribution. Ten species reported from India are *Riccardia cardoti, R. decolyana, R. foreavana, R. indica, R. leveiri, R. multifida, R. palmatiformis, R. pinguis, R. sikkimensis and R. villosa,* as also mentioned by Parihar (1987). It grows luxuriantly in a variety of habitats including wet grounds, moist rocks, moist sandy grounds, decaying wood, ditches, marshy habitats as well as ditches and rocks near streams. *R. multifida* grows extensively in the eastern Himalayan regions and hills of south India while *R. pinguis* grows commonly in western Himalayas and hills of south India.

Originally named as *Riccardius* by SF Gray, the name *Riccardia* was given to this genus later in 1870 by Carrington. Some bryologists treat *Aneura* as a synonymn of *Riccardia.*

The plant body (Fig. 4.18A-D) or gametophytes are either completely thalloid or their terminal branches are thalloid. The gametophytes are either completely prostrate (e.g. *Riccardia indica;* Fig. 4.18 A, B) or bear upright shoots developing from their prostrate, rhizome-like portion. A distinct midrib is usually absent in prostrate species. In *R. multifida* and a few more species, the thalli are pinnately branched. Some ill-defined organs of attachment arise from the lowermost parts of plants. Incurved margins of some species form water sacs-like organs of water retention. Smooth-walled rhizoids and mucilaginous hairs are present on the ventral surface of the thallus in species with prostrate thalli. The prostrate thallus may be thick, broad and slightly branched (e.g. *R. pinguis*), or regularly branched or irregularly branched or even pinnately branched (e.g. *R. multifida*).

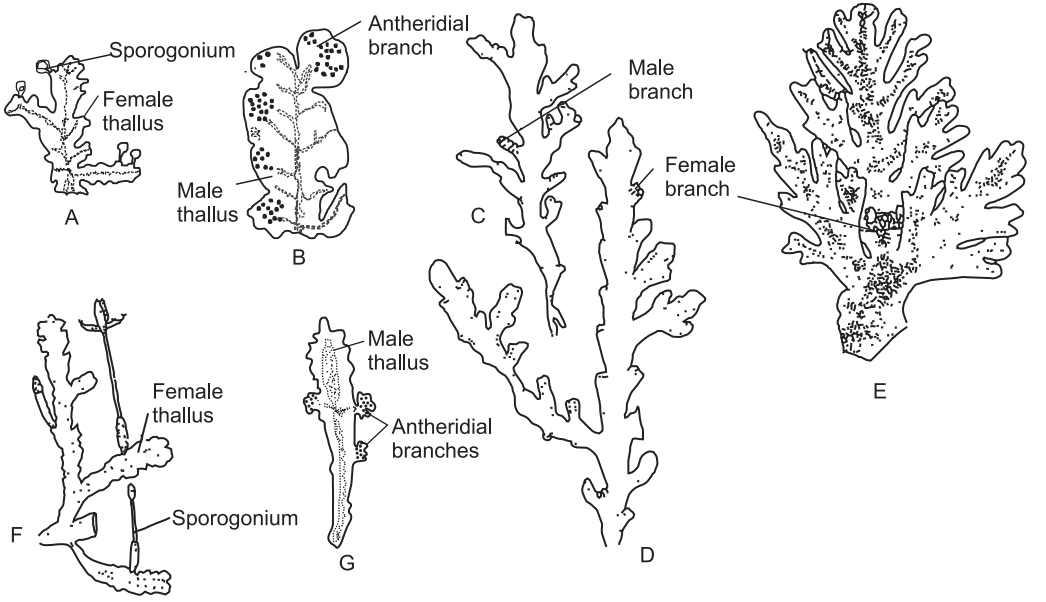


Fig. 4.18 A-G Thalli of some species of *Riccardia*. A-B, *R. indica*; C-D, *R. sikkimensis*; E, *R. prehensilis*; F-G, *R. pinguis*

Anatomically, the thallus lacks any differentiation of tissues and consists of 5 to 15 layers of cellls with cells of superficial layers being comparatively smaller. Thallus is several layers thick in the middle and becomes narrower to even one-cell layer towards the margins. Cells, when young and exposed to sunlight, contain chloroplasts. Some oil bodies are also present in epidermal cells. The number of oil bodies in each epidermal cell varies from 3 to 40 in different species. In a few species only (e.g. *R. prehensilis*), there is some internal differentiation of tissues showing a region of even some thick-walled cells (Fig. 4.19C).

Apical growth takes place by a wedge-shaped apical cell with two cutting faces. It alternately cuts off segments on right and left sides. However, according to showalter (1923), two-faced apical cell "cuts off segments not to the right and left but below and above.

Vegetative reproduction takes place (i) community by progressive death and decay of the older parts of thallus, separating the branches, which develop into new thalli; (ii) by producing stolons or thick cylindrical ventral shoots, which on separation produce new thalli, as in *Riccardia levieri* (Pande and Srivastava, 1958); and (iii) by producing *gemmae* at the apex of branches in several species, including *R. levieri*, *R. multifida* and *R. palmata*. Gemmae in *Riccardia* are small, round, oval or oblong bodies only of few cells. On being detached and germination, each gemma produces a new thallus of *Riccardia*.

Sexual reproduction in *Riccardia* is oogamous like other bryophytes, and takes place by antheridia and oogonia. Species may be monoecious (e.g. *R. decolyana* and *R. multifida*) or dioecious (e.g. *R. indica* and *R. palmata*). Sex organs develop on specialized short lateral branches, which develop from the margins of the thallus.

Antheridia develop on dorsal surface of thallus on lateral branches (Fig. 4.18 B,C) called male or antheridial branches. They remain sunk in the antheridial chambers in the tissues of male branches (Fig. 4.20 A, B). The development of antheridium follows the same pattern as described for *Porella* and other Jungermanniales under Article 4.5.9(1) (Fig. 4.3).

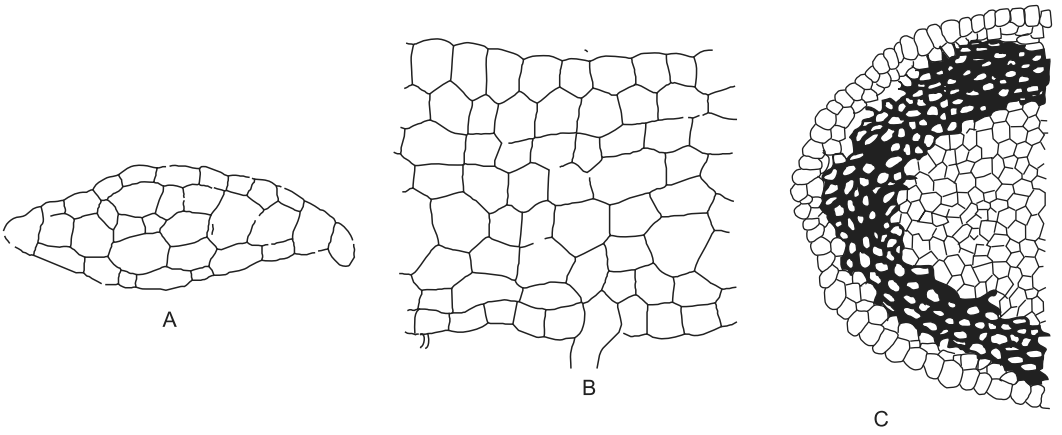


Fig. 4.19 A-C. Transverse sections of the thallus of *Riccardia multifida* (A), *R. indica* (B), and part of axis of *R. prehensilis* (C)

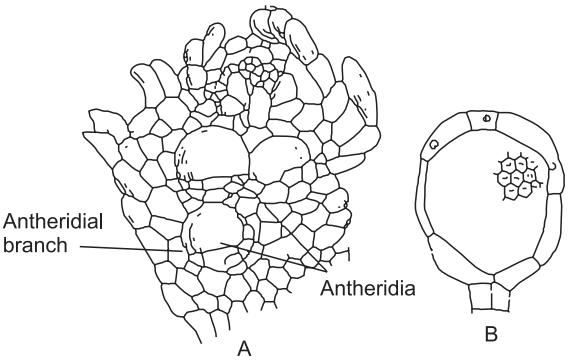


Fig. 4.20 A-B, Antheridia sunken in antheridial branch (A) and a single antheridium (B) of *Riccardia*

The mature antheridium is a globular body with a very short stalk of only 2 or 3 cells in length. It is covered by a single-layered jacket (Fig. 4.20 B). Androcytes present inside the jacket develop into antherozoids. Each antherozoid bears two short flagella.

Archegonia develop on the dorsal surface of the archegonial branches (Fig. 4.18E), which are comparatively shorter than the antheridial branches. Each archegonial branch possesses 4-20 archegonia arranged usually in two alternate rows. The development of archegonium resembles other Jungermanniales as discussed for *Porella* under Article 4.5.10(1) (Fig. 4.5 A-I).

The mature archegonium (Fig. 4.21 A-B) shows only a little differentiation into neck and venter. Usually, the venter as well as the lower part of neck are 2 or 3 cells in thickness. The neck consists of five vertical rows of cells, with its axial row made up of 3 to 6 neck canal cells, a ventral canal cell and an egg (Fig. 4.21C). Involucral scales surround and protect the lower parts of the developing archegonia. The fertilization process also resembles that of *Porella* and other Jungermanniales, as discussed earlier under Article 4.5.11. Fusion of male and female gametes results in the formation of diploid zygotes.

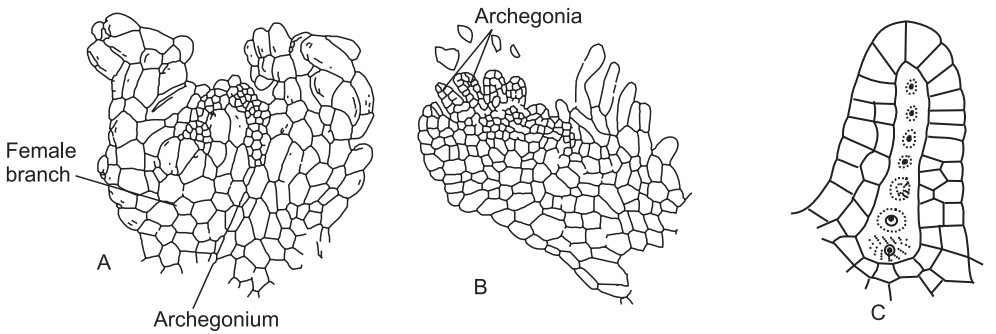


Fig. 4.21. A, An enlarged female branch of *Riccardia diversifolia*; B, Section through an archegonial branch of *R. diversifolia*; C, A mature archegonium of *R. sinuata*

Development of sporogonium starts by a first transverse division (Fig. 4.22A) of the zygote resulting into an epibasal cell and a hypobasal cell. The entire sporogonium develops from the epibasal cell. The lower hypobasal cell simply elongates and develops into a haustorium (Fig. 4.22B), which pierces into

the gametophytic tissue. The epibasal cell divides transversely to form two cells, both of which contain prominent nuclei, dense cytoplasm and many chloroplasts. A transverse division in the uppermost cell makes the young sporogonium a four-celled structure, of which the lowermost is the haustorium. Of the three cells formed by the epibasal cell, the lowermost develops into foot, middle one into seta, and the uppermost into capsule of the sporogonium. Intersecting vertical divisions in these three cells result into the formation of three superimposed tiers, each made up of four cells (Fig. 4.22C). The tier immediately next to haustorium develops into **foot**. Its cells divide by transverse as well as vertical divisions in an irregular fashion and form a compact mass of foot. Vertical and transverse divisions in the cells of middle tier from **seta**. The uppermost tier of four cells develops into **capsule**. A transverse division in this uppermost tier divides this tier into two tiers of four cells each. Now periclinal division in each cell of these two tiers results into the formation of an outer or peripheral amphithecium and inner or axial endothecium (Fig. 4.22D). The amphithecium develops into the jacket of the capsule. Its cells divide first anticlinally and then also periclinally to form a two-layered thick jacket (Fig. 4.22 E, F). The archesporium is endothecial in origin (Fig. 4.22D). Endothecial cells divide irregularly. The cells of apical central region originated from endothecium are larger and develop into **elaterophore** (Fig. 4.22F). From these cells radiate the sporogenous tissue, which later on differentiate into spore mother cells and elaters (Fig. 4.22F). Prior to nuclear division, the spore mother cells attain a four-lobed structure. The diploid nucleus of each spore mother cell divides by two successive divisions to form a tetrad of haploid spores. A massive sheath of gametophytic tissue keeps enclosing the young capsule. At maturity, this sheath breaks and survives at the basal part of the seta in the form of a **collar**.

The mature sporogonium of *Riccardia* (Fig. 4.22 F) is made up of foot, seta and capsule. The *foot* is ill-defined and present in the form of a club-like swelling in the lowermost part of the sporogonium. ***Seta*** consists of several rows of cells, having a diameter of at least six cells. The capsule is a cylindrical to ovoid body (Fig. 4.22F) surrounded by a bilayered jacket. Bands of thickenings are present in the walls of the cells of jacket of most species of *Riccardia.* A well-developed apical elaterophore hangs downwards into the cavity of the capsule up to as much as one-third of the distance from the apex to the base. It forms a central cylinder of long parenchymatous cells. The marginal cells of elaterophore have free tips. Fixed elaters or elater-like cells grow from the surface of the elaterophore. These project from the mass of free elaters and spores. A prominent spiral band of thickening is present in each free elater (Fig. 4.23 A). Ends of the free elaters are pointed.

At the time of the dehiscence of a capsule, cells of the seta start elongating. Seta thus elongates from 2 to 30 mm. Along the line of dehiscence, the capsule dehisces into four valves, which separate out from apex to base. The elaterophore also splits into four parts during this process. The mechanical jerk results into direct and abrupt dispersal of spores. Hygroscopic movement of elaters also helps in spore dispersal.

The spores germinate into gametophytes (Fig. 4.23 B-D). They are small, 12 to 25 μ in diameter, and each remains surrounded by two wall layers, namely exospore and endospore. A nucleus and chloroplasts are also present in each spore. At the time of germination, the spore increases in size, divides transversely and forms two equal or unequal cells. An oblique division in the upper cell differentiates a wedge-shaped apical cell, the further activity of which gives rise to a new gametophytic thallus (Fig. 4.23 D).

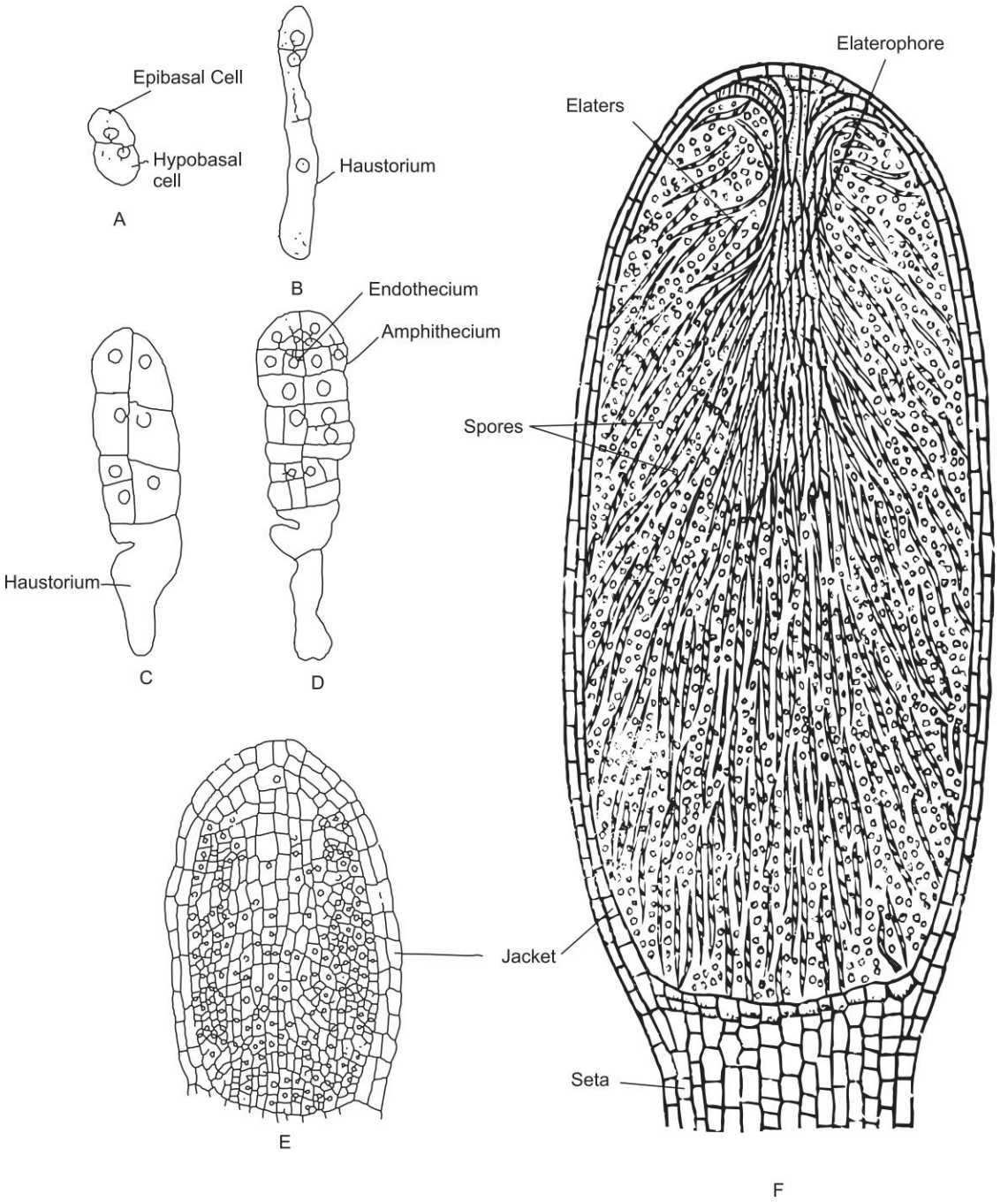


Fig. 4.22 A-F. Showing development of sporogonium in *Riccardia pinguis*

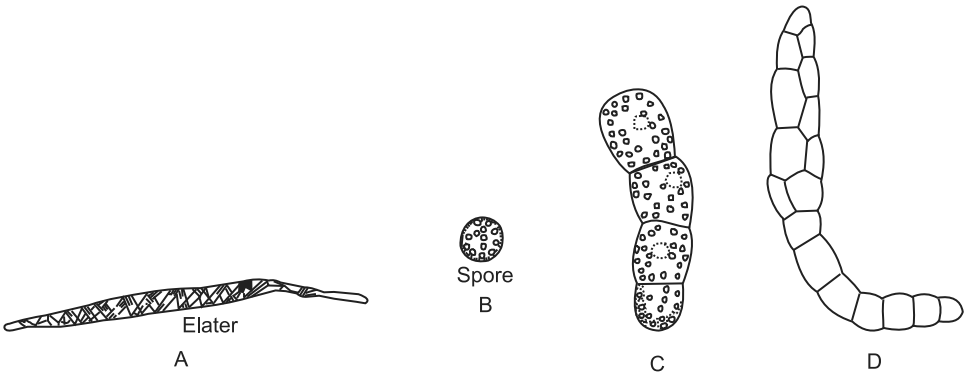


Fig. 4.23 A-D*, Riccardia levieri,* showing an elater (A) and spores (B) and development of young gametophyte

FOSSOMBRONIACEAE 4.13

Fossombroniaceae is one of the seven familes of Metzgerineae. It includes four genera, viz. *Fossombronia*, *Simodon, Petalophyllum* and *Sewardiella*. Majority of the species of Fossombroniaceae, including of *Fossombronia*, have gametophytes differentiated into stem and lateral leaves. Growth of the gametophyte is initiated by a single apical cell.

Only *Fossombronia* is discussed here in some details.

FOSSOMBRONIA 4.14

Fossombronia is represented by about 50 species showing worldwide distribution. Four of its species reported from India are *F. indica*, *F. himalayensis*, F. *cristula* and *F. foreavii*. In India, *Fossombronia* has been reported from south India, Himalayas, Pachmarhi (MP) and Kodaikanal.

The gametophytic plant body is foliose. The thallus is almost completely prostrate with a sparse or profuse branching (Fig. 4.24 A–C). Each branch is made up of a well-developed stem bearing a single row of leaves along both the lateral margins. The arrangement of leaves becomes less organised in some species because of the greatly convoluted margins of their leaves (Fig. 4.24 A). The leaves are 2- to 3-cells thick at the base while their upper portions are only one cell in thickness. The well-developed massive stem shows no indication of any internal differentiation of tissue. Only smooth-walled rhizoids are present on the ventral surface of stem. The apex of the branch contains many multicellular mucilaginous hairs. Their function is to protect the apical region. Older parts of the stem do not bear any mucilaginous hairs.

Growth takes place by an apical cell with two cutting faces. It cuts segments alternately on the right and left sides. The apical cell is semicircular in outline in vertical longitudinal section. It appears narrowly trianglular in HLS. A segment of an apical cell is first cut in a horizontal plane. The ventral daughter cell, formed by this division, gives rise to the ventral portion of the stem while the dorsal daughter cell gives rise to the dorsal portion of the stem and also the leaf. Differing from other members of Metzgerineae, the branching in *Fossombronia* is not initiated by a vertical division of the apical cell

into two equal-sized cells. In this genus, a second apical cell is differentiated in a very young segment derived from the apical cell. The overall growth from the original apical cell and this second apical cell ultimately gives rise to a structure which appears to be a true dichotomy. In reality, however, it is a false dichotomy and not a true dichotomy.

The sex organs develop in acropetal succession on the dorsal surface of the midrib and occur either irregularly scattered or in groups. A majority of the species are monoecious. According to Pande et al. (1954), *Fossombronia himalayensis* is monoecious but protandrous. Rarely, some species are dioecious. Each sex organ generally originates from a single, superficial cell, quite close and just behind the apical cell.

Development of antheridia follows the same pattern as that of other Jungermanniales and explained already for *Porella* under Article 4.5.9(1). Stages of the development of antheridia in *Fossombronia angulosa* are depicted in Fig. 4.25A-G. Mature antheridia burst suddenly and release the antherozoids. The antherozoids are biflagellate, uninucleate structures. Two flagella of each antherozoid remain inserted at different points near the anterior end. Mature antheridium (Fig. 4.25 G) is a stalked structure and contains a globular body surrounded by a jacket layer. The haploid chromosome number in the dividing antheridial cells of *F. himalayensis* is nine (Pande et al., 1954).

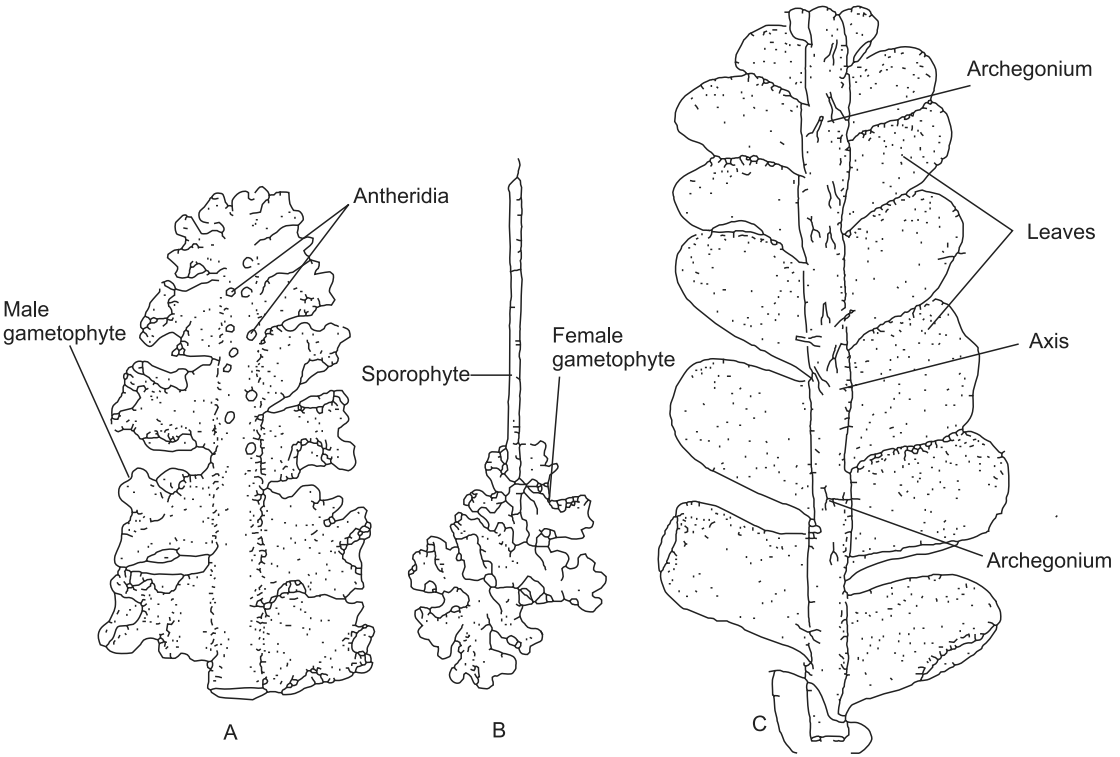


Fig. 4.24 Gametophytes of *Fossombronia*. A, Male gametophyte of *F. longiseta*; B, Female gametophyte of *F. longiseta*; C, Female gametophyte of *F. intestinealis*

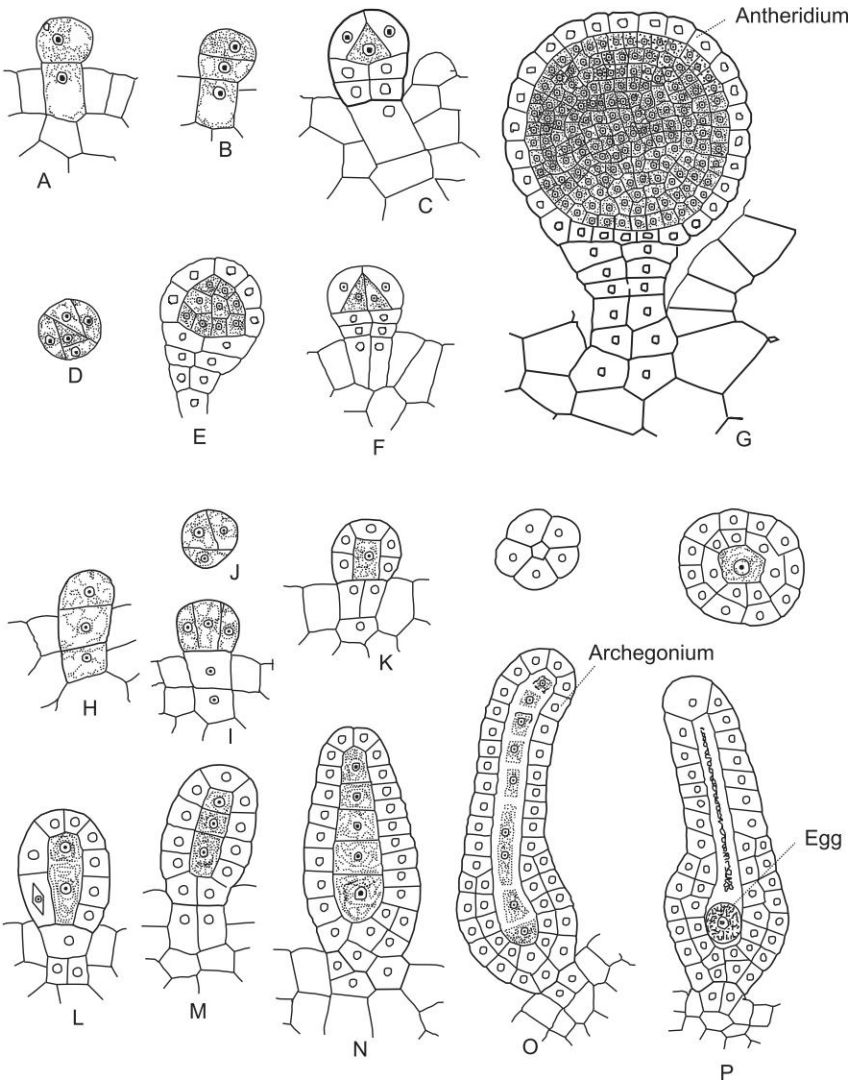


Fig. 4.25 A-G, Stages of the development of antheridia in *Fossombronia angulosa*; H-R, Stages of the development of archegonia in *F. angulosa*. Stages in J, Q and R are in transverse sections

Development of archegonium (Fig. 4.25 H-R) is also in the manner typical for the Jungermanniales, as described for *Porella* under Article 4.5.10(1). A mature archegonium (Fig. 4.25O) consists of 6-8 neck canal cells surrounded by five vertical rows of neck cells. The venter of the archegonium contains a two-cells thick jacket layer. The venter is only slightly broader than the neck of the archegonium.

At the time of fertilization, entrance of antherozoids into archegonia is undoubtedly in response to chemotactic stimuli. Antherozoids entering the venter of an archegonium soon penetrate the egg. Fusion of male and female nuclei takes place 24 to 48 hours after the entrance of the antherozoid, and it results into the formation of a diploid zygote.

According to Showalter (1927), the division of the zygote "takes place six to nine days after gametic union. The zygote first divides transversely into a larger epibasal cell and a smaller hypobasal cell (Fig. 4.26 A). The hypobasal cell develops into the **foot** of the sporophyte. The epibasal cell divides transversely into an upper daughter cell, which develops into the capsule, and a lower daughter cell, which develops into a seta of the sporophyte. (Fig. 4.26 B-E). Periclinal divisions in the capsular region result in the formation of an outer jacket layer or amphithecium and inner endothecial cells. The archesoporium is endothecial in origin.

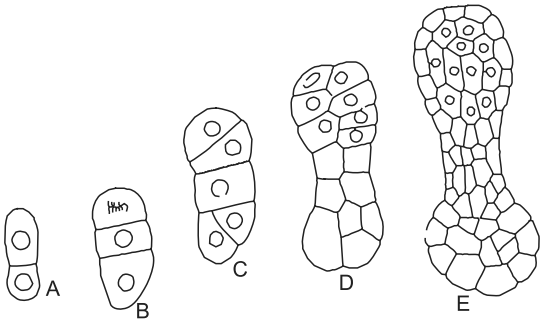


Fig. 4.26 A–E, Stages of the development of embryo in *Fossombronia pusilla*

The jacket or amphithecium soon becomes a two-celled thick layer. Elaters and sporocytes do not differentiate until the last cell generation of the sporogenous tissue of the endothecium. The elaters of *Fossombronia* are unique in that the thickenings on their walls are laid down in 5 to 9 rings instead of the usual 2 or 3 longitudinal thickenings of the other genera. Elaterophore-like structure, when present, is ill-developed.

A calyptra and a cup-like involucre enclose the young sporophyte. Calyptra is actually the part of the old archegonium, while the involucre is produced by the upgrowth of the gametophytic tissue adjacent to the basal part of the archegonium. Until the spores in the capsule attain maturity, the seta is only about 1 mm in length. Soon, it elongates rapidly and pushes the capsule through the calyptra (Fig. 4.24B). After the elongation of seta, the capsule dehisces after about 18 to 36 hours. Capsules in different species either dehisce irregularly or into four valves.

The dehisced spores start germinating in the form of a filamentous protonema of 2 to 12 cells. Rhizoids start developing in the cells nearest the old spore wall. Some distal cells of the protonema start dividing irregularly to form a globose mass of cells. This is actually the termination of the protonemal phase. A cell of this globule mass of cells soon starts functioning as an apical cell with two cutting faces. A thalloid structure soon develops due to the activity of this apical call. There is, however, still no differentiation of stem and leaves. At a later stage, derivatives of the apical cell start differentiating into a leaf and a portion of the stem. Within few days, a foliose gametophyte of *Fossombronia* develops.

TEST YOUR UNDERSTANDING

1. Name the largest order of Hepaticopsida.
2. Write any seven general characteristics of Jungermanniales.
3. Are the rhizoids in Jungermanniales smooth-walled or tuberculate or of both types?
4. Are the scales present or absent in Jungermanniales?
5. Verdoorn (1932) divided Jungermanniales into two artificial groups. These are (a) Jungermanniales Acrogynae, and (b) _____ _____.
6. Evans (1939) divided Jungermanniales into three sub-orders. These are (a) Haplomitrineae, (b) Metzgerineae, and (c) _____.
7. Parihar (1987) divided all Jungermanniales into two sub-orders. These are (a) Jungermannineae, and (b) _____.
8. Write at least five characteristic features of the sub-order Jugermannineae (Jungermanniales Acrogynae).
9. Porellaceae and Frullaniaceae belong to the sub-order _____ of the order Jungermanniales.
10. Porellaceae is also known by the name _____.
11. Write at least four characteristic features of Porellaceae.
12. What do you mean by incubuous arrangement of leaves?
13. Draw well-labelled diagrams of external morphology of the gametophyte of *Porella.*
14. Explain the following terms in reference to the leaf of *Porella:*
    (a) Amphigastria
    (b) Antical lobe
    (c) Postical lobe
    (d) Incubous
15. Describe life-history details of *Porella* in about 500 words.
16. Give an illustrated account of development of antheridium in *Porella.*
17. Explain in brief the generalised process of archegonium development in *Porella* and other Jungermanniales.
18. Describe development of sporogonium and structure of mature sporogonium in *Porella.*
19. Three genera included under Frullaniaceae are *Frullania, Neohattoria* and _____.
20. Write at least four characteristic features of Frullaniaceae.
21. Write a detailed scientific note on the life-history of *Frullania* in about 500 words.
22. The common name "multiform thallose hepatics" is usually given to the members of Metzgerineae. Why?
23. Describe distribution and habitat of *Pellia* in about 100 words.
24. Give an illustrated account of life-history of *Pellia* in about 1000 words.
25. Describe the development of sporogonium and structure of mature sporogonium in *Pellia.*
26. What is elaterophore?
27. In *Pellia,* the archesporium is _____ in origin.
28. Draw a semi-diagrammatic sketch of the life cycle of *Pellia.*
29. Two genera included under the family Riccardiaceae are *Riccardia* and _____.
30. Write a detailed scientific note on the life history of *Riccardia* giving suitable diagrams.
31. Give a brief illustrated account of the life history of *Fossombronia.*

5

Hepaticopsida (Sphaerocarpales)

SPHAEROCARPALES AND THEIR GENERAL CHARACTERISTICS 5.1

Sphaerocarpales is a small order of Hepaticopsida, comprising only three genera, viz. *Sphaerocarpos*, *Geothallus* and *Riella*. The former two (i.e. *Sphaerocarpos* and *Geothallus*) belong to the family Sphaerocarpaceae while the third one (i.e. *Riella*) is the sole member of the family Riellaceae.

Members are commonly called "**bottle-hepatics**" because of the presence of a flask-shaped or globose envelope (involucre) around each of the sex organs. **Sphaerocarpaceae** members have bilaterally symmetrical and thallose gametophytes with no internal differentiation of tissues. On the other hand, **Riellaceae** (*Riella*) members possess asymmetrical gametophytes. A well-organised seta is absent in the sporophyte of the members of Sphaerocarpales.

Some details of the life-history of *Sphaerocarpos* of the family Sphaerocarpaceae and *Riella* of Riellaceae are given here in this account.

SPHAEROCARPOS 5.2

Sphaerocarpos is represented by seven species, and occurs in both northern as well as southern hemispheres. It occurs commonly in the Gulf and Pacific coast states of the United States on fine-textured soil. It prefers a climate where the summer is dry and winter is moderately wet and wild.

The **plant body** is gametophytic and gametophytes are relatively small, orbiculate to cuneate and quite simple or slightly dichotomously branched. Gametophyte is a bilaterally symmetrical thallus. Male and female gametophytic plants (Fig. 5.1 A-B) usually occur together in clumps. A several cells thick, broad midrib is present in each gametophytic thallus. On margins, the wings of the thallus are only one cell in thickness. Wings of the thallus are either entire or incised into leaf-like lobes. Sex organs, each surrounded by an ovoid or flask-shaped involucre, are present on the dorsal surface of a midrib. They remain densely crowded (Fig. 5.1). On the ventral surface of the thallus are present many multicellular glandular hairs and smooth-walled rhizoids. Tuberculate rhizoids and scales are absent.

Anatomically, the thallus lacks any internal differentiation of tissues. Chloroplasts remain filled in almost all vegetative cells of the thallus, except rhizoids.

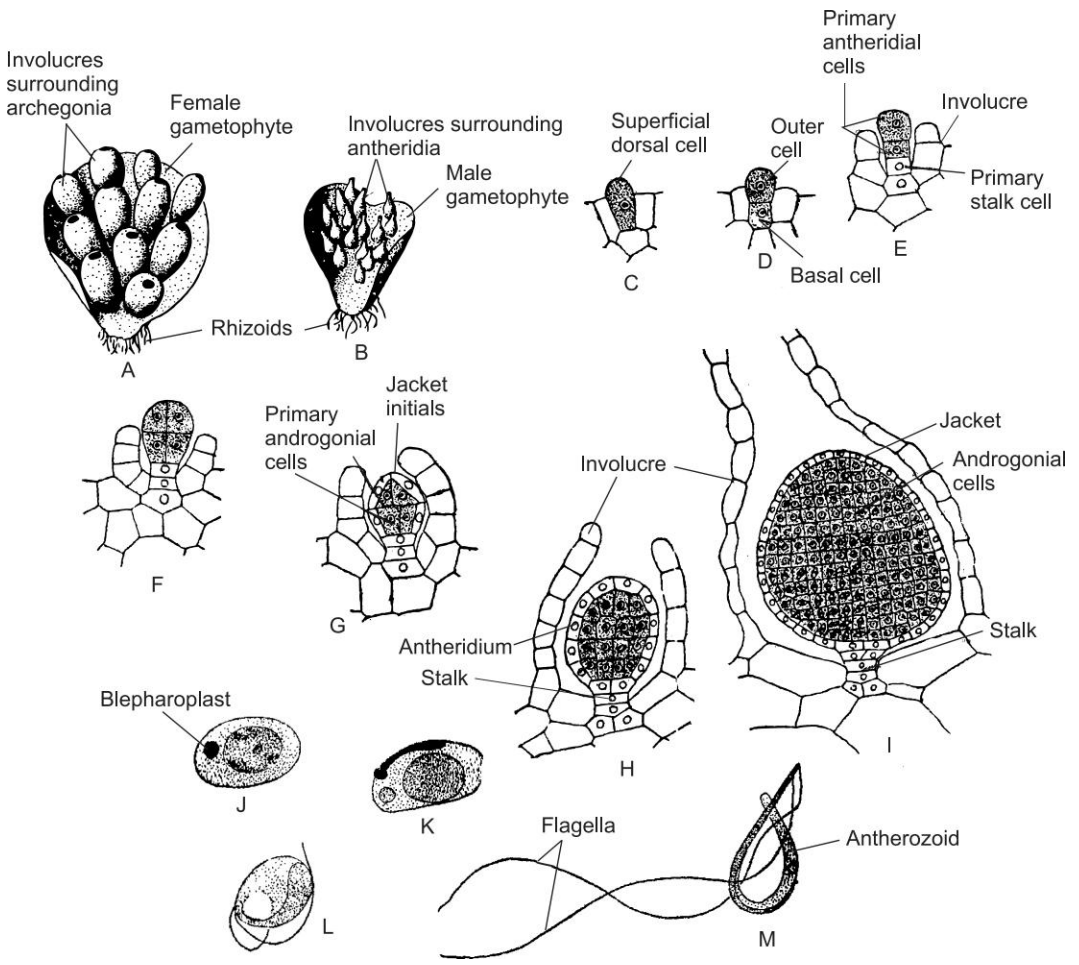


Fig. 5.1 Female (A) and male (B) gametophytes of *Sphaerocarpos californicus*; C-I, Stages of the development of antheridia in *S. cristatus*; J-M, Stages of the metamorphosis of androcytes into antherozoids in *S. donnellii*

Growth takes place by a row of wedge-shaped apical cells, which remain laterally joined to one another. Each apical cell cuts off segments alternately from its dorsal as well as ventral faces. These segments contribute to the midrib of the thallus. The segments, which are cut off from the apical cell at each end of the row, ultimately form wings of the gametophytic thallus. Vertical divisions in the median part of the row of apical cells ultimately contribute to the dichotomous branching of the thallus. Repeated dichotomous branching is common in species like *Sphaerocarpos donnellii*.

Vegetative reproduction takes place by progressive death and decay of the posterior portion of the thallus. When this death and decay process reaches up to the place of dichotomy, the two branches may survive and may continue to develop into two independent plants of *Sphaerocarpos*. Sometimes, plants multiply vegetatively also by the formation of proliferous outgrowth, either from the midrib or from the lateral wings. Such outgrowths may also develop from the involucres in some species, according to Rickett (1920).

Sexual reproduction is oogamous. All the investigated species of *Sphaerocarpos* are heterothallic. Sex differentiation is attributed to sex chromosomes. Male plants (Fig. 5.1 B) differ from female plants by their (i) smaller-sized gametophytes, (ii) flask-shaped involucres, and (iii) purple-tinged gametophytes. Male plants attain a diameter of about 2 mm while the female plants reach up to 1 cm in diameter. In female plants, the archegonia are surrounded by subspherical or cylindrical involucres (Fig. 5.1A).

Development of antheridium (Fig. 5.1 C-I) starts with a superficial dorsal cell (Fig. 5.1C), which enlarges and becomes capitate. It is called **antheridial initial**. It soon divides into a basal cell and an outer cell. The outer cell projects above the thallus (Fig. 5.1 D). The basal cell develops into antheridial stalk. The outer cell develops into the remaining major part of the antheridium. The outer cell divides by successive transverse divisions to form a vertical file of three cells (Fig. 5.1E), of which two upper cells are the primary antheridial cells and develop further into **antheridium proper**. The lowermost third cell forms the **primary stalk cell**. Each of the two primary antheridial cells divide by two successive vertical divisions at right angles to each other and ultimately forms four cells (Fig. 5.1 F). A periclinal division in both tiers of four cells results into the formation of outer four jacket initials and inner four primary androgonial cells (Fig. 5.1.G). Primary androgonial cells now divide by many successive divisions at right angles to one another to form many cubical androgonial cells. Each cell of the last cell generation of the androgonial cells divides diagonally into two androcytes. The jacket initials divide anticlinally to form a well-organised jacket around the antheridium (Fig. 5.1I). Each androcyte metamorphoses into a uninucleate, biflagellate antherozoid (Fig. 5.1 J-M). Free swimming antherozoids are spindle-shaped, curved or variously coiled structures.

Development of archegonium starts with the arrangement of a dorsal cell called **archegonial initial** (Fig. 5.2A). It first divides by a transverse division into a basal cell and an outer cell (Fig. 5.2B). The lowermost part of the archegonium is formed by the basal cell, while its remaining portion is formed by the outer cell. The outer cell first divides by an asymmetrical vertical division to cut off a peripherial initial. Two more unequal vertical divisions form two more peripheral initials. A primary axial cell surrounded by these three peripheral initials now develops (Fig. 5.2 C). All the three peripheral initials now divide vertically to form six jacket initials surrounding the primary axial cell. A transverse division in each jacket initial soon results in the production of six neck initials present above a tier of six venter initials (Fig. 5.2D). An archegonial neck of several cells in length and six cells in perimeter now develops due to transverse division of neck initials and their daughter cells. In *Sphaerocarpos*, the jacket of a mature venter of archegonium consists of 10 or more cells in perimeter. Simultaneously, the primary axial cell divides transversely into a primary cover cell and a central cell (Fig. 5.2D). The primary cover cell divides by two successive vertical divisions to form four cover cells. Side by side, the central cell divides transversely into a smaller upper canal cell and a lower canal cell (Fig. 5.2 E). The upper canal cell divides by two successive transverse divisions resulting into the formation of four neck canal cells within the archeogonial neck. The lower canal cell now divides asymmetrically to form a small venter canal cell and a large egg. Soon, it is observed that the venter canal cell and neck canal cells of the mature archegonium disintegrate to form a mucilaginous mass, and its cover cells are set apart, resulting in the formation of an open passage for permitting and helping the entry of the antherozoids to reach up to the egg. Entrance of antherozoids "into the neck is undoubtedly a chemotactic response" (Smith, 1955).

An **involucre** starts developing in the initial stages of the archegonial development (Fig. 5.2 C-G). The involucre is more prominent around the antheridium (Fig. 5.1 E-I) than that of the archegonium (Fig. 5.2 G).

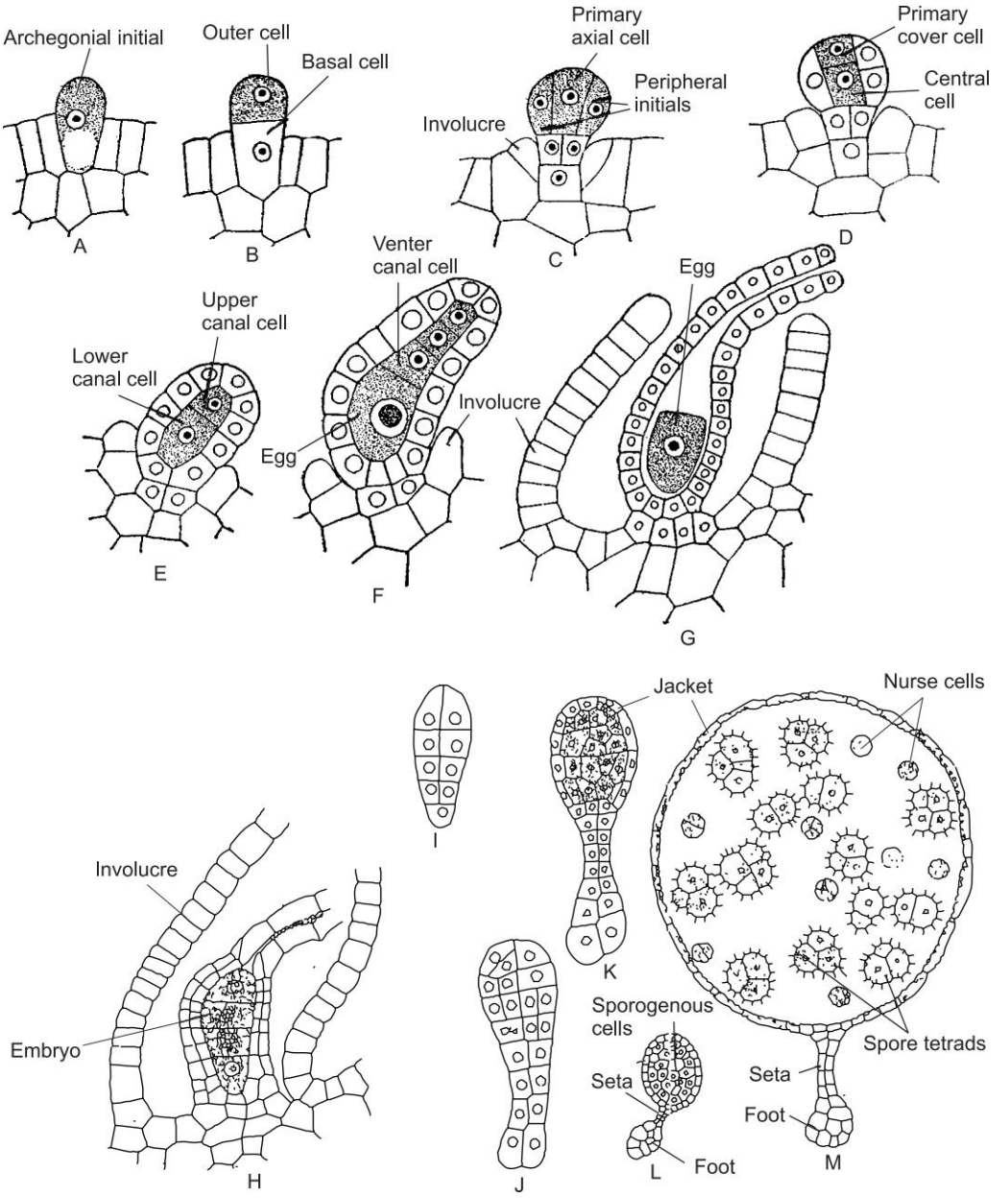


Fig. 5.2 A-M *Sphaerocarpos cristatus.* Development of archegonia (A–G); Development of sporophyte (H-L); M, Mature sporophyte

Fertilization takes place due to the fusion of antherozoids and the egg. Fusing male and female nuclei have organised chromosomes, and fusion of male and female nuclei begins 60 to 70 hours after entrance of an antherozoid. The zygote first divides transversely to form an upper epibasal and a lower

hypobasal cell, and both these cells again divide transversely to form a 4-celled filamentous embryo (Fig. 5.2H). Each of the cells of this young embryo divide by two successive vertical divisions to develop into a tier of four cells. Two tiers of the four cells in the epibasal half of the embryo develop ultimately into a capsule of the sporophyte while the derivatives of the remaining two tiers develop into the remaining parts of the sporophyte. Periclinal division (Fig. 5.2I, J) in the two upper tiers of four cells results into the formation of outer amphithecium and inner or central endothecium. A jacket layer of capsule develops due to anticlinal division in the amphithecium (Fig. 5.2 J-M). **Archesporium is endothecial in origin** in *Sphaerocarpos*. The endothecium develops into sporogenous tissue of the capsule. Some sporocytes or spore mother cells of the sporogenous tissue divide meiotically into four spores. Other cells of the sporogenous tissue remain sterile and mature into sterile **nurse cells**. The function of nurse cells is to supply food to the developing spores. Numerous chloroplasts are present in the nurse cells as well as in the cells of the jacket layer of the capsule. Dispersal of spores takes place after the death and decay of the jacket.

A bulbous **foot** develops simultaneously by the divisions in the basal part of the hypobasal half of the embryo (Fig. 5.2 L,M). The upper part of the hypobasal half of the embryo develops into a small **seta**. Seta in *Sphaerocarpos*, however, does not elongate much. It does not also pushes much to the well-developed capsule of the sporophyte.

Out of the four spores formed by a spore mother cell, two develop into female gametophytes, and two into male gametophytes. A spore first geminates into a long germ tube, which first divides transversely into a small terminal cell and a large basal cell. The terminal cell remains filled with dense protoplasm and divides by transverse and vertical divisions to form a long ribbon-shaped structure of 3 to 4 cells in length and two cells in breadth. The basal cell does not divide any further. Horizontal divisions in the multicellular ribbon give rise to the formation of a germinal disc, which soon grows and forms an asymmetrical structure. Apical cells develop at one side of this disc. Their further activity results into the development of an adult thallus of *Sphaerocarpos*.

RIELLA 5.3

Riella is the only genus of the family Riellaceae of Sphaerocarpales. It differs from Sphaerocarpaceae in possessing asymmetrical plant body of its gametophytes. About 20 species of *Riella* have been reported from the world, of which *R. affinis* and *R. americanum* grow commonly in the United States. *R. affinis* is the only species reported from India.

Riella is an aquatic bryophyte, growing on muddy soil, which remains submerged in calcium-rich waters of shallow pools. *Riella* plants grow entirely submerged, usually several feet below the water surface.

The gametophytic plant body (Fig. 5.3 A) of *Riella* is erect and consists of a thick stem-like axis bearing a well-developed, plate-like wing. The wingh is straight to spirally twisted and only one cell in thickness. The cells of the wing are thin-walled and chlorophyllous. One-cell-thick scales (Fig. 5.3 B) develop along the median part of the axis. These are called **ventral scales**. Some scales also develop at the juncture of the axis and wing. These are called **lateral scales**. Simple spherical oil bodies are present in some cells of the scales. The lower part of the thallus contains some unicellular and smooth-walled rhizoids.

Growth takes place by a single apical cell with two cutting faces. Sometimes the single apical cell is replaced by a row of apical cells.

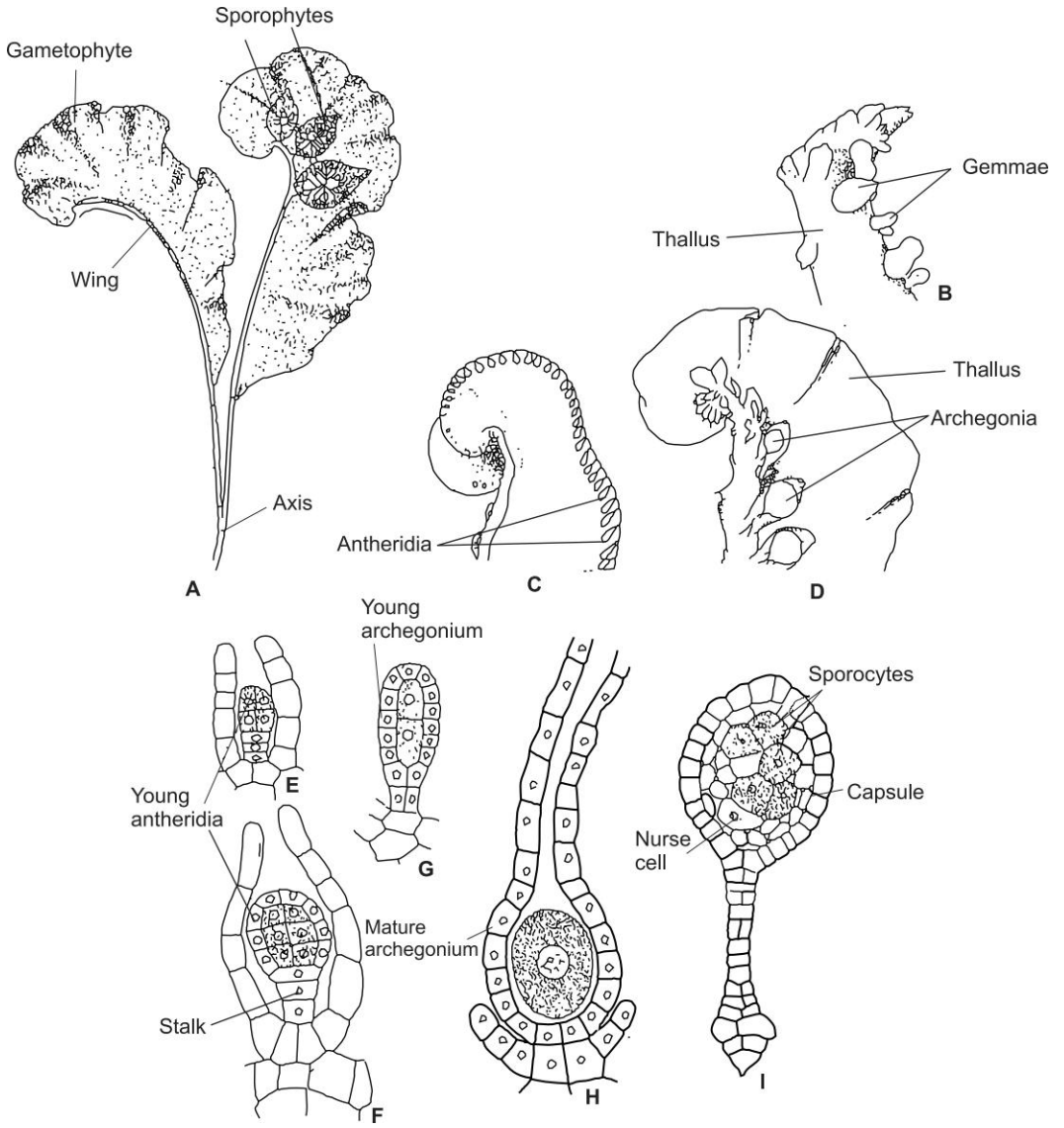


Fig. 5.3 *Riella.* A, Gametophyte with sporophytes of R. americana; B, Thallus with scales and gemmae; C, A part of the thallus with antheridia on the margin; D, A part of thallus with archegonia; E-F, Young antheridia of *R. affinis;* G-H, Young and mature archegonia of *R. affinis;* I, A sporophyte of *R. affinis*

Vegetative reproduction takes place by gemmae (Fig. 5.3 B), which develop between the rows of lateral and ventral scales. A mature gemma is a one-cell thick, spherical or oval structure. It is transversely constricted to two unequal-sized lobes. Studhalter and Cox (1940, 1941) called gemma of *Riella* as a **gemmaling**. On being detached, a gemmaling becomes meristematic in a place between two lobes and develops into an adult gametophytic phase.

Riella may be homothallic or heterothallic. Antheridia always develop in clusters in notches along the margin of the wing of gametophytic thallus. Archegonia develop singly at the juncture of the axis and wing.

Thompson (1943) studied the development of sex organs in *Riella* (Fig. 5.3 E–H) and observed that it is quite similar to that of *Sphaerocarpos*, described earlier under Article 5.2 (Fig. 5.1 C-I and 5.2 A-G). Minor deviations in the development of archegonial involucres, however, exist. Here, in *Riella*, the archegonial involucre originates from the stalk of the archegonium.

Thompson (1942, 1943) also studied the development of sporophyte in *Riella* and reported that it is also quite similar to that of *Sphaerocarpos*. Sporocytes and quadrinucleate nurse cells also develop by the sporogenous tissue of the sporophyte of *Riella* (Fig. 5.3I).

The haploid spore germinates in the form of a long germ tube, at the tip of which differentiate two apical cells. A series of short broad cells result due to the transverse divisions in these apical cells. These cells now divide longitudinally to form a small but flat thallus. Now the active cell division process in the juvenile phase is restricted only up to the margins, and soon a single apical cell is differentiated. Its activity results in the production of an adult phase of gametophyte bearing axis and wing.

TEST YOUR UNDERSTANDING

1. Sphaerocarpales include only three genera, namely *Sphaerocarpos*, *Riella* and _____.
2. The members of Sphaerocarpales are commonly called _____.
3. Why is the name "bottle-hepatics" given to members of Sphaerocarpales?
4. Give only one characteristic feature on the basis of which one can differentiate between Sphaerocarpaceae and Riellaceae.
5. Describe in brief some life-history details of *Sphaerocarpos* in about 500 words.
6. Draw neat and well-labelled diagrams of the following:
   (a) Male gametophyte of *Sphaerocarpos*
   (b) Female gametophyte of *Sphaerocarpos*
   (c) A mature sporophyte of *Sphaerocarpos*
   (d) A mature sporophyte of *Riella*
7. Is *Riella* an aquatic bryophyte or a terrestrial bryophyte?
8. In *Sphaerocarpos*, the archesporium is _____ in origin.
9. In *Sphaerocarpos*, is seta the very small or very long?
10. Write a short scientific note on *Riella* in about 200 words.
11. Draw a labelled diagram depicting external features of the gametophyte of *Riella* bearing sporophytes.

6

Hepaticopsida (Monocleales)

WHAT ARE MONOCLEALES? 6.1

As mentioned earlier under Article 3.4, Monocleaceae is a unigeneric family which shows characters of both Marchantiales and Jungermanniales, and has been placed by some bryologists under Marchantiales and by others amongst Jungermanniales. Due to *Calobryum*-type of archegonial development, Monocleales show closeness to the order Calobryales. It was Schuster (1963), who on the basis of his detailed studies of antipodal Hepaticae, suggested it to be placed in a separate order Monocleales, including a single family Monocleaceae and a single genus *Monoclea*. Schuster (1963) and later on Sandra Holmes (1986) treated Monocleales as an order of Hepaticopsida.

GENERAL CHARACTERISTICS OF MONOCLEALES 6.2

1. Monocleales is a monotypic order represented by a few species of its only genus *Monoclea*.
2. Plant body is thalloid and remarkably large, reaching up to 20 cm or more in length and 5 cm or more in breadth, and that is why these are commonly called "*giant-thallose-liverworts*".
3. Monocleales resemble members of the order Metzgeriales in possessing several characters like (i) lack of air chambers in the gametophyte, (ii) lack of ventral scales, (iii) long seta, (iv) elongate elaters, (v) elaborate calyptra, and (iii) an archegonial pouch.
4. Monocleales also resemble members of the order Marchantiales in possessing several similar characters like (i) specialised antheridial pads, (ii) embedded antheridia, (iii) unlobed spore mother cells, (iv) presence of oil bodies in isolated cells, (v) presence of two types of rhizoids, (vi) structure of neck of archegonia, and (vii) structure and dehiscence of the jacket of the capsule.

   Characters of Monocleales mentioned above under (3) and (4) suggest these members have an independent position as a separate evolutionary line, and hence an independent order of Hepaticopsida.
5. Monocleales differ from Marchantiales in possessing the unique hood-like sheath posterior to the female receptacle.
6. Monocleales also differ from Marchantiales in possessing the elongate capsule.

MONOCLEA 6.3

Monoclea is the sole representative of the only family (Monocleaceae) of order Monocleales. Two of its species reported so far are *M. gottschei* and *M. forsteri. M. gottschei* has been reported from tropical America while *M. forsteri* from tropical America as well as New Zealand.

Smith (1995) stated that "twice to thrice dichotomously branched gametophyte of *Monoclea forsteri* (Fig. 6.1A) is the *largest known thalloid gametophyte among Bryophyta*", and that is why these members are commonly called "*giant-thallose-liverworts*". Thallus lacks a clear midrib. The plant body is only 1 or 2 cells thick on the margins while it reaches up to 10 cells or more in thickness in the middle. The dorsal surface of the thallus is smooth. Rhizoids are confined only on the ventral surface of the thallus. They are smooth-walled as well as some also contain irregular thickenings and thus resemble tuberculate rhizoids. Scales are absent. Growing apex of the thallus is protected by some unicellular mucilaginous hairs.

Internally, the thallus is parenchymatous and remains covered by a layer of dorsal epidermis and ventral or lower epidermis. Cells of the dorsal or upper epidermis and few cells immediately beneath it are filled with chloroplasts. Few cells near the upper epidermis also contain some crystals of calcium oxalate. Walls of some of the cells also have conspicuous pores, which probably provide internal connection for transport of water. Air chambers, characteristic of Marchantiales, are absent in *Monoclea*. Some parenchymatous cells remain filled with oil bodies. Lower or ventral epidermis bear both smooth-walled and tuberculate rhizoids, and no scales.

Reproduction in *Monoclea* resembles *Riccia*, specially the ontogeny of antheridium as well as archegonium. *Monoclea* is heterothallic. The antheridia of each receptacle are produced in acropetal succession. They remain enclosed in semicircular to elongate, cushionlike pads called **receptacle**, which is present behind the growing point. Continuous growth and succession of male receptacles is observed because the apical initial is not utilised in their formation. Each antheridium develops in an antheridial chamber (Fig. 6.1B), which opens to the exterior by a long narrow canal. The mature antheridium is an ovoid shortly-stalked structure, somewhat pointed towards the apex. Each antheridial chamber opens on the dorsal surface by a pore.

The **archegonia** develop within a pouch-like, tubular structure called **involucre** (Fig. 6.1 C). The involucre develops in the form of a hood-like outgrowth covering the archegonia. It may attain a length of as much as 1.5 cm. Archegonia remain situated behind growing points of thallus. *Monoclea* resembles *Riccia* in ontogeny of its archegonium. A **mature archegonium** contains a swollen venter and a long neck of six vertical rows of jacket cells, and thus resembles *Riccia* as well as *Marchantia*. The neck contains as many as 10 neck canal cells. Since production of archegonia does not check apical growth in *Monoclea*, it is anacrogynous.

Two, three or even more sporophytes may be observed emerging from an involucral cavity (Fig. 6.1A). A young sporophyte also remains surrounded by a long calyptra (Fig. 6.1C). A mature sporophyte possesses a long and massive seta reaching up to a length of as much as 4 cm. At the top of the seta is present a dark-brown cylindrical capsule, which is broader than seta and attains a diameter of as much a 1.5 mm. Great seta length and elongate capsule in the mature sporophyte are the characters of *Monoclea* which bring it more close to Jungermanniales than that of Marchantiales.

Diploid zygotic nucleus divides first by many free nuclear divisions, and walls start appearing slightly at a later stage. Foot, seta and capsule become quite clear during the early embryogeny. A

single-layered amphithecium soon gets differentiated by periclinal division in the region of capsule. The sporogenous tissue is endothecial in origin. **Elaters**, having 2 or 3 helical thickenings, soon start differentiating in the sporogenous tissue. The fertile sporogenous cells form 8 isodiametric sporocytes, each of which divides reductionally to form 4 haploid spores.

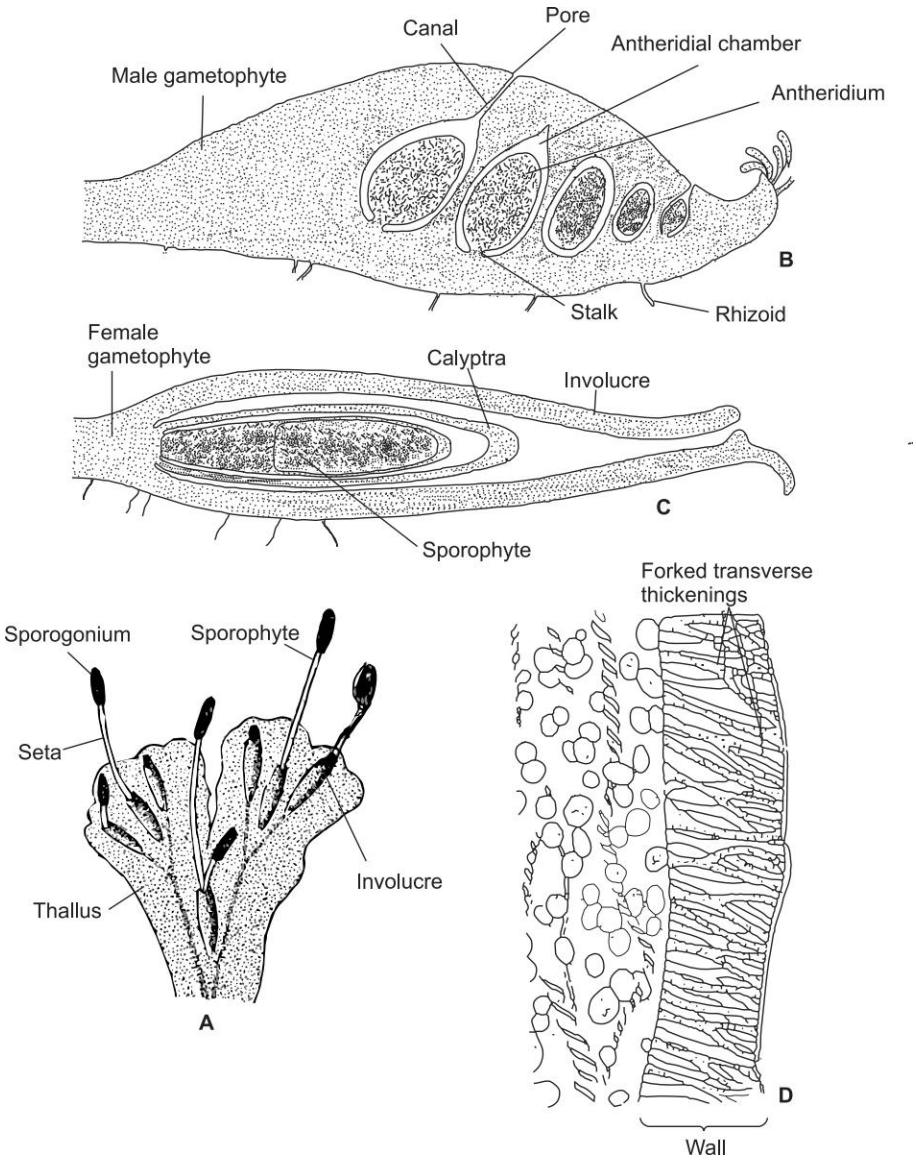


Fig. 6.1 A, A gametophyte of *Monoclea forsteri* bearing many sporophytes; B, Longitudinal vertical section through a male gametophyte of *M. gottscheri;* C, Longitudinal vertical section through a female gametophyte of *M. gottescheri* bearing a young sporophyte surrounded by calyptra and involucre; D, A part of the capsule wall with forked transverse thickenings

The wall of the capsule is single-layered and contains forked transverse thickenings (Fig. 6.1), a unique feature of *Monoclea*. Dehiscence of capsule takes place by a single longitudinal slit, through which elaters uncoil abruptly and help in dispersal of spores. It never dehisces into four valves. Each spore is a very small structure. It starts germinating almost immediately after dispersal. A multicellular mass of cells is produced, from which the rhizoids start developing soon. An apical cell soon develops, the activity of which results in the formation of a young gametophyte. Sporocytes in *Monoclea* also get partitioned into four parts by furrowing, and this type of cytokinesis is seen commonly in members of Jungermanniales. In Marchantiales, this type of cytokinesis is rarely seen.

TEST YOUR UNDERSTANDING

1. What are Monocleales?
2. Monocleales shows characters of both Jungermanniales and _____.
3. Who was the first to suggest that Monocleaceae should be placed under an independent order Monocleales?
4. How many genera do Monocleales include?
5. Write any four resemblances of Monocleales with Marchantiales.
6. What is the common name of Monocleales?
7. Write a detailed note on the life history of *Monoclea* in about 500 words.
8. In *Monoclea*, are scales present or absent?
9. Write a note on involucre of *Monoclea* in about 100 words.
10. Describe sporophyte of *Monoclea* in about 200 words.

7

Hepaticopsida (Marchantiales)

LIMITS OF MARCHANTIALES? 7.1

Marchantiales is the most prominent order of the class Hepaticae or Hepaticopsida (Rothmaler, 1951). As mentioned earlier under Article 3.4, "recent studies of molecular biology, genosystematics, phylogeny, diversification and classification of bryophytes (Newton et al., 2000; Norris, 2003; Shaw and Renzaglia, 2004; Zander, 2006; and Triotsky et al., 2007) treat all bryophytes under an independent subkingdom (*Bryobionta*) and divided it further into three phyla, of which one is *Marchantiophyta* (= Liverworts or Hepaticopsida or Hepaticae)". Here, Marchantiales is treated as circumscribed by Parihar (1987) and Rashid (1998), and also as detailed earlier under the classification of Hepaticopsida under Article 3.4.

Out of about 280 genera and approximately 9500 species of the class Hepaticopsida, Marchantiales is represented by about 35 genera and approximately 420 species (Parihar, 1987). Marchantiales are commonly called **chambered hepatics**.

COMMON GENERA 7.2

Besides *Riccia* and *Marchantia*, some of the other common genera of Marchantiales are *Aitchinsoniella*, *Asterella*, *Athalamia*, *Conocephalum*, *Cyathodium*, *Dumortiera*, *Mannia*, *Plagiochasma*, *Preissia*, *Reboulia* and *Targionia*.

GENERAL CHARACTERISTICS 7.3

Some of the salient features of Marchantiales are listed below:

1. Plant body is gametophytic, and gametophytes are usually prostrate, with dorsiventral thalli.
2. The thallus is usually dichotomously branched.
3. The dorsal surface is usually green, contains a midrib or mid-dorsal groove.
4. The ventral surface of thallus contains scales and rhizoids.

5. The rhizoids are of two types, smooth-walled and tuberculate.
6. The male and female sex organs (i.e. antheridia and archegonia) are either scattered along the midrib, or they are grouped in usually raised receptacles.
7. Internally, the thallus shows well-marked specialisation of tissues in most Marchantiales. In a few genera (e.g. *Dumortiera*), however, the differentiation of tissues is not well-marked.
8. The dorsal region contains several air chambers. Each air chamber opens outside by a well-defined air pore.
9. The green tissue is mainly confined to the dorsal region of the thallus.
10. The ventral region of the thallus is usually made up of compact colourless parenchymatous storage tissue.
11. Sometimes, some mucilage cells and cells filled with oil bodies are also present in the storage region.
12. Gemmae, when present, are in a cup-shaped structure called **gemma cup** (e.g. *Marchantia*).
13. Archeogoniophore usually bears several archegonia, which ultimately develop into several sporophytes.
14. The seta in the sporophyte is either short or absent.
15. The jacket or wall of the capsule is unistratose, i.e. single-layered in thickness.
16. In the sporogonia of Marchantiales, the columella is absent.
17. The capsule never opens by four regular valves. It dehisces in a variety of ways.

CLASSIFICATION 7.4

Campbell (1918) divided Marchantiales into three familes, viz. Ricciaceae, Corsiniaceae and Marchantiaceae.

Verdoorn (1932) recognised six familes under Marchantiales. These are Marchantiaceae, Operculatae, Astroporae, Targionaceae, Corsiniaceae and Ricciaceae.

Evans (1939) also recognised six families under Marchantiales, but these were not the same which were recognised by Verdoorn. Six familes of Marchantiales recognised by Evans were Marchantiaceae, Sauteriaceae, Rebouliaceae, Targionaceae, Corsiniaceae and Ricciaceae.

Campbell (1940) then revised his classification of Marchantiales on the basis of several new features, including (i) nature and development of the receptacle, and (ii) structure of the sporophytes, and divided this order into five families, viz. Ricciaceae, Corsiniaceae, Targionaceae, Monocleaceae and Marchantiaceae.

Shiv Ram Kashyap, a well-known Indian bryologist, made detailed studies of liverworts of western Himalayas and Punjab Plains and opined that all Marchantiales should be included only in three families, namely Ricciaceae, Monocleaceae and Marchantiaceae.

In the later years, Carr (1956) and Proskauer (1961) also made detailed studies of several curious thalloid hepatics (e.g. *Carrpos sphaerocarus*) and suggested several new changes in the classification of Marchantiales.

Only Ricciaceae and Marchantiaceae are discussed here in some detail.

RICCIACEAE 7.5

A family of only three genera (*Riccia*, *Ricciocarpos* and *Oxymitra*) and about 150 species, Ricciaceae members show the following general characteristics:

1. Ricciaceae are the simplest members of the order Marchantiales containing a gametophytic thalloid plant body, which is usually prostrate, flat, dorsiventral and ribbonlike.
2. Upper or dorsal region of the thallus is called **photosynthetic region**, which contains either large air chambers or narrow air canals enclosed by filaments of green, chlorophyll-containing cells.
3. Well-marked pores are either absent or rudimentary.
4. A median longitudinal groove or strip, extending backwards from the growing apex, is present on the dorsal surface.
5. Usually, the sex organs are borne in the region of the median longitudinal groove.
6. The sex organs (antheridia and archegonia) are usually immersed singly in cavities on the dorsal surface of the thallus.
7. The neck and the apical portion of the archegonium usually remains projected above the surface of the thallus.
8. The sporogonium remains usually sunken in the tissue of the thallus.
9. The sporogonium usually consists of only a saclike capsule. The foot and seta are absent.
10. The archesporium forms only the spores.
11. The elaters are absent.
12. The spores are disseminated or become free only when the thallus breaks down.

Life-history details of only *Riccia* are given here.

RICCIA 7.6

7.6.1 Systematic Position

Division—Bryophyta
Class—Hepaticopsida
Order—Marchantiales
Family—Ricciaceae
Genus—*Riccia*

7.6.2 Distribution and Habitat

Riccia is a cosmopolitan genus of bryophytes. More than 200 of its species have so far been reported, the majority of which are the inhabitants of the southern hemisphere. All the so-far reported species of *Riccia* are terrestrial, except *R. fluitans*, which is the only aquatic, free-floating or submerged species. The terrestrial species grow luxuriantly on damp soil and rocks. More than 30 species of *Riccia* have so far been reported from India, specially from eastern Himalayas and the hills of southern India. Some of the Indian species, growing commonly on moist soils, garden beds, stones and river banks are *Riccia discolor*, *R. cruciata*, *R. crystallina*, *R. pathankotensis, R. gangetica, R. billarderi, R. frostii* and *R. melanospora* (Fig. 7.1 A-F).

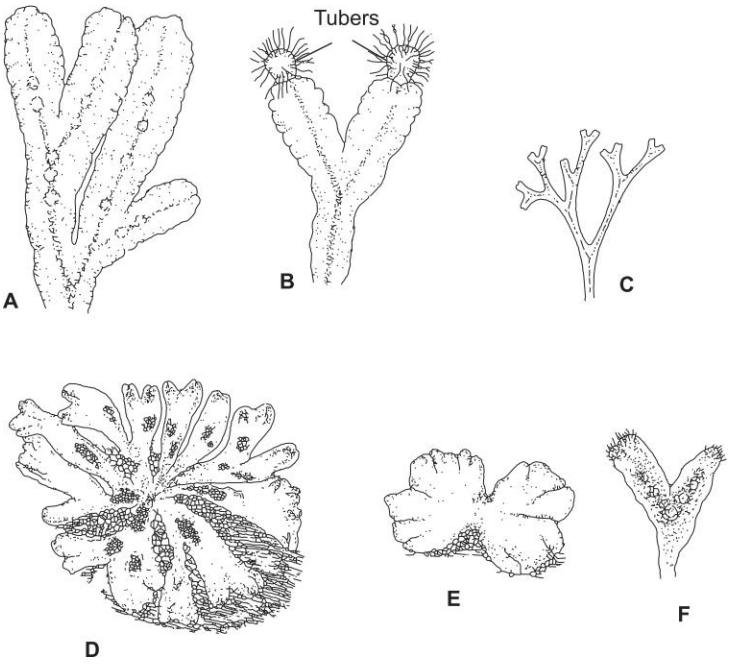


Fig. 7.1 A-F, External features of the gametophytes of some Indian species of *Riccia.* A, R. discolor *(R. himalayensis);* B*, R. billardieri;* C*, R. fluitans;* D*, R. pathankotensis;* E*, R. cruciata;* F*, R. melanospora*

Riccia fluitans, the only aquatic species, occurs floating in stagnant water or submerged a little below the standing water surface.

The name *Riccia* has been given to the genus in honour of a Florentine politician, P F Ricci.

7.6.3 External Features of Gametophyte

The gametophytic plant body of *Riccia* is thalloid, flat, prostrate, fleshy and dorsiventral. The thallus branches dichotomously, and due to repeated dichotomy, it becomes a rosette-shaped structure (Fig. 7.2 A). Each branch of the thallus is usually obcordate and sometimes linear to wedge-shaped and ribbonlike.

A thickened mid-dorsal groove is present on the dorsal surface of the thallus (Fig. 7.2 B). This groove extends up to the apical portion of the thallus, where it forms an apical notch. The apical notch bears the growing point of the thallus.

The ventral surface (Fig. 7.2C) of the thallus possesses rhizoids and scales. The rhizoids are hairlike elongated structures. Their main functions include (i) attachment of thallus to the substratum, and (ii) absorption of water and soil solutes. Rhizoids of *Riccia* thus function as roots of higher plants. Rhizoids are of two types, smooth-walled and tuberculate. The **smooth-walled rhizoids** (Fig. 7.2 D, E) are unicellular, smooth-walled and elongated structures with colourless contents.

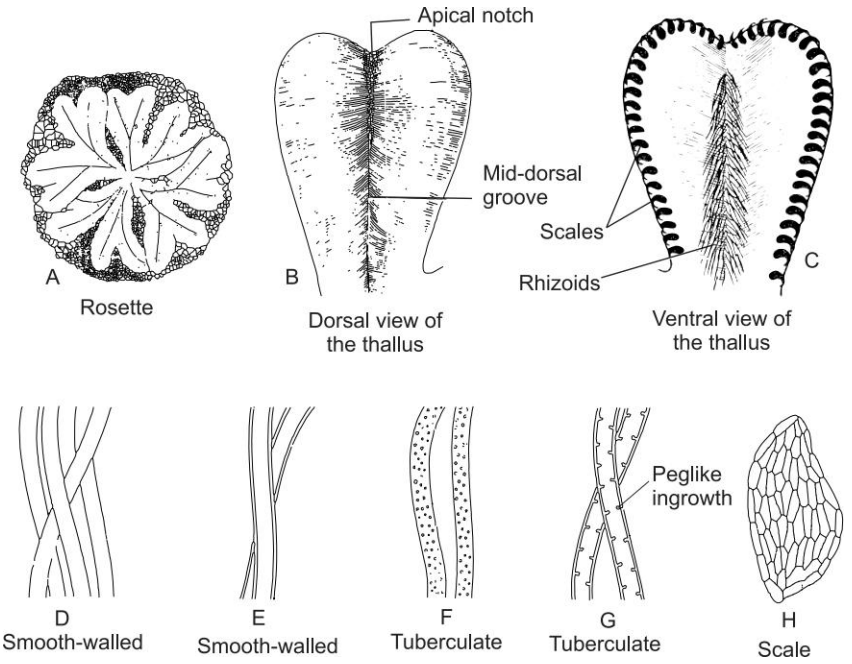


Fig. 7.2 External features, scales and rhizoids of *Riccia.* A, A rosette; B, Dorsal surface of thallus; C, Ventral surface of thallus; D, Smooth-walled rhizoids in surface view; E, Smooth-walled rhizoids in optical section; F, Tuberculate rhizoids in surface view; G, Tuberculate rhizoids in optical section; H, A scale.

The **tuberculate rhizoids** (Fig. 7.2 F, G) have peglike or platelike ingrowths, which project into the lumen from the wall. Rhizoids are absent in *R. fluitans*, the only aquatic species of the genus.

Scales (Fig. 7.2 H) are multicellular, one-cell-thick structures present on the ventral surface of the thallus. These are violet-coloured bodies present on the margin. The violet colour is due to the presence of a pigment, which remains dissolved in the cell sap. Scales are poorly developed or even absent in some species, e.g. *Riccia crystallina*. The scales project forward near the growing point and thus protect the young growing apex of the thallus.

Sex organs are present in the mid-dorsal groove region on the dorsal surface of the thallus. The sporophytes, however, may be seen as black dots, when mature.

Riccia fluitans (Fig. 7.1C), the only aquatic spacies of *Riccia*, has a long, narrow, delicate, flattened, ribbonlike, thalloid plant body. Its thalli are dichotomously branched. It lacks scales and rhizoids. In the terrestrial conditions, the thalli of *R. fluitans* become thick, broadly channelled and also develop numerous rhizoids as well as scales. Such scales are, however, confined to near the apex of the lobes of the thallus.

7.6.4 Anatomy of the Thallus

The thallus appears like a boat-shaped structure in a vertical transverse section (Fig. 7.3 A), when viewed under a dissecting microscope. It is thick in the midrib region and gradually becomes thin towards the margins. The thallus is dorsiventrally differentiated into an outer or upper green **photosynthetic region**

and an inner or lower colourless storage region (Fig. 7.3 A, B). The **storage region** remains bounded on the lower side by a layer of lower epidermis (Fig. 7.3 B), which bears two types of rhizoids in the central region. These are *smooth-walled rhizoids* and *tuberculate rhizoids*. Compactly arranged, parenchymatous, starch-containing cells are present in this ventral region, which is primarily a storage tissue.

The upper, green photosynthetic region consists of more or loss erect vertical rows of unbranched photosynthetic filaments or assimilatory filaments. These filaments remain separated by narrow air-filled spaces called ***air chambers***. Each cell of these filaments possesses numerous chloroplasts. Each air chamber opens to the outside through a simple pore called ***air pore***. The air pores are actually the intercellular spaces between the upper epidermal cells (Fig. 7.3 B). The uppermost cells of the photosynthetic filaments are comparatively large, lack chloroplasts and are thus colourless. These cells form an ill-defined upper epidermis, the continuity of which is broken by air pores. The air chambers communicate with the outer atmosphere on the dorsal surface of the thallus by air pores. Boat-shaped vertical transverse sections of the thallus contain violet-coloured *scales* (Fig. 7.3 A), which are multicellular structures, one cell in thickness.

In *Riccia fluitans*, the chlorophyllous tissue is made up of variously directed lamellae consisting of one layer of cells (Fig. 7.3 C) enclosing large polyhedral air chambers. They are closed by an almost continuous dorsal epidermis. Only a few air pores are present. Anatomy of some species is depicted also in Fig. 7.3 D, E.

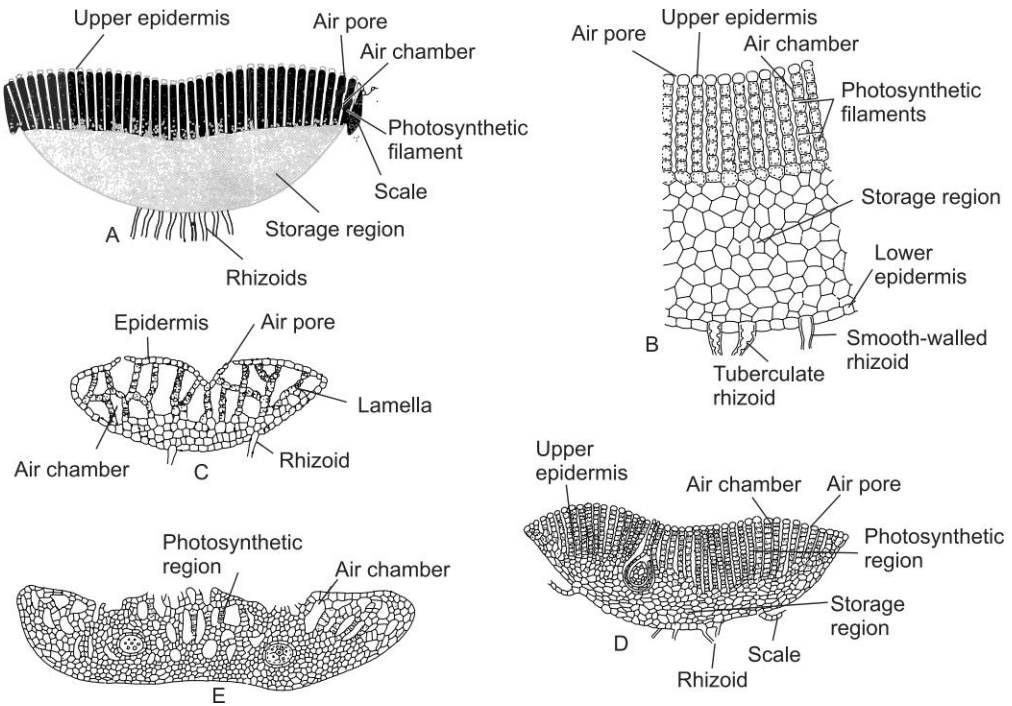


Fig. 7.3 *Riccia.* A, VTS of thallus (diagrammatic); B, VTS of thallus (a part cellular); C, VTS of thallus of *Riccia fluitans*; D, VTS thallus of *R. glauca*; E, VTS thallus of *R. crystallina*

7.6.5 Apical Growth

Thallus grows by the activity of a growing point located at the apex. This growing point consists of three to five or more apical cells which are meristematic in nature. Each apical cell has four cutting faces, of which one is dorsal, another is ventral and the remaining two are lateral.

In surface view, each apical cell appears rectangular, but in vertical longitudinal section, it appears triangular (Fig. 7.4 A, B). Growth of the thallus is mainly contributed by segments which are cut off from the dorsal and ventral faces of the apical cells. A major part of the thallus tissue is derived from the dorsal segments. However, the lowermost cell layer of the thallus, rhizoids and scales are contributed by the ventral segments.

Portions of the thallus contributed by five dorsal segments (D1, D2, D3, D4 and D5) and five ventral segments (V1, V2, V3, V4 and V5) are shown in Fig. 7.4. Dichotomy in the thallus originated by the cessation of the meristematic activity of one or more cells in a row of apical cells. Meristematic activity of other adjacent apical cells results in the formation of two separate groups of cells, giving rise ultimately to dichotomy.

Regarding the origin of the air chambers, some bryologists believed that the air spaces are depressions in the surface of the thallus where growth of the tissue stops, and growth is more vigorous in the adjacent parts, thus resulting in the formation of air chambers. This view has now been discarded.

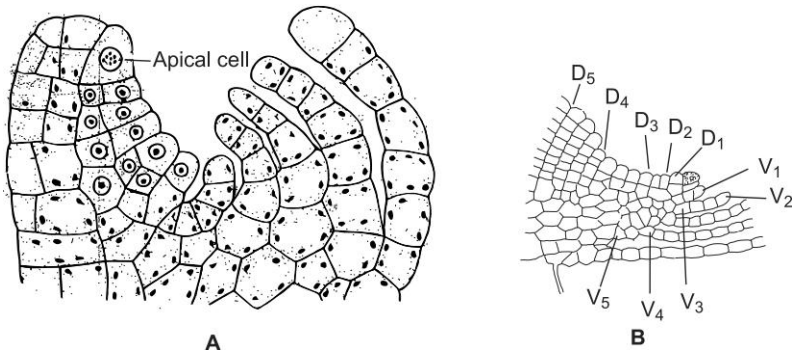


Fig. 7.4 A, Vertical longitudinal section through the growing point of thallus; B, Vertical longitudinal section of the thallus apex of *Riccia glauca* showing a triangular apical cell and its derivatives

Bryologists supporting the second view believe that air chambers develop "by splitting of the internal cell walls in the originally compact upper tissue of the thallus, their origin being schizogenous like that of the intercellular spaces in the parenchyma of vascular plants" as stated by Parihar (1987). Such splitting of the internal cell walls begins endogenously, i.e. below and extends upwards (Pietsch, 1911). Some others, however, opine that splitting starts exogenously, i.e. begins at the surface and extends downwards.

7.6.6 Vegetative Reproduction

Some common methods of vegetative reproduction in *Riccia* are listed below:

1. Progressive Death and Decay This is the most common method of vegetative reproduction in almost all species of *Riccia*. Progressive decay starts from the posterior part of the thallus, and

ultimately the older parts die. When this process of death and decay reaches up to the place of dichotomy, the surviving branches of the thallus start behaving as independent thalli.

2. Adventitious Branches In species like *Riccia fluitans*, adventitious branches develop from the ventral surface of the thallus. These branches, on separation from the main thallus, may develop into new thalli.

3. Apex of Thallus In species, like *R. himalayensis*, the apex of the thallus grows down into the moist soil and becomes thick at the end of the growing season. It develops into a new thallus when favourable conditions return in the next season.

4. Apex of Rhizoids In a few species, like *R. glauca*, the apical part of the rhizoid has the ability to form a thallus, in much the same way as a germinating spore forms a germ tube and then a young thallus.

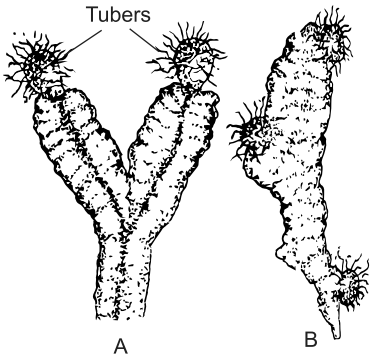


Fig. 7.5 Tubers of two species of *Riccia.* A, *R. billardieri;* B, *R. discolor.*

5. Tubers Thalli sometimes develop perennating tubers, which have the ability to survive in unfavourable conditions. On return of favourable conditions, these tubers may grow into new thalli, as in *R. billardieri* (Fig. 7.5 A), *R. discolor* (Fig. 7.5 B), *R. perennis*, etc.

7.6.7 Sex Organs

The two sex organs in *Riccia* are **antheridia** and **archegonia**. In monoecious or homothallic species (e.g. *R. billardieri*, *R. crystallina*, *R. gangetica*, *R. glauca* and a majority of other species), both antheridia and archegonia develop on the same thallus. But in dioecious or heterothallic species (e.g. *R. bischoffi*, *R. curtisii*, *R. discolor* and some more species), antheridia and archegonia develop on separate thalli.

The sex organs develop in the region of median longitudinal furrow on the dorsal surface of the thallus. This furrow extends backwards from the growing point. Sex organs develop in acropetal succession, and serial sections through a thallus may reveal almost all stages of their development. They arise from the segments which are cut off by an apical cell usually very close to, i.e. only 2-3 cells away from the apical cell. Sex organs, in the different stages of their development, can be seen on the same thallus. Due to the rapid development of the tissue surrounding the sex organs, they soon appear to be embedded in the thallus (Fig. 7.3 D) or surrounded by a chamber-like structure called **antheridial chamber** in case of male sex organ (i.e. antheridium) and **archegonial chamber** in case of female sex organ (i.e. archegonium).

7.6.8 Development of Antheridium

Development of antheridium starts from a single superficial initial cell. This cell can be identified due to its upward growth, and dense contents in relation to its neighbouring cells on the dorsal furrow, a few cells behind the apical cells. It is known as **antheridial initial** (Fig. 7.6 A). Soon it becomes papillate and divides transversely into a lower **basal cell** and an **outer cell** (Fig. 7.6 B). The basal cell remains

embedded in the thallus and forms the stalk of the antheridium. The outer cell projects slightly above the thallus, undergoes several divisions and forms the rest of the antheridium. A series of transverse divisions in the outer cell forms a filament of four superimposed cells (Fig. 7.6 C), of which two upper cells are the primary antheridial cells and the two lower ones are the **primary stalk cells**. Two lower primary stalk cells form the stalk of the antheridium, on which develops the globular body of the antheridium. Two upper primary antheridial cells divide by two successive vertical divisions at right

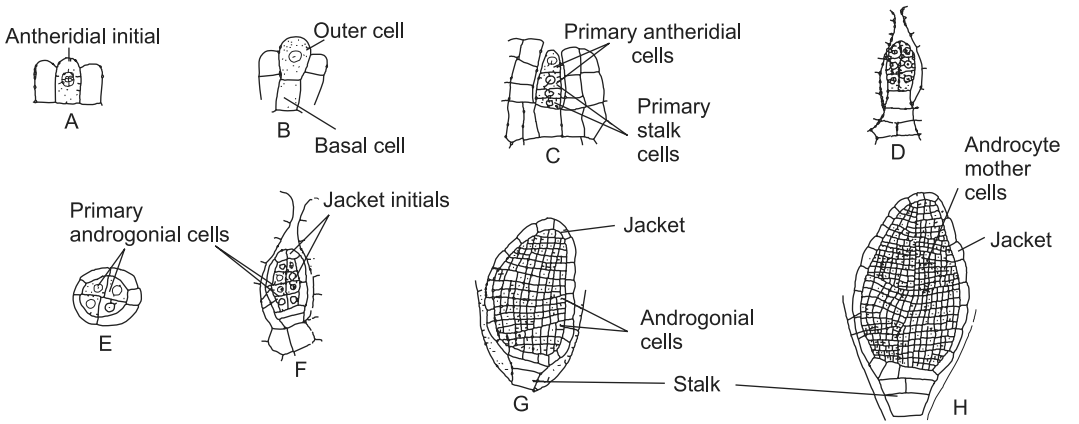


Fig. 7.6 A-H, Development of antheridium in *Riccia*

angles to one another, and thus develop two tiers of four cells each (Fig. 7.6 D). Both the tiers of four cells each now divide periclinally to from an outer layer of eight **jacket initials**, which are sterile, and a central group of eight **primary androgonial cells** (Fig. 7.6 E, F), which are fertile. Jacket initials now divide anticlinally to form a single layer of sterile jacket around the antheridium (Fig. 7.6 G). Repeated divisions in the primary androgonial cells give rise to small cubical fertile androgonial cells, the last generation of which are known as **androcyte mother cells** (Fig. 7.6 H).

Each androcyte mother cell divides diagonally into two triangular androcytes (Fig. 7.7 A). Each androcyte is uninucleate and metamorphoses into an antherozoid (Fig. 7.7 B-F). During the process of metamorphosis, each androcyte contains a prominent nucleus and an extranuclear granule called **blepharoplast** (Fig. 7.7 B). The blepharoplast granule develops in the peripheral part of the protoplast of androcyte. Soon the androcyte looses its triangular shape, and becomes a spherical body (Fig. 7.7 C). The blepharoplast elongates in the form of a cordlike structure and occupies about 3/4th of the way of the developing androcyte. The nucleus assumes a crescent shape, moves towards the periphery of the protoplast and comes in contact with the blepharoplast (Fig. 7.7 D, E). Two flagella are produced from one thickened end of the blepharoplast, which is quite a prominent structure (Fig. 7.7 F).

A mature antherozoid is uninucleate with a homogeneous nuclear portion, which occupies the major part of the antherozoid. Blepharoplast, the extranuclear granule, ends in a head bearing two long flagella (Fig. 7.7 F). The antherozoid moves with the help of its flagella. Both the flagella are attached at the same level on opposite sides. The function of one flagellum is to help in propulsion while the other flagellum helps in rotation and also in changing the direction of the antherozoid.

A **mature antheridium** (Fig. 7.6 H) consists of a small stalk and a globular or club-shaped body. The stalk is short and few-celled and remains attached at the base of the antheridial chamber. The

body of the antheridium is composed of a central mass of either androcytes or antherozoids. It remains surrounded by a single layer of sterile jacket, made up of tangentially elongated cells.

Antherozoids are liberated through a pore of the antheridial chamber, present on the dorsal surface of the thallus. All cell walls within the mature antheridium disappear, and a semiliquid or viscous content develops within. The antherozoids lie there in this viscous substance. Water drops enter within the antheridial chamber. Cells of the antheridial jacket absorb this water by imbibition. They become softened and finally break open to liberate the antherozoids, along with the semifluid mucilaginous mass.

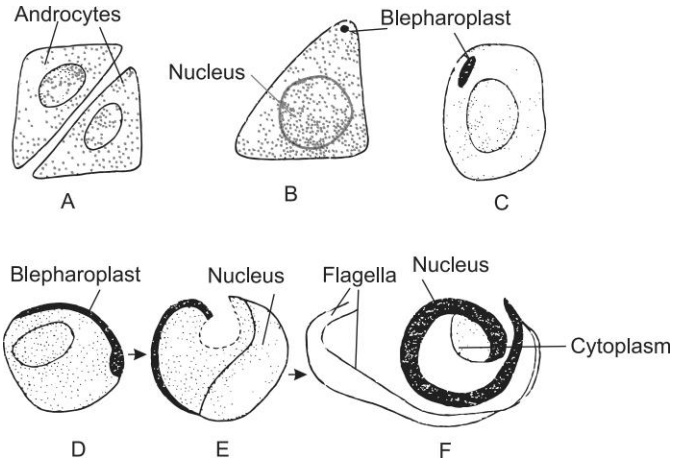


Fig. 7.7 A-F, Process of spermatogenesis and formation of an antherozoid in *Riccia*

7.6.9 Development of Archegonium

Development of archegonium starts from a single superficial cell on the dorsal surface of the thallus, quite close to the apical cell. This is called **archegonial initial**, which soon becomes papillate (Fig. 7.8 A) and divides by a transverse division into an **outer cell** and a **basal cell** (Fig. 7.8 B). The outer cell ultimately forms the body of the archegonium while the basal cell finally develops into the embedded portion of the archegonium. The outer cell divides by three successive intersecting vertical divisions to form three **peripheral initials** and a fourth median cell called **primary axial cell** (Fig. 7.8 C-E).

Three **peripheral initials** divide by radial longitudinal walls to form six **jacket initials**, which again divide by transverse walls to form two superimposed tiers of six cells each. Upper tier of six cells form the neck and are called neck initials while the lower tier forms the venter, called **venter initials**. Simultaneously, the **primary axial cell** divides transversely to form upper smaller **primary cover cell** and the lower larger **central cell** (Fig. 7.8 F-I).

Repeated transverse divisions in the neck initials form a tube-like neck. It is made up of 6 to 9 cells in height and of six vertical rows of neck cells, as can be seen in the transverse section (Fig. 7.8 J). Simultaneously, six **venter initials** divide by several transverse and vertical divisions to form the **jacket of the venter**. It is made up of 12 to 20 cells in perimeter.

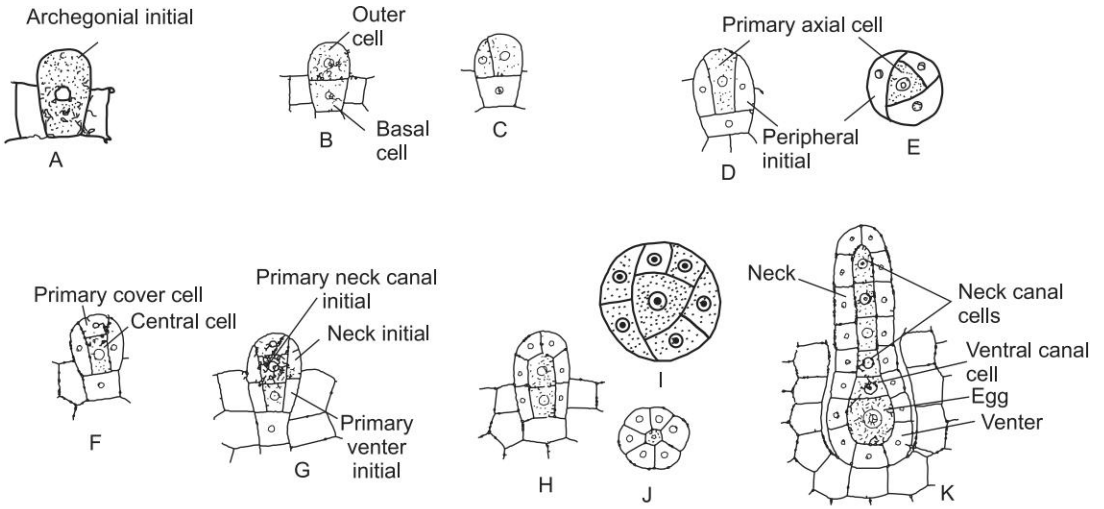


Fig. 7.8 A-K, Showing development of archegonium in *Riccia* (Note: E, I and J are in transverse sections)

At the top of the neck is present the primary cover cell (Fig. 7.8 F). It divides by two successive vertical divisions at right angles to each other and gives rise to four **cover cells**. The central cell (Fig. 7.8 F) divides transversely into an upper **primary neck canal initial** and a **primary venter initial** (Fig. 7.8 G). The primary neck canal initial divides transversely to form a row of four **neck canal cells** (Fig. 7.8 K). The primary venter initial also divides by one transverse division to form an upper small **ventral canal cell** and a lower large **egg** (Fig. 7.8 K).

A **mature archegonium** (Fig. 7.9) is a flask-shaped, long-necked structure. It remains attached to the thallus tissue on the dorsal surface by a short stalk. It contains a swollen venter and an elongated neck. The neck is a single-layered, tube-like structure made up of 6 to 9 tiers of elongated cells arranged in six vertical rows and surrounding a fine narrow canal. At the upper part of the neck are present four cover cells. The canal of the neck contains four neck canal cells. The venter contains a one-layered wall and encloses a small ventral canal cell and a large egg. Immediately prior to fertilisation, the neck canal cells and ventral canal cell disintegrate and form a mucilaginous mass. Due to the pressure of this mucilaginous mass, all the four cover cells of the neck separate apart from one another, and some of the mucilaginous mass also extrudes from the tip of the archegonial neck.

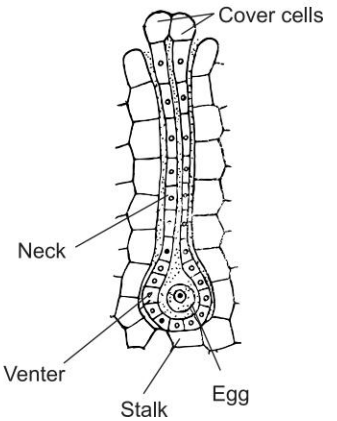


Fig. 7.9 A mature archegonium of *Riccia.*

7.6.10 Fertilization

The mucilaginous mass, formed by the disintegration of neck canal cells and venter canal cell imbibes water, swells up and exerts a pressure on cover cells to separate. Due to all these activities, the canal is open up to the venter. This mucilaginous mass also attracts spermatozoids swimming in the surface film of water. The attraction is a chemotactic phenomenon due to the presence of some proteins and

inorganic salts in the mucilage. The spermatozoids are guided up to the egg due to this chemotactic phenomenon. A spermatozoid (X) fuses with the egg (X), resulting into the formation of a diploid structure called **zygote** (2X). The zygote soon secretes a wall, increases in volume and finally occupies the entire lumen of the venter (Fig. 7.10 A–C).

7.6.11 Sporophyte

1. Development of Embryo The diploid zygote is the first cell of the sporophytic generation or asexual generation. It soon secretes a cell wall of its own, enlarges and almost fills the cavity of the **venter** (Fig. 7.10 C). Cells of the venter start dividing periclinally and then also anticlinally to form a bilayered calyptra. Simultaneously, the zygote divides first by a transverse division (Fig. 7.10 D) to form two almost equal-sized cells. Both these cells now divide vertically to form a four-celled embryo or *quadrant-stage* (7.10 E). Soon follows one more vertical division at right angles to the first one and thus results an eight-celled or **octanct stage** of the embryo. In this usual course of divisions resulting in octanct stage of the embryo, there may be variations in different species of *Riccia*.

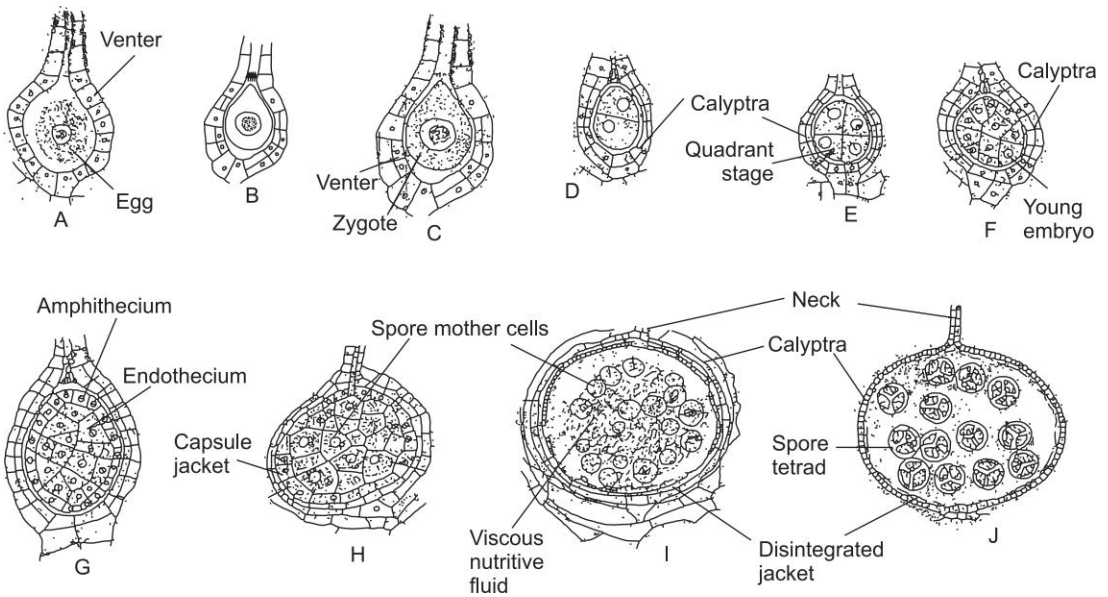


Fig. 7.10 A-J Some stages in the development of sporogonium, formation of nutritive fluid and spore tetrads in *Riccia*

The young eight-celled embryo now divides in all the planes without any definite sequence to form a multicellular (20 to 40-celled) spherical mass of cells (Fig. 7.10 F). It now divides periclinally into an outer layer of amphithecium and an inner mass of cells, which represents the endothecium (Fig. 7.10 G). The amphithecium forms the **jacket** layer of the young sporogonium while the **endothecium is archesporial in origin**. Cells of the jacket layer divide only by radial walls to form a single layer of jacket. This layer is sterile and protects the sporogonium.

The endothecial archesporium, which is the first cell generation of sporogenous tissue, divides and redivides (Fig. 7.10 H) several times to form a large mass of sporogenous cells. All these cells

are potential **sporocytes** or **spore mother cells**. Each of these spore mother cells is diploid, divides **reductionally** and forms four haploid spores (Fig. 7.10 I, J). In *Riccia crystallina* and a few more species, some spore mother cells fail to produce spores. Such spore mother cells form abortive **nutritive cells**. Some bryologists (Pagan, 1932) opined that nutritive cells are forerunners of elaters, found in some other Marchantiales (e.g. *Marchantia*).

The dividing spore mother cells are present in large amount of viscous nutritive fluid (Fig. 7.10 I), which serves as nourishment for these spore mother cells and developing spores.

2. Sporogenesis Formation of haploid spores from the diploid spore mother cells is called **sporogenesis**. The sporogenesis starts with the contraction of cytoplasmic contents of spore mother cells or sporocytes. Each spore mother cell divides by two successive divisions and develops into a tetrad of spores (Fig. 7.10 J). It also results in a reduction division, thereby the chromosome number is reduced to half, i.e. each diploid spore mother cell changes into four haploid spores arranged first in the form of a tetrad. The cell plate is incomplete during the first division, and after the completion of the second division, the cell plates delimiting four spores are formed simultaneously. All the four spores of a spore tetrad remain opposed to one another and also remain surrounded by the wall of the spore mother cell (Fig. 7.11 A-F) till the maturity of the spore wall.

3. Spore Each spore (Figs. 7.12 A-B; 7.13) is a uninucleate structure surrounded by three wall layers:

(a) The outermost **perispore** or **exosporium** is thin, mucilaginous but very strongly cutinized;

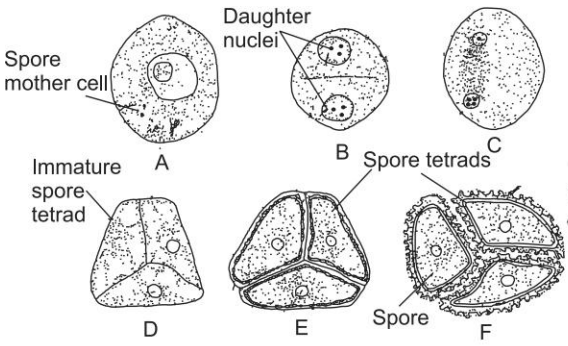


Fig. 7.11 A-F, Process of sporogenesis in *Riccia.*

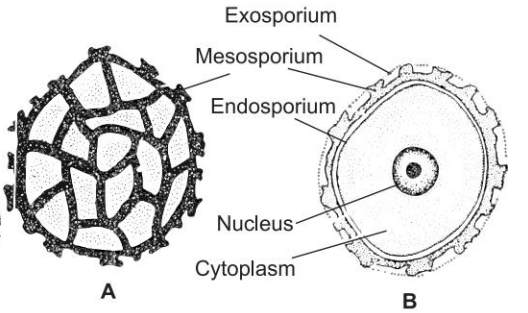


Fig. 7.12 *Riccia* spores. A, Surface view; B, Optical view.

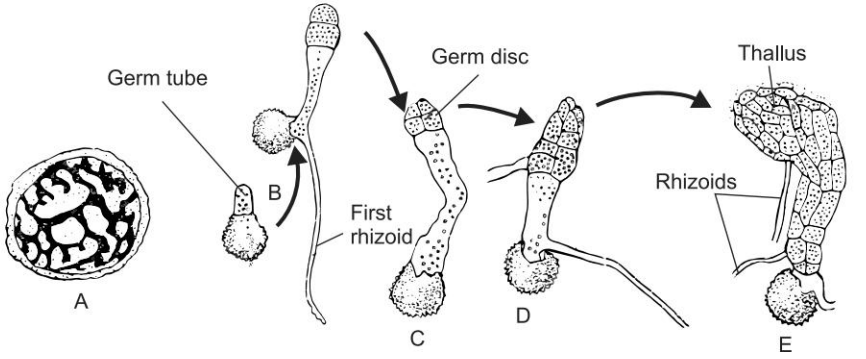


Fig. 7.13 A-E. A mature spore (A) and stages of its germination and initiation of a gametophyte (B–E) in *Riccia*

(b) **Exine** or **mesosporium** is a tough outer spore coat, in three concentric layers, and;
(c) **Intine** or **endosporium** is the innermost layer which is thin and homogenous.

The exine is variously ornamented. It shows reticulate sculptures, irregular reticulum or even tubercles. Different species of *Riccia* may be identified on the basis of ornamentation patterns of exine. In a majority of the species of *Riccia*, each spore of a tetrad has two faces, the convex distal face and opposite to it are three flattened faces which form a pyramid-like structure.

4. Dispersal of Spore Spores in *Riccia* are dispersed without any definite mechanism, simply (i) by disorganisation of wall of capsule or sporogonium, and (ii) by decaying of the surrounding tissue of the thallus. Due to the absence of any definite mechanism, the spores may remain inside the thallus for as long as one year or even more. Finally, they are dispersed by air currents or even by splashing raindrops. On being dispersed, they germinate into gametophytes.

5. Germination of Spore Spores start germinating only in moist conditions. At the time of germination, a spore absorbs some water swells, and starts producing a **germ tube** (Fig. 7.13 A). Usually, the spores remain adhered in tetrads in the initial stages of their germination. The germ tube is an elongated structure and remains filled with chloroplasts and oil globules. Its cell contents start accumulating towards the apex. Soon the apical part of the germ tube is separated by a transverse division. The so-formed cell now again divides by one more transverse division and then by a vertical division in both these cells, resulting into a 4-celled body or **germ disc** (Fig. 7.13 B-C). From the lowermost part of the germ tube also develops the first rhizoid (Fig. 7.13 B). Out of the four cells of the germ disc, one starts functioning as an **apical cell** with two cutting faces. The activity of this apical cell results in the formation of a multicellular young thallus (Fig. 7.13 D-E). It gets fixed in the soil by the development of some more rhizoids from the newly-formed and young multicellular thallus. Sex organs develop on such newly-formed thalli, and the life history (Fig. 7.14A-N) keeps on repeating again and again.

7.6.12 Life Cycle of *Riccia*

Diagrammatic life cycle is depicted in Fig. 7.14A–N.

MARCHANTIA 7.7

7.7.1 Systematic Position

Division—Bryophyta
Class—Hepaticopsida
Order—Marchantiales
Family—Marchantiaceae
Genus—*Marchantia*

7.7.2 Distribution and Habitat

Marchantia, the best-known genus of the family Marchantiaceae, is represented by about 65 species, distributed widely all over the world. The name to the genus was given in honour of Nicolas Marchant, a French botanist. Chopra (1943) reported about 11 species of *Marchantia* from India, mainly from the

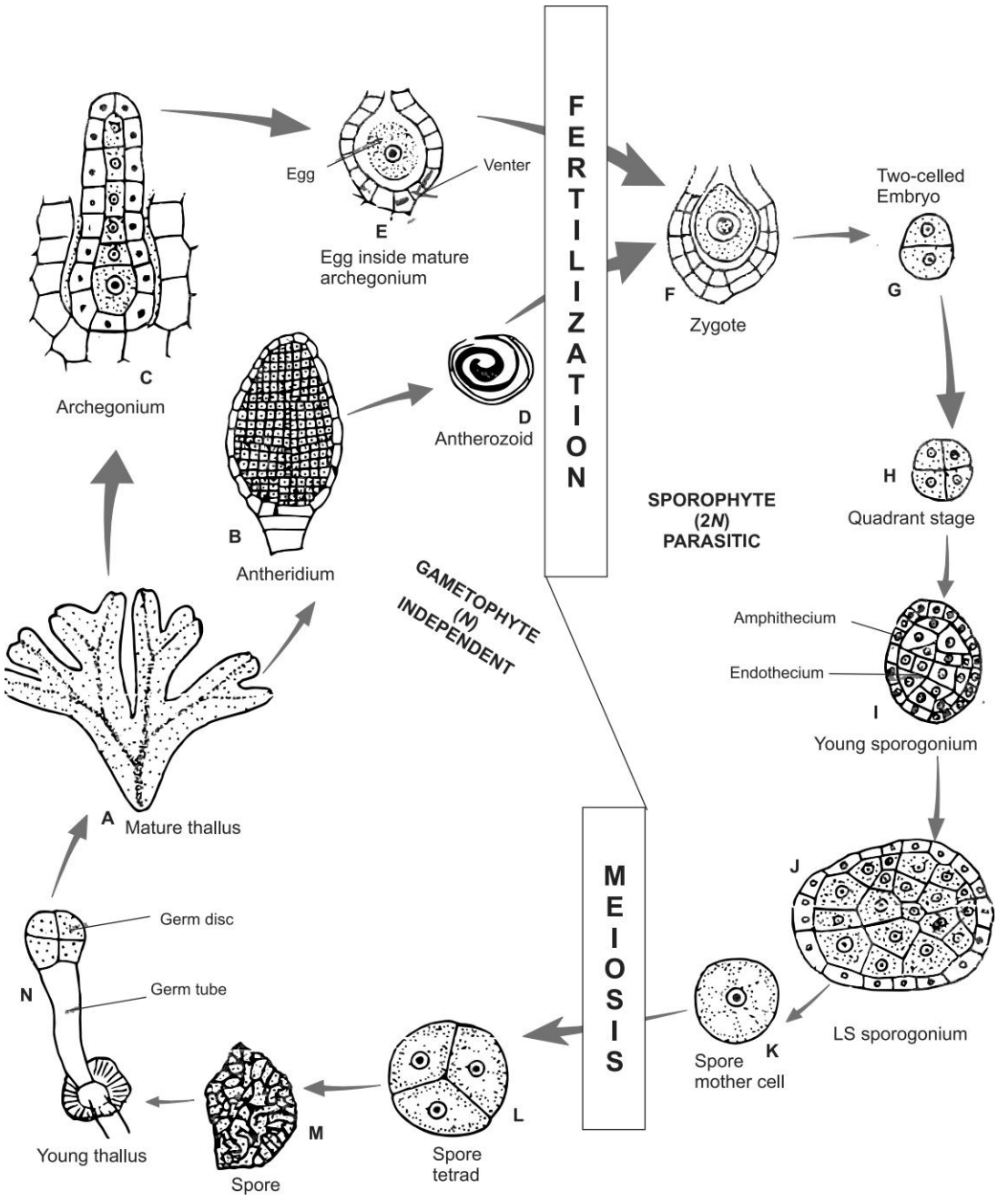


Fig. 7.14 A–N Diagrammatic representation of the life cycle of *Riccia*

Himalayas. All the so-far reported species are terrestrial and grow on the ground or soil in moist, shady and cool conditions. It is also commonly seen on the sides of streams, wet rocks, damp burnt soil, walls of the wells, swampy meadows and similar other surroundings.

Marchantia polymorpha is the best-known species. Kashyap (1919) reported *M. palmata*, *M. nepalensis* and *M. polymorpha* from various parts of India. Udar (1970) reported 6 species from different parts of India. The genus occurs commonly in almost all the hilly regions of India.

GAMETOPHYTIC PHASE

7.7.3 External Features of Gametophyte

The gametophytic plant body is a thalloid, green, prostrate and dichotomously branched structure with a dorsiventral symmetry. Thalli attain a length of 2 to 10 cm or more. Each lobe or branch of the thallus has a notch at the apex. At the bottom of the notch is located the growing point.

On the **dorsal** or **upper surface** of the thallus (Fig. 7.15) is present a clear midrib. Several diamond-shaped rhomboidal or polygonal areas are also present. The boundaries between these areas mark the limit of the underlying air chamber. A dotlike structure, present in the centre of each polygonal area, represents the **air pore**. Several thalli bear many cup-shaped, subsessile **gemma cups** (Fig. 7.15) on the dorsal surface. Many **gemmae** are present in each gemma cup. They are the means of vegetative reproduction.

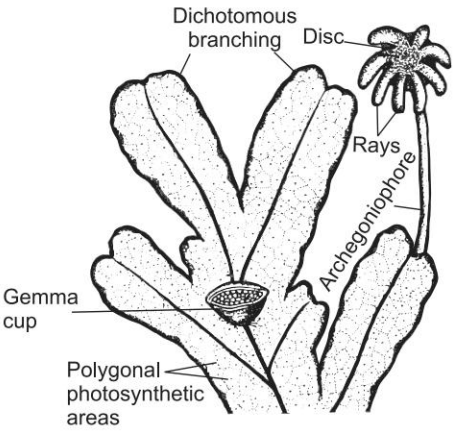


Fig. 7.15 *Marchantia polymorpha* showing dorsal surface of the thallus

Mature thalli bear a few stalked, upright, fertile branches, having either antheridia or archegonia at their top portion. These antheridia-bearing branches are called **antheridiophores**, while the archegonia-bearing branches are called **archegoniophores** (Fig. 7.15).

On the ventral or lower surface of the thallus are present **scales** and **rhizoids** (Fig 7.16).

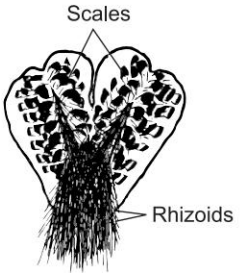


Fig. 7.16 *Marchantia nepatensis* showing ventral surface of the thallus

Scales are violet to purple-coloured structures. They are multicellular but one-celled thick structures. Scales are arranged in 2 to 4 or more distinct rows on each side of the midrib. Scales are of two types, i.e. appendiculate and ligulate. The **appendiculate** scales are situated usually in one row just on both the sides of the midrib, and each contains an appendage at its apical side (Fig. 7.17). The **ligulate** scales are present in one to three rows on either side of the midrib. Each ligulate scale is ligule-like and is devoid of any appendage. The ligulate scales are smaller than the appendiculate scales. The function of scales is to protect the growing apex and to retain the moisture.

Rhizoids are unicellular, elongated and hairlike structures. They are of two types, i.e. smooth-walled and tuberculate (Fig. 7.18). The **smooth-walled rhizoids** are broad, thin-walled, unicellular and possess both the outer and inner smooth wall layers. The tuberculate rhizoids are comparatively narrow

and their inner wall layer contains many peglike ingrowths. Absorption and fixation are the functions of the rhizoids.

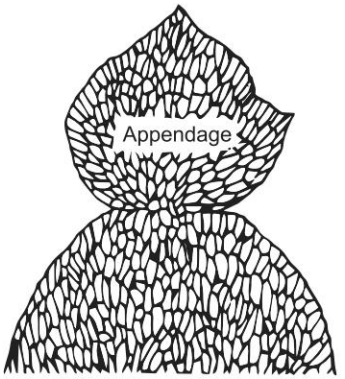


Fig. 7.17 An appendiculate scale of ***Marchantia nepalensis***

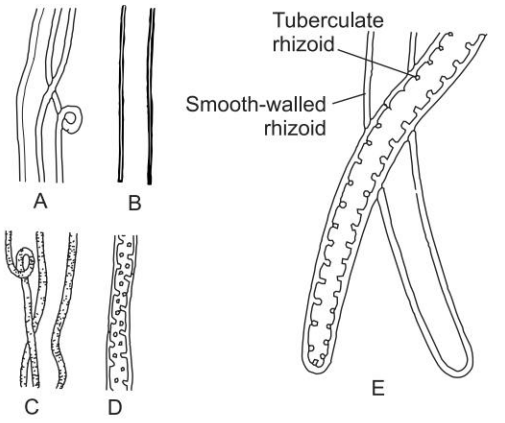


Fig. 7.18 Rhizoids of *Marchantia.* A, Smooth-walled rhizoids in surface view; B, Cross section of a smooth-walled rhizoid; C, Tuberculate rhizoids in surface view; D, Cross section of a tuberculate rhizoid; E, Both the rhizoids in cross section

7.7.4 Anatomy of the Gametophyte

Anatomically, the thallus is divisible into two different regions, i.e. upper **photosynthetic region** and lower **storage region** (Fig 7.19, 7.20).

The **photosynthetic region** is the green, dorsal or upper region of the thallus, made up of upper epidermis, air pores, air chambers and photosynthetic filaments. The **upper epidermis** is the outermost layer made up of thin-walled cells. Its continuity is broken by many air pores. Each **air pore** is a barrel-shaped, structure, usually surrounded by 4-8 rings of superimposed cells (Fig. 7.21 A-C). Each ring has 4-5 cells. The wall of the pore lies half above and half below the epidermis. Below the upper epidermis is present a single horizontal layer of **air chambers**. The air chambers remain separated from each other by 2- to 6-celled partition walls. These cells may or may not contain chloroplasts. Each air chamber opens outside by a barrel-shaped **air pore**. Several green, chlorophyll-containing **photosynthetic filaments** are present in each air chamber. These filaments consist of 2 to 6 or more cells and are branched or unbranched. The chlorophyll-containing cells of these filaments constitute the main photosynthetic tissue of the gametophyte.

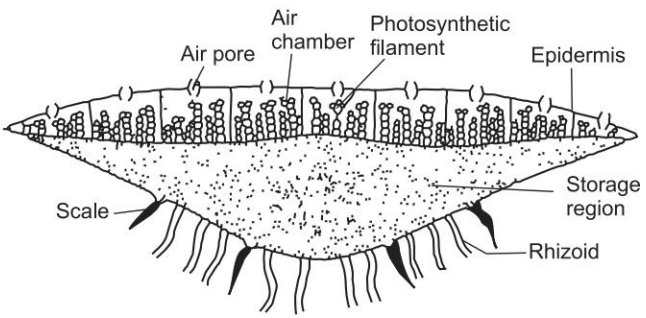


Fig. 7.19 VTS Thallus of *Marchantia polymorpha* (diagrammatic)

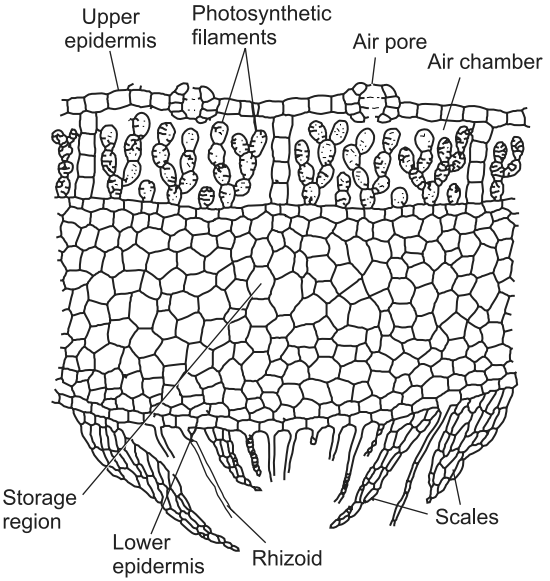


Fig. 7.20 VTS Thallus of *Marchantia polymorpha* (a part cellular)

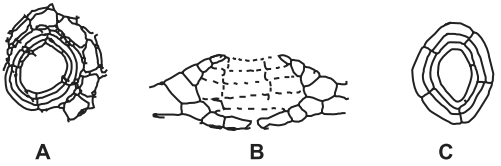


Fig. 7.21 A, Air pore of *Marchantia polymorpha (in surface view); B, Air pore of* M. nepalensis *in vertical cross section; C, Air pore of* M. palmata *(in surface view).*

The **storage region** represents the ventral tissue of the thallus and lies below the photosynthetic region. It consists of several layers of thin-walled parenchymatous cells. However, on the margins, there are only 1 to 3 layers of this tissue. Usually, the cells are isodiametric in this region except along the midrib. Most of the cells contain **starch** and are usually devoid of chloroplast. A few cells of this region either contain a large oil body, or remain filled with **mucilage**. The cells of the midrib region are marked with some reticulate thickenings. The cells of the lower epidermis contain both the types of **scales** and **rhizoids**.

7.7.5 Vegetative Reproduction

Marchantia reproduces vegetatively by a variety of ways mentioned below:

1. Death and Decay In this most common process of vegetative reproduction of thalloid bryophytes, the basal or posterior part of the thallus starts rotting or disintegrating due to ageing or drought. When this process of disintegration or decay reaches up to the place of dichotomy, the lobes of the thallus get separated. All lobes, so detached, develop into independent plants by apical growth.

2. Adventitious Branches The adventitious branches may develop from the ventral surface or from any other part of the thallus, and on getting detached, they develop into new thalli of *Marchantia*. Kashyap (1919) reported the development of such branches from the stalk and disc of the archegoniophore in *M. palmata*.

3. Gemmae

Gemmae are the specialised means of vegetative reproduction in several species of *Marchantia*. They develop in special cup-shaped structures, on the dorsal surface of the thallus, called **gemma cups**. Each gemma cup (Fig. 7.15) is a circular or cup-shaped body with fringed margins, and usually develops in the midrib region. Each **gemma** is a small, green, disclike and bilobed structure having a short, delicate and unicellular stalk. Several small mucilaginous hairs also develop in the cavity of the gemma cup along with the gemmae. Large amount of the mucilage is secreted by these mucilaginous hairs, which finally help in the detachment of gemmae from the gemma cup.

(a) Development of Gemma Certain superficial initial cells, lining the floor of the gemma cup, become active and appear as papillate outgrowths. These initial cells are called **gemma initials.** Each gemma initial divides transversely into a lower basal cell and an **upper cell**. There is no further division in the lower basal cell, and it forms the single-celled **stalk**. The upper cell divides transversely, and both the so-formed cells undergo one more similar division resulting in a row of four cells. These four cells divide several times in horizontal and vertical planes resulting in the formation of a thin plate-like, multicellular **gemma** (Fig. 7.22 A-F). Several such gemmae, in different stages of development, are seen in a gemma cup (Fig. 7.22 G).

(b) A Mature Gemma A mature gemma is a multicellular, lens-shaped structure, several cells thick in the middle but only one-celled thick on the margins. It is deeply notched on the two opposite sides. A growing point lies in each marginal notch. Each gemma contains a single-celled stalk. Majority of the gemma cells contain abundant chloroplasts and are green. Some of its cells contain oil bodies instead of chloroplasts. These are called **oil cells**. Some **rhizoidal cells** are also present on both the surfaces of gemma.

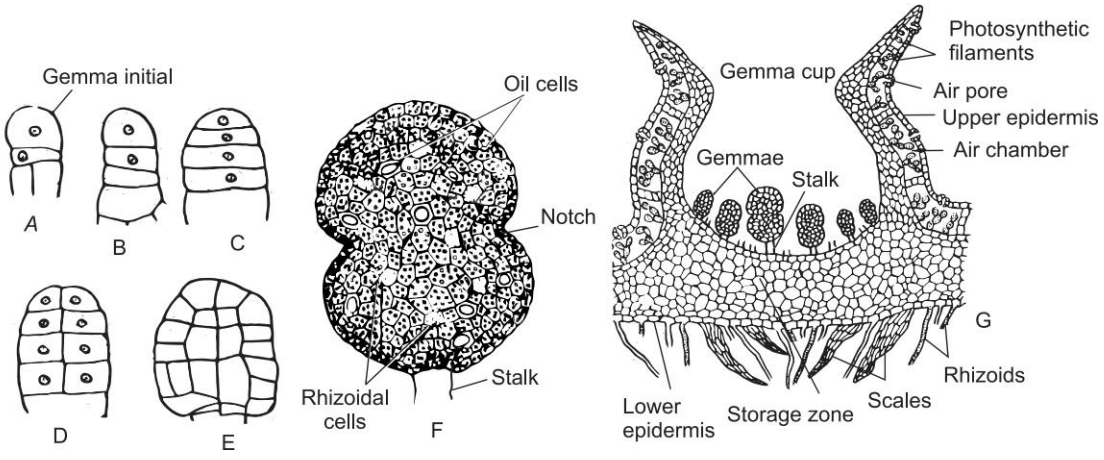


Fig. 7.22 *Marchantia.* A-E, Stages of the development of a gemma; F, A mature gemma; G, Vertical cross section of thallus passing through gemma cup

(c) Germination of Gemma The gemmae are dispersed by the wind or water current easily because of their weak fragile single-celled stalk. When they fall on a suitable soil, the rhizoidal cells become active and develop rhizoids. The meristematic cells, situated in both the marginal notches, start growing in opposite directions and develop into two young thalli. The central portion of the parent gemma dies leaving the production of two newly formed thalli of *Marchantia*.

7.7.6 Sexual Reproduction

The sexual reproduction is oogamous. The sex organs, i.e. **antheridia** and **archegonia**, develop on special erect, stalked branches of the thallus. The antheridia-bearing erect branches are called **antheridiophores**, and the archegonia-bearing branches are called **archegoniophores**. *Marchantia* is strictly dioecious. The male thallus bears antheridiophores whereas the female thallus bears archegoniophores. The **stalk** of both antheridiophores and archegoniophores contains a terminal horizontal **disc**. These erect sexual branches are the direct continuations of the thallus, and this reflects also in their anatomical details.

7.7.7 Antheridiophore

1. Structure of Antheridiophore Antheridiophore has a long stalk of about 1-3 cm, bearing a lobed disc at the apex. The disc is usually eight-lobed and rarely four-lobed. A growing point is situated at the tip of each lobe. Each lobe of the disc contains 2-7 or more antheridia arranged acropetally, i.e. the oldest antheridium in the centre of the disc while the youngest antheridium near the apex of the lobe. The antheridia are present on the dorsal surface of the disc. Each antheridium is enclosed in an antheridial chamber.

2. Development of Antheridiophore It starts developing (Fig 7.23 A-F) as an outgrowth on the male plant. Later on, the horizontal tubular outgrowth becomes erect and swells up at the tip. This swollen tip develops into a lobed, concave, antheridial disc, bearing groups of antheridia on the dorsal surface, and scales and rhizoids on the ventral surface.

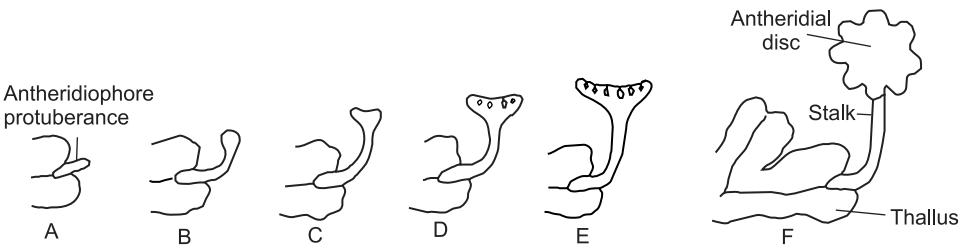


Fig. 7.23 A-F, Development of antheridiophore in *Marchantia polymorpha*

3. Anatomy of the Stalk of Antheridiophore The stalk (Fig. 7.24) is more or less a prismatic, five-faced structure, of which three faces are furrowed and two faces are curved outward. Two longitudinal furrows or grooves run down the length of the stalk. Scales and rhizoids are present in the grooves, and thus the surface containing the grooves corresponds with the ventral surface of the thallus. Several air pores, air chambers and photosynthetic filaments are present on the posterior side, which thus corresponds with the dorsal surface of the thallus. The stalk thus shows a dorsiventral symmetry, typical of the thallus.

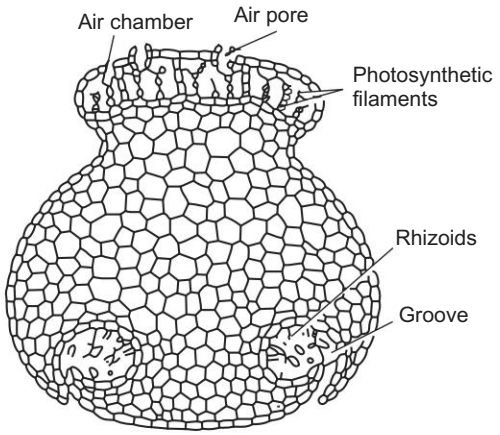


Fig. 7.24 T.S. Stalk of antheridiophore of Marchantia polymorpha

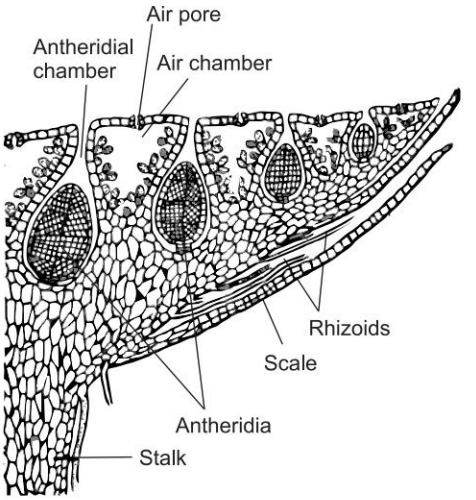


Fig. 7.25 Longitudinal section (a part) of the disc of antheridiophore of *Marchantia polymorpha*

4. Anatomy of the Disc of Antheridiophore Anatomically, the disc also resembles the thallus (Fig 7.25). The disc is surrounded by a layer of epidermis, the continuity of which is broken by many barrel-shaped air pores. Each air pore opens in an air chamber having several photosynthetic filaments. A growing region is situated at the apex of each lobe of the massive disc. Along with the air chambers are also present several flask-shaped cavities called 'antheridial chambers'. Each antheridial chamber contains an antheridium and opens outside by a pore or **ostiole**. The antheridia remain arranged acropetally, i.e. the oldest antheridium is present in the centre and the youngest near the apex of each lobe of the disc.

5. Development of the Antheridium The development of antheridium (Fig 7.26 A-I) starts from a superficial **antheridial initial cell** on the dorsal surface of the disc of the antheridiophore (Fig 7.26 A). The antheridial initial enlarges in size, becomes papillate and divides first by a transverse

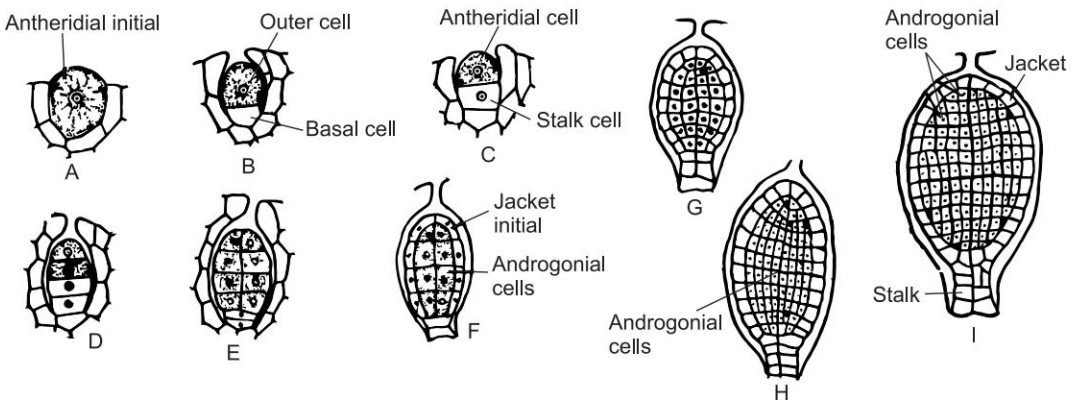


Fig. 7.26 A-I, Development of antheridium in *Marchantia polymorpha*

division forming an upper **outer cell** or **primary antheridial cell** and a lower **basal cell** (Fig. 7.26 B). The outer cell or primary antheridial cell divides transversely into an upper **antheridial cell** and a lower stalk initial cell (Fig. 7.26 C). The stalk initial cell divides by a few transverse and vertical divisions and ultimately forms a small stalk of the antheridium. The upper antheridial cell divides transversely to form a four-celled structure. This is followed by two vertical divisions at right angles to one another forming a sixteen-celled structure, in which the cells are arranged in four tiers of four cells each (Fig. 7.26 D–E). A periclinal division in this sixteen-celled structure results in the formation of 16 outer **primary jacket cells** and 16 inner **primary androgonial cells** (Fig. 7.26 F). The primary androgonial cells divide by several repeated transverse and vertical divisions resulting in hundreds of **androgonial cells** (Fig. 7.26 F-I). The primary jacket cells divide by several anticlinal divisions to form a single layer of sterile antheridial **jacket** (Fig. 7.26 I).

Simultaneously, the cells, neighbouring the antheridial initial cell, also become active and develop into a chamber-like structure around the antheridium. This chamber is called **antheridial chamber**.

6. Spermatogenesis The process of metamorphosis of androgonial cells into antherozoids is called **spermatogenesis**. Each **androgonial** cell (Fig. 7.27 A) or **androcyte mother cell** is a cubic structure and divides by a diagonal mitotic division to form two triangular **androcytes**. (Fig. 7.27 B). Both the androcytes remain enclosed in the wall of the androcyte mother cell with no separating wall.

Each androcyte (Fig.7.27 C) has a prominent **nucleus** and a small extranuclear granule called **blepharoplast**. The blepharoplast granule is present near the periphery of the protoplast. Soon the androcyte loses its triangular shape and becomes somewhat round or oval. Its blepharoplast elongates into a cord and occupies about two-third of its part. Simultaneously, the nucleus also becomes crescent-

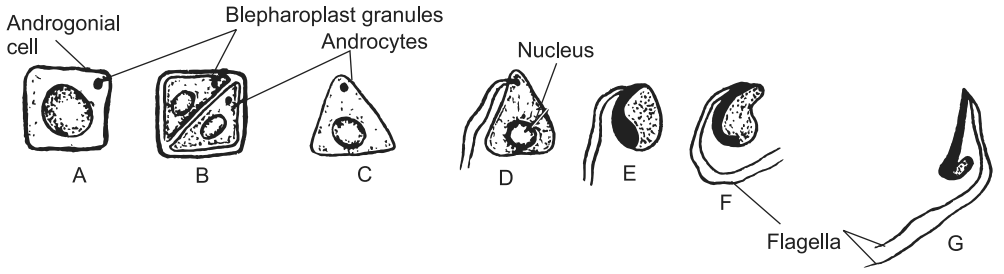


Fig 7.27 A-G, Spermatogenesis in *Marchantia polymorpha*

shaped and homogeneous, and ultimately comes into contact with the blepharoplast. Two long flagella are produced from the conspicuously thickened end of the blepharoplast. Thus, a uninucleate and biflagellate antherozoid develops from each androcyte (Fig. 7.27 G).

6. Dehiscence of Antheridium Water helps in the dehiscence of antheridium. From the slightly concave disc of antheridiophore, water enters into the antheridial chamber through its narrow canal. When water comes into contact with some sterile cells of the jacket of the antheridium, they start disintegrating. This results in the rupturing of antheridium. The androcytes in a group start emerging out of the dehisced portion of antheridium in the form of a long smoke-like column. This mass of androcytes breaks on reaching an air-water surface. Thus, the androcytes spread on the surface of water.

7. Mature Antheridium and Antherozoids A mature antheridium is a short-stalked, globular and ovoid or club-shaped body present singly in an antheridial chamber. A single-layered sterile jacket encloses the mass of androgonial cells.

Electron microscopic studies conducted by Sato (1951) indicate that the antherozoid of *M. polymorpha* is a rod-like, uninucleate and biflagellate structure. Each flagellum is made up of several fibrils. When the antherozoids swim in water, they resemble the crawl of a snake.

7.7.8 Archegoniophore

1. Structure and Development of Archegoniophore Similar to antheridiophore, the archegoniophore or *carpocephalum* also consists of a stalk and a disc. The stalk is simply the modified branch of the thallus. The disc is usually eight-lobed. In *M. polymorpha*, the stalk of archegoniophore terminates in a nine-rayed stellate disc. The stalk of the archegoniophore is comparatively smaller than the stalk of antheridiophore.

When very young, the apex or growing point of the archegoniophore protuberance becomes swollen (Fig. 7.28 A, B). The dichotomy is repeated in quick succession in this swollen apex, which ultimately becomes a rosette-like, eight-lobed disc. From the original branch initial, an eight-lobed disc develops by three successive dichotomies. Each lobe of the disc contains a growing point. Soon a group of archegonia develops in each lobe in acropetal succession, i.e. youngest near the apex and the oldest archegonium in the centre of the disc. Thus, eight groups of archegonia are seen on the upper surface of the disc.

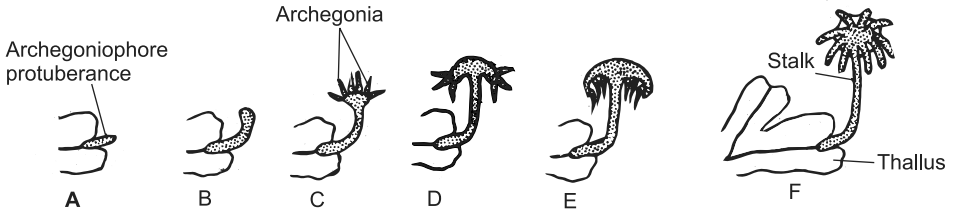


Fig 7.28 A-F, Development of archegoniophore in *Marchantia polymorpha*

The archegonia develop in erect position on the archegonial lobe with their necks directed upwards (Fig. 7.28 C). The erect position of the archegonia is seen only when the stalk of the archegoniophore is very short and the disc is only slightly raised above the thallus. Fertilization takes place at this stage.

Immediately after fertilisation, following changes occur in quick succession:

(a) Stalk of the archegoniophore begins to elongate with the simultaneous overgrowth in the central sterile part of the disc.

(b) Because of the overgrowth of the central part of the disc, the groups of archegonia and the marginal apical regions of the disc are shifted towards the lower side (Fig. 7.28 D, E). This brings the curvature of the apices of lobes.

(c) The growing apex of each lobe of the disc now lies near the stalk of the archegoniophore.

(d) The archegonia are now hanging towards the lower side with their necks pointing downwards.

(e) Because of the curvature of the apices, the youngest archegonium is now present near the stalk of the archegoniophore while the oldest archegonium near the periphery of the disc (Fig 7.29).

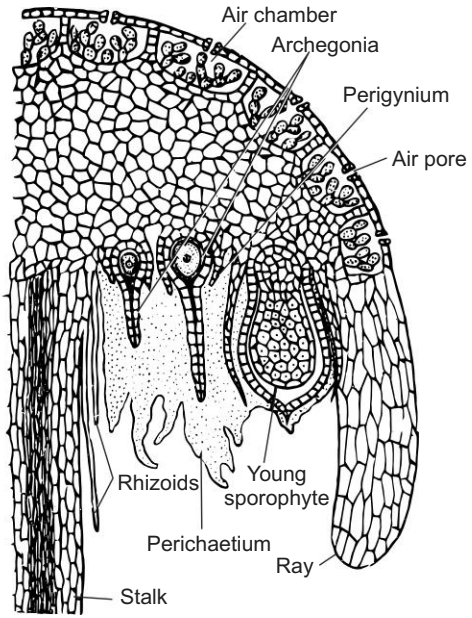


Fig 7.29 LS (a part) of archegoniophore disc after fertilization, showing the youngest archegonium near the stalk

(f) At the base of each archegonium develops a ring of cells in the form of a collar-like structure called **perigynium** or **pseudoperianth**.

(g) A bilipped, pendant, one-celled thick sheath, with fringed margins, develops from both the sides of the group of archegonia. This involucral sheath encloses the group of archegonia and is known as perichaetium (Fig. 7.29).

(h) Between the groups of archegonia, in some species, develop long, green, cylindrical processes from the peripheral portion of the disc. These processes are called **rays**. The rays provide an umbrella-shaped structure to the disc. In *M. polymorpha*, the rays are usually nine in number.

2. Anatomy of Archegoniophore Anatomically, the stalk of an archegoniophore resembles the stalk of an antheridiophore (Fig. 7.24). Its morphologically ventral side has two longitudinal grooves having scales and rhizoids, whereas its morphologically dorsal side, resembling the dorsal surface of the thallus, contains air chambers, air pores and photosynthetic filaments. In the upper side of the disc portion are also present the air chambers, air pores and photosynthetic filaments (Fig. 7.29), Groups of archegonia, perigynium, perichaetium and rays are also present in the disc region of the archegoniophore.

3. Development of Archegonium The development of archegonium starts from a dorsal superficial cell which acts as an **archegonial initial** (Fig. 7.30 A). The archegonial initial enlarges, becomes papillate and first divides transversely into a lower **basal cell** and an upper **outer cell** (Fig 7.30 B). There is no further division in the basal cell, and thus the entire archegonium develops from the outer cell.

The outer cell divides by three successive intersecting walls or periclinal vertical divisions resulting in the formation of three outer **peripheral cells** and a central **axial cell** (Fig. 7.30 C-H). The axial cell divides transversely and unequally, forming a small upper **cover initial cell** and a large **central cell** (Fig.7.30 G). Each of the three peripheral cells divides by an anticlinal vertical division forming two cells. In this way, the axial cell gets surrounded by six peripheral cells (Fig. 7.30 J). All the peripheral cells divide transversely into upper **neck initial tier** and lower **venter initial tier**. Simultaneously, the large central cell also divides transversely into an upper **neck canal initial** and a lower **central cell** (Fig. 7.30 I). The primary neck canal initial divides by a series of transverse divisions to form 4 to 6 neck canal cells. The central cell divides transversely only once and forms a small **venter canal cell** and a large **egg** (Fig. 7.30 J).

The cover initial cell divides by two vertical divisions at right angles to one another forming four **cover cells** which form the mouth of the archegonial neck. The cells of the neck initial tier divide by repeated transverse divisions to form a long **neck**. The cells of the venter initial tier also divide by repeated transverse divisions to form a single-layered swollen venter (Fig. 7.30 K,L).

4. Mature Archegonium A mature archegonium (Fig. 7.30 L) is a flask-shaped structure with a long neck and a globular venter. The neck consists of six vertical rows of cells enclosing 4 to 6 neck canal cells. The venter consists of a single-layered jacket enclosing a venter canal cell and an egg. Four cover cells form the mouth of the archegonium.

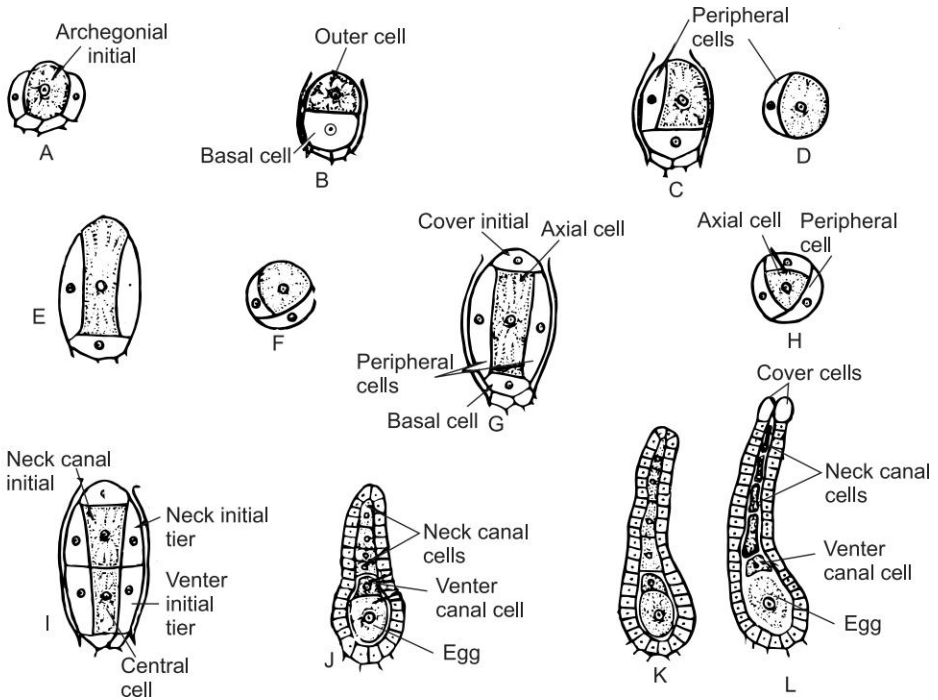


Fig. 7.30 A-L. Development of archegonium in *Marchantia polymorpha*

7.7.9 Fertilization

Fertilization takes place at a time when the archegoniophores are only slightly elevated above the thallus, and the necks of the archegonia are facing upwards. Water is essential for fertilization. A mass of antherozoids exudes from the canal of the antheridial chamber. Antherozoids keep freely swimming in the water. The antherozoids are positively chemotactic to certain substances, such as proteins, inorganic salts of potassium, etc. An antherozoid enters the archegonial neck because of the chemotactic response. Two gametes, i.e. antherozoid and egg, fuse, but, according to Anderson (1929), the nuclei of the two gametes fuse only after a long time. The fusion of the nuclei of male and female gametes results in the formation of a diploid structure called **zygote**.

SPOROPHYTIC PHASE

7.7.10 Post-fertilization Changes

After fertilization, the oospore or fertilized egg, enlarges until it completely fills the cavity of the venter of the archegonium. A cellulose cell wall is then secreted around the oospore. The surrounding gametophytic tissue is also affected due to the developing oospore, which is the first cell of the sporophytic generation. A few noticeable changes take place in the developing sporogonium and the surrounding tissues. These are mentioned below:

1. The stalk of the archegoniophore starts elongating and becomes 3 to 4 cm long.
2. Periclinal divisions take place in the cells of the venter. This makes the venter two- to three-layered, and it is'now called **calyptra**.
3. The calyptra later on expands and protects the young developing sporogonium.
4. Several cells, in the form of a ring, at the base of the venter become active, divide and redivide and form a thick, collar-like outgrowth called **perigynium** or **pseudoparianth**. When young, the perigynium is only one-cell thick. It forms a close covering at the base of the archegonium enclosing the young sporogonium. Its function is to provide protection to the developing sporogonium.
5. The group of archegonia, a few of which contain the eggs and a few others the developing sporogonia, is also covered by yet another protective covering called **perichaetium**.

The young sporogonium is thus surrounded by three protective coverings of gametophytic origin, i.e. calyptra, perigynium and perichaetium.

7.7.11 Development of Sporogonium

The oospore or zygote (Fig. 7.31 A) first divides by a transverse division to form an upper epibasal cell and a lower hypobasal cell (Fig. 7.31 B). Further development of the young embryo is different in different species. In several species, including *M. polymorpha*, the second division is at right angles to the first one to form a 4-celled quadrant stage (Fig. 7.31 C). The epibasal derivatives of this quadrant stage form the capsule while the hypobasal ones form the **seta** and **foot**.

In *M. domingensis*, the quadrant stage develops as in *M. polymorpha*, but the epibasal part of the quadrant develops into a capsule and a part of seta while the hypobasal part gives rise to the remaining basal part of seta and capsule.

In *M. chenopoda*, the second transverse division is parallel to the first transverse division resulting in a 3-celled filamentous embryo, of which the uppermost cell gives rise to the capsule, the middle cell to seta and the lowermost cell to foot.

In the 4-celled stage of *M. polymorpha*, the next division is also a vertical division but at right angles to the first one to form an 8-celled stage of the embryo called **octant stage**. The young embryo now begins to elongate at this stage. There are now differences in the subsequent divisions in both hypobasal and epibasal regions. Four cells of the hypobasal region of the octant stage of the embryo divide and redivide to form a parenchymatous tissue (Fig. 7.31 D). From the lower cells of this parenchymatous tissue develops the foot while from its upper cells develop the **seta**.

Foot is the lowermost region of the sporogonium. It is made up of a bulbous mass of cells, which presses itself into the gametophytic tissue. It functions as an anchoring and absorbing organ of the sporogonium.

Seta is the middle region of the sporogonium. It arises from the upper cells of the parenchymatous tissue which develop from the hypobasal region of the embryo in *M. polymorpha*. The cells in the seta are arranged in regular vertical rows. When young, the cells of the seta region are isodiametric in shape, but, they soon divide by repeated transverse divisions which ultimately result in an increase in the seta length. The elongating seta pushes the capsule, which ruptures the calyptra and other membranes surrounding the sporogonium (Fig 7.31 E-G).

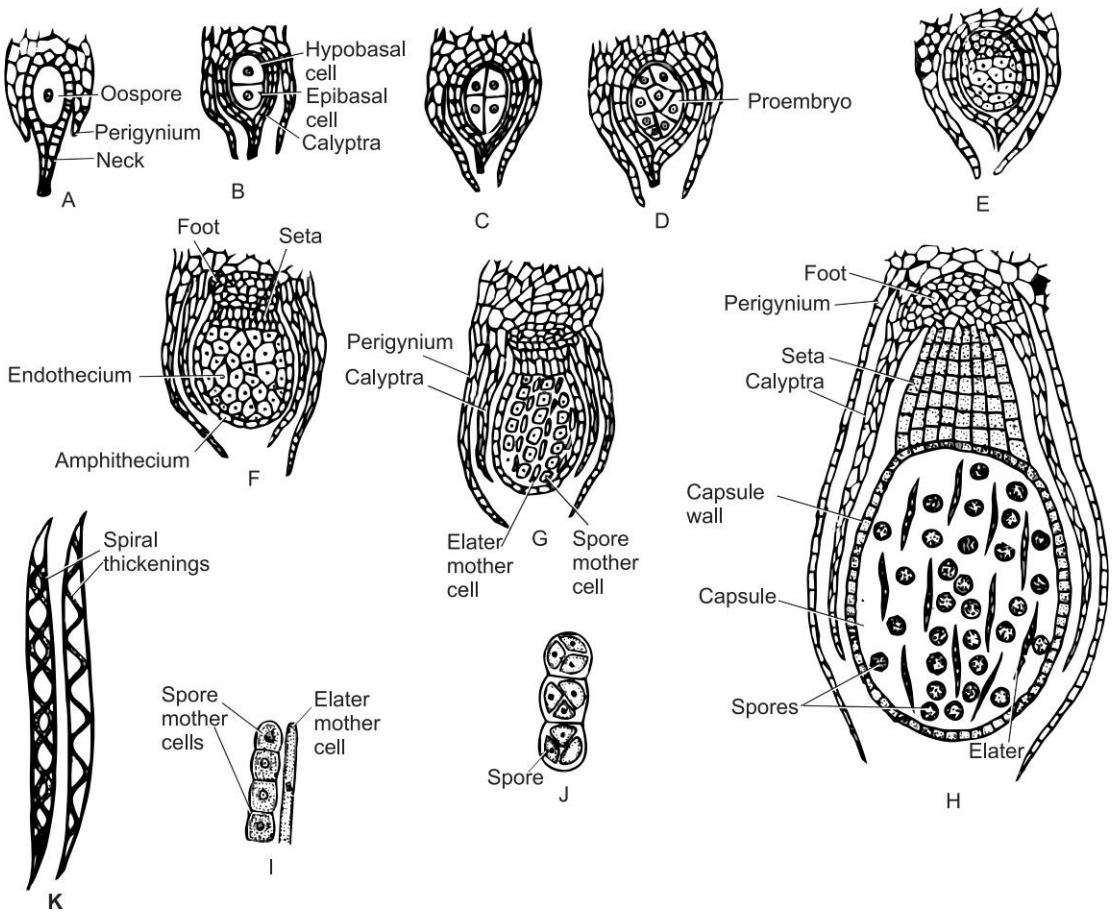


Fig. 7.31 A–G, Development of sporogonium in *Marchantia polymorpha*; H, L.S. of a mature sporogonium; I, spore mother cells and elater mother cell; J, spore tetrad; K, Two elaters.

Capsule is the uppermost part of the sporogonium. It develops from the four cells of the epibasal region of the octant stage of embryo in *M. polymorpha*. The cells of this region divide irregularly to form a round mass of cells. With the help of a periclinal division, in the cells of the peripheral region of this mass of cells, two layers are formed, an outer layer of **amphithecium** and the inner cellular mass called **endothecium**. The cells of the amphithecial layer divide only by anticlinal walls and form a single-layered jacket or **capsule wall**. Some annular thickenings may also develop in the cells of the capsule wall in the later stages.

The archesporium is endothecial in origin in *Marchantia*. Massive sporogenous tissue develops by several divisions in the cells of the endothecium. About half of the cells of the sporogenous tissue divide by several transverse divisions to form fertile **spore mother cells** or **sporocytes**. These spore mother cells are more or less cubic in shape and arranged in the form of vertical rows. According to O'Hanlon (1926), each sporogenous cell in *M. polymorpha* divides by five successive divisions to form 32 spore mother cells. However, only 8 or 16 spore mother cells are formed by three or four successive divisions of a sporogenous cell in *M. domingensis*, as reported by Andersen (1929).

The remaining half of the cells of the sporogenous tissue become sterile and form **elaters**. The elaters (Fig. 7.31 K) are long, spindle-shaped, slender cells possessing tapering ends. On the inner surface of the cell walls of each of these elaters are present two spiral thickenings, formed by the partly disappearance of their protoplasm. The elaters are hygroscopic in nature and help in loosening of spore mass and dispersal of spores. In *M. polymorpha*, an elater is equivalent to a sporogenous cell. As mentioned above, a fertile sporogenous cell produces 32 spore mother cells by five successive divisions. Thus, there are 32 spore mother cells (or 128 spores) to each elater in the sporogonium of *M. polymorpha*.

Each spore mother cell is diploid and divides meiotically to form four haploid spores (Fig. 7.31 I, J), which remain arranged tetrahedrally for quite some time (Fig. 7.31 J). The spores later become free and remain enclosed by the capsule wall along with elaters. It has been estimated that as many as 300,000 spores may be produced in a single sporogonium of *M. polymorpha* (O'Hanlon, 1926).

7.7.12 Mature Sporogonium

A mature sporogonium of *Marchantia* is an elongated structure differentiating into three regions, i.e. foot, seta and capsule (Figs 7.31 H, 7.32). The **foot** is multicellular, bulbous, anchors the sporogonium to the disc of the archegoniophore, and also helps in the absorption of food for the developing sporogonium from the gametophyte. The **seta** is a thick, stalk-like structure in between the foot and capsule. It consists of cubic cells arranged in vertical rows, and its function is elongation. The **capsule** is the uppermost, spherical or oval, and spore-producing region of the sporogonium. The capsule is surrounded by an outer layer of sterile wall called jacket or **amphithecium**. The cells of the wall have ringlike thickened bands.

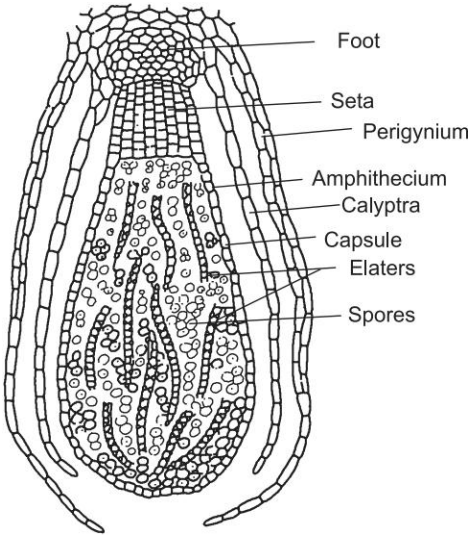


Fig. 7.32 L.S. mature sporogonium of *Marchantia polymorpha*

Inside the wall are present the fertile spore mother cells and sterile elaters. Elaters are long, spirally thickened structures with tapering ends. The spore mother cells divide reductionally to form haploid spores. Ruptured calyptra, perigynium and perichaetium coverings are also present around the mature sporogonium.

7.7.13 Dehiscence of Capsule

After the formation of haploid spores from the diploid spore mother cells in the capsule, the seta elongates very fast. It pushes the capsule out of the protective coverings of calyptra, perigynium and perichaetium. The exposed capsule starts drying from the top. The long elaters start twisting and create tension inside the capsule. Due to this process, the jacket of the capsule splits longitudinally, from the apex to about the middle, into a variable number of valves. The hygroscopic nature of elaters and cells of the capsule jacket also helps in the splitting of the capsule. The jerking action of elaters also helps in loosening the spore mass. Wind helps in the spore dispersal from the dehisced capsule.

YOUNG GAMETOPHYTE

7.7.14 The Spore

The spores are very small (from 0.012 to 0.03 mm in diameter), haploid, round or spherical, uninucleate structures surrounded by two layers, i.e. an outer thick, smooth or ornamented exine, and an inner thin and smooth intine. Granular cytoplasm surrounds the nucleus. The spores in species, such as *M. polymorpha* and *M. faleacea* are **apolar**, i.e. they lack a definite polar axis and are globose in outline, while in species, such as *M. tonasa*, the spores are **cryptopolar**, i.e. they possess a polar axis and are not globose in outline.

The spores are of about 10-12 μ in diameter in *M. polymorpha*, 18-25 μ in diameter in *M. nepalensis*, and 24-30 μ in diameter in *M. palmata*.

7.7.15 Germination of Spore and Formation of Young Gametophyte

The spore germination (Fig 7.33 A-H) starts immediately if favourable conditions persist. The viability of spores is almost 100% for one full year. At the time of germination, the spore first swells and becomes nearly double the original size. Out of the four spores of a tetrad, usually two develop into male thalli and the remaining two into female thalli.

The early divisions in the germinating spore are in one plane only, and thus develop short filamentous structures. In the later stages, however, the divisions are in all planes. When about a dozen cells are formed in the young gametophyte of *M. polymorpha*, a marginal row of cells become conspicuous according to O'Hanlon (1926). This row of cells is responsible for further growth of the young gametophyte. A notch develops in the apical region when the gametophyte contains about 25-40 cells. However, Menge (1930) opined that when the young gametophyte is only 6- to 8-celled in *M. polymorpha*, there develops an apical cell with two cutting faces. This apical cell cuts cells in both left and right sides by repeated divisions, and thus develops a young gametophytic thallus of *Marchantia.*

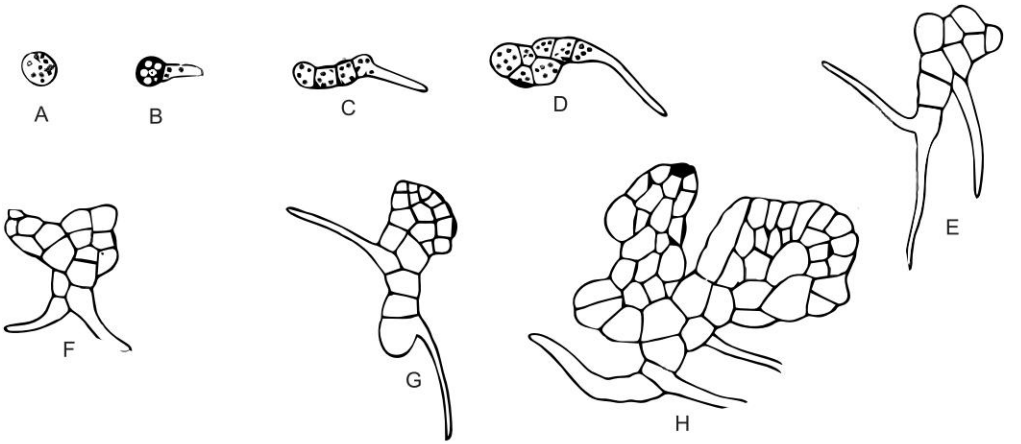


Fig. 7.33 A–H, Spore germination in *Marchantia polymorpha.*

7.7.16 Life Cycle of *Marchantia*

See Fig 7.34.

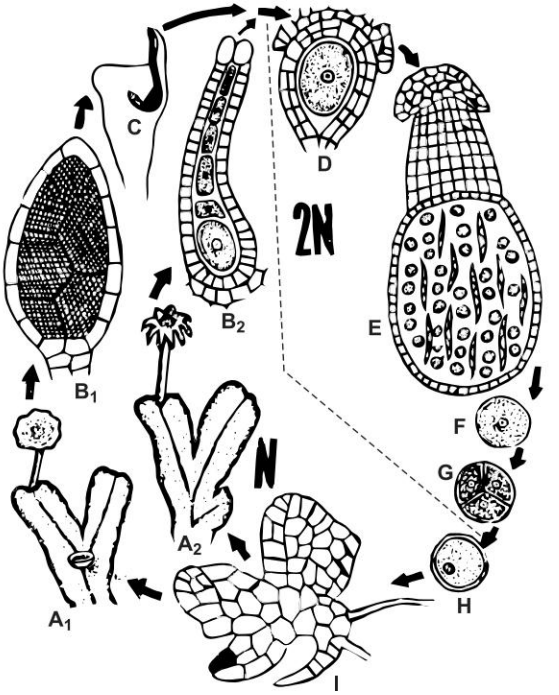


Fig. 7.34 Diagrammatic life cycle of *Marchantia*

COMPARISON OF SPOROGONIUM OF *RICCIA* AND *MARCHANTIA* 7.8

Table 7.1 *Comparison of sporogonium of Riccia and Marchantia*

S. No.	*Riccia* sporogonium	*Marchantia* sporogonium
1.	Sporogonium is simplest amongst bryophytes.	Sporogonium is a very complex structure.
2.	It is made up of only capsule or spores. It lacks foot and seta.	It is made up of well-developed foot, seta and capsule.
3.	The mature sporogonium remains almost sunken in the thallus.	It remains attached to the thallus only by foot. It hangs from the undersurface of the female receptacle.
4.	The sporogonium remains surrounded by a jacket layer made up of sterile cells.	Only the capsule remains surrounded by a single-layered capsular wall.
5.	Jacket layer surrounds the fertile spore mother cells. There are no elater mother cells.	Jacket layer of capsule surrounds the mass of fertile spore mother cells and sterile elater mother cells.
6.	Few sterile nurse cells are present in the sporogonium.	Nurse cells are absent. The sterile tissue of the sporophyte is in the form of foot, seta, capsule wall and elater mother cells.
7.	Elaters are absent.	Elaters are present.
8.	Mature sporogonium has almost no diploid tissue. The outer layer of sporogonium represents parent gametophyte and spores represent future gametophyte.	Mature sporogonium completely made up of diploid tissues, except spores which represent the new gametophyte.
9.	A bilayered calyptra surrounds the sporogonium. The layers like perigynium and perichaetium are absent.	A bilayered calyptra, and well-developed coverings or layers of perigynium and perichaetium are present.
10.	Dehiscence of capsule never occurs. The dispersal of spores is simply by the disintegration of the capsule wall.	Dehiscence of capsule takes place by 4-6 valves, and spores are dispersed into the air.
11.	Mature haploid spores are simply left behind on the soil due to the decay of the surrounding thallus tissue.	Mature haploid spores are dispersed by the wind under a specialised process.

ORIGIN AND EVOLUTION OF MARCHANTIACEOUS THALLUS 7.9

Bryologists may be grouped in two different categories in suggesting their theories regarding the origin and evolution of Marchantiaceous thallus. Some believe that the simple looking thallus of members of Marchantiales is due to **retrogressive evolution** while other bryologists believe that simplicity of thallus of these members is the result of **progressive evolution**. Let us explain both these theories as under.

7.9.1 Retrogressive Evolution

Bryologists believing retrogressive evolution of Marchantiaceous thallus may also be placed in two different groups. Majority of them believe that retrogressive evolution has taken place by progressive simplification, called **reduction**. On the other hand, some believe that it has been brought about by **condensation**. The former view has been termed **reduction theory**, while the latter view has been expressed under **condensation theory**.

1. Reduction Theory

(a) Theory of Von Wettstein Von Wattstein (1908) was the first to propose the reduction theory of retrogressive evolution of origin of Marchantiaceous thallus, and received the support of several top bryologists of those days, including Church (1919), Kashyap (1919), Goebel (1930) and Evans (1939). In his theory, Von Wettstein opined that "the primitive gametophyte of Hepaticae was nearest to the erect, leafy Acrogynous Jungermanniaceous forms". He treated Acrogynous Jungermanniales of the *Calobryum*-type first. Plant body in *Calobryum* is an erect, leafy gametophyte showing radial symmetry and containing leaves in three rows. During the course of reduction, the first step was the adoption of a prostrate habit. Because of the development of dorsiventral habit, the leaves on the ventral side gradually reduced in size, and finally in some cases, they disappeared completely. These changes in habit and reduction of size of ventral leaves were soon accompanied by the flattening of central axis of the gametophyte. The lateral leaves were first partially and then completely eliminated. The ***final result*** of all these changes was the "formation of a leafless, flat, dorsiventral Acrogynous Jungermanniaceous gametophyte of *Pellia*-type" (Von Wettstein, 1908). In the later stages, there was "gradual progressive internal differentiation of tissues", which finally resulted into the "formation of externally simple but internally highly differentiated thallus of Marchantiales" (Von Wettstein, 1908). He believed that **scales** on the ventral surface of the Marchantiaceous thallus as 'modifications of the leaves of the ventral row of the prostrate, foliose ancestor'.

(b) Kashyap's Reduction Theory of Pteridophytean Origin of Marchantiales SR Kashyap (1919) believed in the reduction theory but opined differently from that of the theory of Von Wettstein. He postulated the theory of Pteridophytean origin and opined that liverwort thallus, in general, and Marchantiaceous thallus, in particular, shows great resemblance in external form and structure with the prothalli of *Lycopodium cernuum* and *Equisetum debile* of pteridophytes. He also correlated the erect, chlorophyll-containing branched lobes of dorsal photosynthetic region of *L. cernuum* and *E. debile* with the erect photosynthetic filaments and walls of air chambers of Marchantiales. On the basis of these similarities between some pteridophytes and Marchantiales, Kashyap (1919) suggested that "Marchantiales probably arose by reduction from these pteridophytean ancestors".

Kashyap's reduction theory of pteridophytean origin of Marchantiales was, however, opposed by P N Mehra, another Indian bryologist, on the basis of the following arguments:

(i) Pteridophytes have a well-developed vascular system, while liverworts, in general, and Marchantiales, in particular, have no evidence of any lost vascular system.

(ii) Simple sporophytes of Marchantiales have many clear dissimilarities with the sporophytes of *Lycopodium* and *Equisetum*.

(iii) Scales, present on the ventral surface of the thallus of Marchantiales, have no similarity with any structure of the undersurface of the prothallus of *Lycopodium cernuum* and *Equisetum debile*.

(iv) There exists no similarity between the sex organ-bearing erect structures (antheridiophores and archegoniophores) of *Marchantia* and sex organ-bearing parts of *Lycopodium* and *Equisetum*.

2. Condensation Theory

Mehra and Vasisht (1950) proposed that the thalloid forms of Marchantiales and other liverworts have been derived from the foliose forms by the process of condensation, and this theory is known as **condensation theory**. On the basis of these findings in the later years, Mehra (1957) observed the real phylogenetic connection between thalloid forms of Marchantiales and foliose forms of Jungermanniales and explained the origin of Marchantiaceous thallus by compaction, condensation and fusion of leaves of Jungermanniales. Major outlines of the condensation theory are listed below:

(a) The lateral leaves of the foliose ancestors overlapped succubously or incubously.
(b) The lower portions of these leaves **fused** at the points of contact. This resulted in the formation of single-layered wings on either side of the central axis. This also resulted in the formation of lamellae on the upper side of wings.
(c) Thus formed **lamellae** were one-cell thick.
(d) These lamellae were directly obliquely outwards and were responsible for the **formation of open chambers**.
(e) Then there was the inward growth of the margins of the cavities of these open chambers, and this resulted in the formation of **roof of these air chambers**.
(f) In the early stages, the communication of these roofed chambers with the exterior area was by **large gaps**.
(g) These gaps were later on replaced by **air pores**.
(h) Development of the air pores was also helpful in protection against loss of water by **transpiration** process.
(i) Simultaneously, there was a **gradual flattening of central axis**.
(j) **Flattening** of the central axis reached **up to the margins of the wings**.
(k) Along with the flattening process, there occurred the **development of secondary partitions** across the air chambers.
(l) **Horizontal partitions** also developed between the lamellae in xerophytic conditions, resulting in the formation of several-layered chambers, as in *Plagiochasma*.
(m) Along with all the above-mentioned changes, there developed **photosynthetic filaments** from the floor of air chambers, as in *Marchantia*.
(n) In *Marchantia* and a few other Marchantiales, there also developed **barrel-shaped air pores** in air chambers.

7.9.2 Progressive Evolution

Originally proposed by Schiffner (1893), the theory of progressive evolution was supported by some famous bryologists, such as F Cavers (1903), FO Bower(1935), DH Campbell (1936), GM Smith (1955) and others. The progressive evolution theory suggests that the Hepaticae members "originated from a simple thallose gametophyte". The ancestral thallus was simple, prostrate, and exhibited no external or internal differentiation. According to Cavers (1903), the forms like *Sphaerocarpos*, are the present-day Hepaticae, while Campbell (1936) opined that forms like *Metzgeria* are the present-day Hepaticae which exhibited a nearest approach to the primitive Hepaticean gametophyte. The following two types of gametophytes evolved from these primitive types by progressive evolution process:

1. Marchantiaceous Gametophytes Marchantiaceous gametophytes evolved from the primitive thallose gametophyte by progressive evolution as under:

(a) Simple, prostrate, thallus-like form of primitive thalloid gametophyte has been retained as such.

(b) During evolution, there has been a gradual but progressive internal differentiation of tissues. Finally developed the thallus, made up of (i) a definite epidermis, (ii) well-developed air pores opening into the air chambers, (iii) air chambers containing photosynthetic filaments, and (iv) well-organised parenchymatous and compact region representing the ventral surface or storage tissue of the thallus.

(c) Sex organs aggregated into specified areas called *receptacles*, e.g. antheridia on antheridiophore, and archegonia on archegoniophores.

2. Jungermanniaceous Gametophytes Jugermanniaceous gametophytes evolved from the primitive thallose gametophyte by progressive evolution as under:

(i) Simple internal structure of primitive thalloid gametophyte has been retained.

(ii) There has been a gradual but progressive elaboration of the external form.

The above-mentioned changes resulted in the evolution of a leafy, prostrate thallus of members of Jungermanniales.

TEST YOUR UNDERSTANDING

1. What do you mean by Marchantiophyta?
2. Marchantiales are commonly called _____.
3. Two major genera of Marchantiales are *Marchantia* and _____.
4. Name any five common genera of Marchantiales.
5. Enlist any seven general characteristics of Marchantiales.
6. Ventral surface of the thallus of Marchantiales contain rhizoids and _____.
7. Two types of rhizoids of Marchantiales are smooth-walled and _____.
8. In *Dumortiera*, the differentiation of tissues is _____ well-marked
9. In the thalli of Marchantiales, the green tissue is mainly confined to which region: dorsal or ventral?
10. Usually, the jacket wall of the capsule of Marchantiales contains how many layers?
11. In the sporogonia of Marchantiales, the columella is _____
12. Write a note on classification of Marchantiales in about 100 words.
13. Three genera of Ricciaceae are *Riccia*, *Ricciocarpos* and ____.
14. Write any five general characteristics of the family Ricciaceae.
15. Name the aquatic species of *Riccia*.
16. Are a majority of the species of *Riccia* aquatic or terrestrial?
17. Write a brief life-history account of *Riccia* in about 1000 words
18. Give in detail an illustrated account of the external features of the gametophyte of *Riccia*.
19. Write short notes on the following:
    (a) Scales of *Riccia*
    (b) Rhizoids of *Riccia*
    (c) Anatomy of the thallus of *Riccia fluitans*
    (d) Apical growth in *Riccia*

20. How does *Riccia* reproduce vegetatively?
21. Discuss in brief the development of sex organs in *Riccia*. Support your discussion with suitable diagrams.
22. Give an account of spermatogenesis and formation of an antherozoid in *Riccia*
23. How many flagella does a mature antherozoid of *Riccia* contain?
24. Write illustrated notes of the structure of mature sex organs of *Riccia*.
25. A mature archegonium of *Riccia* is _____ shaped.
26. Discuss in detail the sporogonium and its various stages of development in *Riccia*.
27. Write a note on nutritive cells of the sporogonium of *Riccia*.
28. Draw diagrammatic representation of the life-cycle of *Riccia*.
29. Name the best-known species of *Marchantia*.
30. Explain in detail the external features of the gametophyte of *Marchantia*.
31. Write a detailed note on the gemma cups in *Marchantia*.
32. Write one major difference between the scales of *Riccia* and *Marchantia*.
33. What are the major differences between the scales of *Riccia* and *Marchantia*?
34. Discuss the anatomy of the *Marchantia* thallus.
35. Air pores of *Marchantia* are _____ shaped.
36. What are gemmae? Explain their development in *Marchantia*.
37. Write major details of the life history of *Marchantia* in about 1000 words.
38. Write detail illustrated notes on:
    (a) Antheridiophore of *Marchantia*
    (b) Archegoniophore of *Marchantia*
39. Explain in detail the sporophyte and its development in *Marchantia*.
40. In the sporophyte of *Marchantia*, what are calyptra, perigynium and perichaetium?
41. *Marchantia* sporophyte is divisible into foot, _____ and capsule
42. Make a well-labelled diagram of LS of the mature sporogonium of *Marchantia*.
43. Compare the sporogonia of *Riccia* and *Marchantia.*
44. Explain in detail the origin and evolution of the Marchantiaceous thallus.

8

Anthoceropsida

WHAT IS ANTHOCEROPSIDA? 8.1

The class *Anthoceropsida* (Rothmaler, 1951), variously named as *'Anthocerotes'* (Howe, 1899; Campbell, 1918), or *'Anthocerotae'* (Smith, 1938, 1955; Takhtajan, 1953; Wardlaw, 1955) or *Anthocerotopsida (Proskauer,* 1957), is a small group of bryophytes, and its best known genus is *Anthoceros*. The members of this class are commonly known as **horned liverworts**.

GENERAL CHARACTERISTICS 8.2

Some of the generalized characteristics are described here:

1. The plant body is gametophytic and the gametophytes are dorsiventral, thalloid and variously lobed.
2. The thallus does not show any internal differentiation of tissues.
3. On the ventral surface of the thallus are present smooth-walled rhizoids. The tuberculate rhizoids, found in several members of Hepaticopsida (e.g. *Riccia, Marchantia),* are absent.
4. The scales are absent.
5. The air chambers and the air pores are absent.
6. Each cell of the thallus contains one or sometimes more, large, laminate chloroplasts, and each chloroplast contains a *pyrenoid*.
7. Oil bodies are absent in the cells.
8. Antheridia develop from the hypodermal cells on the dorsal side of the gametophyte.
9. Antheridia are present either singly or in groups, in closed cavities called **antheridial chambers**.
10. Archegonia are almost completely embedded in the gametophytic tissues on the dorsal surface of the thallus.
11. The sporophyte consists of a bulbous foot, an intercalary meristematic region instead of seta, and a long capsule.

12. Owing to the presence of the intercalary meristem, the sporophytes continue to grow indefinitely, i.e. show indeterminate growth.
13. A well-developed central columella is present in each sporophyte.
14. The sporogenous tissue is amphithecial in origin.
15. The archesporium develops into fertile spore mother cells and sterile pseudoelaters. The pseudoelaters may or may not possess spiral thickenings.
16. The capsule starts maturing from the tip downwards.
17. The capsule usually dehisces by two valves.

CLASSIFICATION 8.3

Majority of the bryologists believe that the class Anthoceropsida includes only a single order *(Anthocerotales)* having only a single family *(Anthocerotaceae).* However, Proskauer (1951) and Reimers (1954) believe that there should be two families (*Anthocerotaceae* and *Notothylaceae*) under the order Anthocerotales.

Only 6 genera and about 300 species are recognised to belong to the class Anthoceropsida. These 6 genera include *Anthoceros, Aspiromitus, Dendroceros, Megaceros, Notothylas* and *Phaeoceros.* Four of these genera *(Anthoceros, Dendroceros, Megaceros* and *Notothylas)* are recognised universally by all the bryologists to belong to Anthoceropsida. Stephani (1916) separated about 55 species of *Anthoceros* in the form of a separate independent genus *Aspiromitus,* while several species of the same genus *(Anthoceros)* have been delinked in the form of a new genus, i.e. *Phaeoceros* by Proskauer (1951).

ANTHOCEROTACEAE 8.4

1. Plant body is gametophytic and thalloid. The thallus is dark green, dorsiventrally flattened and lobed. The lobes with divided margins overlap each other.
2. Thallus lacks distinct midrib.
3. The ventral surface lacks scales, tuberculate rhizoids and mucilage hairs.
4. The archegonia are almost completely embedded in the gametophyte.
5. The sporophytes are long, upright, cylindrical structures.
6. At the base of each sporophyte is present a tubular sheath called involucre.
7. The sporogonium is differentiated into a bulbous foot, a meristematic zone and a long capsule.
8. "Cells of the capsule do not mature at the same rate and the cells in the basal portion of a capsule remain embryonic even after those in the apical portion are fully mature" (Smith, 1955).
9. A mature capsule dehisces from the apex downwards.
10. Capsule wall is several-layered thick, and its outermost layer contains stomata.
11. Chloroplasts are present in the cells of the sub-epidermal layers of the capsule wall.
12. Columella is present. It is endothecial in origin.
13. Columella remains overarched by archesporium.
14. Simple and branched pseudoelaters are present.

The life history of *Anthoceros* is discussed here in some detail.

ANTHOCEROS 8.5

8.5.1 Systematic Position

Class—Anthoceropsida
Order—Anthocerotales
Family—Anthocerotaceae
Genus—*Anthoceros*

8.5.2 Distribution and Habitat

Anthoceros is a cosmopolitan genus but occurs mainly in temperate and tropical parts of the world. Out of a total of about 200 species reported so far from different parts of the world, about 25 species of *Anthoceros* have been reported from India. It grows commonly in both plains and hills, on moist shady places, on the sides of ditches, and also in moist shady hollows among rocks. Dry conditions are not usually liked by *Anthoceros*. Some common Indian species, along with their places of common occurrence, are *A. erectus* (Kumaon Himalayas, Kulu, Manali, Mussoorie), *A. himalayensis* (Himalayas at an elevation of 5000–8000 ft), *A. gollani* (South India, including Chennai, Travancore), *A. longii* (Shimla, Nainital) and *A. chambensis* (Punjab, Chamba Valley).

GAMETOPHYTIC PHASE

8.5.3 External Features of Gametophyte

The plant body of *Anthoceros*, like other bryophytes, is gametophytic, and the gametophytes are thalloid, dark green, dorsiventral, usually prostrate (Fig. 8.1A-F) and smaller than *Marchantia*. In a majority of the species (e.g. *A. laevis*, *A. punctatus*), the thalli are variously lobed. The plant body is somewhat erect or raised over a short stalk in *A. erectus*, while it is pinnately branched in *A. halli*, and somewhat elongated in *A. himalayensis*.

Margins of the thallus, in most of the species, are irregularly lobed. The branching of the thallus appears to be of dichotomous type.

The dorsal surface of the thallus may be smooth (*A. laevis*), or rough with spines or ridges (*A. fusiformis*), or velvety because of the presence of several lobed lamellae (*A. crispulus*).

The ventral surface of the thallus contains only smooth-walled rhizoids. Tuberculate rhizoids and scales are absent. Mucilage hairs are also not found. Several dark, bluish-green spots are also seen on the ventral surface of the thallus. These spots are actually the cavities filled with *Nostoc,* an alga.

8.5.4 Anatomy of Thallus

Anatomically (Fig. 8.2A), the thallus is homogeneous, i.e. shows no differentiation of tissues. Both the surfaces are marked by an epidermal layer, i.e. **upper epidermis** on the upper side and the **lower epidermis** on the lower side.

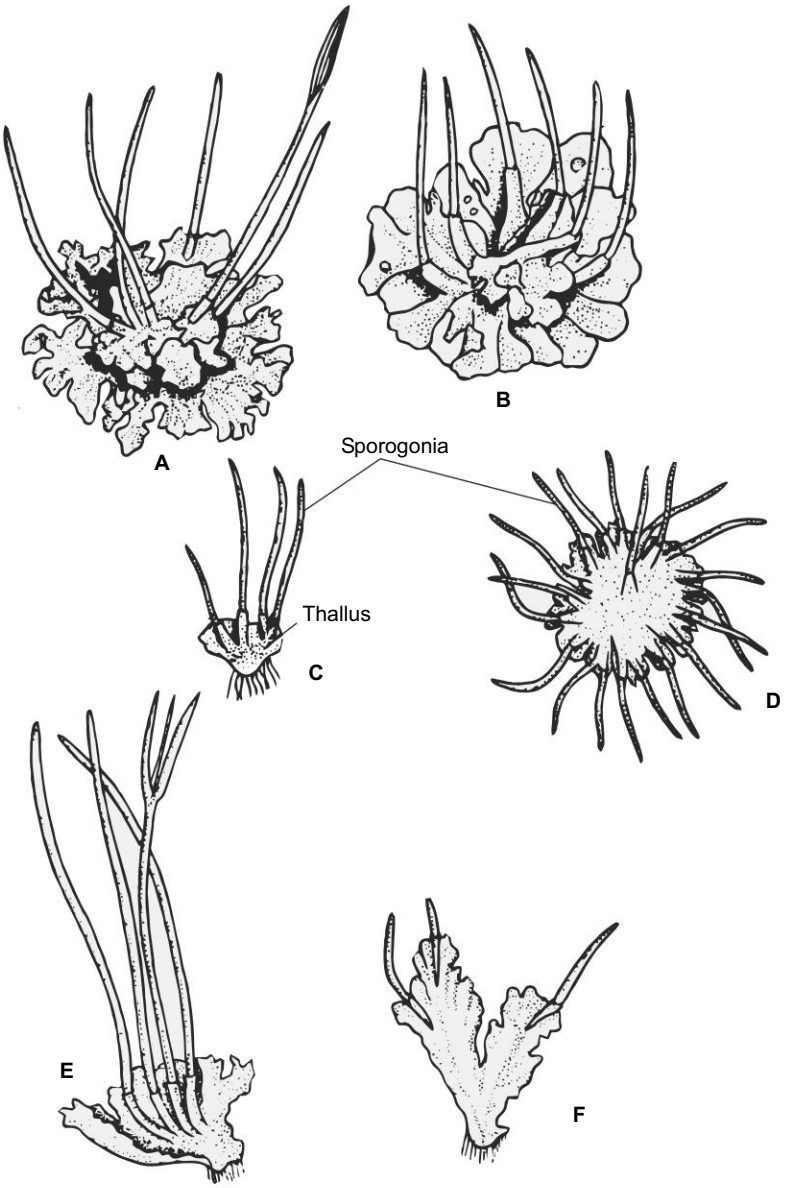


Fig. 8.1 A-F, External features of some species of *Anthoceros.* A, *A. punctatus;* B, *A. laevis;* C, *A. erectus;* D, *A. crispulus;* E, *A. fusiformis;* F, *A. himalayensis*

In between the two epidermal layers is present a soft, parenchymatous region of more or less uniform cells. The epidermal cells are comparatively smaller-sized, green, photosynthetic with chloroplasts somewhat larger than that of the cells of underlying tissues, and are more regularly arranged. The middle region of the thallus is usually 6 to 8 cells thick in most of the species. But, in a few species, it becomes 30 to 40 cells thick.

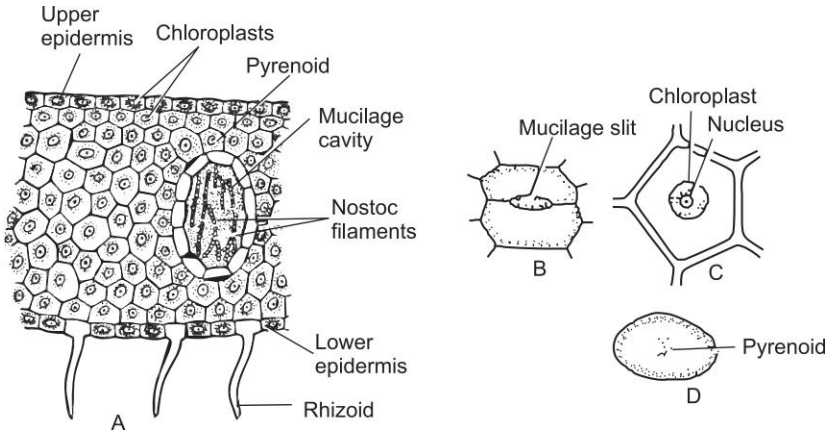


Fig. 8.2 A, VTS thallus of *Anthoceros*; B, A mucilage slit on the ventral surface of the thallus; C, An enlarged cell; D, A much enlarged chloroplast with a pyrenoid.

The air chambers and the air pores are absent in *Anthoceros*. However, some intercellular mucilage-filled cavities, each opening externally on the ventral surface by a stomata-like slit (Fig. 8.2B) or slime pore are present in the ventral region of the thallus. According to Parihar (1961), the slime pores appear to represent vestigial stomata. *Nostoc*, a blue-green alga, usually remains inhabited endophytically in these mucilaginous cavities, and hence these are also called *Nostoc - cavities*. The mucilage slits provide entry to the *Nostoc* filaments inside the thallus. Several schizogenous tubular cavities also develop in *A. punctatus* and several other species along with the *Nostoc* cavities.

Unlike other bryophytes, the cells of *Anthoceros* are peculiar in that each possesses a single large chloroplast (Fig. 8.2C), resembling several members of Chlorophyceae (green algae). Some species have variable number of chloroplasts in their cells. Each cell contains 2 chloroplasts in *A. pearsoni* while 4 chloroplasts in *A. halli*. The chloroplast is also peculiar in possessing a single large pyrenoid, resembling that of algae (Fig. 8.2D). The pyrenoids of *Anthoceros* consist of 25 to 300 spindle-shaped bodies grouped together in the form of a compact body. A rudimentary starch grain is also formed by each of these spindle bodies of the pyrenoid. The pyrenoids are absent in other members of bryophytes. The nucleus of each cell is located usually near the pyrenoid in close apposition to the chloroplast.

8.5.5 Apical Growth

The apical growth takes place in the thalli of *Anthoceros*, but whether it takes place by a single apical cell or by a group of apical cells is not clear. Mehra and Handoo (1953) opined that in *A. erectus* and *A. himalayensis* the apical growth is initiated by a group of apical cells. On the other hand, Campbell (1918) observed that the apical growth in *A. fusiformis* takes place by a single apical cell which cuts off the segments on dorsal, ventral as well as on both the lateral sides.

8.5.6 Vegetative Reproduction

Progressive decay and death of older parts of the thallus, formation of tubers, gemmae formation and survival of only the growing points of the thalli, are the major methods of vegetative reproduction in *Anthoceros*.

1. When the **progressive death and decay process** of the older posterior parts of the thallus reaches up to the dichotomy, the apical regions of the thallus may survive and start to function as new plants.
2. **Tubers** are usually swollen (*A. laevis*), stalked (*A. himalayensis*) or unstalked, and storage perennating bodies which develop during unfavourable conditions, such as prolonged drought. Other portions of the thallus die during such unfavourable conditions. When moisture and other favourable conditions are again available, the tuber germinates readily into a new thallus. Starch grains, aleurone granules and oil globules usually remain present in the inner tissues of a tuber in *Anthoceros*. *A. halli*, *A. himalayensis*, *A. laevis*, *A. pearsoni* and *A. tuberosus* are some of the tuber-forming species.
3. **Gemmae** develop either on the dorsal surface or along the margin of the thallus in several species, such as *A. formosae* and *A. glandulosus*.
4. Except the growing point and a small adjacent portion, the remaining parts of the thallus die during summer in *A. fusiformis*. On return of the favourable conditions, the surviving growing points develop into the new thalli.

8.5.7 Sexual Reproduction

The sexual reproduction in *Anthoceros* is oogamous, as in most of other bryophytes. The species may be monoecious (e.g. *A. fusiformis*, *A. punctatus*) as well as dioecious (e.g. *A. dixitianus*, *A. erectus*, *A. halli*, *A. laevis*). The monoecious species are usually protandrous, i.e. antheridia develop first on the thallus and the archegonia develop later on. The sex organs remain embedded and develop quite close to the apical cell, i.e. near the growing point.

8.5.8 The Antheridium

1. Development of Antheridium It starts from a superficial dorsal cell which does not become papillate (Fig. 8.3A). It divides periclinally into an inner antheridial initial and an outer **roof initial** (Fig. 8.3B). A mucilage-filled space appears between the roof initial and the antheridial initial. This space enlarges gradually and forms the **antheridial chamber** (Fig. 8.3C-G). There is no contribution of roof initial in the formation of antheridium proper. The roof initial divides anticlinally as well as periclinally to form a bi-layered roof (Fig. 8.3F-G) outside the antheridial chamber. Further development of antheridium differs in different species. In some species (e.g. *A. pearsoni*), the antheridial initial develops directly into a single antheridium, whereas in other species it divides by vertical divisions into two, four, eight or more daughter cells, each such cell developing into an antheridium. In the latter case, several antheridia develop inside an antheridial chamber, as in *A. punctatus* (Fig. 8.3G). However, in all the species, further development of antheridium from the antheridial initial is same as described below:

The antheridial initial first divides by two vertical divisions at right angles to one another, thus forming four cells. The next division is a transverse division forming an upper tier of four **antheridial cells** and a lower tier of four **stalk initials** (Fig. 8.3D). The stalk initials divide only by transverse divisions to form a long four-rowed stalk of the antheridium (Fig. 8.3G). Upper four antheridial cells (Fig. 8.3D) divide transversely to form an eight-celled octant stage (Fig. 8.3E). All the cells of the octant stage divide periclinally to form eight central **primary androgonial cells** and eight outer **primary jacket cells**. Several rapid transverse and vertical divisions take place in the primary androgonial cells

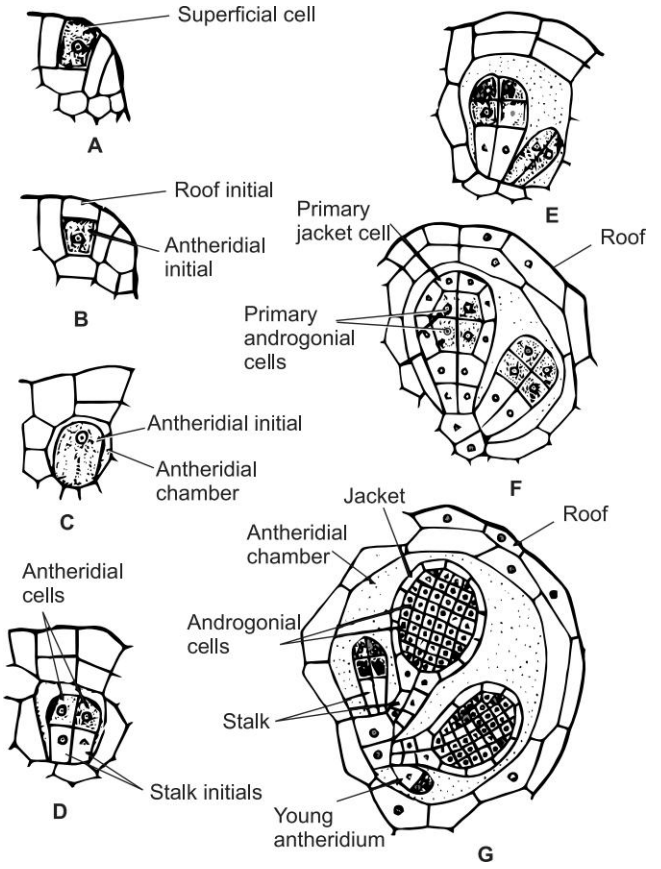


Fig. 8.3 A-G, Development of antheridium in *Anthoceros punctatus*

forming a mass of **androgonial cells** (Fig. 8.3F,G). All of the androgonial cells ultimately function as **androcyte mother cells**. The androgonial mother cells give rise to androcytes. The **spermatogenesis** is similar to that of other members of bryophyta. Each of the androcytes metamorphoses into a single biflagellate **antherozoid**. The primary jacket cells divide by several anticlinal divisions to form a single-layered sterile **jacket**.

Either a single or several antheridia are present in an antheridial chamber. Several antheridia, in different stages of their development, may be seen developing in an antheridial chamber (Fig. 8.3G). The secondary antheridia arise as young buds from the base of the mature antheridia. Proskauer (1951) reported as many as 22 antheridia in an antheridial chamber in *A erectus*, and up to 25 antheridia in an antheridial chamber in *A. punctatus*.

2. Mature Antheridium It is a stalked, club-shaped (Fig 8.4A) or pouch-like body, surrounded by a single-layered sterile jacket. The stalk usually consists of four rows of cells. Each cell of the jacket contains a well-developed plastid. The sterile jacket encloses several androcytes, each of which metamorphoses into a biflagellate antherozoid.

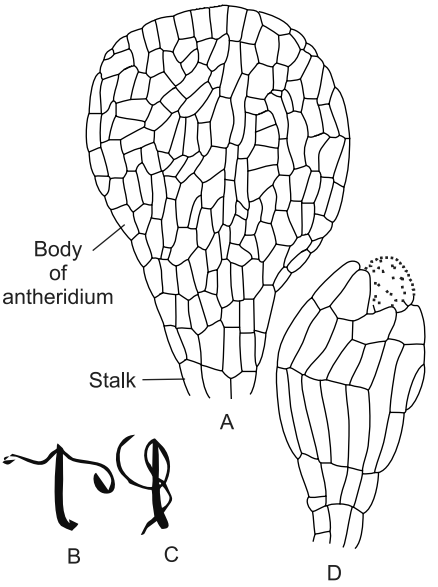


Fig. 8.4 A, A mature antheridium of *Anthoceros laevis;* B-C, Antherozoids of *A. laevis;* D, An antheridium of *A. punctatus* showing dehiscence

3. Antherozoids Each antherozoid is a unicellular, uninucleate and biflagellate structure having a linear body (Fig. 8.4B, C) with a slightly broader head. The length of the flagella is almost the same as that of the body of the antherozoid. An elongated swelling, probably representing a **blepharoplast**, is present just beneath the flagella.

4. Dehiscence of Antheridium The mature antheridia soon become exposed due to the irregular breaking of the roof of the antheridial chamber. The antheridia now start absorbing water. Soon, some of the cells of the apical region are separated from each other forming an apical aperture in the antheridium. The mass of the androcytes come out through this apical aperture (Fig. 8.4D).

8.5.9 The Archegonium

1. Development of Archegonium The archegonia are produced in acropetal succession near the growing points. The archegonia remain embedded in the thallus. Each archegonium is characteristically surrounded externally by a mucilaginous mound (Fig. 8.5).

The **development of archegonium** starts from a superficial dorsal cell which starts to function as an **archegonial initial** (Fig. 8.6A). Differing from *Marchantia*, the archegonial initial does not project from the surface of the thallus. Mehra and Handoo (1953) reported that the archegonial initial starts to function directly as the **primary archegonial cell**. (*Anthoceros* thus differs from *Marchantia* because in the latter, the archegonial initial first divides transversely into an outer primary archegonial cell and an inner stalk cell).

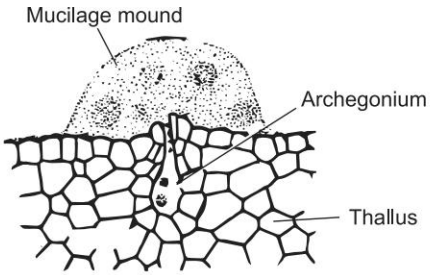


Fig. 8.5 An embedded archegonium of *Anthoceros laevis* surrounded by a mucilaginous mound

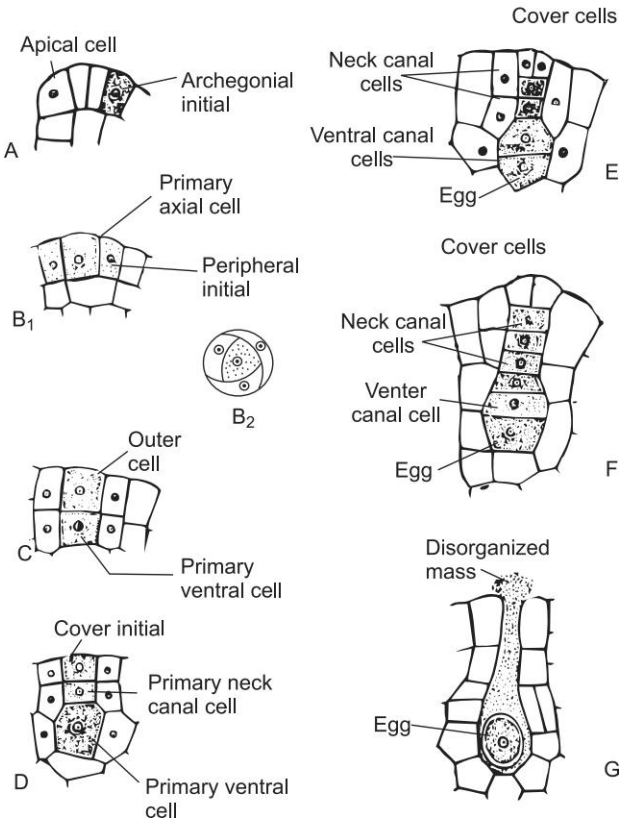


Fig. 8.6 A-G, Archegonial development in *Anthoceros* (B_2 is the T.S. of B_1)

In *Anthoceros*, the primary archegonial cell divides by three vertical intersecting divisions, forming three **peripheral initials** or **jacket initials** and a central **primary axial cell** (Fig. 8.6B_1, B_2). The primary axial cell divides transversely into two equal-sized cells called **outer cell** and **primary ventral cell** (Fig. 8.6C). The primary ventral cell soon becomes distended, whereas the outer cell divides transversely into an upper **cover initial** and an inner **primary neck canal cell** (Fig. 8.6D). The cover

initial divides by one or two vertical divisions at right angles to one another to form two or four **cover cells** (Fig. 8.6E). The primary neck canal cell divides by transverse divisions to form four to six or more **neck canal cells** (Fig. 8.6E, F). The primary ventral cell divides by a transverse division to form a **ventral canal cell** and an **egg** (Fig. 8.6E).

Along with all these developments, the three **jacket initials** divide transversely to form two tiers of cells (Fig. 8.6C). The three cells of the upper tier, surrounding the neck, divide by vertical divisions to form six vertical rows of cells. These vertical rows of cells surround the neck canal cells. Owing to the embedded nature of the archegonium, further development of the lower tier of the cells of the jacket initials is indistinguishable from that of the surrounding cells of the thallus.

2. Mature Archegonium Except that of the cover cells, the major parts of the mature archegonium remain embedded in the tissues of the thallus. The axial row consists of four to six neck canal cells, a venter canal cell and an egg (Fig. 8.6F). Soon, the cover cells are thrown off without leaving any of their traces. The neck canal cells and venter canal cell disintegrate and form a mucilaginous mass, leaving only the egg in the cavity of the venter of the archegonium (Fig. 8.6G).

3. Fertilization It is exactly similar to that of *Marchantia* discussed under Article 7.7.9.

SPOROPHYTIC PHASE

8.5.10 Development of Sporogonium

Immediately after fertilization, the fertilized egg enlarges in size and keeps on enlarging till it completely fills the cavity of the venter. A cellulose wall is secreted outside this developing zygote (Fig. 8.7A). Usually, the zygote first divides by a vertical division (Fig. 8.7B) to form two equal cells. It is followed by a transverse division in each cell forming four equal- or unequal-sized cells (Fig. 8.7C). If the four unequal-sized cells are formed after first two divisions, then the two basal cells are smaller while the two upper cells are larger (Fig. 8.7C). In the four-celled embryo, the next division is a vertical division at right angles to the first vertical division. Thus, an eight-celled octant stage of the embryo is resulted. According to Bhardwaj (1950), however, the first division in the zygote is a transverse division, followed by two successive vertical divisions at right angles to one another, thus forming an eight-celled octant stage.

Further development of the eight-celled embryo is different in different species. In *Anthoceros erectus*, the lower four cells develop into **foot** whereas the upper four cells form the **intermediate zone** (seta) and **capsule**. In *A. himalayensis* and *A. pearsoni*, however, the upper four cells of the eight-celled embryo divide by transverse walls to form a three-tier embryo (Fig. 8.7D) in which each tier contains four cells. Of these three tiers, the uppermost tier forms the capsule, the middle tier forms the intermediate zone (seta) and a small part of the foot, while the lowermost tier of four cells forms the remaining major part of the foot.

Foot develops further by regular (*A. erectus*) or irregular (*A. himalayensis*) divisions in the cells of the lowermost tier of the embryo. It ultimately becomes broad, bulbous and multicellular (Fig. 8.7G, H). Its cells are parenchymatous. In most of the species, the superficial cells of the foot tend to become rhizoidal or haustorial. These cells penetrate deeply into the adjoining tissues of the thallus and absorb food, and thus behave like cells of haustorium.

The **capsule** develops from the uppermost tier of four cells. This uppermost tier divides by one or two transverse walls to form the cells arranged in two or three tiers containing four cells each (Fig. 8.7E). These cells now divide periclinally to form an outer layer of **amphithecium** and an inner layer of **endothecium** (Fig. 8.7E). The entire endothecium, consisting of four vertical rows of cells, gives rise to **columella**. The columella in the mature capsule consists of 16 vertical rows of cells. In *A. fusiformis*, the columella in the mature sporogonia becomes very massive and consists of as many as 36-49 rows of cells, according to Campbell (1924).

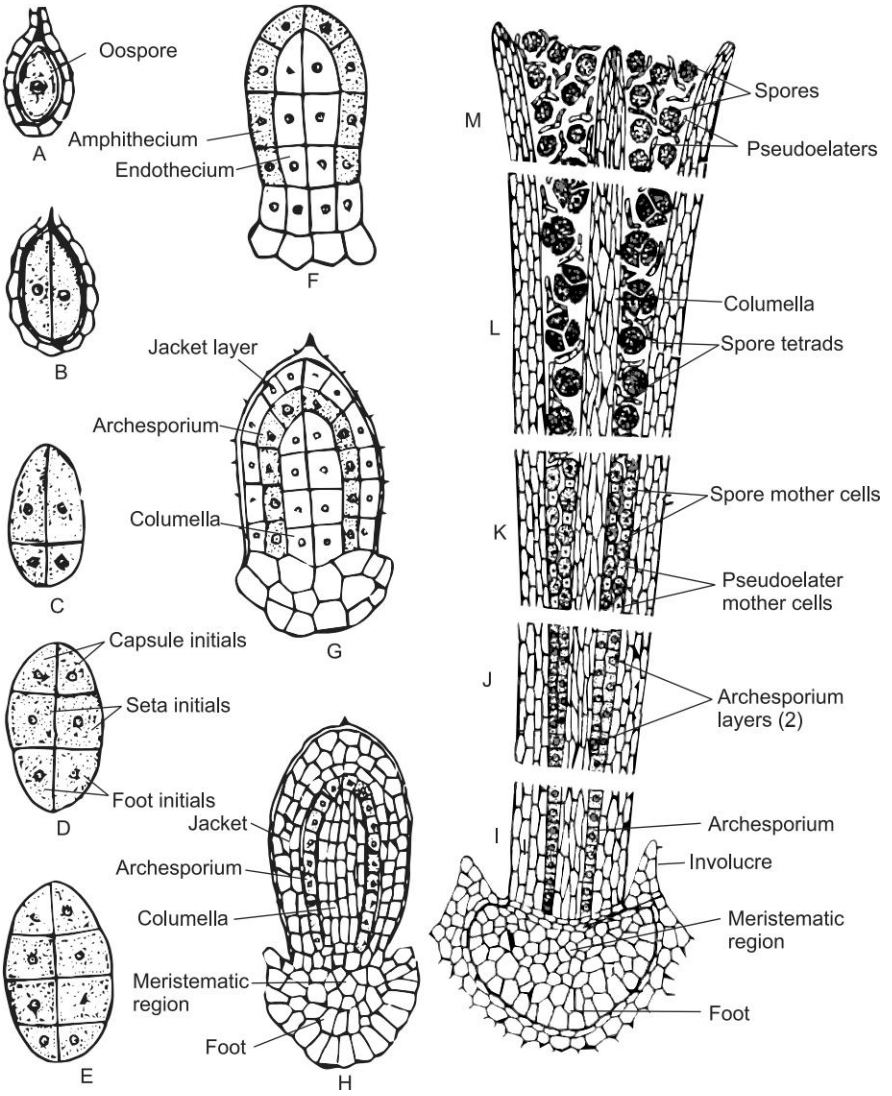


Fig. 8.7 A-H, Development of the sporogonium in *Anthoceros*; I-M, LS of the mature capsule through different portions of the sporogonium (Note the single-layered archesporium in I, bilayered archesporium in J, formation of spore mother cells and elater mother cells in K, formation of spore tetrads in L, and formation of spores and pseudoelaters in M)

A periclinal division in the amphithecium divides it into an outer sterile layer of the **initials of jacket layer** and an inner fertile layer of the sporogenous tissue called **archesporium** (Fig. 8.7G). The jacket layer initials divide periclinally several times to form a four- to six-layered **wall** of the capsule (Fig. 8.7H-M). The outermost layer of the wall of the capsule functions as **epidermis**. In mature capsule, the epidermis is thickly cutinised and also bears some pore-like **stomata**. The cells of the other wall layers are green, parenchymatous and bear intercellular spaces. The number of chloroplasts in the parenchymatous cells of the inner wall layers may vary from one to four in different species.

The **archesporium** overarches the apex of the columella in young sporogonia (Fig. 8.7H). Several stages of the archesporium development may be seen and studied in a single sporogonium. At the base of the capsule, the archesporium is single-layered and present in between the columella and the wall layers (Fig. 8.7I). In species, such as *A. himalayensis* and *A. pearsoni*, the archesporium becomes bilayered slightly above the base (Fig. 8.7 J). In *A. hallii*, it even becomes 2 to 4 cells in thickness. At a slightly higher level in the maturing sporogonium, the archesporium gets differentiated into two types of cells, i.e. fertile **spore mother cells** and sterile **pseudoelater mother cells** (Fig. 8.7K). The spore mother cells are oval to spherical, large cells with dense granular cytoplasm, chloroplast and prominent nucleus. The pseudoelater mother cells are elliptical cells with less prominent nuclei. In several species, the spore mother cells and pseudoelater mother cells are alternately arranged. Both are soon separated from each other as well as from the columella due to the unequal growth of the wall layers and the columella.

The **spore mother cells** are diploid in nature. Each enlarges in size, becomes globular and divides reductionally to form four haploid **spores**, arranged in a tetrad manner (Fig. 8.7L). The **pseudoelater mother cells** divide either transversely or by oblique divisions to form a loose net of sterile cells, which are soon separated into one- to three-celled **pseudoelaters** (Fig. 8.7 L, M; Fig. 8.8). When young, the pseudoelaters contain starch and protein, and are nutritive in function. But mature pseudoelaters are dead cells and help in the dispersal of spores.

The middle tier of the young embryo (Fig. 8.7D) usually gives rise to the **intercalary meristem**, which functions like that of the **seta** of *Marchantia* and other Hepaticopsida. After the formation of the columella, the archesporium and the jacket, further growth of the sporogonium takes place mainly due to the activity of this intercalary meristem (Fig. 8.7H, I). Due to activity of this meristematic region, the capsule increases in length, its tip portion is dehisced, and ultimately the mature spores are liberated (Fig. 8.7M).

The **calyptra** or **involucre** protects the young developing sporogonium in the form of a sheath or fleshy covering. It is formed mainly by the thallus tissues surrounding the young sporogonium and partly by the tissues of the embedded archegonium. When the sporogonium grows more, the involucre is ruptured and ultimately remains only in the form of a sheath at the base of the sporogonium (Fig. 8.7I). Structurally, the involucre resembles the thallus because it is mainly the part of the latter.

8.5.11 Mature Sporogonium

It consists of a bulbous **foot**, an intermediate **meristematic zone** in place of seta, and an erect cylindrical **capsule**, varying between 2 and 15 centimetres in length in different species (Fig. 8.7I-M). The **foot** is a bulbous body consisting mainly of parenchymatous cells and some superficial cells showing haustorial processes. The latter penetrate deep into the tissues of the thallus and absorb food.

The **capsule** is a long structure, having sterile columella and fertile sporogenous tissue or archesporium. The columella extends from the base up to the tip of the capsule and consists of 16 vertical rows of cells. Campbell (1924) opined that the columella functions as a water-conducting tissue of the capsule in *A. fusiformis*. However, it mainly provides mechanical support to the long sporogonium and helps in spore dispersal.

The columella is surrounded by sporogenous tissue. It consists of a one-layered archesporium at the base, while mature spores and pseudoelaters are at the top of the capsule. The pseudoelaters are multicellular and branched or unbranched structures. Spiral thickenings are absent in pseudoelaters (Fig. 8.8). The capsule wall consists of 4 to 6 layers of cells, of which the outermost layer is the epidermis. The continuity of the epidermis is broken by a few pore-like stomata.

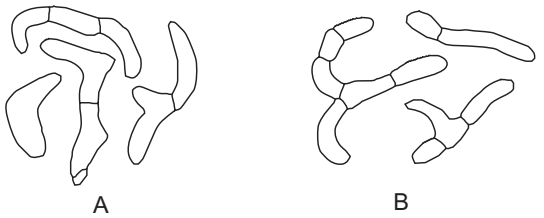


Fig. 8.8 A-B, Pseudoelaters of *Anthoceros erectus* (A) and *A. himalayensis* (B)

8.5.12 Dehiscence of the Capsule

In a mature capsule, the tip becomes brownish or blackish in colour and ultimately shrinks due to the loss of water in the dry conditions. Because of this shrinkage, the capsule wall comes in contact with the fertile sporogenous region containing spores and pseudoelaters. Actual dehiscence occurs because of slits or dehiscence lines formed in different species. Spiral twisting is also observed in the tip region of the capsules because of the excessive loss of water. Enlarging columella and somewhat hygroscopic nature of the pseudoelaters also help in the dehiscence of the capsule. Spores are dispersed over a long distance from the dehiscing capsule by strong air currents.

GAMETOPHYTE

8.5.13 Spore

The haploid spores, formed after the reduction division of the diploid spore mother cells (Fig. 8.9 A-B) are the starting points of the gametophytic generation. Each spore is surrounded by a thin endospore and a thick outer layer of exospore. The spores may have short papillae on the outer surface or may be reticulate with furcate spines. Each spore is uninucleate and usually contains oil globules, a plastid and other food materials. The diameter of the spore in different species usually ranges between 0.03–0.06 mm. The colour of the mature spores may be yellow, dark brown or smoky black.

8.5.14 Germination of Spore and Formation of Young Gametophyte

Spore germination has been studied only in a few species of *Anthoceros*, such as *A. fusiformis* (Campbell, 1928), *A. erectus* and *A. punctatus* (Mehra and Kachroo, 1962). The exospore layer of the spore ruptures along the triradiate ridge (Fig. 8.9A) and the endospore comes out in the form of a germ tube (Fig. 8.9C). The plastid, oil globules and other food materials of the spore pass into the

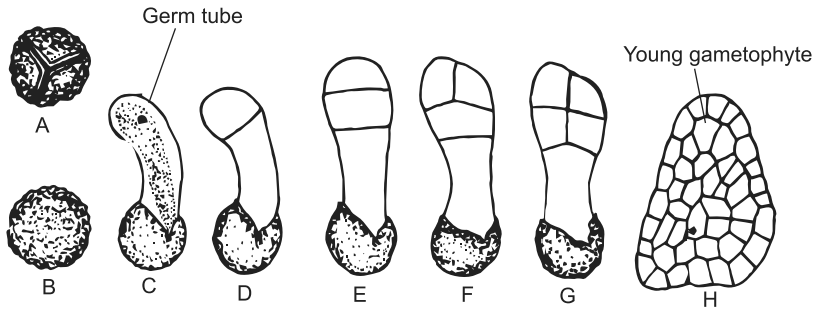


Fig. 8.9 A-H, Spore germination in *Anthoceros*

germ tube. Usually, the first two divisions in the germ tube are transverse, forming a three-celled short filament (Fig. 8.9D, E). The uppermost cell now divides by a vertical division (Fig. 8.9F). Soon, the same type of vertical division takes place in the lower cell (Fig. 8.9G). All the so-formed four cells now divide by yet another vertical division at right angles to the first one, forming an eight-celled stage. Further growth of the young gametophyte (Fig. 8.9H) usually takes place by the four upper cells of this eight-celled germling. A cylindrical elongated young gametophyte is soon resulted. The first rhizoid develops from the young multicellular gametophyte, from any cell containing chloroplast.

8.5.15 Life History of *Anthoceros*

Life history of *Anthoceros* is depicted in Fig. 8.10.

APOSPORY IN *ANTHOCEROS* 8.6

"Production of a diploid gametophyte from vegetative cells of the sporophyte, that is, without the production of spores is known as **apospory**. It was first reported in *Anthoceros laevis* by Lang (1901). He discovered that pieces cut off from the sporogonium of this species, when placed in conditions suitable for their growth, are able to develop into masses of cells which grow into thalli. Commonly, such masses of cells develop from sub-epidermal cells. Since such a gametophyte was produced directly from the vegetative cells of the sporophyte, this clearly represents a case of the phenomenon of apospory. Later on, apospory was reported in several species of *Anthoceros*. Schwarzenbach (1926) observed that in many species of this genus, any cell of the young sporophyte can produce a gametophyte, except that of the cells of the meristematic region. The gametophytes producted aposporously appear quite normal to that of other normal thalli, except the fact that the number of chromosomes in their cells is diploid ($2x$).

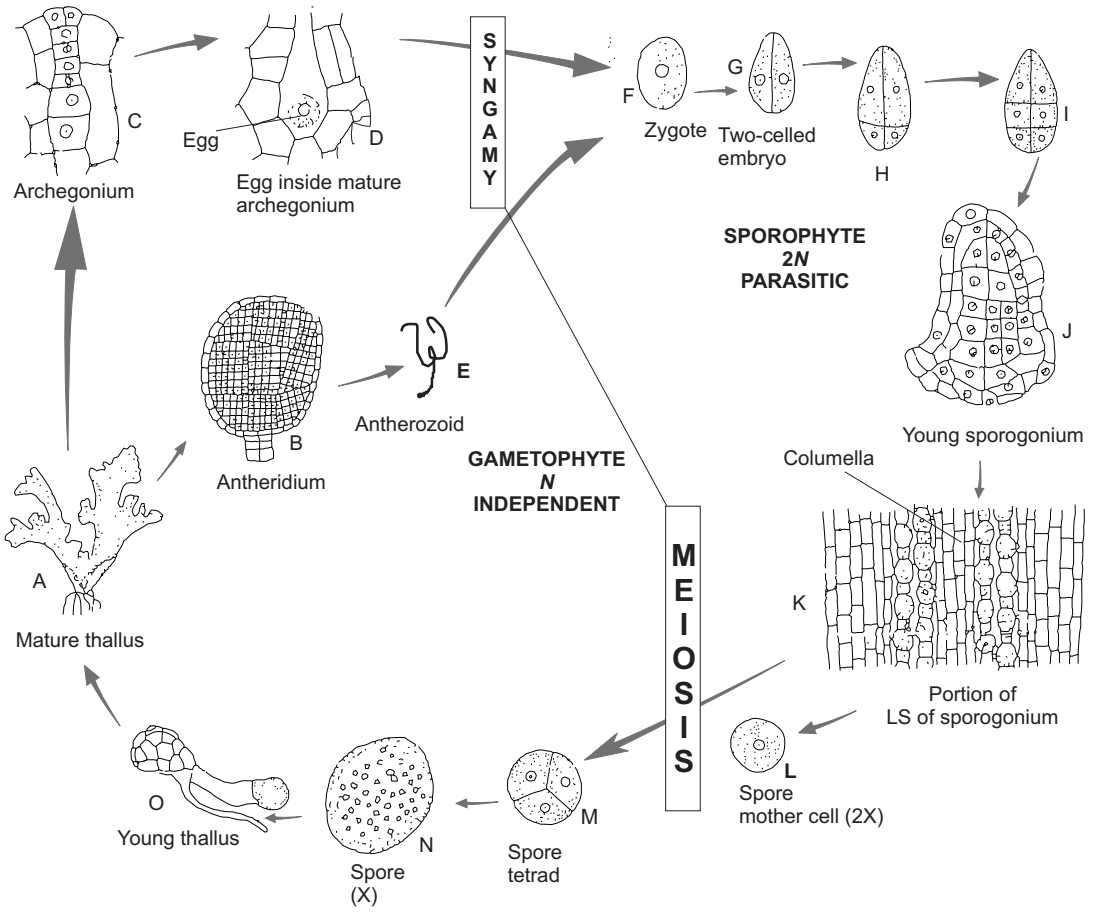


Fig. 8.10 *Life history of Anthoceros*

NOTOTHYLACEAE 8.7

1. The sporophytes grow out horizontally from the fertile lobes of thallus.
2. In comparison to Anthocerotaceae, the sporophytes in Notothylaceae are shorter, more compact and marginal in position.
3. Capsule wall lacks photosynthetic tissue.
4. The outermost layer of capsule wall lacks stomata.
5. In some species of this unigeneric family, columella is absent. In others, however, it is well-developed.
6. Pseudoelaters are simple, and are equal-sized or sometimes larger than the spores.
7. Pseudoelaters contain spiral or oblique bands.

The only genus of the family Notothylaceae is *Notothylas*, and some details of its life history are discussed here.

NOTOTHYLAS 8.8

Systematic Position

Class—*Anthoceropsida*
Order—*Anthocerotales*
Family—*Notothylaceae*
Genus—*Notothylas*

About a dozen species of *Notothylas* have been reported so far, growing in damp, shady places, either on moist soil or on rocks or on moist floor walls of old buildings. They are widely distributed in temperate as well as tropical regions. Five species have been reported so far from India. These are *Notothylas chaudhurii*, *N. indica*, *N. javanicus*, *N. levieri* and *N. pandei*. Two most common Indian species, growing in Himalayas, are *N. indica* and *N. levieri*. *N. indica* also occurs commonly in the plains.

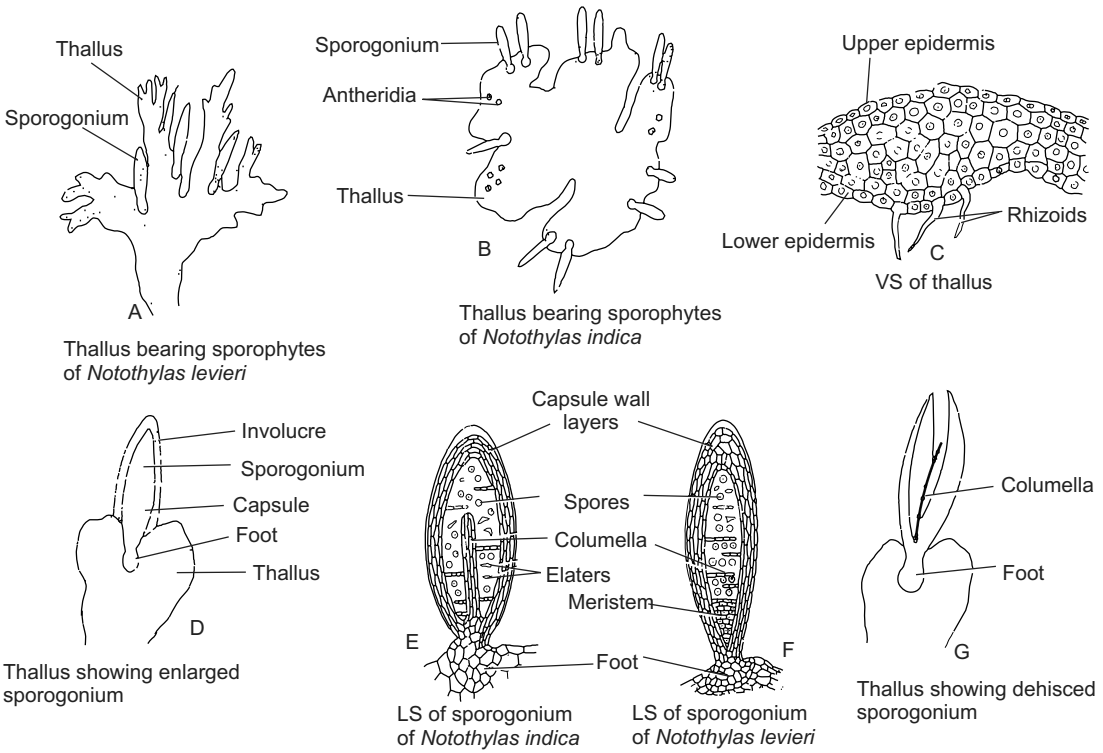


Fig. 8.11 *A-G, Notothylas.* A, Thallus of *N. levieri* bearing sporophytes; B, Thallus of *N. indica* bearing sporophytes; C, Vertical section of the thallus; D, Thallus showing an enlarged sporogonium; E, LS sporogonium of *N. indica;* F, LS sporogonium of *N. levieri;* G, Thallus showing dehisced sporogonium

Plant body is gametophytic, prostrate, thalloid, delicate, light green and orbicular or sub-orbicular in outline. The thalli are variously lobed, and the lobes are either toothed, seriate or fimbriate (Fig. 8.11A-B). Thalli of *Notothylas indica* form bluish-green rosettes while that of *N. levieri* are pale green, elongated and irregularly branched. *N. indica* thalli attain a diameter of 2–5 mm. Horizontally borne sporophytes and cyanobacterial auricles are present on the dorsal surface of the thallus. Only smooth-walled rhizoids are present on the ventral surface. Tuberculate rhizoids and scales are absent.

Anatomy of the thallus reveals that it is 6–8 cells thick in the middle and only one or two cells thick on the margins (Fig. 8.11C). Cells of the upper and lower epidermal layers are generally smaller than the other inner cells. Soft parenchymatous cells are present in between the two epidermal layers. Mucilage cavities containing the *Nostoc* colonies are common in the thallus. These colonies are, however, absent in *Notothylas javanicus*.

The structure and development of sex organs in *Notothylas* (Fig. 8.12 A, B) is exactly similar to *Anthoceros*, as described earlier under Articles 8.5.7 to 8.5.9.

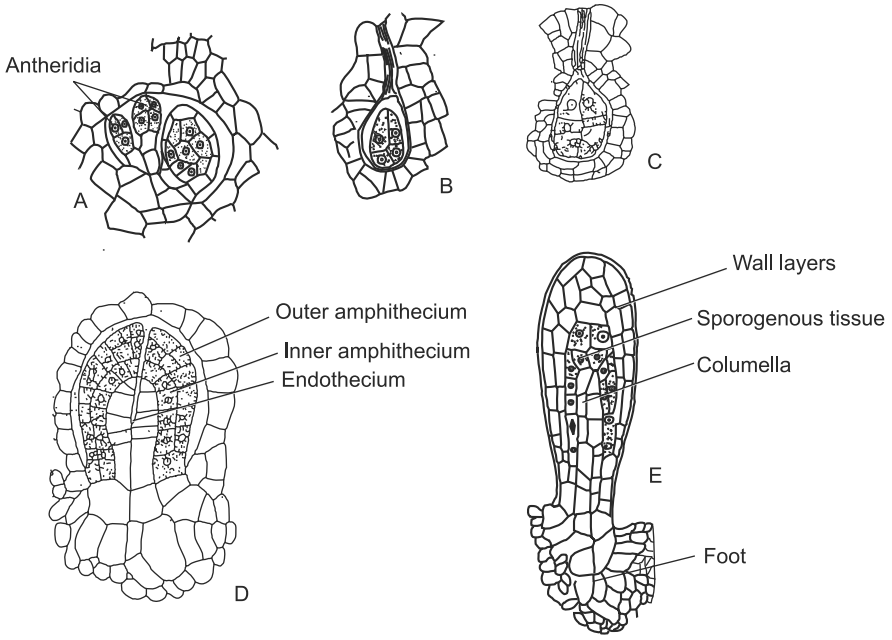


Fig. 8.12 *Notothylas.* A, Antheridia in different stages of development; B, An archegonium bearing young embryo; C, Three-tiered embryo; D-E, Differentiation of outer and inner amphithecial layers and endothecium.

The **zygote** first divides by transverse division in *N. indica* and *N. orbicularis*. In some other species (*N. javanicus and N. levieri*), however, the first division in the zygote is a longitudinal division. In all species of *Notothylas*, further divisions result in the development of a three-tiered embryo, in which each tier contains four cells (Fig. 8.12C). The lower two tiers develop into the foot, while the uppermost tier of this three-tiered embryo produces the **capsule**. Periclinical division in the cells of the uppermost tier demarcates the outer **amphithecium** and inner zone of **endothecium**. The embryo development is similar in all species up to this stage only. After this stage, it is different in different species.

In *Notothylas indica*, the amphithecium cells divide periclinally and form outer amphithecium and inner amphithecium. The outer amphithecium forms the wall of the capsule, while the inner amphithecium forms the sporogenous tissue. The endothecium develops into columella (Fig. 8.12 D-E). In this way, *N. indica* resembles *Anthoceros* in its embryo development. In *N. levieri*, however, the entire amphithecium develops into the wall of the capsule while the entire endothecium develops into sporogenous tissue. Thus, the embryo development in *N. levieri* resembles with members of *Hepaticopsida*. This species, therefore, serves as a connecting link between Anthoceropsida and Hepaticopsida. In *N. indica*, therefore, the archesporium is a layer of cells in between the capsule wall and columella. The archesporium becomes many-layered towards the apex of the sporophyte in this species.

Regarding the fate of archesporium in *Notothylas,* two bands of sterile and fertile tissues are formed. Bands of the sterile tissue form **elaters** and of fertile tissue form **spore mother cells**. Structurally, the elaters are short, often curved, unicellular structures with bands of thickenings on their walls. The diploid spore mother cells divide reductionally and form haploid **spores**. A meristematic zone of intercalary meristem is present at the base of the capsule. The meristematic zone is short-lived in activity and contributes to various tissues in the capsule. Due to this short-lived activity of meristematic tissue, the sporophyte in *Notothylas* is shorter (only 2–3 mm in length) than that of *Anthoceros*.

Mature sporophytes (Fig. 8.11 D-F) of *Notothylas* are pointed, oval or cylindrical structures. Usually, they are cylindrical with pointed ends. When young, the sporophyte is completely enclosed within a membranous structure. Each sporophyte has a massive foot, meristematic zone and capsule. The **foot** is triangular and some of its basal cells elongate to form rhizoidal outgrowths. Intermediate **meristematic zone** is short, less active and exhibits very little meristematic growth. **Capsule** remains surrounded by a 3–4 layered wall, which lacks stomata and photosynthetic tissue. Columella is present in the centre. The sporogenous tissue contains elaters and haploid spores. The **spores** are dark brown in colour, and their wall is differentiated into thick exospore and thin endospore. One to four lines of dehiscence in the form of rows of thick-walled cells can be observed. They are seen running along the entire length of the capsule, and they meet at the apex of the capsule.

Dehiscence of capsule and dispersal of spores take place along lines of dehiscence. At the time of spore germination, a four or eight-celled mass of cells is formed. It is called **germ disc**. Rhizoids start developing from one or two basal cells of the germ disc. Differentiation of a marginal meristem is responsible for the further growth of the thallus of *Notothylas*.

BIOLOGICAL IMPORTANCE OF THE SPOROPHYTE OF *ANTHOCEROS* 8.9

The sporophyte of *Anthoceros* is remarkably different from the sporophytes of other bryophytes, and it is thus considered unique and also of advanced type. Its advanced characteristics show evolutionary trends.

8.9.1 Some Advanced Features of Sporophyte

1. Capsule Wall of the Sporophyte The wall of the capsule of the sporophyte of *Anthoceros* is multilayered, contains chlorophyll-containing green cells with several intercellular spaces between

them. On the external side is present a layer of epidermis with several stomata, here and there, like that of higher plants. The presence of amply ventilated photosynthetic tissue in the wall is an advanced feature, and certainly a step towards the beginning of physiological independence of the sporophyte. To some extent, it can prepare its own food. Inspite of this, it never becomes completely independent of the gametophytic thallus.

2. Decentralization and Sterilization of the Central Fertile Region, i.e. Endothecium Differing from many other bryophytes, the archesporium is amphithecial in origin in *Anthoceros*. Decentralization and complete sterilization of the central fertile tract is very clear in this genus. The central core of sterile tissue forms the **columella** in the capsule. The columella is made up of narrow, vertically elongated conducting cells, the walls of which are uniformly thickened. The presence of central columella in the sporophyte of *Anthoceros* suggests of the **origin of the vascular tissue** in plants. Vascular elements (xylem, phloem, etc.), however, never develop in columella. But its central location in the sporophyte may be compared with the vascular cells of the early tracheophytes. Like vascular tissue of higher plants, the columella in *Anthoceros* provides mechanical support to the sporophyte. Some scientists believe that presence of columella is an evolutionary step towards the development of protostele.

Archesporium, being amphithecial in origin, is also an evolutionary steps because the spore-producing region is shifted from central to the superficial region, and this position promotes easy dispersal of spores.

3. Importance of Development of Archesporium into Alternate Bands of Fertile and Sterile Tissues Fertile spore mother cells and sterile pseudoelater mother cells develop in between columella and wall layers in alternate bands in the capsule of *Anthoceros*. This is also an evolutionary tendency, which has great potentialities. It is thought by some bryologists to be an initial step towards the origin of sporangia and sporophylls. Bower thought it to be a step towards the origin and evolution of leaves and sporangia in pteridophytes. This theory of Bower is called **theory of origin of strobilus**.

4. Presence of Basal Intercalary Meristem Presence of intercalary meristem at the capsule base provides strength and also unlimited power to the entire sporophyte to grow. The meristem keeps on adding new cells at the base of the capsule. These cells keep on differentiating into columella, archesporial region and also photosynthetic region of capsule wall. All these activities of meristematic cells prolong the period of spore production. Only because of these characteristics, *Anthoceros* sporophyte is long-lived in comparison to other bryophytes, and keeps on producing spores as long as the gametophytic thallus is surviving.

5. Massive Foot Foot is well-developed, massive and remains embedded in the thallus. It produces many short, rhizoid-like processes, which penetrate into the thallus and keep on absorbing the nutrients. Presence of rhizoid-like processes in the foot is an advanced feature which also indicates evolutionary trends.

6. Upright Cylindrical Body of the Capsule The upright cylindrical body of the capsule helps in the easy dispersal of spores, and it is also thus an advanced feature of the sporophyte in *Anthoceros*.

8.9.2 Anthoceros Sporophyte and Origin of Pteridophytes

The above-mentioned six unique and advanced features of the sporophyte of *Anthoceros* also indicate the evolutionary trends or possible lines of biological progress in this genus. On the basis of such characteristics, Campbell (1940) formulated the well-known theoery of **Anthocerotalean Origin of Pteridophytes**. In this theory, "the sporophyte of *Anthoceros* and its allies was considered to be on the line of evolution leading to the simplest and primitive independent sporophyte of the pteridophytes" (Campbell, 1940). In *Anthoceros fusiformis* Campbell also collected some very large and bulky specimens of the sporophyte, attaining a length of about 15 cm or even more, and suggested that these have evolved into some simplest and most primitive free-living sporophytes of pteridophytes. Such large sporophytes of *A. fusiformis* also survived in unusually favourable habitats for a large period of as long as 9–10 months or even more. The following peculiarities were seen in such specimens of *A. fusiformis*:

1. The sporogenous tissue was suppressed or ill-developed at the base of the capsule of the sporophyte.
2. In comparison to normal sporophytes, there was seen amply ventilated photosynthetic system in the capsule wall of *A. fusiformis*.
3. Bulky growth of the columella was seen. It became nearly double in diameter in *A. fusiformis* than that of the normal sporophytes of other species of *Anthoceros*.
4. Some columella cells at the base of the capsule became elongated, functioned like conducting strands and thus can be compared with the simple vascular bundles of tracheophytes.
5. Bulky and unusually large foot may come in direct contact of the soil due to disorganisation of the adjacent tissue of the thallus.

These characteristics of *A. fusiformis* suggest that such sporophytes have attained a "condition comparable to that of the young pteridophyte after it has established its first root" (Campbell, 1940). This theory of Anthocerotalean Origin of Pteridophytes has, however, been criticised by several other later bryologists.

AFFINITIES OF ANTHOCEROTALES 8.10

Available details of life history (gametophytic and sporophytic generations) of Anthocerotales, in general, and *Anthoceros,* in particular, lead us to the conclusion that this group has characteristic features common with algae on one hand and other groups (like Hepaticopsida, Bryopsida and also pteridophyta) on the other. Let us have a glimpse of some features of Anthocerotales common with all these other groups.

8.10.1 Features Common with Algae

Anthocerotales show features common with algae, in general, and green algae (Chlorophyceae), in particular. Some of such features are listed below:

1. Presence of at least a single large **chloroplast** in each cell of the gametophyte. In *Megaceros*, however, many chloroplasts are present in each cell, and this has been interpreted as an intermediate condition between the single chloroplast of *Anthoceros* and many chloroplasts of other Embryophyta.

2. Presence of **pyrenoid** in the chloroplast of each cell (**Pyrenoid** is actually a small grain of protein in the chloroplast of an algal cell, around which starch is deposited. Pyrenoids are the characteristics of cells of green algae, i.e. Chlorophyceae).
3. Presence of simple, green, thallus-like gametophytic plant body, resembling in outline and branching.
4. Presence of biciliate antherozoids in both algae and Anthocerotales.

All these above-mentioned similarities suggest that *Anthoceros* is close to the evolutionary line leading from algae (Chlorophyceae) to the land plants.

8.10.2 Features Common with Hepaticopsida

Anthocerotales show many features common with Hepaticopsida, yet another major group of bryophytes. Some of such features are listed below:

1. Presence of simple, thallus-like gametophyte in both Anthocerotales and most of the species of Hepaticopsida.
2. Appendages are absent on the thalli of both.
3. In both Anthocerotales and many Hepaticopsida, there is not much differentiation of tissues in the plant body.
4. Apical growth is almost similar in members of both groups.
5. There exists similarity in the essential construction of mature sex organs in members of both the groups.
6. Both Anthocerotales and Hepaticopsida possess biflagellate antherozoids.
7. In both groups, amphithecium and endothecium separate in almost the same way by periclinal divisions.
8. In both the groups, archesporium gives rise to fertile spores and sterile elaters or pseudoelaters.
9. In *Megaceros*, walls of the sterile cells of the capsule are spirally thickned to form elaters, quite similar to that of members of Hepaticopsida.
10. *Notothylas levieri* is a noncolumellate species of Anthocerotales. The entire endothecium in this species forms the archesporium, and the amphithecium forms the jacket of the capsule. Due to these similarities, *N. levieri* forms a connecting link between Anthocerotales and Hepaticopisida.

8.10.3 Features Common with Bryopsida or Mosses

Features of sporophyte of *Anthoceros* common with that of mosses (Bryopsida) are listed below:

1. Highly differentiated and ventilated photosynthetic region is present in the capsule wall of both *Anthoceros* and mosses.
2. Columella, the central solid core of sterile cells, is present in both *Anthoceros* and *Funaria*.
3. Greatly reduced sporogenous tissue present only in a small part of the capsule in both.
4. Presence of functional stomata in the wall of both *Anthoceros* and *Funaria*.
5. *Anthoceros* resembles some Bryopsida (e.g. *Sphagnum*) in their common characteristic of origin of archesporium from inner amphithecium. In some species of *Notothylas*, however, the archesporium is endothecial in origin, and this characteristic may form a link between Bryopsida and *Anthocerotopsida*.

8.10.4 Features Common with Pteridophyta

Some characteristics of Anthocerotales common with pteridophytes include the following:

1. Overall general similarity in the thalli (gametophytes) of Anthocerotales and prothallus of ferns.
2. Deeply sunken sex organs in the thalli of Anthocerotales and prothallus of several pteridophytes.
3. Similarity in the structure of mature female sex organs, i.e. archegonia.
4. Similarity in the sporophyte of Anthocerotales with the rootless and leafless dichotomously branched sporophytes of some fossil pteridophytes belonging to Psilophytales.

8.10.5 Anthocerotales: A Synthetic Group

The characteristics outlined above under Articles 8.7.1 to 8.7.4 suggest that Anthocerotales are a distinct but *synthetic group of plants*. It forms a bridge or connecting link between the (i) Hepaticopsida and Bryopsida (mosses) on one hand, and (ii) bryophytes and pteridophytes on the other. Simultaneously, Anthocerotales also have some features common with green algae (i.e. Chlorophyceae). In this connection, SK pande (1932, 1934), a noted Indian bryologist, suggested that *Notothylas levieri* forms a connecting link between Anthocerotales and Hepaticopsida. Pande, however, opined that both Anthocerotae and Hepaticae should be retained as two separate independent classes of Bryophyta.

DIFFERENCE BETWEEN ANTHOCEROTOPSIDA AND HEPATICOPSIDA 8.11

Some striking differences between Anthocerotopsida and Hepaticopsida are listed below in Table 8.1:

Table 8.1 *Difference between Anthocerotopsida and Hepaticopsida*

S. No.	*Anthocerotopsida*	*Hepaticopsida*
1.	Each cell contains a single chloroplast.	Numerous chloroplasts are present in each cell.
2.	Each chloroplast contains a pyrenoid.	Pyrenoids are absent in the chloroplast.
3.	Sex organs are deeply sunken in the thallus.	Sex organs are superficial in nature, and not deeply sunken.
4.	A very narrow meristematic zone is present in the sporogonium in between foot and capsule.	Meristematic zone is absent in sporogonium (e.g. *Riccia*), or it is replaced by a well-differentiated seta in between foot and capsule (e.g. *Marchantia*).
5.	Columella is present as a slender core of sterile tissue in the capsule.	Columella is absent.
6.	Archesporium is originated from amphithecium.	Archesporium is endothecial in origin.
7.	An amply ventilated photosynthetic system is present in the capsule wall of the sporogonium.	Amply ventilated photosynthetic system is absent in the capsule wall of the sporogonium.
8.	Stomata are present in the outermost layer of capsule.	Stomata are absent in the capsule wall.
9.	Pseudoelaters, without spiral thickenings, are present.	Instead of pseudoelaters, the elaters with spiral thickenings are present (*Marchantia*).
10.	The usual chromosome number is 5 or 6.	10. The number of chromosomes are usually 8 or 9.

A NOTE ON THE ORIGIN OF ANTHOCEROTALES 8.12

Origin of Anthocerotae is still difficult to be finalised because of the fundamental differences in the genetic relationship of this group and Hepaticopsida. Campbell (1925) believed that the nearest affinities in the thallus and sporophyte of Anthocerotae are with some pteridophytes. The view of Campbell was supported by Kashyap (1929) and proved by showing several striking structural similarities between the thallus of *Anthoceros erectus* and prothallus of *Equisetum debile*. Kashyap (1929) tried to prove that Anthocerotae originated from *Equisetum debile* by reduction. In 1953, PN Mehra and ON Handoo opposed the views of Campbell and Kashyap and gave several reasons to support their contention. Some of these reasons include the following: (i) There are basic and fundamental differences between the sporophytes of Anthocerotae and pteridophytes, (ii) Vascular tissues (xylem and phloem) are completely absent in Anthocerotae while present in all pteridophytes, and (iii) Vast difference in the basic chromosome number of Anthocerotae and pteridophytes, 5 in Anthocerotae but 10 in *Equisetum debile*. They, however, proposed that Anthocerotae and Rhyniaceae have sprung up from the same ancestral stock, i.e. *Anthorhyniaceae* in pre-Devonian (Mehra and Handoo, 1953). The *Anthorhyniaceae*, according to them, evolved from a hypothetical pro-liverwort stock from which have also arisen Marchantiales, Jungermanniales and Sphaerocarpales. Pro-liverwort stock originated in some Chlorophyceae (green algae). GM Smith (1955) has shown the phylogenetic relationship between Anthocerotae and Psilophytales (e.g. *Rhynia* and *Horneophyton*) of pteridophytes, which are some of the oldest and most primitive of all the known vascular plants. Further evidence in favour of Psilophytalean ancestry of Anthocerotales was given by J Proskauer (1962) on the basis of his studies of *Dendroceros crispus* (of Anthocerotales) and *Rhynia* and *Horneophyton* (of Psilophytales). Professor Ram Udar and DK Singh (1978) supported the views of Proskauer on the basis of their studies on thickened bands in the capsule wall of *Notothylas levieri*. Their research has been published in *The Bryologist*.

TEST YOUR UNDERSTANDING

1. What are Anthocerotes?
2. Who was the first to propose the name Anthocerotopsida to Anthoceropsida?
3. Anthocerotopsida members are commonly named as _____.
4. Write at least seven general characteristics of Anthoceropsida.
5. Whether Anthoceropsida members contain tuberculate rhizoids?
6. Are scales in Anthoceropsida present or absent?
7. Each cell of Anthoceropsida contains at least one chloroplast and one _____.
8. Instead of seta, the sporophyte of Anthocerotes contain _____?
9. In Anthoceropsida, the sporogenous tissue is _____ in origin.
10. Two families of Anthocerotales are Anthocerotaceae and _____.
11. Six genera of Anthoceropsida are *Anthoceros*, *Aspiromitus*, *Dendroceros*, *Phaeoceros*, *Notothylas* and _____.
12. Write a brief note on the classification of Anthoceropsida.
13. Write at least five characteristic features of Anthocerotaceae.

14. Write a short note on the distribution and habitat of *Anthoceros* with particular reference to India.
15. Write an illustrated essay on the life history of *Anthoceros* in about 1000 words.
16. Thalli of which of the following are smaller: *Marchantia* or *Anthoceros*?
17. Give an illustrated account of the anatomy of thallus of *Anthoceros* in about 200 words.
18. Which of the following are present in thallus of *Anthoceros*?
    (a) Stomata (b) Scales (c) Nostoc colonies (d) Tuberculate rhizoids
19. Explain means of vegetative reproduction in *Anthoceros*.
20. Describe development of antheridium in *Anthoceros* making suitable diagrams.
21. What do you mean by protandrous?
22. In *Anthoceros*, the archegonia remain embedded in the thallus or projected on the thallus?
23. Give a detailed accout of development of sporogonium in *Anthoceros*.
24. Explain structure of a mature sporogonium of *Anthoceros*.
25. Write a short note on the pseudoelaters of *Anthoceros*.
26. Depict life history of *Anthoceros* with suitable illustrations only.
27. Write a note on the apospory in *Anthoceros*.
28. Write any four characteristics of the family Notothylaceae.
29. Write a detailed scientific note on the life history of *Notothylas* in about 500 words.
30. Discuss the biological importance of the sporophyte of *Anthoceros*.
31. Write some advanced features of the sporophyte of *Anthoceros* and explain their implications.
32. Give a detailed account of the affinities of Anthocerotales.
33. Write some such features of Anthocerotales which are common with Hepaticopsida and pteridophytes.
34. Anthocerotales is a synthetic group. Explain
35. Write some of the basic differences between Anthocerotopsida and Hepaticopsida.
36. Write a note on the origin of Anthocerotales.

9

Bryopsida (General Account)

WHAT IS BRYOPSIDA? 9.1

Bryopsida or Musci is a class of bryophytes that includes **mosses**. It includes different evolutionary lines, most prominent amongst which is Bryales, and due to this it has been given the name **Bryopsida**. The class Bryopsida includes about 660 genera and 15000 species. These are the bryophytes which have a leafy (not thalloid) gametophyte with the leaves not strictly in 2 or 3 ranks, multicellular rhizoids and, in most, a capsule (sporophyte) with both a columella and a lid (operculum).

The gametophyte in Bryopsida is the dominant generation and exhibits two distinct morphological stages. The first, which arises on germination of the spore, is the filamentous **protonema**, which, except for its oblique cross walls, resembles a heterotrichous green alga. The protonema produces buds, from which the familiar leafy **moss** plant arises.

Although the group does not generally have a very rich fossil record but earliest fossil mosses are seen in the rocks of Permian.

GENERAL CHARACTERISTICS 9.2

1. Bryopsida or Musci includes the bryophytes called “mosses”.
2. Mature gametophyte is foliose, i.e. divisible into rhizoids, stem and leaves. It is never thalloid. The gametophyte may be **acrocarpous** or **pleurocarpous**. In **acrocarpous gametophytes**, the main axis is terminated by the development of the reproductive organs, and so subsequent growth is sympodial. In such mosses, the main axis is almost always erect. On the other hand, in **pleurocarpous gametophytes,** the reproductive organs are produced laterally and the main axis is usually creeping.
3. The rhizoids are multicellular, well-branched, and contain oblique septa or cross walls.
4. The leaves are spirally arranged on the stem.
5. The sex organs are present in the apical portions of the gametophore.
6. The sporogonium consists of foot, seta and spherical or a cylindrical capsule.

7. The sporogonium is determinate in growth.
8. The seta elongates gradually.
9. The capsule wall is several-layered, and its outermost layer is the epidermis containing some functional or nonfunctional stomata.
10. The capsule opens by operculum or by four slits.
11. A well-developed sterile columella is usually present in the centre of the capsule.
12. The lower part of the capsule may be green and photosynthetic.
13. The sporogenous tissue or archesporium develops either from the endothecium or from the amphithecium, and usually encloses the columella.
14. Only spores develop from the archesporium. The elaters or other sterile cells are usually absent.
15. The capsule dehisces in dry weather, and the dehiscence is often controlled by hygroscopic peristomial teeth.
16. The spore germinates usually into an extensive and filamentous protonema.

CLASSIFICATION 9.3

Bower(1935) and Campbell (1940) divided the class Bryopsida into three orders, viz. Bryales, Sphagnales and Andreaeales.

Bryales are commonly called **true mosses**. It is the largest order of about 600 genera including *Polytrichum*, which shows some internal differentiation. **Sphagnales** are commonly termed **bog** or **peat mosses**. It contains the single genus, *Sphagnum*, characteristic of waterlogged acid areas. The third order is **Andreaeales**, which also contain only one genus *Andreaea*, the members of which are known as **granite mosses**.

Engler et al. (1954) divided Bryopsida into five subclasses, i.e. Sphagnidae, Andreaeidae, Bryidae, Buxbaumiidae and Polytrichidae.

However, Parihar (1965) and Holmes (1986) divided the class Bryopsida (Musci or mosses) into three subclasses, viz. Sphagnidae (peat or bog mosses), Andreaeidae (granite mosses) and Bryidae (true mosses).

For details of the classification proposed by Holmes, refer Chapter 2, Article 2.1. For latest views on classification of mosses, consult details proposed by Goffinet and Buck (2004), and Troitsky et al. (2007) as outlined in Chapter 2, Article 2.3.2.

DISTRIBUTION AND HABITAT 9.4

Mosses are distributed throughout the world and in almost all types of habitats, except in seas and oceans. A few species of mosses have even been reported from very high altitudes, as much as 20000 feet above the sea level (e.g. *Aongstroemia julacea*). Mosses, however, flourish most in the wet and humid regions, and prefer to grow in moist plains and mountain forests of tropical and subtropical regions. *Sphagnum* and a few more mosses grow in bogs. (A **bog** is a region of badly drained permanently wet land that is subject to high rainfall and has a persistently moist atmosphere). A few mosses are even aquatic (e.g. *Fontinalis antipyretica*). Some have been reported even from deserts (e.g. *Torula desertorum*). Majority of mosses, however, grow in damp situations and form extensive mats.

HABIT 9.5

Plant body of mosses is gametophytic, and gametophytes are green and independent. Mosses can be divided into the following two broad categories on the basis of their habit:

(a) **Acrocarpous mosses**, in which the main axis is almost always erect.

(b) **Pleurocarpous mosses**, in which the main axis is usually crreping.

In acrocarpous mosses, the main axis terminates by the development of the reproductive organs, and thus the subsequent growth is sympodial. But in pleurocarpous mosses, the main axis does not terminate by the reproductive organs, which are therefore produced laterally.

9.5.1 Growth Phases of Moss Gametophyte

Protonema stage and leafy stage (Fig. 9.1A-D) are the two growth phases of the moss gametophyte.

1. Protonema Stage This stage of mosses is creeping, green, branched, multicellular and often filamentous. It develops from the spore. It is a vegetative phase and bears no sex organs. It is also called juvenile stage. In a majority of mosses, the protonema dies and disappears soon, thus making the leafy gametophytic plants independent. In some mosses, however, the protonema persists for a long time (e.g. *Buxbaumia aphylla*).

2. Leafy Stage It is the adult stage of moss plant, and due to the presence of leaves it is called *leafy stage*. The gametophyte in this stage consists of an upright, slender axis, bearing spirally arranged leaves. Sex organs develop on the leafy stage. Actually, it is the so-called **moss plant**, which we see in the form of gametophyte. Leafy stage develops as a lateral bud from the protonema stage. From the single protonema stage of the mosses develop many leafy moss plants.

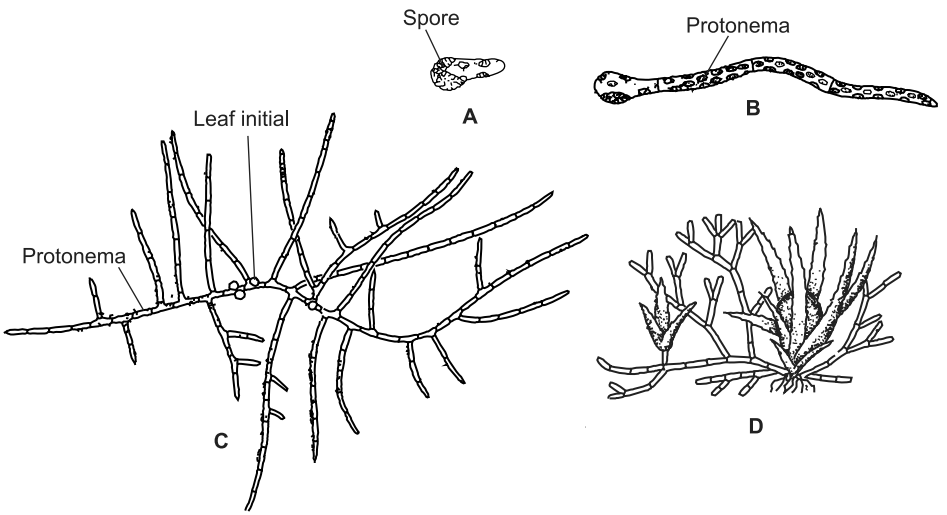


Fig. 9.1 Some stages of the development of protonema and leafy stages. A, A young germinating spore; B, Protomena; C, Protonema and initials of gametophore of *Splachnum ovatum;* D, Protonema with mature male and female gametophores of *Ephemerum serratum.*

9.5.2 Moss Gametophore

Moss gametophore remains differentiated into a stem-like axis bearing many green, leaflike expansions. Some prefer to call them **stem** and **leaves** while others term **cauloid** to the stem and **phylloids** to the leaves. The plant body remains attached to the substratum by many brown-coloured filaments known as **rhizoids**. Three major or basic organs of a moss gametophore are **stem**, **leaves** and **rhizoids**.

The **stem** or central axis is branched or unbranched, and erect or prostrate in different species. The branching, if present, is usually lateral and never dichotomous.

The **leaves** are green, sessile and the main photosynthetic organs of the gametophore. The basal part of the leaves is usually broad. The form of the leaf is highly variable in different species. It may be ovate to linear or sub-orbicular. The cells of the leaves remain filled with chloroplasts. Each leaf contains a midrib. In some mosses, however, the midrib is absent (e.g. *Sphagnum*). The lamina of each leaf is usually one cell in thickness. Basically, the leaves remain arranged spirally in three ranks on the stem, and, therefore, the gametophore has radial symmetry. Typical 3-ranked spiral arrangement with 1/3 divergence is seen in *Fontinalis*, but this arrangement may be different in different genera, e.g. 2/5 in *Sphagnum*, 3/8 in *Funaria* and 5/13 in *Polytrichum*.

The **rhizoids** are multicellular, well-branched and septate. The septa in moss rhizoids are oblique. They keep the plants attached to the substratum, and their main function is anchoring. Rhizoids are brown or dark brown in colour. They develop in tufts in pleurocarpous mosses.

VEGETATIVE OR ASEXUAL REPRODUCTION 9.6

Mosses have exceptional ability to reproduce vegetatively, and that is how they form dense mats over large areas. Almost all parts of moss gametophore (rhizoid, axis, leaf) or any portion of all of these parts have the capacity to reproduce vegetatively. Some such methods of vegetative or asexual reproduction in mosses include (i) branching of leafy stems, (ii) formation of stolons, (iii) detachment of a specially modified branch of bud-like form as in *Pohlia*, (iv) formation of lateral buds from the extensively branched **primary protonema**, (v) **secondary protonema**, (vi) persistent apices, (vii) **gemmae**, which are green, oval, multicellular buds produced on short stalks (e.g. species of *Torula*, *Leptobryum* and *Barbula*), and (viii) **tubers**, which are underground resting buds (e.g. *Funaria*, *Bryum* etc.).

APOSPORY IN MOSSES 9.7

Production of a diploid gametophyte from vegetative cells of the sporophyte, that is, without the production of spores is called **apospory**. Several mosses show extraordinary power of regeneration through apospory. Any undamaged cell of the moss sporophyte, besides the gametophyte, can grow into a protonema-like body. Green protonema-like filaments are commonly produced by wounding of the unspecialised cells of any of the parts of sporophyte. Many leafy gametophytes are developed from such green protonema-like filaments. Thus, the moss plants are produced directly from the sporophyte without the production of spores under the phenomenon of apospory. Such plants have a diploid chromosome number, instead of haploid. They are quite normal like that of haploid plants, except that they are slightly larger-sized. They also produce gametes, but such gametes are not haploid but diploid. Their fusion, under the process of fertilization, results in the formation of a tetraploid sporophyte.

However, if such a diploid gamete fuses with a normal haploid gamete, it results in the formation of a sporophyte which is triploid (i.e. possesses three sets of chromosomes).

SEX ORGANS 9.8

9.8.1 Distribution of Sex Organs

Two sex organs (antheridia and archegonia) are borne in clusters, generally at the top of the main axis or lateral branches. However, in some (e.g. *Sphagnum*) the antheridia occur singly in the axil of perigonial leaves. Several sterile green filaments (**paraphyses**) are also present intermixed with sex organs in each cluster. Mosses are **monoecious** as well as **dioecious**. Monoecious mosses (e.g. *Mnium medium*) possess male and female sex organs on the same individuals. But dioecious mosses (e.g. *Buxbaumia*) possess male and female sex organs on different individuals of the same plant species.

9.8.2 Categories of Monoecious Mosses

The following three different categories can be recognised in monoecious mosses on the basis of the distribution of sex organs:

1. Paroicous Mosses These are the monoecious mosses in which two different sex organs develop in the same cluster or head in separate groups. A few perichaetial leaves separate groups of two sex organs.

2. Autoecous Mosses These are the monoecious mosses in which two different sex organs develop on separate branches of the same plant.

3. Synoicous Mosses These are the monoecious mosses in which two different sex organs develop in the same cluster or head intermingled with each other.

Some mosses show four conditions, viz. paroicous, autoicous, synoicous and dioecious (e.g. *Pohlia*).

9.8.3 Antheridia

Moss antheridia are elongate, club-shaped structures with a short and multicellular stalk (Fig. 9.2 A). They are comparatively longer and narrower than that of antheridia of liverworts. Their size ranges between 0.2 mm and 2.00 mm, with an average length of 1.5 mm. Mature antheridia are usually orange in colour and remain surrounded by a jacket layer enclosing a mass of androcytes or male gametes. The tip of each antheridium usually contains one to many large-sized cells. Each male gamete or sperm is a spirally coiled, motile, biflagellate, uninucleate and unicellular structure.

9.8.4 Archegonia

Except that of a comparatively longer stalk, massive venter and longer neck, the archegonia of mosses (Fig. 9.2B) are similar to those of liverworts. Each archegonium consists of a long neck and a globular venter. The neck encloses 35 to 50 neck canal cells, a ventral canal cell and an egg. The primary cover cells are present at the tip of the archegonium.

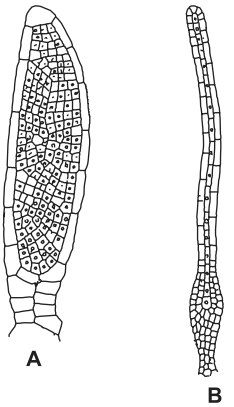


Fig. 9.2 Sex organs of mosses. A, An antheridium of *Funaria hygrometrica*; B, An archegonium of *Cyathophorum bulbosum*

9.8.5 Fertilization

Fertilization is effected through the agency of water. In paroicous and synoicous mosses, the presence of a connecting film of water between archegonia and antheridia is a necessity. In autoecious and heterothallic mosses, the antherozoids are transported up to the archegonia generally through water. It has been finally established that antherozoids enter the archegonium in response to the chemical stimuli. Union of male and female gametes (i.e. **plasmogamy**) is followed by **karyogamy** (i.e. fusion of two nuclei), and thus a diploid zygote is resulted.

9.8.6 Embryo and Sporophyte

A wall is soon secreted around the fertilized egg. The so-formed zygote increases in size, divides and redivides to form an **embryo**. The embryo is actually the product of repeated mitotic divisions of the zygote. The growth of the moss embryo is due to the activity of two apical cells located in opposite directions for quite some time. The apical cell, situated at the upper end of the embryo, is more active and from its derivatives are differentiated the **capsule** and a large part of the **seta**. The foot and lower remaining portion of the seta are differentiated from the derivatives of the lower apical cell. The young embryo is long and slender. The lower end of the embryo burrows through the stalk of the archegonium and into the apex of the gametophore. Simultaneously, there is an enlargement of the surrounding archegonium, which is known as **calyptra**.

The sporophyte of most of the mosses consists of foot, seta and capsule. It resembles those of Jungermanniales in showing the formation of a long **seta**, which elevates the capsule above the surrounding leaves of the gametophore. In most mosses, the seta contains a well-defined central strand. Its main function is conduction of food material to the developing capsule. Seta also functions as a mechanical tissue. The **foot** is the basal part of the sporophyte. Its functions include attachment and also as an absorbing organ. The foot remains embedded in the tissues of the tip of the leafy gametophore.

Capsule is the uppermost, most complex region of the sporophyte of mosses. In true mosses (e.g. *Funaria hygrometrica*), it is divisible into three major regions, viz. apophysis, theca and operculum (Fig. 9.3). **Apophysis** is the basal region, **theca** is the middle region and **operculum** is the uppermost region of the capsule.

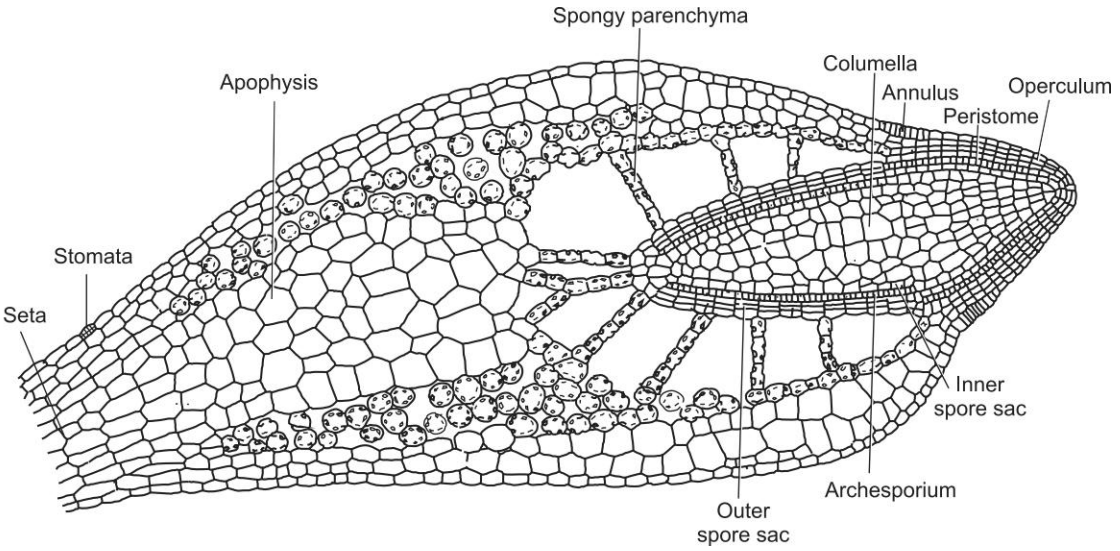


Fig. 9.3 Longitudinal section of the capsule of *Funaria hygrometrica*

Apophysis is the green photosynthetic region, containing several chlorenchymatous cells and stomata in its outermost layer. **Theca** is the spore-producting region of the capsule. It consists of several parts including outermost epidermis, wall layers, air cavities traversed by trabeculae, spore sacs and centrally-located columella. The archesporium is endothecial in origin. Sporogenous tissue forms spore mother cells, which divide meiotically to form haploid spores. Elaters are absent. The uppermost region of capsule matures into **operculum** and **peristome**. The peristome contains teeth-like projections that surround the mouth of the capsule. The number of peristomial teeth varies between 4 and 64, but in various mosses they are in multiples of 4, such as 8, 16, 32 or 64.

In some mosses (e.g. *Polytrichum*), the peristomial teeth are solid structures made up of bundles of dead cells. Such a peristome is known as **nematodontous peristome**. They are arranged in a single series and they do not show any hygroscopic movements. In some other mosses, the peristome is made up of thin, membranous teeth made up of thickened portions of cell walls of the adjacent cells. Such a peristome is known as **orthodontous peristome**, and their teeth are hygroscopic in nature. They are either arranged in single series or in two series. When arranged in one series, the peristome is known as **haplolepidous**, but if arranged in two series, the peristome is known as **diplolepidous** (e.g. *Funaria hygrometrica*).

9.8.7 Spore and its Germination

Moss spore is a unicellular, uninucleate structure surrounded by a thin spore wall. The reserve food is in the form of lipid and a little starch. Mitochondria and endoplasmic reticulum and rarely Golgi bodies are also present in the cytoplasm of the spore. Three wall layers, which constitute the spore wall are perine, exine and intine from outside within. A fourth separating opaque layer may or may not be present. When present, it is actually a sub-unit of the exine.

Spores start germinating immediately if they fall on a suitable soil. In some species, however, the length of time varies if the conditions are unfavourable. Acording to Meyer (1941), in some species, the spores remain "capable of germinating eight to sixteen years after shedding". At the time of germination, a spore increases somewhat in size, ruptures the outer spore wall layer and then sends out one or two germ tubes. A cross wall is soon formed near the point of emergence of the germ tube. The cell thus cut off by this cross wall soon develops into a branched, multicellular, filamentous structure known as *protonema*. Two types of branches are soon differentiated in this protonema. These are (i) **chloronemal branches** or **chloronema**, which usually grow along the surface of the substratum or into the air for some time, and (ii) **rhizoidal branches** or **rhizoids**, which penetrate into the substratum. The chloronemal branches have (i) colourless cell walls, (ii) septa at right angles to lateral walls, and (iii) several well-defined chloroplasts. On the other hand, rhizoidal branches possess (i) brown cell walls, (ii) oblique or diagonal septa, and (iii) ill-defined chloroplasts or leucoplasts. A number of the leafy gametophores develop as lateral outgrowth from the protonema. They bear sex organs and represent the adult stage of moss gametophyte.

Most of the genera of mosses have a disappearance of protonema after leafy gametophores produced by them have attained a stage where they have rhizoids and several leaves. In a few genera, however, protonema persists throughout the entire life of the gametophytic generation. Protonema functions as the major photosynthetic portion of the gametophyte in some mosses, e.g. *Ephemerum* (Fig. 9.1D).

RESEMBLANCES AND DIFFERENCES BETWEEN HEPATICOPSIDA (LIVERWORTS) AND BRYOPSIDA (MOSSES) 9.9

9.9.1 Resemblances

There are only a few resemblances between liverworts and mosses:

1. Both show heteromorphic type of alternation of generations.
2. Both lack meristematic tissue in their sporogonia. Some meristematic tissue, however, develops in Anthocerotopsida.
3. Plant body is gametophytic in both.
4. Both possess biflagellate antherozoids.
5. Members of both groups possess calyptra.

9.9.2 Differences between Hepaticopsida and Bryopsida

Differences between the two groups are many. Some such differences are tabulated in Table 9.1.

Table 9.1 *Differences between Hepaticopsida and Bryopsida*

S. No	*Hepaticopsida (Liverworts)*	*Bryopsida (Mosses)*
1.	Development of gametophytic plant body from a spore is a continuous process.	Development of gametophytic plant body from a spore is not a continuous process. It passes through two phases, viz. (i) **juvenile stage** which includes formation of protonema from spore, and (ii) **adult leafy gametophore stage**.
2.	Spore first germinates into a sporeling, which develops into a mature gametophytic plant body.	Spore first develops into a well-branched filamentous protonema, from which develop many gametophores.
3.	Plant body is dorsiventral and thalloid or foliose.	Plant body is radial and always foliose.
4.	Plant body of most liverworts lacks a central conducting strand.	Central conducting strand is present in the axis of mosses.
5.	Leaves, present in foliose liverworts, lack midrib.	Leaves of all mosses have a midrib.
6.	Growth of leaves in foliose members is usually intercalary.	Growth of leaves in mosses is by the activity of an apical cell.
7.	Scales are present on the ventral surface in thalloid liverworts.	Scales are absent in mosses.
8.	Rhizoids are unbranched and unicellular.	Rhizoids are well-branched and multicellular.
9.	Oblique septa are absent in the rhizoids.	Rhizoids of most mosses have oblique septa.
10.	Sex organ development is intercalary and not apical.	Sex organ development is due to the activity of an apical cell.
11.	Antheridia are ovoid or subglobose in shape.	Antheridia are longer, narrower and club-shaped bodies.
12.	Archegonial neck contains lesser number (usually 6–9) neck canal cells.	Archegonial neck is very long and contains more (usually 35–45) neck canal cells.
13.	Early growth of the embryo is intercalary.	Early growth of embryo is usually biapical.
14.	Seta, when present, is soft and lacks any internal differentiation of tissues.	Seta is long, tough and contains a central conducting strand.
15.	Seta lengthens, and due to this the sporophyte breaks through the calyptra, but quite late.	Seta lengthens, and due to this the sporophyte breaks through the calyptra at an early stage.
16.	Sporophyte is quite simple in its organization.	Sporophyte is quite complex in its organisation.
17.	Sporophyte lacks apophysis and operculum region.	In most mosses, the sporophyte contains regions like apophysis and operculum.
18.	Stomata are absent on the capsule wall.	Capsule wall of mosses contains stomata.
19.	Sporophyte lacks annulus.	Capsule of most mosses contain annulus.
20.	Capsule lacks columella.	Columella is present in moss capsule.
21.	Sporophyte lacks peristomial teeth.	Peristomial teeth are present.
22.	Elaters are present.	Elatere are absent.
23.	Usually, the entire endothecium is archesporial in origin.	Usually, only the outermost layer of endothecium is archesporial in origin.

TEST YOUR UNDERSTANDING

1. What is Bryopsida? Explain in about 100 words.
2. Bryopsida includes bryophytes which are commonly called _____.
3. Write at least ten general characteristics of Bryopsida.
4. Do Bryopsida have thalloid gametophores?
5. In mosses, a spore germinates into a multicellular, branched, filamentous structure known as _____.
6. In mosses, the gametophyte may be acrocarpous or _____.
7. What are acrocarpous gametophytes in mosses?
8. In the centre of the moss capsule, a well-developed sterile region is present. It is known as _____.
9. Elaters in mosses are _____.
10. Write a short scientific note on the classification of Bryopsida.
11. Sphagnales are commonly known as peat or _____ _____.
12. The name "granite mosses" is given to the members of _____.
13. What are true mosses?
14. Write a note on the distribution and habitat of mosses in about 100 words.
15. Do mosses occur in seas or oceans?
16. What are the two growth phases of moss gametophyte? Explain briefly.
17. Name five major types of the vegetative reproduction found in mosses.
18. Write a brief scientific note on apospory in mosses.
19. How will you differentiate between the following?
    (a) Paroicous mosses, (b) Autoecous mosses, (c) Synoicous mosses
20. Draw labelled diagrams of an antheridium and an archegonium of any moss.
21. What is calyptra?
22. Differentiate between apophysis, theca and operculum of a moss capsule.
23. What is peristome?
24. How can you differentiate between nematodonous peristome and orthodontous peristome?
25. Describe structure and germination of moss spore in about 200 words.
26. Enumerate any four resemblances between liverworts and mosses.
27. What are the ten major differences between Hepaticopsida and Bryopsida? Tabulate them.

10 Bryopsida (Selected Mosses)

SPHAGNALES OR BOG MOSSES 10.1

10.1.1 What are Bog Mosses, Bogs and Peat?

Sphagnales are commonly known as "*bog mosses*" or "*peat mosses*". They are characteristic of waterlogged acid areas.

Bog is actually a region of badly drained permanently wet land that is subject to high rainfall and has a persistently moist atmosphere. Bogs are commonly found in upland and waste areas of temperate regions. Besides several angiospermic plants like rushes (e.g. *Juncus*) and sedges (e.g. *Carex*), the most common bryophyte of bogs is *Sphagnum*.

Peat is actually the partially decomposed plant material. It builds up in areas with poor drainage, namely bogs and fens. Acid bog peat or "peat moss" is composed primarily of the remains of bog plants such as *Sphagnum* mosses and sedges.

10.1.2 Differences between Bog Moss and Other Mosses

Bog moss differs from other mosses in possessing the following:

1. Thalloid protonema which develops into gametophore
2. No midrib in the leaves
3. Leaves usually composed of markedly different types of cells
4. Axillary antheridia, which show a clear differentiation of fertile part
5. Acrogynously formed archegonia
6. Archesporium is amphithecial in origin
7. Pseudopodium in the sporophyte, which is an elongation of a stalk of gametophytic tissue.

SPHAGNUM 10.2

10.2.1 Distribution, Habitat and Some Other Details

Sphagnum is the only genus of Sphagnales, which contains only one family Sphagnaceae. It is commonly known as **bog moss**. Some bryologists also name *Sphagnum* as **turf moss** or **peat moss**.

Sphagnum is a cosmopolitan genus which grows from north and south tropics through the temperate regions and extends up to sub-arctic and sub-antarctic regions. It is particularly abundant in the northern circumpolar regions. It occurs as dense masses in ponds, lakes and other such surroundings where due to seepage such soft water is available which contains only a little amount of lime. In cooler temperate regions of the northern hemisphere, *Sphagnum* usually dominates the vegetation of wetlands. Over 350 species of *Sphagnum* have been reported so far, of which were than 20 species occur in India. The pH of the water in which *Sphagnum* grows ranges from 3.7 to 4.9. The size of *Sphagnum* plants varies from a few inches to a maximum of 7 inches.

Sphagnum is a perennial moss and keeps on growing year after year. Water around *Sphagnum* plants is so much acidic that there develops only a little decay of dead basal portions. Regularly, the older parts of the plants of *Sphagnum* die and the dead organic remains of these plants, in combination with the remains of other surrounding plants, form a compact mass known as **peat**. Due to the formation of peat, this moss is known as **peat moss**, and being a peat-former, it is of great commercial importance for us.

10.2.2 Mature Gametophore

Structurally, the plant is erect, branched and differentiated into stem and leaves. The rhizoids are colourless and develop at the base but do not survive for too long. They disappear soon. Mature gametophores usually lack rhizoids. At the apex of the gametophore, there are present a number of short branches densely crowded in a cluster, called **coma** (Fig. 10.1A). In the posterior part of the stem, the branches arise in tufts in the axil of every fourth leaf, and in each tuft, there are 3 to 8 branches. The branches are of two types (Fig. 10.1A, B): (i) **divergent branches**, which are short, stout and grow outward and upward, and (ii) **drooping branches**, which hang downward quite close and around the stem. These are also called **flagelliform branches**. In submerged plants, these drooping branches are absent. At certain intervals, one of the branches in the tuft grows and develops into an apical cluster of branches like the main stem. This is known as **innovation**. On being separated from the main branch, the innovation develops into a

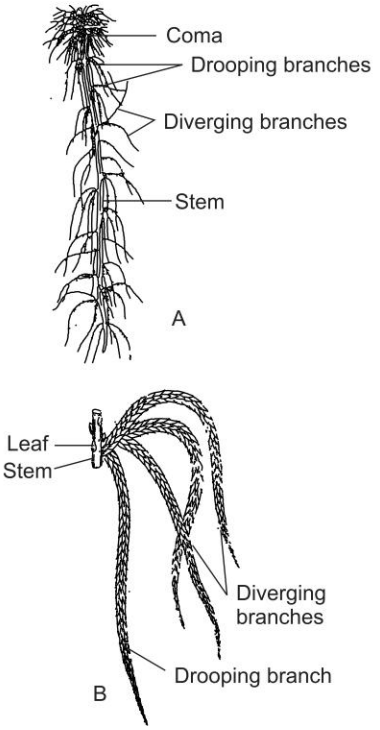


Fig. 10.1 *Sphagnum.* A, A part of gametophore; B, Portion of a plant showing tuft of branches

new plant, and hence it functions as an organ for vegetative propagation. The first-formed leaves are in three vertical rows or 3-ranked. The arrangement, however, changes to 2/5 in the later stages. The stem is only a few inches in length, and close aggregation of short and stumpy branches towards the apex (Fig. 10.1 A) provides it an appearance like that of a head or capitulum. An exceptional feature of the *Sphagnum* leaves is the absence of a midrib.

10.2.3 Apical Growth

Terminal growth of the stem is due to a tetrahedral apical cell with three cutting faces (Fig. 10.2). Each segment is first cut off by a periclinal division giving rise to an inner cell and an outer cell. The inner cell forms the axis of the shoot while the outer cell gives rise to the cortex and a single leaf. In this fashion, each segment develops into a single leaf and the subtending part of the stem. When young, the leaves are in three vertical rows, corresponding to the three cutting faces of the tetrahedral apical cell. But during course of time, as the stem and leaves grow, the leaves show some displacement, and they finally loose their 3-ranked arrangement. At maturity, the leaves get arranged on the stem in a spiral with a divergence of 2/5, i.e. each leaf gets separated from the next leaf above it by $2/5^{th}$ of the circumference of the stem.

Fig. 10.2 Longitudinal section through the apex of a gametophore of *Sphagnum subsecundum.*

10.2.4 Leaves

Leaves show an orderly arrangement of two types of cells (Fig. 10.3A), viz. (i) green, narrow and elongate chlorophyll-containing cells, and (ii) hyaline or colourless, large, polygonal cells which lack cell contents. In the cross section of a mature leaf (Fig. 10.3B), the large and dead hyaline cells, and green, wedge-shaped chlorophyllous cells are present alternately. Thickening bands and pores are present in hyaline cells. With reference to size, shape and structure, the leaves of the main stem are different from those present on the branches. The leaves present on the main axis or stem have very little or no chlorophyll, and their hyaline cells lack thickening bands and pores. On the other hand, the leaves present on the branches consist of a network of green, long, chlorophyll-containing cells. Some of these green cells surround one hyaline dead porose cell.

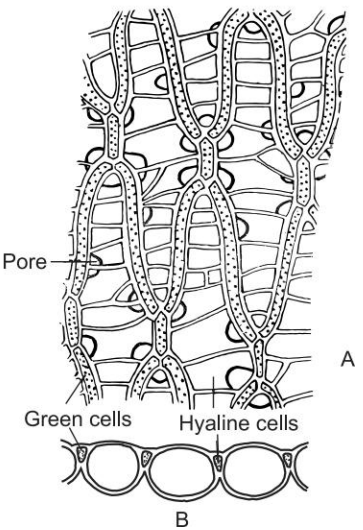


Fig. 10.3 *Sphagnum.* A, A part of mature leaf showing green and hyaline cells; B, Section of a leaf showing green and hyaline cells

10.2.5 Anatomy of Axis

Transverse sections of the axis (Fig. 10.4 A-D) show an outermost layer of cortex made up of compactly arranged cells. In some species, the cortex becomes 3-5 cells thick. Mature cortical cells get devoid of protoplast, become hyaline and dead. In some other species (e.g. *S. cymbifolium*), they develop spiral thickenings and even develop pores. Such cortical cells contain water and air. In *S. molluscum* and *S. tenellum*, some cortical cells become greatly enlarged and flask-shaped. They accumulate water and are known as **retort cells** (Fig. 10.4B, C). Such type of cortex is known as **hyalodermis**. The cells inner to the cortex are prosenchymatous and provide mechanical support to the stem. This region of axis is known as **hadrome** (Fig. 10.4A). In such stems, the innermost region is known as **medulla**. Medulla cells are vertically elongated, colourless and parenchymatous.

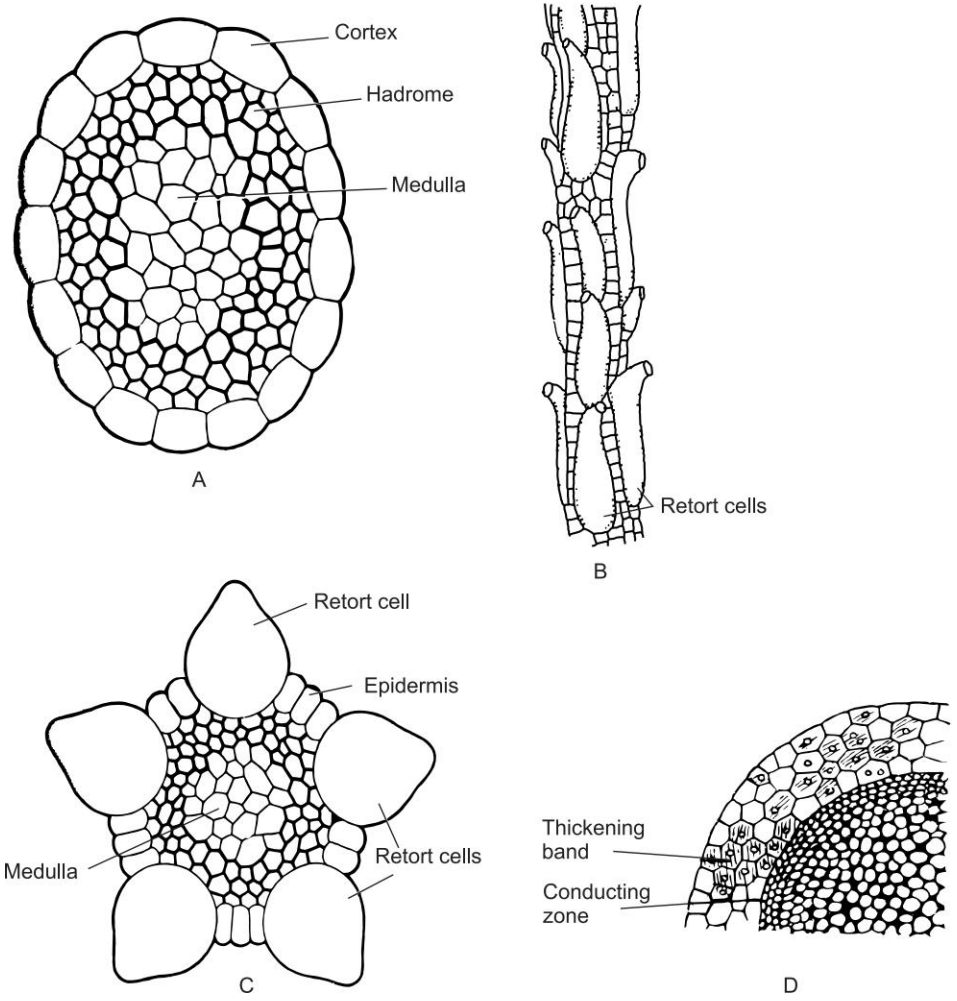


Fig. 10.4 *Sphagnum.* A, TS Young stem; B, Part of stem showing retort cells; C, TS stem of S. molluscum showing retort cells; D, TS of old stem showing thickening band and conducting zone

10.2.6 Reproduction

Sphagnum reproduces vegetatively and sexually.

1. Vegetative Reproduction

Special branches, known as *innovations*, are the means of vegetative reproduction. They develop in the axis of leaves on the main axis in a similar fashion like ordinary branches. They are strong and remain directed towards the upper side. They get separated because of the progressive death of the basal part of the main axis and establish themselves as the new plants of *Sphagnum*.

Some species of *Sphagnum* multiply by *primary protonema*. Few marginal cells of the thalloid primary protonema become meristematic and develop into a multicellular filament. The apical part of this multicellular filament develops into a thallus-like, flat *secondary protonema*. A leafy gametophore of *Sphagnum* may develop from any of the marginal cells of this secondary protonema.

2. Sexual Reproduction

Sphagnum has both monoecious as well as dioecious species. The archegonia and antheridia develop on different branches of the same plant in monoecious species. Development of sex organs takes place usually in the beginning of the winter season. They develop on specialised branches, formed in the axis of leaves. Sex-organ-bearing branches are comparatively much smaller than that of the other vegetative branches of the plant

(a) Antheridium

(i) Antheridial or Male Branches The male branches are catkin-like, small structures (Fig. 10.5 A), arranged usually spirally or in straight rows on the main axis. They possess many small, coloured leaves. The colour of these leaves may vary from yellow or brown or even reddish. In the axil of each leaf of the antheridial branch develops an antheridium (Fig. 10.5B). The development of antheridia in the antheridial branch is in acropetal succession, i.e. oldest antheridium is present at the base and the youngest at the apex of the antheridial branch.

(ii) Development of Antheridium It starts from a superficial cell of the antheridial branch. This is known as **antheridial initial** (Fig. 10.6A), which soon enlarges and appears like a papillate outgrowth. The antheridial initial first divides by some transverse divisions to form a small filamentous structure (Fig. 10.6B). Its terminal cell divides by two intersecting divisions, and thus differentiates an **apical cell** (Fig. 10.6B) with two cutting faces. It forms its derivatives in both the planes, resulting into a 10- to 15-celled structure. Upper 2–5 cells of this structure differentiate into the body of the antheridium while the remaining lower cells form the stalk of the antheridium. The upper cells, responsible for the formation of the antheridium body divide periclinally to form outer **jacket initials** and inner **primary androgonial cells** (Fig. 10.6C). The jacket initials divide and form a single-layered jacket. The primary androgonial cells divide and redivide in different planes to form many androgonial cells. The last generation of these cells forms **androcytes** (Fig. 10.6C-G). The antheridium of *Sphagnum* is unique in its characteristic that its apical cell stops dividing eventually and starts functioning as a cell of jacket. Each androcyte metamorphoses into a unicellular, spirally coiled, biflagellate antherozoid.

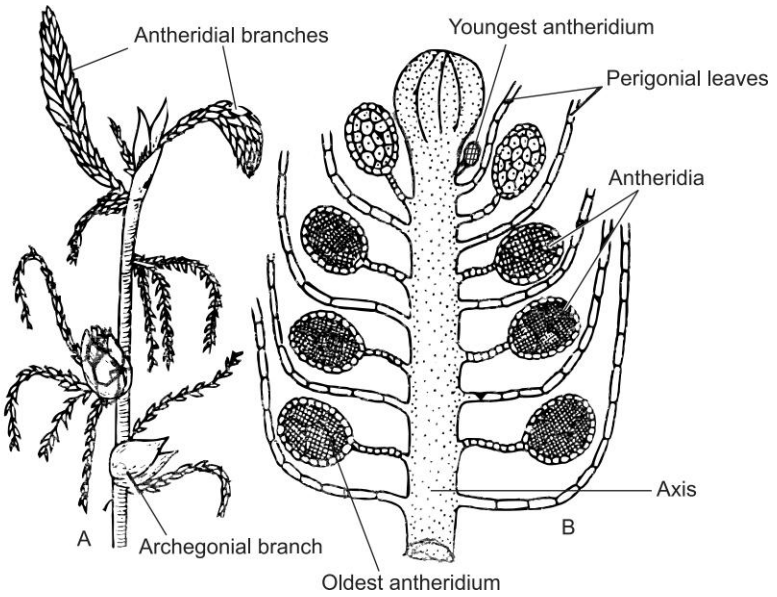


Fig. 10.5 Sex organs of *Sphagnum.* A, A lateral branch bearing antheridial and archegonial branches; B, Longitudinal section of antheridial branch

(iii) Mature Antheridium and its Dehiscence The **mature antheridium** (Fig. 10.6G) has a long stalk and a globular body. The stalk is made up of 2-4 row of cells. The body is surrounded by a single layer of sterile jacket, which encloses a mass of androcyte cells. Each androcyte metamorphoses into a biflagellate, unicellular, uninucleate antherozoid (Fig. 10.6H).

The mature antheridium dehisces and liberates the antherozoids. Apical cells of the sterile jacket absorb water and become swollen. Due to this, the turgor pressure increases and the wall of the antheridium breaks into several irregular lobes or valves at the apex. These valves turn backward, and thus the mass of androcytes is exposed and finally liberated. During this process, the antherozoids come out of the androcytes and start swimming in the surrounding liquid.

(b) Archegonium

(i) Archegonial or Female Branches Archegonial branches (Fig. 10.5A) are shorter than antheridial branches. They are bud-like structures bearing either a single or a group of 2–5 archegonia surrounded by leaves. These leaves are green and larger than those of the leaves of vegetative branches. The leaves which surround the archegonia are known as **perichaetium** (Fig. 10.7).

Two types of archegonia develop in an archegonial branch. The archegonium, which develops from the apical cell of the archegonial branch, is situated at the top and known as **primary archegonium**.

On the other hand, the archegonia, which develop from the derivatives of the apical cell, are known as **secondary archegonia** (Fig. 10.7). However, the process of the development of both the types of archegonia is the same.

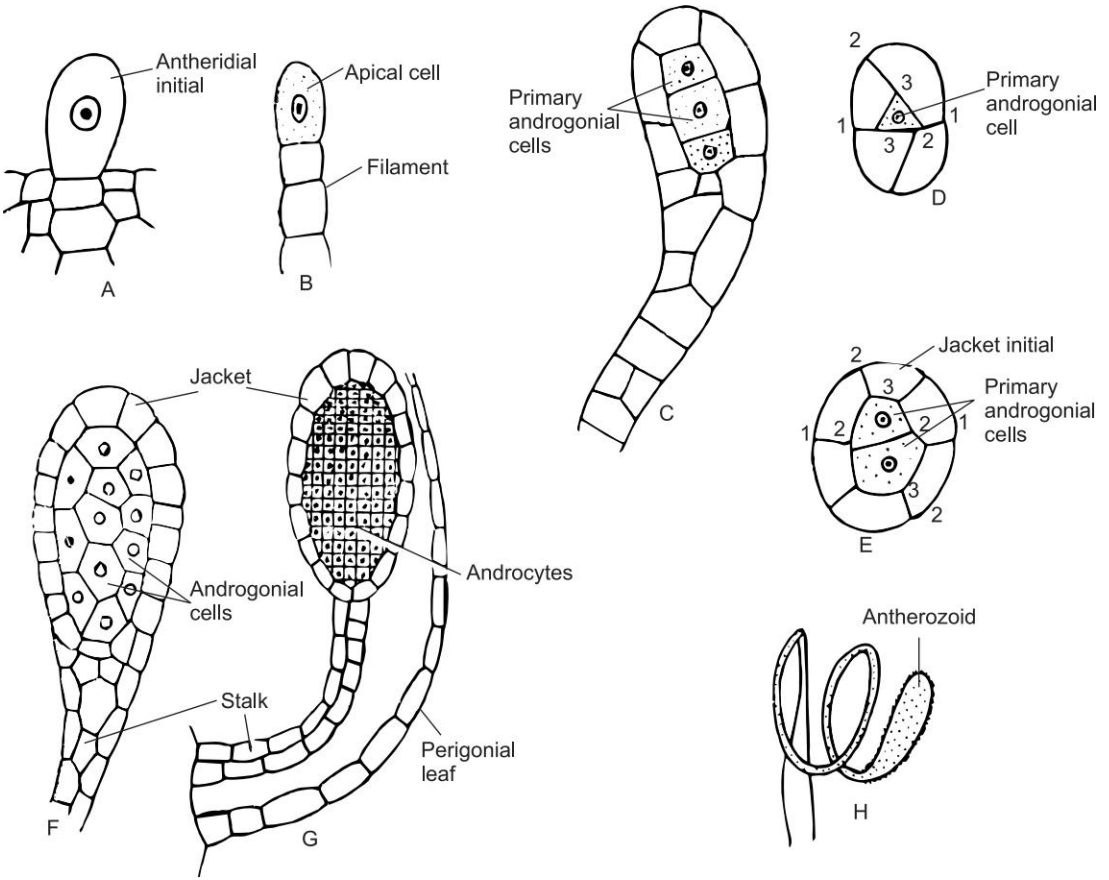


Fig. 10.6 A-H *Sphagnum* showing development of antheridium

(ii) Development of Archegonium The development of archegonium starts from an **archegonial initial**, which divides by repeated transverse divisions to form a short filament of 4–6 cells (Fig. 10.8A-C). The uppermost or terminal cell of this filament divides by three intersecting vertical divisions, resulting in the formation of three peripheral **jacket initials** and a central primary **axial cell** (Fig. 10.8D). The primary axial cell now divides transversely to form an upper **cover initial** and a lower **central cell** (Fig. 10.8E). Vertical divisions in the cover cell result into a group of eight or more **cover cells**, which form the jacket of the upper or terminal part of the neck of the archegonium (Fig. 10.8F,G, J). Simultaneously, the lower central cell also divides transversely to form an upper **primary neck canal cell** and a lower **primary**

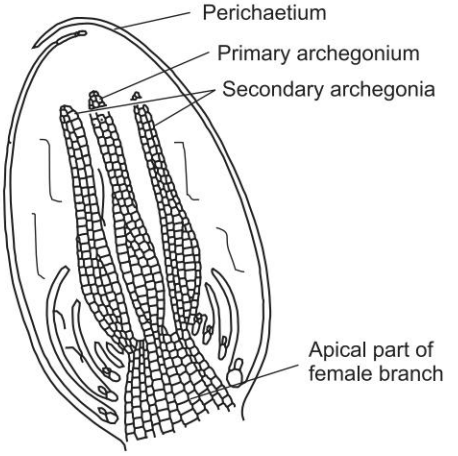


Fig. 10.7 LS of apical portion of female branch bearing archegonia and perichaetium

venter cell (Fig. 10.8F). Repeated transverse divisions take place in the primary neck canal cell and thus develops a row of 8–10 **neck canal cells** (Fig. 10.8 J). Side by side, the primary venter cell divides by only one transverse division to form an upper **venter canal cell** and a lower **egg** (Fig. 10.8J). Side by side, each of the three jacket initials (Fig. 10.8 H) divides anticlically as well as periclinally to form the middle and basal parts of the jacket of the archegonium (Fig. 10.8J). Now, jacket cells divide by repeated transverse divisions to ultimately form five or six vertical rows of neck cells (Fig. 10.8 H,J). The jacket becomes two- to three-layered in the basal parts of the neck due to periclinal divisions.

(iii) Mature Archegonium The mature archegonium of *Sphagnum* (Fig. 10.8J) has a long stalk, a twisted neck and a massive venter. The neck jacket is two- to three-celled thick in its basal and middle parts. Eight or sometimes more cover cells are present in the apical part of the neck. The neck cavity contains 8–10 neck canal cells, and the venter contains a venter canal cell and an egg.

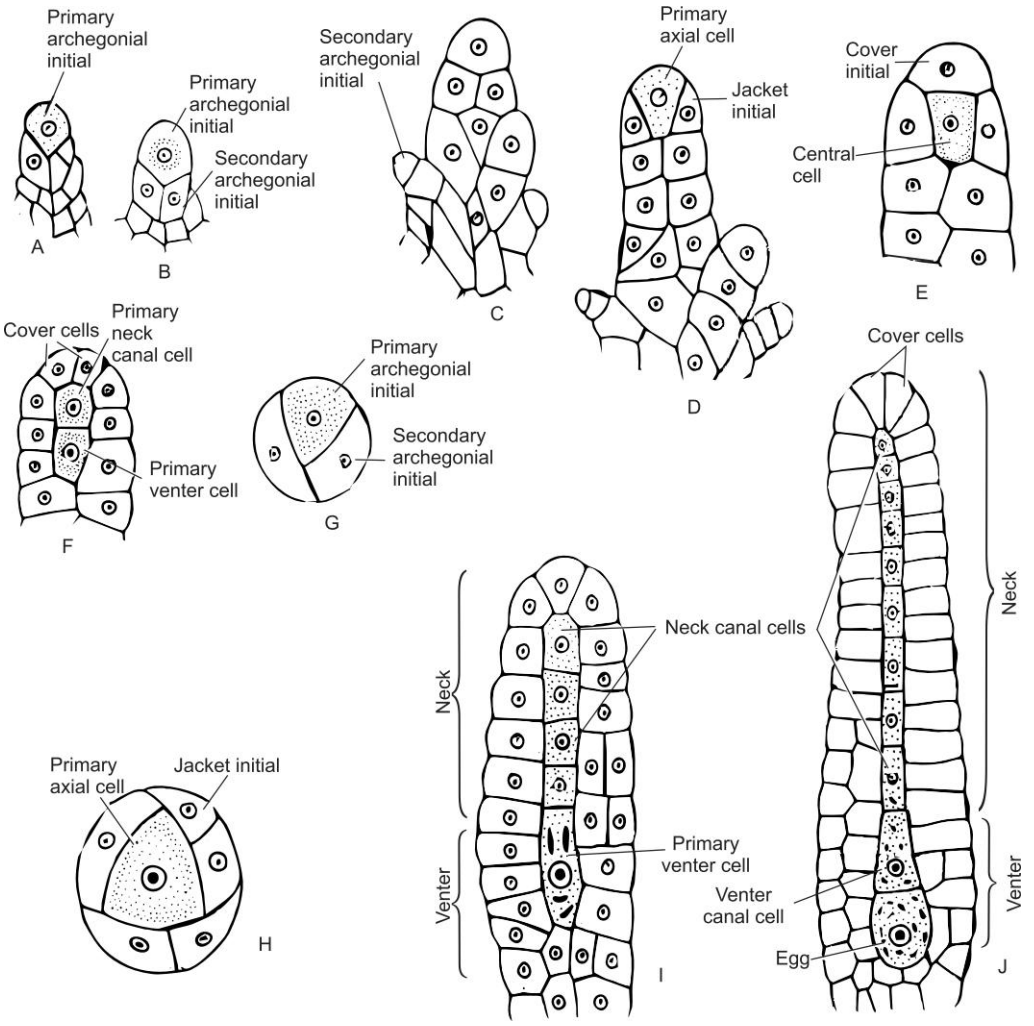


Fig. 10.8A-J Development of archegonium in *Sphagnum*

(c) Fertilization Fertilization takes place only in the presence of water. The liberated antherozoids keep freely swimming in this water and reach near the neck of the archegonium. Inside the archegonium, the neck canal cells and venter canal cell disintegrate and disorganise, and form a passage for the antherozoids. Only the egg is now present inside the venter. One of the antherozoids fuses with this egg and the fusion product results in the formation of a diploid egg.

(d) Sporophyte

(i) Development of Sporophyte The diploid zygote (Fig. 10.9A) is the first cell of the sporophytic generation. A single sporophyte usually develops on an archegonial branch. The zygote enlarges and soon divides by a transverse wall to form a lower **hypobasal cell** and an upper **epibasal cell** (Fig. 10.9B). Its further fate is different in different species. In *Sphagnum subsecundatum*, both the epibasal as well as hypobasal cells divide by repeated transverse divisions to form a young filamentous embryo of 6–12 cells (Fig. 10.9C). In some other species (e.g. *S. acutifolium*), only the epibasal cell of the bicelled embryo divides transversely, while the hypobasal cell divides by a vertical division, followed by many irregular divisions resulting ultimately into the formation of a bulbous parenchymatous foot (Fig. 10.9E-I).

In the filamentous embryo (Fig. 10.9C), usually the 3 or 4 upper cells give rise to the **capsule**, and from the remaining cells develop the **foot** and **seta** (Fig. 10.9C-E). The upper cells divide by two vertical divisions at right angles to each other, and thus a quadrant is resulted from each cell, They divide periclinally to form the outer or peripheral **amphithecium** and inner or central **endothecium** (Fig. 10.9J). Repeated transverse divisions of the endothecium give rise to **columella**, which forms the central sterile part of the capsule. The amphithecium divides periclinally to form an outer sterile layer, and an inner fertile layer of **archesporium**. **The archesporium** is thus **amphithecial in origin** (Fig. 10.9I-L). A 3–7-layered capsule wall is resulted as a result of periclinal divisions of the outer sterile layer. The archesporium forms a dome-shaped arch over the columella (Fig. 10.9I). It divides periclinally to form a 2–4-layered **sporogenous tissue**, of which all cells start functioning as **spore mother cells**. They divide meiotically to form haploid spores, which remain enclosed in a **spore sac** in the capsule.

(ii) Mature Sporophyte The mature sporophyte contains foot, seta and capsule (Fig. 10.10A-B). The foot is made up of parenchymatous cells. It is a bulbous or cylindrical body. **Foot** in *Sphagnum* is haustorial in function. The **seta** is ill-developed, inconspicuous and has a very narrow structure. The **capsule** is well-developed, quite conspicuous and has a spherical structure (Fig. 10.10B). The mature capsule is a dark-brown or black-coloured body, surrounded by a 2–7 layered wall, of which the outermost layer is differentiated into an **epidermis** bearing several nonfunctional stomata. Several cells of the capsule wall contain chloroplasts, which shows photosynthetic nature of the capsule. At the apical part of the capsule is present the **operculum**. It is a circular, biconvex disc-shaped structure. A circular groove of thin-walled cells separates the operculum from the capsule. It is known as **annulus**. In mature sporophytes, the operculum gets separated from the annulus and due to this the spores are dispersed

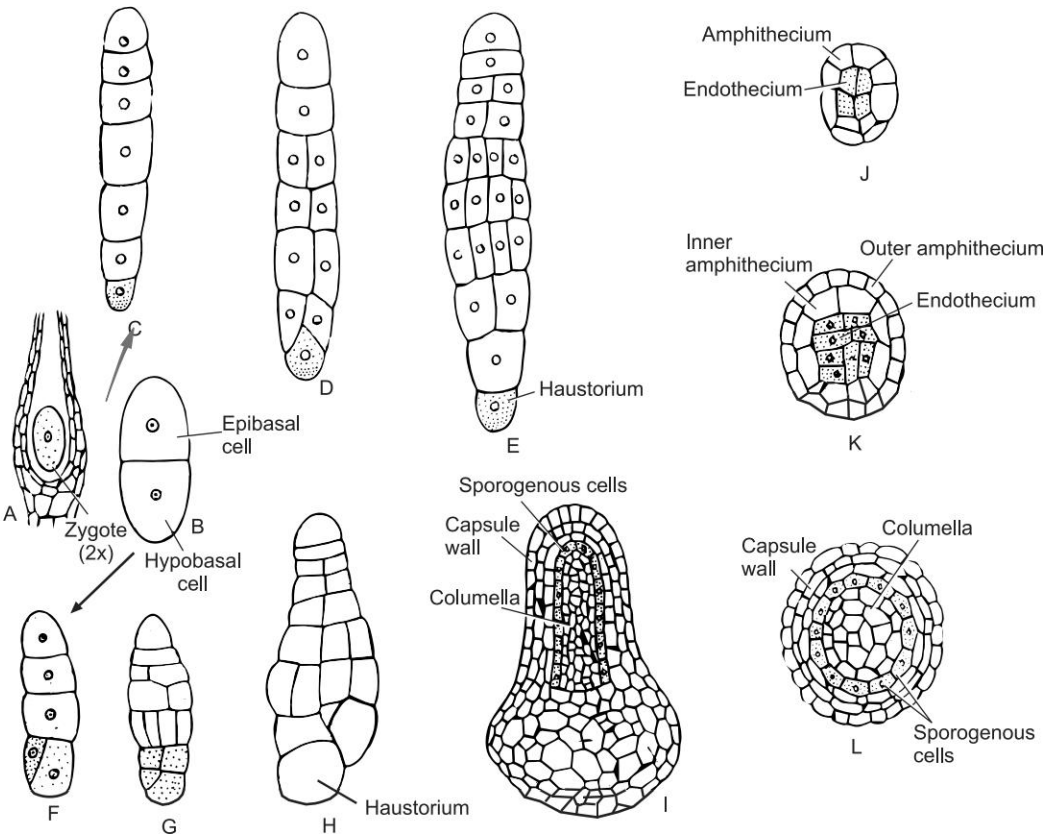


Fig. 10.9 A *-Development of sporophyte (Note that J-L are the stages of differentiation of amphithecium and endothecium in transverse sections)*

Columella is the central part of the capsule. It is made up of sterile cells. A dome-shaped arch of fertile sporogenous tissue is present over the columella. The calyptra and perichaetium surround the sporophyte in young conditions.

At maturity, the axis of the archegonial branch elongates, and the capsule thus comes out of the protective covering of calyptra and perichaetium. The leafless, elongated axis of the archegonial branch, present at the base of the sporophyte, is known as **pseudopodium** (Fig. 10.10A). It is mainly a post-fertilization development. A sac-like structure, formed by the distal end of the pseudopodium and basal part of calyptra, is known as **vaginula** (Fig. 10.10B). The foot remains embedded in the vaginula of the sporophyte.

(iii) Dehiscence of Capsule The capsule dehisces by a special **explosive mechanism**, usually on a bright sunny day. This mechanism is also known as **air-gun mechanism**. Due to heat of the sunny day, the columella and wall of the capsule become dry and get shrivelled. This promotes the development of an air space under the spore sac, and the capsule also changes its shape from spherical to cylindrical. The air present inside the capsule gets compressed, and a pressure also develops inside the capsule. Due to this, the operculum breaks off at the annulus. The spore sac ruptures and the spores are blown to a height of several centimetres.

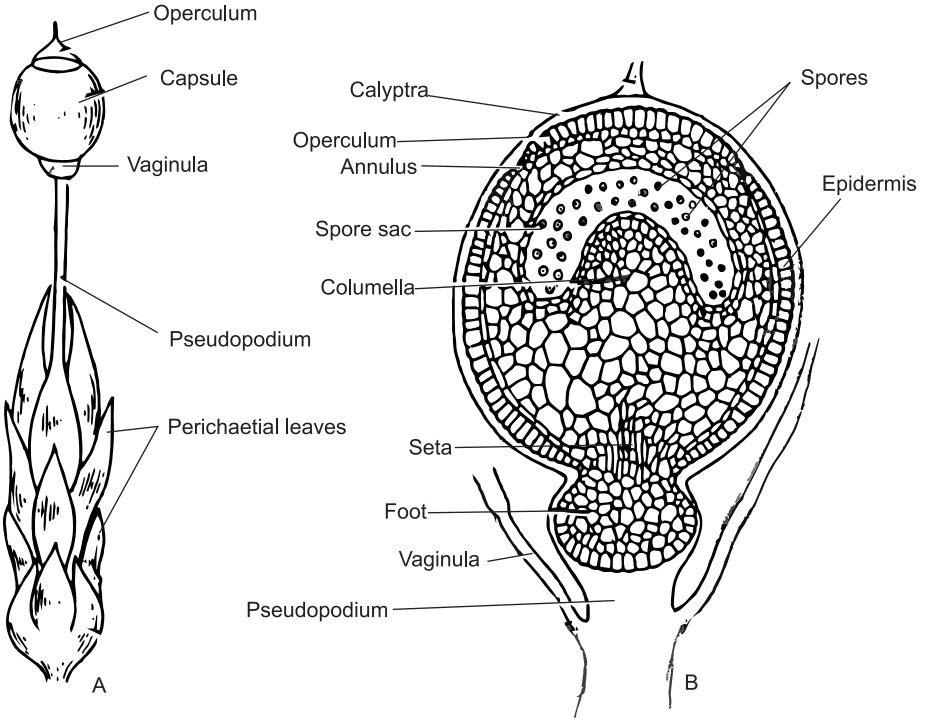


Fig. 10.10 *Sphagnum.* A, A female branch bearing perichaetial leaves and sporophyte; B, LS of sporophyte

(e) Young Gametophyte The haploid spore develops into a young gametophyte, and is thus the first cell of the gametophytic generation. The spores, when young, are arranged tetrahedrally. Each spore varies from 15 to 40 μm in diameter. They are uninucleate bodies, and their wall is made up of a thin inner endospore and a rough or papillose outer exospore. The spores of *Sphagnum* remain viable for as much as 4–6 months. In suitable conditions, the spores may germinate even within 2–3 days after dispersal.

At the time of germination, the exospore ruptures along the triradiate ridge, and the endospore comes out in the form of a germ tube (Fig. 10.11A-B). The germ tube divides by transverse divisions to form a green filament of 2-4 cells. An apical cell with two cutting faces develops in the uppermost cell of this filament due to two oblique vertical divisions (Fig. 10.11C-D). A plate-like multicellular, thallus-like structure develops due to the activity of the apical cell. This is known as **primary protonema** (Fig. 10.11E). Some marginal cells of this green primary protonema become meristematic and form **secondary protonema**, which contain rhizoids and leafy buds (Fig. 10.11F). It is these leafy buds which develop into mature gametophore of *Sphagnum*. Secondary protonema does not develop in many species of *Sphagnum*, and in such conditions, the leafy gametophores develop from the primary protonema only.

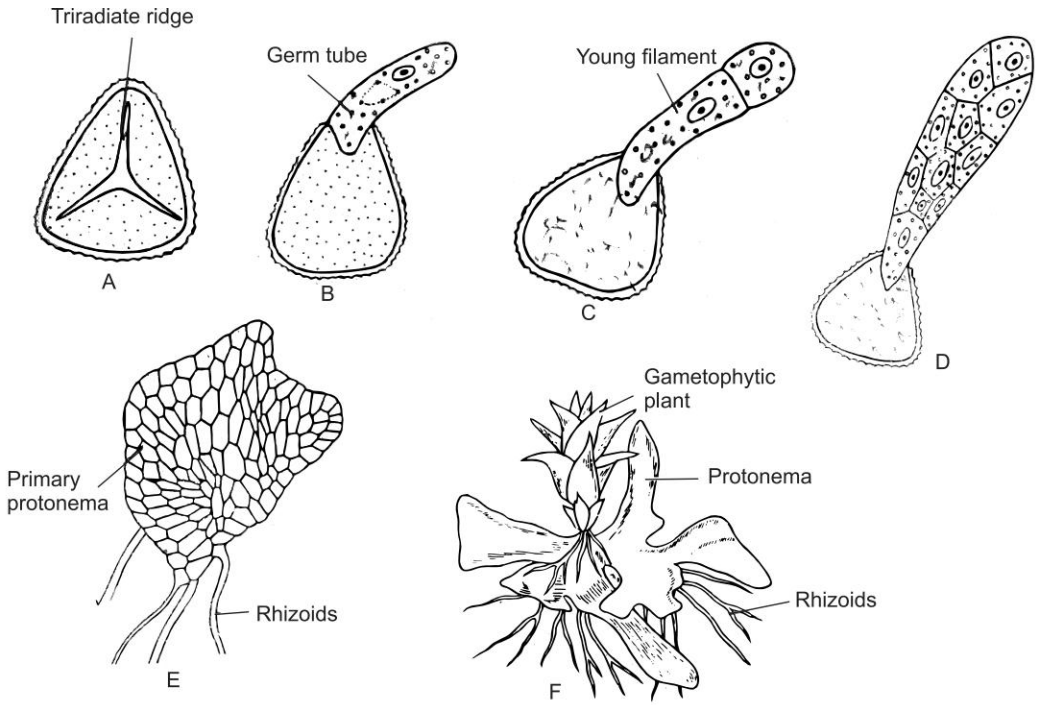


Fig. 10.11 A-F *Sphagnum.* Successive stages of spore germination and formation of young gametophytic plant

AFFINITIES OF *SPHAGNUM* 10.3

Sphagnum is unique among bryophytes because on one hand it shows resemblances with Hepaticopsida, Anthocerotopsida and also with Bryopsida but, on the other hand, it has some unique features of its own. Some, therefore, consider *Sphagnum* as **a synthetic group**. A glimpse of all such resemblances and unique characters is presented here.

10.3.1 Resemblances of *Sphagnum* with Hepaticopsida

1. Thalloid protonema of *Sphagnum* (Fig. 10.11E) resembles with that of several liverworts including acrogynous Jungermanniales.
2. Growth in thalloid protonema of *Sphagnum* occurs by an apical cell with two cutting faces, as in some acrogynous Jungermanniales.
3. Mechanism of dehiscence of antheridium of *Sphagnum* resembles with that of *Porella* and some other acrogynous Jungermanniales.
4. The mode of development, position and structure of archegonium of *Sphagnum* is also same as that of many acrogynous Jungermanniales.

10.3.2 Resemblances of *Sphagnum* with Anthocerotopsida

1. Apical growth is not shown by young sporogonium of *Sphagnum* and the same is true also in hornworts.
2. The entire endothecium in *Sphagnum* develops into sterile columella, as is also the case in Anthocerotopsida.
3. Archesporium in *Sphagnum* is amphithecial in origin and the same is the case in Anthocerotopsida.
4. Wall of the capsule of both *Sphagnum* and Anthocerotopsida contains several chlorophyll-containing cells and is thus photosynthetic in nature.
5. Sporophyte in both *Sphagnum* and hornworts is differentiated into a large bulbous foot, an ill-developed seta and a well-developed capsule.

10.3.3 Resemblances of *Sphagnum* with Mosses

1. Presence of erect, leafy gametophores in both.
2. Presence of multicellular rhizoids in both.
3. Presence of oblique septa in the rhizoids of both.
4. Resemblance of leaves of *Sphagnum* and *Leucobryum* in possessing alternate living green cells and dead hyaline cells.
5. Development of antheridium of *Sphagnum* resembles with that of several mosses.
6. Presence of stalked archegonium in both.
7. Presence of a massive venter in the archegonia of both.
8. Dehiscence of capsule with the help of a lid-like operculum in both *Sphagnum* and mosses.

10.3.4 Unique Characters of *Sphagnum*

1. Absence of rhizoids in the adult gametophore.
2. Development of branches in tufts, and that too from the axil of every fourth leaf.
3. Absence of midrib in the leaves.
4. Cortex of mature stem is made up of dead, empty and colourless cells.
5. Several spiral thickenings develop in the dead cells of the cortex.
6. Cortex cells have large oval pores on their walls in many species of *Sphagnum*.
7. Dead empty cells of cortex absorb water and thus behave like velamen of orchid roots.
8. Flask-shaped retort cells develop in the cortex of side branches of *Sphagnum*.
9. In spite of being a hydrophytic plant, *Sphagnum* shows several typical xerophytic characters.
10. The cell walls of this unique bryophytic plant contain some organic substance of colloidal nature, due to which it absorbs bases and releases acids. Water is, therefore, highly acidic where *Sphagnum* grows.

ANDREAEALES 10.4

General Characteristics

1. Andreaeales includes the mosses containing a capsule, which resembles a Chinese lantern, hence called **lantern mosses**.

2. Since these mosses grow exclusively on siliceous rocks, these are also called **granite mosses**.
3. Gametophores are small, quite brittle, dark brown or reddish in colour.
4. The conducting strand is absent in the stem.
5. The perichaetial leaves are quite large, stiff, erect and convolute.
6. The endothecium gives rise to archesporium and columella.
7. A dome-shaped spore sac overarches the columella.
8. Capsule wall lacks spongy photosynthetic tissue.
9. Foot is well-developed, and seta is very short or ill-developed or even may be absent.
10. The mature capsule gets elevated on a specialised gametophytic structure, called **pseudopodium**.
11. Dehiscence of capsule takes place by four longitudinal slits, which may sometimes be as many as ten in number.
12. The protonema is a thalloid and parenchymatous body.

Andreaeales has a single family Andreaeaceae, which includes genera like *Andreaea*, *Neuroloma*, *Andreaeobryum* and *Acroschisma*. Some details of the life history of *Andreaea* are given here.

ANDREAEA 10.5

Andreaea is worldwide in distribution and prefers to grow on siliceous rocky substratum, specially on exposed rocks in high mountain tops of tropics and colder temperate regions. It grows well in extremely dry situations on noncalcareous granite rocks, and that is why it has been commonly named "*granite moss*". Five species of *Andreaea* have been found from different regions of eastern and western Himalayas. These include *A. commutata*, *A. densifolia*, *A. indica*, *A. kashyapii* and the most common cosmopolitan species, i.e., *A. rupestris.*

The gametophores of *Andreaea* (Fig. 10.12 A) are green only when young, but even slightly mature plants are deeply pigmented being orange to deep purple or dark brown to even black. Plants are small-sized, reaching as much as 2 cm or only slightly more. They form irregular branching to provide a look of dense compact tuft. The leaves are spirally arranged on the stem, and tend to be imbricate when dry but divergent when moist. They vary in shape from subulate to ovate and their margin is entire or sometimes toothed. They are usually unistratose, with or without costa in different species.

Plants grow prostrate along the rock surface. Many multicellular and cylindrical rhizoids develop from the lower parts of the stem. They usually penetrate into the rock crevices. The stem is very brittle in dry conditions and can divide easily into fragments, from which new plants may develop, thus proving to be a method of vegetative propagation.

In *Andreaea*, the stem grows by means of an apical cell with three cutting faces, and therefore three rows of leaves are present.

Anatomically, the stem is almost uniform in structure and shows no differentiation into cortex and central conducting strands (Fig. 10.12B).

Majority of the *Andreaea* species are monoecious. The sex organs (antheridia and archegonia) are present on separate branches and are terminal in position. Some species (e.g. *A. nivalis*) are dioecious. Growth of the branch containing these sex organs stops after initiation of the sex organs because the apical cell is responsible for sex-organ formation. The last-formed segments of the apical cell form

other antheridia or archegonia. Perigonial leaves resemble the vegetative leaves while perichaetial leaves are bigger than that of remaining leaves. It has also been observed that sometimes a new apical cell differentiates near the base of the perichaetial leaves. This apical cell develops into new branches known as **innovation organs**.

Development of both the sex organs (antheridia and archegonia) follows the same pattern as in *Funaria*, and is described in detail under articles. 10.7.7(2) and 10.7.7(6). **Antheridia** are, however, ellipsoidal bodies, each with a long stalk which is usually uniseriate and sometimes biseriate (Fig. 10.12C). The **archegonium** is a short-stalked, flask-shaped body (Fig. 10.12 D) with a long and broad neck and a slightly globular venter. The first archegonium develops directly from the apical cell of the female branch.

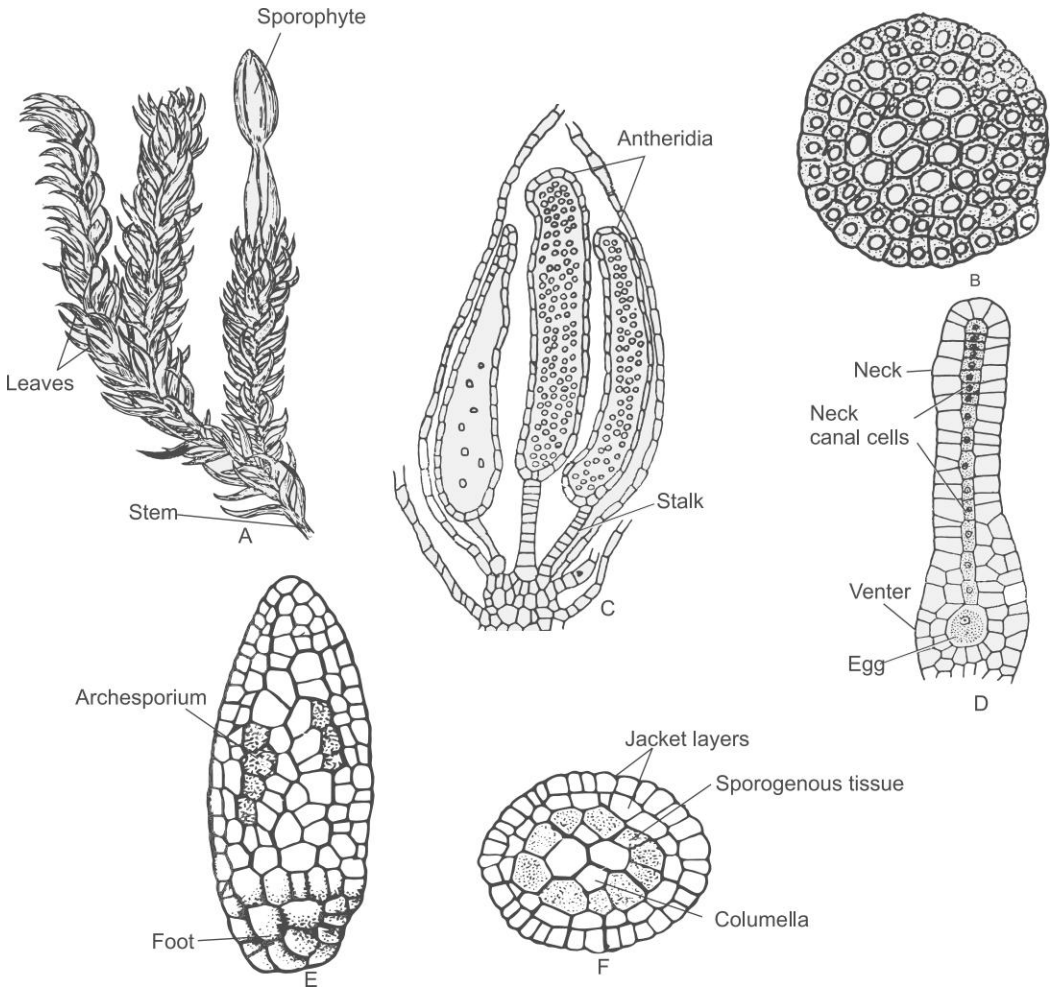


Fig. 10.12 *Andreaea rupestris.* A, Part of gametophore (enlarged) with sporophyte; B, TS stem; C, LS apex of male plant showing antheridia; D, An archegonium; E, Young sporophyte showing differentiation of archesporium and foot; F, TS young sporophyte showing differentiation of jacket layers, archesporium and columella

The zygote divides first by a transverse division to form a bicelled embryo. Its lower cell divides irregularly to form a **foot**, and the upper cell divides and differentiates an apical cell with two cutting faces. The foot is an unorganised mass of cells (Fig. 10.12E). The apical cell derived from the upper cell cuts several segments on each side to form a multicellular body which divides periclinally to form an outer amphithecium and inner endothecium. A three- to eight-celled thick jacket of the capsule in derived from the amphithecium. The endothecium again divides periclinally to form two layers, or the inner endothecium matures into **columella** (Fig. 10.12F).

The **capsule** is an elliptical body, and the sporophyte lacks seta (Fi. 10.13A). Some gametophytic cells elongate and push the capsule through the perichaetial leaves and form a long, leafless stalk known as **pseudopodium** (Fig. 10.13B). The jacket of the capsule gets heavily impregnated with black or dark-brown pigments. **Capsule lacks peristome** and also the **operculum**.

Mature sporophyte of *Andreaea* consists of a well-developed foot and a small capsule. It lacks structures like seta, operculum and peristome. Some have opined that seta is suppressed in *Andreaea*. The capsule attains a length of only 0.5 mm. The capsule tapers a little towards the apex and base. It remains covered by a wall of 2-6 layers. The centre of the capsule remains occupied by a club-shaped columella. The spore sac is dome-shaped and bears only **spores**. The young sporophyte remains enclosed by a thick calyptra and perichaetial leaves. The elongating function of seta is taken by a body of gametophytic tissue called **pseudopodium**.

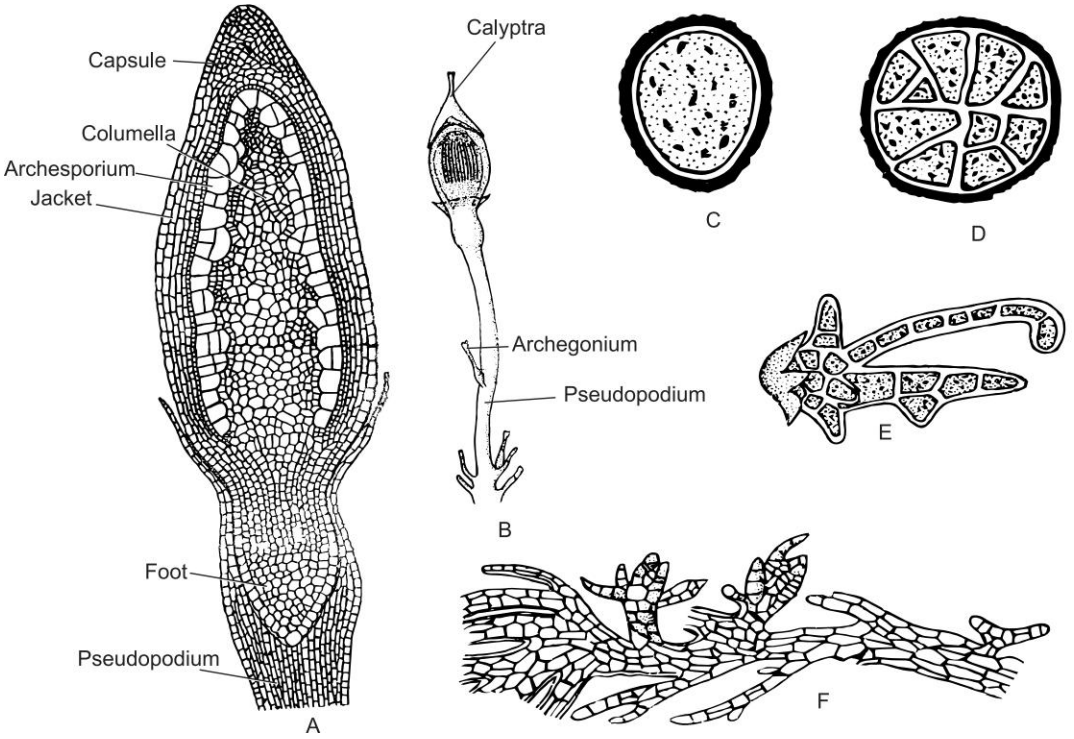


Fig. 10.13 A, LS of a sporophyte of *Andreaea rupestris*; B, A sporophyte showing pseudopodium; C, A spore; D-F, Development of spore and young gametophyte

Dehiscence of capsule takes place by four lines of dehiscence. The spores are dispersed through the slits. The dispersed spores remain viable for a few months.

The spore divides and redivides and earlier few divisions occur within the spore coat (Fig. 10.12C-D). A multicellular body comes out from the spore coat (Fig. 10.12E), and a well-developed protonema develops. From this develop the gametophores of *Andreaea*.

BRYALES 10.6

As mentioned earlier under Article 9.3, *Bryales* are commonly known as **true mosses**. This is the largest order of mosses including more than 675 genera and over 14000 species. Parihar (1987) has treated Bryales as equivalent to the subclass Bryidae of the class Bryopsida.

General Characteristics

1. Plant body is foliose, and leaves of the gametophore usually possess a distinct midrib.
2. The midrib region is more than one cell in thickness.
3. The spore develops into a protonema, which is usually filamentous.
4. The rhizoids are multicellular with oblique septa.
5. The zygote divides transversely into an epibasal and a hypobasal cell, and both usually grow by a two-sided apical cell.
6. The endothecium develops into columella and archesporium.
7. The columella is well-developed. It usually penetrates the sporogenous layer and reaches up to the apex of the capsule.
8. In between the wall of the capsule and spore sac is usually present an intercellular space traversed by many filaments of cells.
9. Differing from Andreaeales, the sporogonium in these mosses is never elevated on the pseudopodium.
10. A well-developed and elongated seta is present in these mosses.
11. The capsule, when mature, is a very complicate structure, and remains differentiated into several types of tissues.
12. The capsule opens usually by an operculum.
13. A peristome usually covers the spore cavity.
14. Peristome is hygroscopic in nature and helps in spore dispersal.

FUNARIA 10.7

10.7.1 Systematic Position (According to Holmes, 1986)

Division —Bryophyta
Class—Bryopsida
Subclass—Bryidae
Cohort—Eubryiidae
Order—Funariales
Family—Funariaceae
Genus—*Funaria*

10.7.2 Distribution and Habitat

Funaria is one of the most common mosses, distributed widely throughout the world. It includes over 120 species, of which more than 15 species have been reported from India. *Funaria hygrometrica* is cosmopolitan and best known of all species of different mosses. It grows on moist grounds in close tufts and also on damp and shady moist rocks, wells, crevices, tree trunks and other similar surroundings.

10.7.3 Mature Gametophyte

Plant body is gametophytic and foliose, consisting of an erect leafy axis attached to the substratum by means of rhizoids.

The **axis** or **stem** is erect, slender, usually branched and attains a height of 1–4 cm. It remains covered with many leaves, arranged spirally in 3/8 phyllotaxy, i.e. three complete spirals contain eight leaves. The leaves are simple, ovate, sessile, green and each possesses a broad membranous base and a pointed apex (Fig. 10.14 B). A distinct midrib is also present in each mature leaf. The midrib is, however, not present in very young leaves.

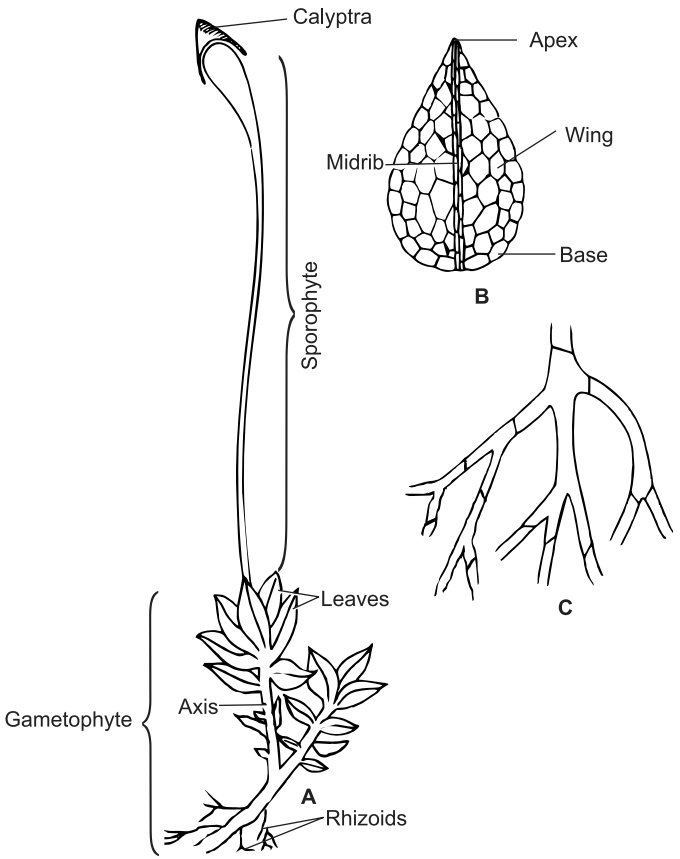


Fig. 10.14 *Funaria hygrometrica.* A, Plant body with sporophyte; B, A leaf; C, Rhizoids showing oblique septa

Many rhizoids are present at the base of the gametophores. They are multicellular, slender and well-branched. Rhizoids contains oblique septa (Fig. 10.14C). They are colourless when young but mature rhizoids become brown or black-cloloured. The chloroplasts may also develop in the cells of rhizoids, when they are exposed to sunlight. The main functions of rhizoids are anchoring as well as absorption.

10.7.4 Apical Growth

The growth of the stem takes place by a pyramidal apical cell with three cutting faces. Its three lateral faces cut off three rows of cells by successive divisions. Each of the so formed cells divides periclinally into inner daughter segment and an outer segment. The inner daughter segment gives rise to the inner tissues of the stem while the outer segment contributes to the leaf and the outer tissues of the stem. The leaves in the young apical part of the axis are thus arranged in three vertical rows.

10.7.5 Anatomy

1. Stem or Axis Internally the mature axis is divided into **epidermis**, **cortex** and **central strand** (Fig. 10.15A, B).

Epidermis is the outermost layer made up of tangentially elongated cells filled with chloroplasts. Pores or stomata are absent.

Cortex is the well-developed, parenchymatous region of the axis present just inner to the epidermis and extends up to the central strand or central cylinder. In the young axis, the cells of the cortex also contain chloroplasts, which disappear in the mature stems. In mature stems the cells of the outer layers of cortex may also become thick-walled and somewhat reddish-brown, while the cells of the inner cortex are thin-walled. Isolated small leaf traces may also be seen near the periphery.

Central strand or central cylinder is made up of long, narrow, colourless, thin-walled cells. They lack protoplasm and are thus dead cells. They help in conduction of water and other nutrients.

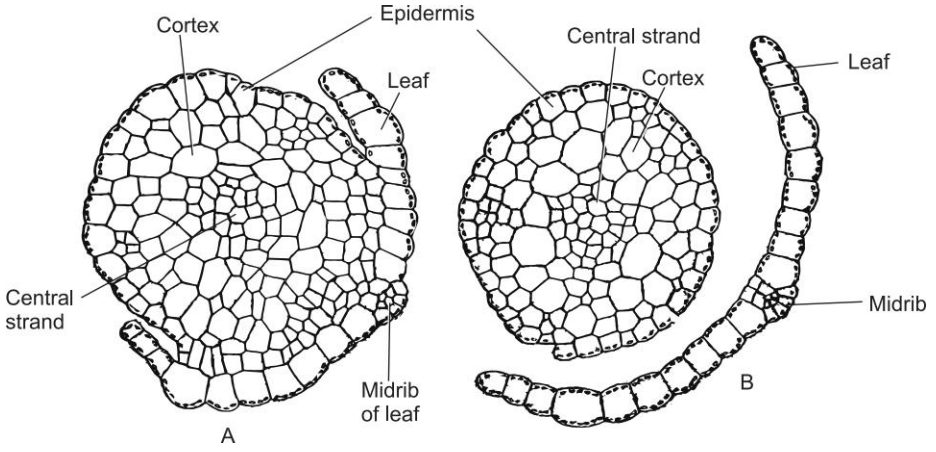


Fig. 10.15 *Funaria hygrometrica.* A, T.S. of a gametophore at a level of junction of a leaf with the stem; B, TS of stem and leaf cut at a slightly higher level

2. Leaf

Internally, the leaf is very simple in structure. Its lamina or wings are composed of a single layer of large thin-walled cells. They remain filled with chloroplasts, and thus represent the main photosynthetic tissue of the gametophore. In the centre of the lamina is present a midrib. It is made up of small strands of narrow and thick cells. The cells of the central strand help in conduction. Hairs or stomata are absent on the leaf.

10.7.6 Vegetative Reproduction

Funaria reproduces vegetatively by various methods including gemmae, bulbils, primary protonema, secondary protonema and apospory.

1. Gemmae

When conditions are unfavourable, some of the terminal cells of protonema form green multicellular bodies called gemmae. They are both transversely as well as vertically septate. On being detached from the plant, and if the conditions are favourable, each gemma germinates into a new gametophore of *Funaria*.

2. Bulbils

Gemmae-like structures developing on rhizoids are known as bulbils. They lack chloroplasts and are thus nongreen structures. On being detached, each bulbil germinates into a new plant.

3. Primary Protonema

Spore germinates into a branched filamentous structure known as **primary protonema**. Accidentally or due to death and decay of some of its cells, the primary protonema gets broken into small fragments. Buds develop on such fragmented parts of the primary protonema. Each of these buds develops into gametophore of *Funaria*.

4. Secondary Protonema

The protonema formed on the injured stems, leaves, reproductive parts or even rhizoids, are known as **secondary protonema**. Buds also develop on secondary protonema, and each such bud matures into a new foliose gametophore.

5. Apospory

Sometimes, diploid gametophores are produced from the vegetative cells of the sporophyte of *Funaria*, that is, without the production of spores. This phenomenon is known as *apospory*. Such gametophores resemble normal haploid gametophores in appearance but they have diploid cells. Such plants also produce gametes but they are also diploid. On being fused with the gametes of the opposite sex, the resultants are 4n zygotes and produce sterile sporophytes.

10.7.7 Sexual Reproduction

Funaria is a monoecious and autoecious moss, i.e. male and female reproductive structures develop on different branches of the same plant. Usually, the female or archegonial branches are longer than that of male or antheridial branches.

1. Antheridial Branches

The main axis becomes expanded at the apex, and bears groups of antheridia (Fig. 10.16A) in different stages of their development. A rosette of spreading leaves also surround the groups of antheridia, and these are known as perichaetial leaves. Many multicellular, long, capitate and green hairs, intermingled with antheridia and perichaetial leaves are also present. These are known as **paraphyses**. Being green, they contain chloroplasts, and help in photosynthesis. Antheridia are also protected by these paraphyses.

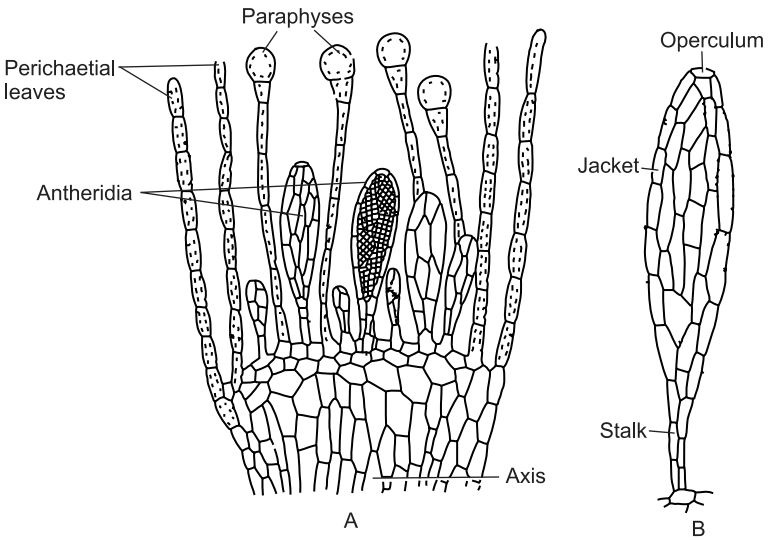


Fig. 10.16 *Funaria.* A, LS of an antheridial branch; B, A single antheridium

2. Development of Antheridium

The development of antheridium starts from a superficial **antheridial initial** (Fig. 10.17A) situated at the apex of the antheridial branch. This initial soon enlarges, becomes papillate and divides to form an **outer cell** and a **basal cell** (Fig. 10.17B). The basal cell forms the lower part of the stalk of the antheridium which remains embedded in the tissue. The outer cell divides and redivides transversely to form a small 2-4 celled filament (Fig. 10.17C). The uppermost cell of this filament divides by two vertical intersecting divisions, resulting into an apical cell with two cutting faces (Fig. 10.17D). This apical cell cuts off segments in a regular sequence in two rows (Fig. 10.17E). Few upper cells of this filament divide diagonally by vertical divisions, each forming two unequal cells, of which the smaller peripheral cell functions as the first **jacket cell** (Fig. 10.17F) and the larger daughter cell divides in a similar fashion to form second jacket initial on the outer side and primary androgonial cells on the inner side (Fig. 10.17G). Two jacket initials and one primary androgonial cell are thus formed by each cell of the filament. Many anticlinal divisions in the jacket initial give rise to a single-layered jacket of the antheridium (Fig. 10.17H). Jacket cells, when young, are green in colour because of the presence of chloroplasts. An **operculum** is formed by the apical cell of the filament (Fig. 10.17I). Repeated divisions in the primary androgonial cell make it a multicellular mass of cells which develop into androgonial cells (Fig. 10.17I). Further division in each androgonial cell results in the formation of two **androcytes**. Each of the androcytes differentiates into a single, uninucleate and biflagellate antherozoid (Fig. 10.17 K).

3. Mature Antheridium

The **mature antheridium** (Fig. 10.17 J, K) possesses a long multicellular stalk and a dark-coloured club-shaped body. The mass of androcytes remains enclosed in the body by a single-layered antheridial jacket (Fig. 10.17J). A comparatively larger hyaline cell of the operculum is present at the tip of the jacket layer. Sometimes the operculum consists of two cells (Fig. 10.17 J).

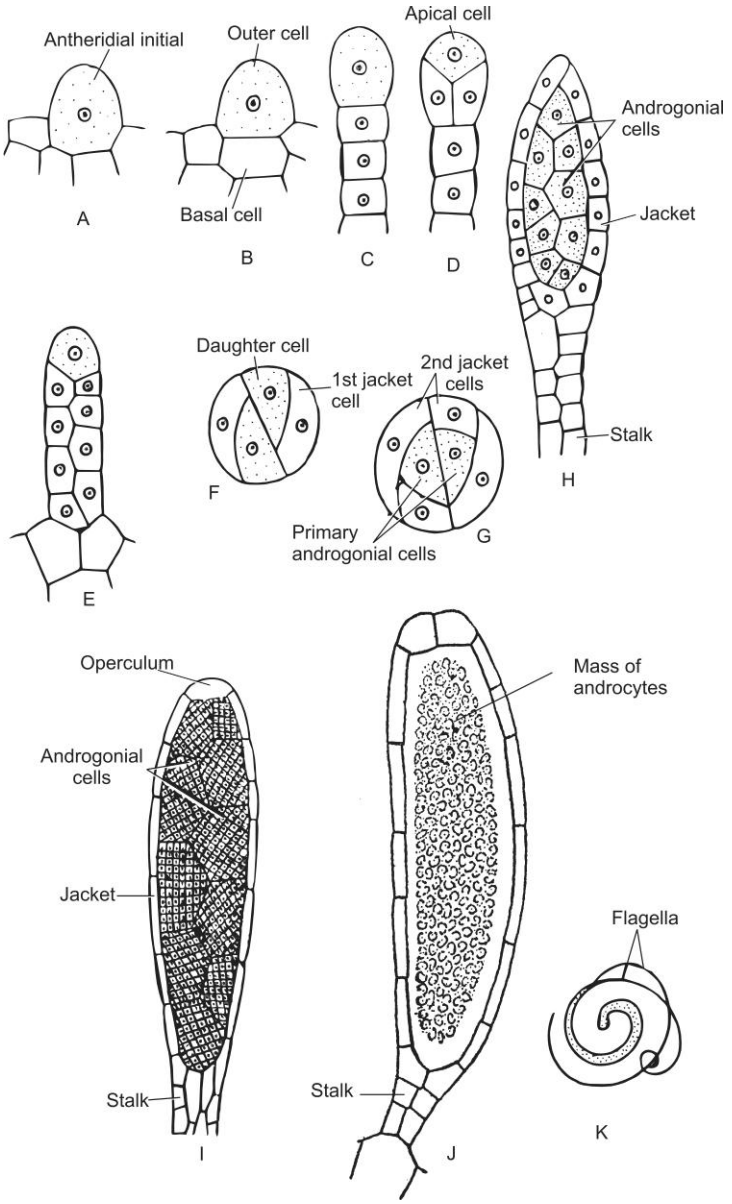


Fig. 10.17 A-K. *Funaria hygrometrica*. Development of antheridium

4. Dehiscence of Antheridium

Fully mature antheridium dehisces when it comes in contact with water. The operculum cell absorbs water, becomes mucilaginous and swells up. Due to pressure, it bursts forming a pore-like structure at the distal end of the antheridium. The mass of androcytes surrounded by the viscous fluid oozes out through this pore. Contraction of the antheridial wall also helps in releasing the mass of androcytes. The androcytes spread out in the form of a thin film, their membranous walls dissolve in water, this all finally liberates the spirally coiled biflagellate antherozoids.

5. Archegonial Branches

The female or archegonial branches in *Funaria* usually develop laterally at the base of the male branch. At the apex of these branches develop archegonia (Fig. 10.18) surrounded by many leaves known as **perichaetial leaves**. Along with archegonia and perichaetial leaves are also present several **paraphyses** on the archegonial branch. The cells of both perichaetial leaves and paraphyses remain filled with several chloroplasts.

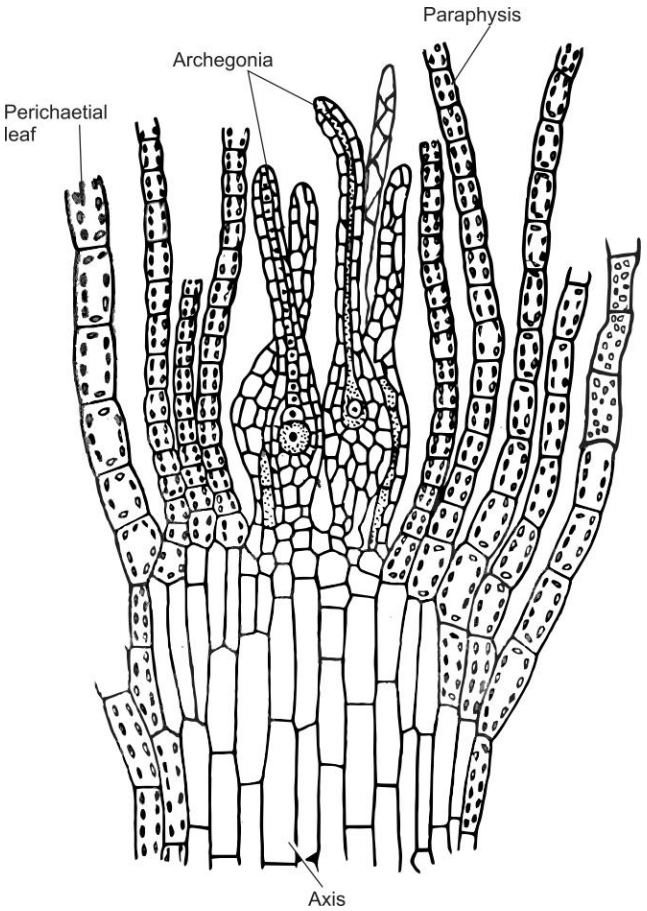


Fig. 10.18 *Funaria hygrometrica*. Longitudinal section of an archegonial branch bearing archegonia

6. *Development of Archegonium*

It starts from a superficial cell, known as **archegonial initial** (Fig. 10.19A), which gets differentiated at the tip of the archegonial branch. It first divides transversely to form a **lower cell** and an **upper cell** (Fig. 10.19B). Repeated divisions in the lower cell results in the formation of the basal part of the archegonium which remains embedded in the tissues of the archegonial branch. Upper cell starts functioning as **archegonial mother cell** and divides by two intersecting oblique walls to form an **apical cell** with two cutting faces (Fig. 10.19C). This apical cell cuts many (4–8) segments alternately on both sides and forms the archegonial stalk (Fig. 10.19D). The apical cell now divides by three intersecting oblique divisions to form three **peripheral cells** surrounding an **axial cell** (Fig. 10.19E). Each peripheral cell divides anticlinally and forms a single-layered jacket of the venter. By further divisions, it becomes bilayered. The derivatives of the axial cell develop into the neck of the archegonium.

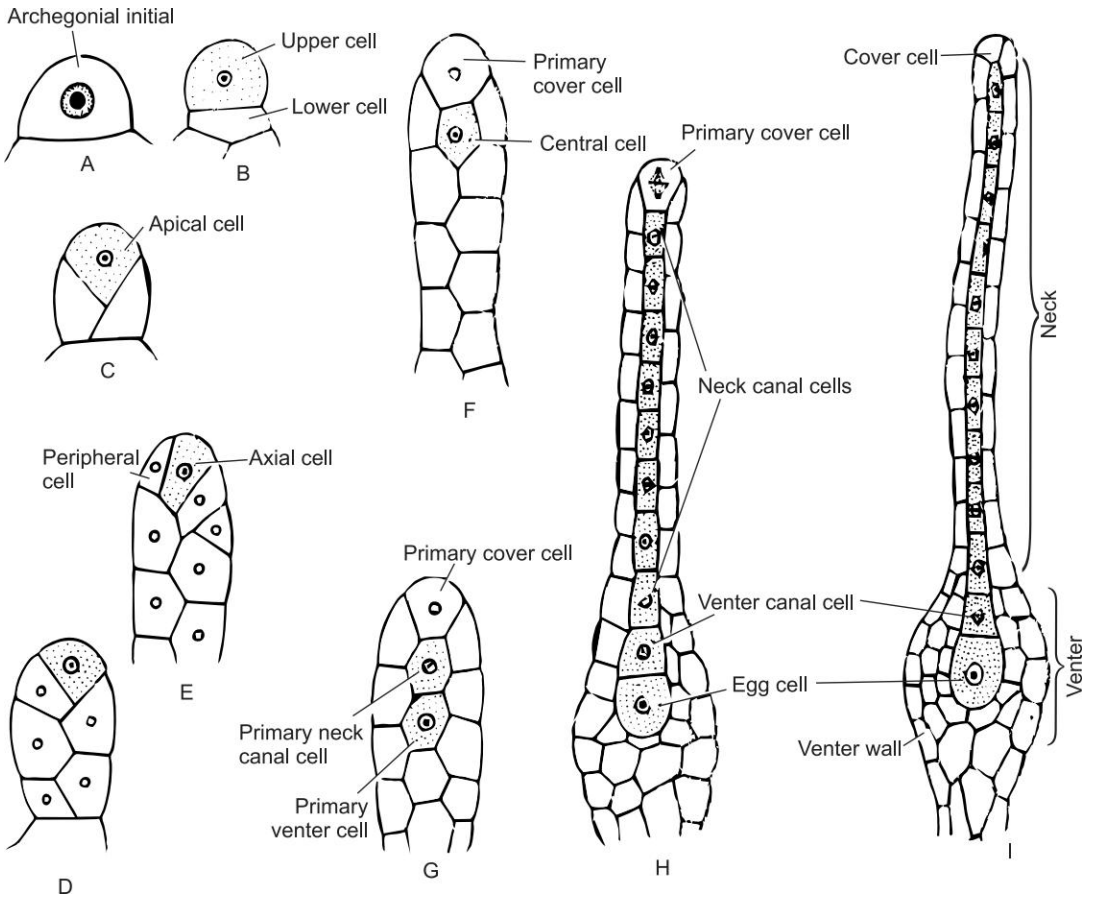


Fig. 10.19 *A-I. Funaria hygrometrica* showing successive stages of the development of archegonium

The axial cell (Fig. 10.19E) divides transversely into a **primary cover cell** and an inner **central cell** (Fig. 10.19 F). The primary cover cell now behaves as an apical cell with four cutting faces. The

derivatives of three of these faces form the jacket of the neck whereas the fourth basal face forms a row of neck canal cells. The **central cell** divides transversely into an outer **primary neck canal cell** and inner **primary venter cell** (Fig. 10.19G). The primary neck canal cell divides transversely to form a row of neck canal cells and all these occupy the median and lower part of the neck. In *Funaria*, the neck canal cells, therefore, have double origin, i.e. those present in the median and lower part of the neck originate from the primary neck canal cells while those present in the upper part of the neck originate from the basal derivatives of the cover cell. The **primary venter cell** divides transversely to form a venter canal cell and an egg (Fig. 10.19 H,I).

7. Mature Archegonium

Mature archegonium (Fig. 10.19I) consists of a well-developed stalk, a swollen venter and an elongated neck. The venter region is surrounded by a bilayered archegonial jacket while in the neck region, it is single-layered. The neck contains a row of 6-9 or more neck canal cells, and the venter contains a venter canal cell and an egg cell (Fig. 10.19 H, I).

8. Fertilization

Fertilization is facilitated by rain or dew water. Biflagellate antherozoids are set free during the process of dehiscence of antheridium. On the other hand, the neck canal cells and the venter canal cell of the archegonium disintegrate and degenerate, and form a mucilaginous mass. This mass absorbs water, and due to this the cover cells present at the top of the neck of the archegonium are forced apart. A free passage for the entry of antheridium is thus formed inside the archegonium. Dew or rainwater helps in the transfer of antherzoids from antheridial head to the archegonial head. Water drops containing antherozoids easily tickle down from antheridial to archegonial head because the archegonial heads are usually at the lower level than the antheridial heads. Water current helps in transfer of antherozoids from antheridial heads to archegonial heads in submerged species of *Funaria*.

The antherozoids enter into the archegonium due to the chemotactic imfluence of the mucilaginous substances of the neck. Many antherozoids enter inside the archegonial neck, but ultimately only one of them fuses with the egg and forms a diploid zygote.

10.7.8 Sporophyte

Fusion of antherozoids and an egg in the process of fertilization results in the formation of a diploid zygote, which is the first cell of the sporophytic generation. A wall is secreted around the zygote. It also increases in size and fills the cavity of the venter (Fig. 10.20A).

1. Development of Sporophyte

The diploid zygote first divides by a transverse division into an upper **epibasal cell** and a lower **hypobasal cell** (Fig. 10.20B). Both of these cells divide further by two oblique intersecting walls, resulting in the formation of a two-sided apical cell in both epibasal cell as well as hypobasal cell (Fig. 10.20C). Two growing points, represented by two apical cells, are thus present in the young embryo at this stage. Each of these apical cells has two cutting faces. The **epibasal cell** (Fig. 10.20B) and its derivatives give rise to **capsule** and a part of the seta while the **hypobasal cell** and its derivatives give rise to **foot** and remaining part of the seta. The cells of the wall of the venter divide and redivide to form a **calyptra**, which is a protective covering and covers the capsule till it matures.

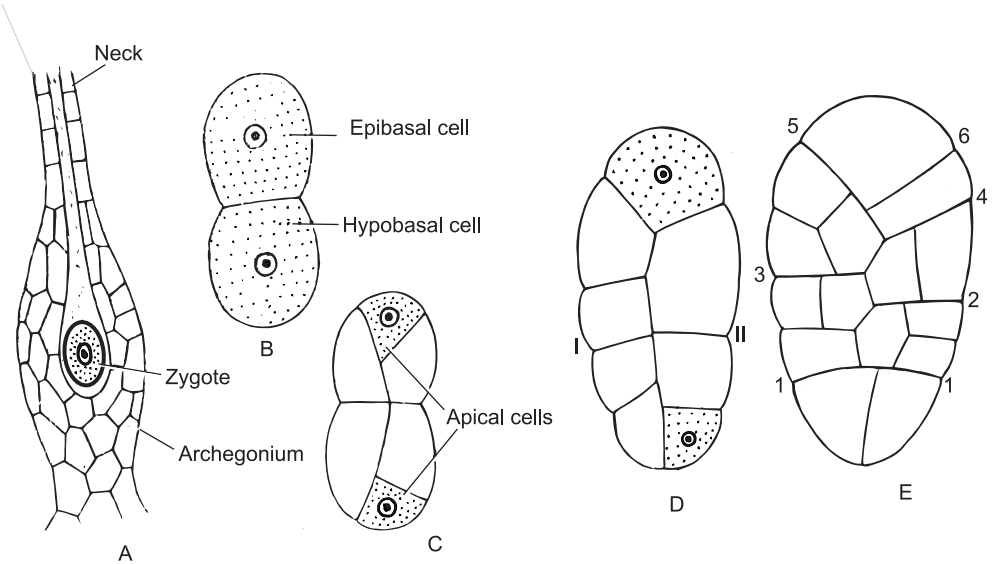


Fig. 10.20A-E *Funaria.* A, Mature zygote inside the archegonium; B-E, Early stages of the development of sporophyte

(a) Development of Capsule

Study of the serial transverse sections of the young sporophyte can provide us a clear picture of the development of the capsule. If a transverse section just below the apical cell is cut, its two derivatives form an almost spherical segment (Fig. 10.21 A). These two derivatives are one each from two faces of the epibasal apical cell. A vertical division in both these derivatives forms the quadrant stage of the embryo. (Fig. 10.21B). In this quadrant embryo, each cell divides by an anticlinal division in such a way that two such cells are resulted, of which one is smaller and almost triangular while the other one is larger and more or less rectangular in shape (Fig. 10.21C). This stage contains eight cells of the embryo, in which four are triangular cells while the remaining four are rectangular cells, and these are alternately arranged. Each rectangular cell divides by a periclinal division. In this way, at this stage eight peripheral cells, which form **amphithecium**, surround the centrally-located four cells of the **endothecium** (Fig. 10.21D). These two (amphithecium and endothecium) are fundamental embryonic layers of the sporophyte. Cells of these two layers divide in a definite pattern and form three regions of the capsule, i.e. **apophysis**, **theca** and **operculum**, from base towards top.

(i) Early Fate of Amphithecium

The amphithecial cells (Fig. 10.21D) divide periclinally and develop into two concentric rings made up of 8 cells each. The inner ring is designated as the **first ring** (Fig. 10.21 E). In the outer ring, the cells first divide anticlinally and then periclinally forming two concentric rings of 16 cells each. The inner one of these two concentric rings is designated as the **second ring** (Fig. 10.21G). The cells of the outer ring divide first anticlinally resulting into 32 cells and then periclinally forming two concentric rings of 32 cells each. The inner ring of 32 cells is the **third ring**, and the outer ring divides again periclinally, thus resulting into two rings of 32 cells each (Fig. 10.21G). Of these two rings of 32 cells each, the inner one is designated as **fourth ring** and the outer one is known as the **fifth ring** (Fig. 10.21H, I). An additional **sixth ring** is formed in the opercular region.

(ii) Early Fate of Endothecium As mentioned above, the endothecium is present in the form of a central core of four cells (Fig. 10.21 D,E). These cells repeat the same pattern of divisions that differentiates the amphithecium and endothecium. Due to this, a group of four endothecial cells is differentiated by eight peripheral cells (Fig. 10.21F,G). Two subsequent divisions in the endothecial cells give rise to 16 cells, which form **columella**. Eight peripheral cells divide first by radial wall and then by a periclinal division. Two layers of 16 cells each are thus differentiated. The inner layer, which is adjacent to the columella, matures into the **inner spore sac**, while the cells of the outer layer divide again by radial walls to form the single-layered **archesporium**. The single-layered archesporium divides periclinally and soon becomes double-layered. All archesporial cells are fertile and behave as spore mother cells. Reduction division in each archesporial cell results in the formation of four haploid spores.

(iii) Fate of the Rings in the Development of Operculum, Theca and Apophyses in the Young Capsule

- ***Fate of Endothecium in the Operculum*** It develops into central parenchymatous region. The first ring contributes to outer peristomial layer. The second ring gives rise to the middle peristomial layer. The third ring contributes to the inner peristomial layer.

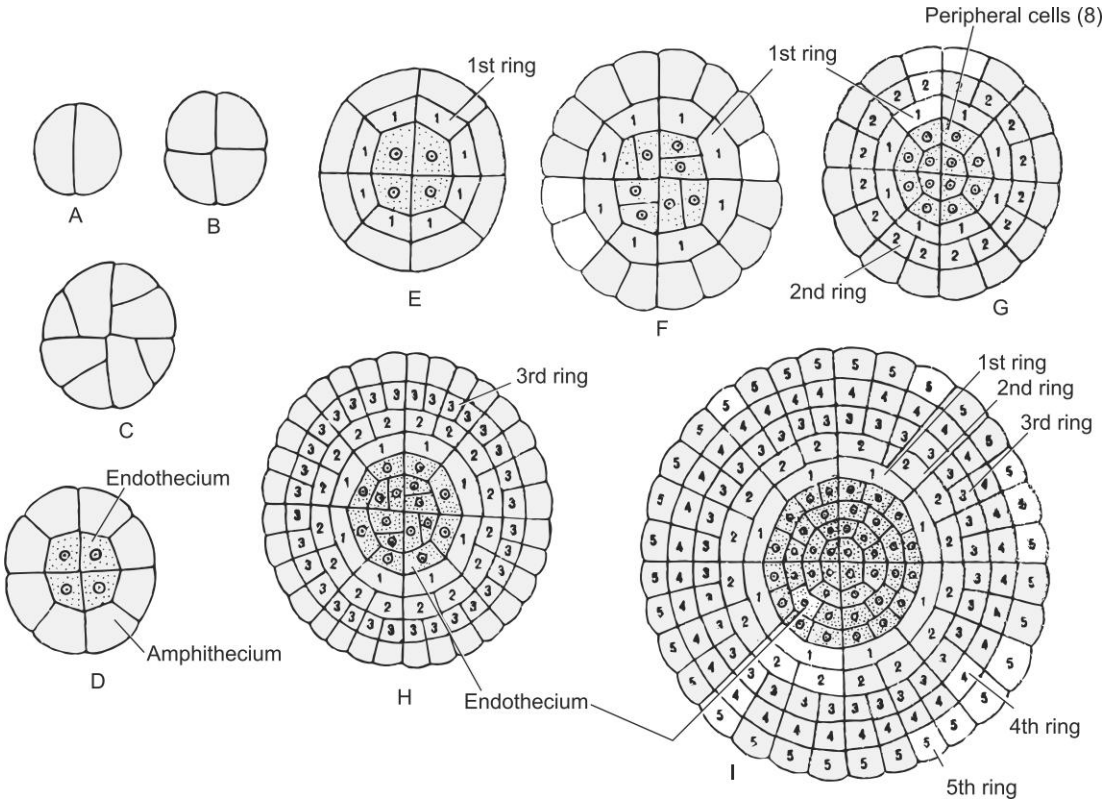


Fig. 10.21 A-I *Funaria.* Stages of the development of sporophyte, including differentiation of amphithecium and endothecium (A-D) and formation of five rings of amphithecial cells in the region of capsule (E-I)

- ***Fate of Amphithecium in the Operculum*** The fourth and fifth rings contribute to the inner layer of the operculum. The sixth ring, present only in the operculum region, contributes to the epidermis of the operculum and annulus.
- ***Fate of Endothecium in the Theca*** Four central cells contribute to the columella. Inner layer of 16 peripheral archesporial cells form the inner wall layer of the spore sac. Peripheral cells form the outer layer. The outer layer of 16 peripheral archesporial cells form the archesporium which forms spore mother cells.
- ***Fate of Amphithecium in the Theca*** The first ring contributes to the outer wall of the spore sac. The second ring gives rise to trabeculae. The third ring forms chlorenchymatous layers. The fourth ring forms the hypodermis. The fifth ring contributes to the epidermis.
- ***Fate of Endothecium in the Apophysis*** It contributes to the central conducting strand. Four inner layers form spongy tissue around the conducting strand.
- ***Fate of Amphithecium in the Apophysis*** The outermost fifth layer contributes to the epidermis of the apophysis region of the young capsule.

3. Structure of Mature Sporophyte

The sporophyte (Fig. 10.22A) is differentiated into **foot**, **seta** and **capsule**. The **foot** is a small, conical body embedded in the tip of the archegonial branch. The **seta** is very long, more or less twisted and a stalk-like structure which supports the capsule at its tip.

Internally, the seta is differentiated into an outermost layer of epidermis, enclosing somewhat thick-walled cells of the cortex and a centrally-located central conducting strand (Fig. 10.23) made up of thin-walled elongated cells. Functions of seta include (i) transport of water and nutrients to the capsule, and (ii) to provide mechanical support to the capsule.

The capsule is erect and green, when young, but at maturity it becomes curved and bright orange coloured. The capsule can be divided into three major regions (Fig. 10.22B), viz. (i) apophysis, (ii) theca proper, and (iii) apical region.

(a) Apophysis The apophysis is the basal sterile part of the capsule which connects the capsule with the seta of the sporophyte. It is made up of the central conducting strand, which extends down into the seta. Around the central strand are present loosely arranged chlorophyll-containing cells. On its outermost side is present a layer of epidermis, the continuity of which is broken by stomata. Because of the presence of chlorophyllous cells, the apophysis performs the function of photosynthesis. The *Funaria* sporophyte is, therefore, partially dependent on the gametophyte.

(b) Theca Proper Theca is the middle part of the capsule, present in between the apical region and apophysis. It is the fertile part of the capsule, and contains various parts, including columella, spore sac, air space and capsule wall.

- ***Columella*** It is the centrally-located, cylindrical, pith-like part of the theca made up of parenchymatous cells. Its distal end projects into the operculum. At its base, the columella remains connected with the apophysis.
- ***Spore Sacs*** Two elongated spore sacs surround the columella. On the outer side, each spore sac remains covered by a 3–4 layered wall. The wall present on the inner side of the spore sac

is single-layered. Each spore sac contains many spore mother cells, when young. At maturity, each spore mother cell forms four haploid spores. *Funaria* lacks elaters.

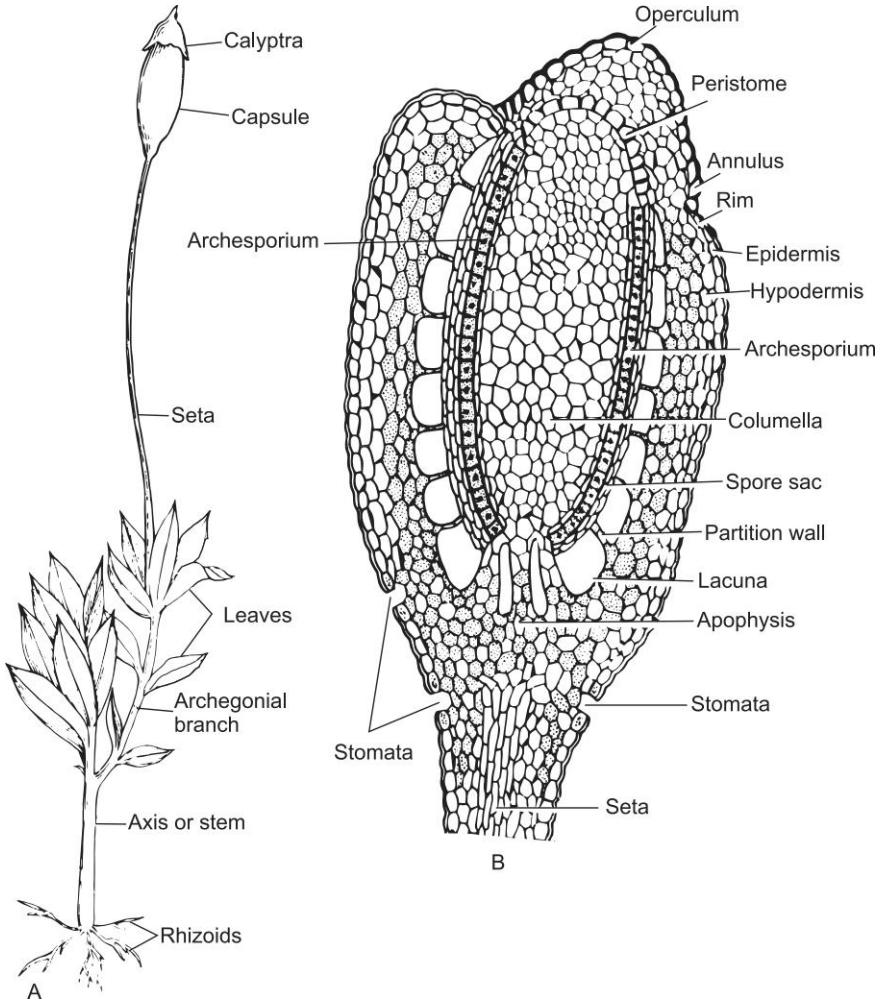


Fig. 10.22 *Funaria.* A, A gametophyte with sporophyte; B, LS capsule

- ***Air Space*** Outside each spore sac is present a large air space or air cavity. It remains traversed by many filaments which are green, delicate and contain chlorophyll-containing cells. These filaments are known as **trabeculae**.
- ***Capsule Wall*** The wall of the capsule is made up of many layers of thin-walled parenchymatous cells. The epidermis, followed by 2-3 layered hypodermis, is present on the outermost side of the capsule wall. Inner to the parenchymatous hypodermis are present 2–3 layers of chlorophyllous cells, which enclose many intercellular spaces. Through trabeculae, the innermost layer of the capsule wall remains connected with the outer wall of the spore sac.

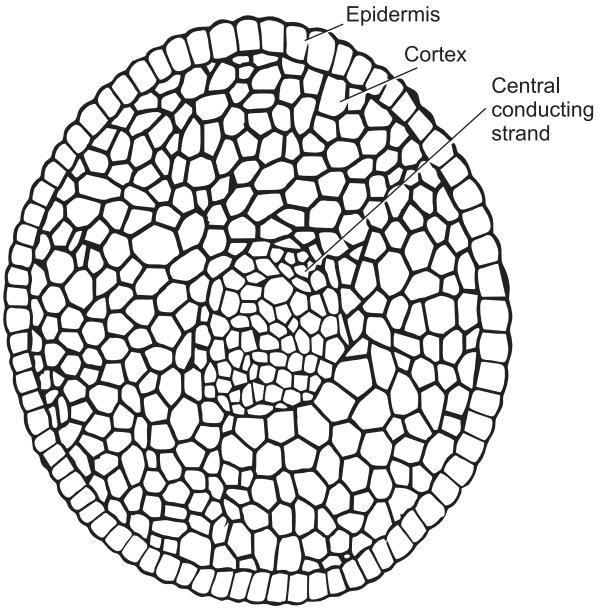


Fig. 10.23 *Funaria*. TS of seta

(c) Apical Region

Two main parts of the apical region of the capsule are **operculum** and **peristome** (Fig. 10.22B). A constriction is present at the juncture of the theca and apical regions. A **rim** or **diaphragm** is present immediately below this constriction. The rim, made up of 2–3 layers of radially elongated cells, demarcates the upper limit of the theca.

- ***Operculum*** The operculum is a lid-like conical structure (Fig. 10.22B) which closes the mouth of the capsule. It is made up of 2–3 layers of thin-walled cells. The cells of its outermost layer have thickened outer walls. At the broader lower end of the opercular lid, a few layers form a ring of large, well-developed cells, which represent the annulus. The annulus is composed of thin-walled cells. It helps in the dehiscence of the capsule.
- ***Peristome*** Immediately below the operculum lies the **peristome** (Fig. 10.22B). It remains attached below the edge of the diaphragm. The peristome consists of two rings of long, curved, triangular teeth-like structures known as **peristomial teeth**. 16 teeth are present in each ring of peristome. The outer peristomial teeth are large, thicker and red-coloured structures, while the inner peristomial teeth are smaller, delicate and colourless structures (Fig. 10.24 A-C). Well-marked transverse thickening bands are present in the outer peristomial teeth.

4. Dehiscence of Capsule and Dispersal of Spores

Water supply is almost cut off when the sporophyte is fully mature. This results into drying up of all tissues of the capsule. Soon the thin-walled cells of the annulus break and the operculum is thrown away. In spite of all these conditions, the spores are not dispersed because the mouth of the theca is covered by the peristome. Being hygroscopic in nature, the outer peristomial teeth bend outwards in **dry conditions** while the inner peristomial teeth remains as such in their normal position. Due to jerky movement

of the outer peristomial teeth, the slits present in between inner peristomial teeth become broader, and through these slits the spores are dispersed. During **humid** or **moist conditions**, the outer peristomial teeth absorb moisture and they show a bending towards the inner side. Due to this, the slits close and this prevents the escape of spores. Dispersal of spores in *Funaria* is also facilitated due to twisting and bending nature of seta of the mature sporophyte.

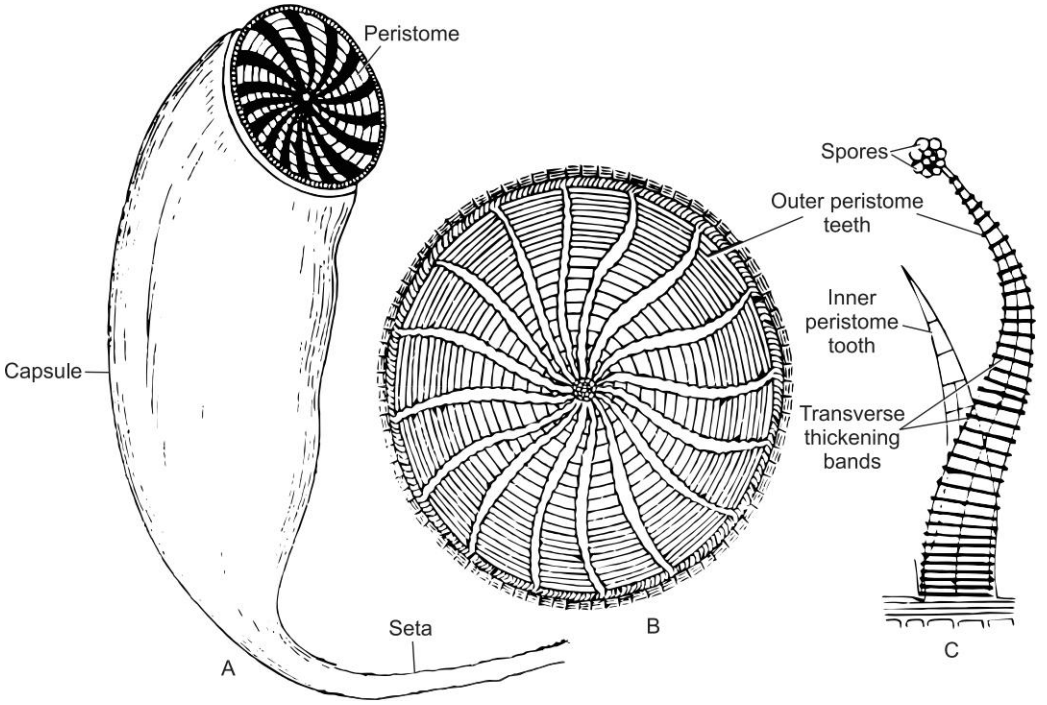


Fig. 10.24 *Funaria.* A, A capsule showing peristome; B, Outer peristome in surface view; C, An outer and an inner peristomial teeth

10.7.9 Young Gametophyte

The dispersed spore germinates (Fig. 10.25A-E) readily to form one or two germ tubes, which elongate to form a branched filamentous **protonema**. Initially, the protonema is made up of highly chlorophyllous, green short cells with transverse septa. This stage of the protonema is known as **chloronema**. The chloronema matures into **caulonema**, which is a shoot-producing protonema. The caulonema is made up of erect filaments and also prostrate filaments, which comprise green elongated cells with oblique septa. An initial develops from the cell of prostrate filament, and this initial either develops into a branch or a gametophore. The branch initial divides by transverse divisions to form a branch but a bud initial divides by oblique transverse walls to form an apical cell with three-cutting faces. It produces stem and leaves. From the base of the bud develop the rhizoids, and thus develops a young gametophore.

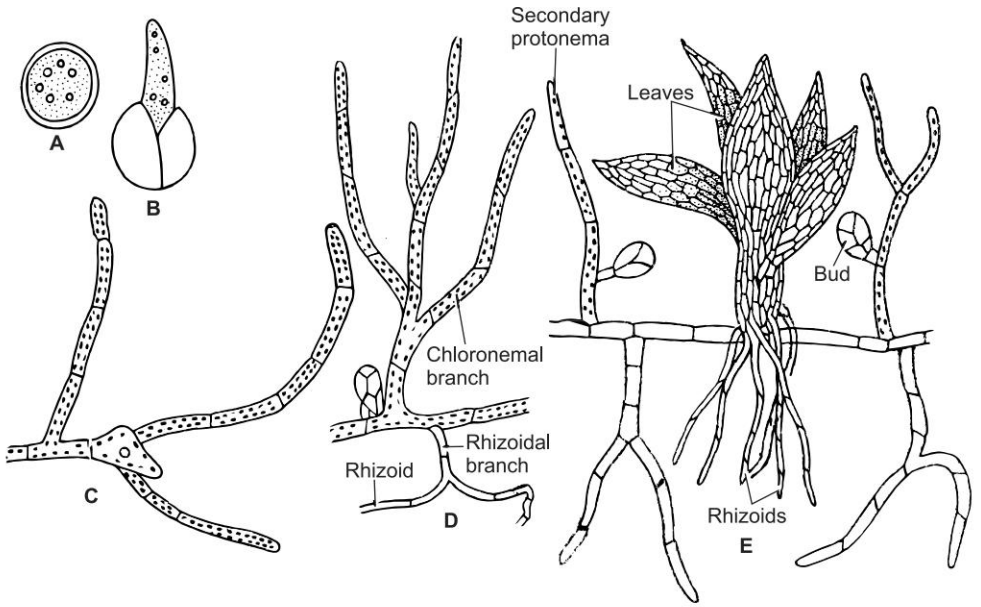


Fig. 10.25 A-E *Funaria,* showing germination of spore (A, B) and successive stages (C-E) of the formation of primary protonema, secondary protonema and young gametophore

BUXBAUMIA: A BOTANICAL NOTE 10.8

Systematic Position

Division—Bryophyta
Class—Bryopsida
Subclass—Bryidae
Cohort—Buxbaumiidae
Order—Buxbaumiales*
Genus—*Buxbaumia*

Buxbaumia is a microscopic moss, occurring on nutrient-poor soil, decaying logs and other similar organic substances. It bears very small gametophytes and a bug-like dorsiventrally flattened sporophyte. The sporophytes attain a length of about 2 cm, and only after their formation the microscopic gametophytes can be noticed easily. It is a moss, mainly of temperate regions of the northern hemisphere, and about 15 of its species have so far been reported. Udar et al. (1971) reported *Buxbaumia himalayensis* from India.

The perigonium of this microscopic moss is the most reduced gametophyte known in bryophytes (The leaves or bracts surrounding the sex organs of bryophytes, specially those around the antheridia, are termed perigonia). The male gametophyte (Fig. 10.26 A,B) comprises a single unistratose flap of tissue which surrounds a single, spherical, short-stalked antheridium. In the female gametophyte, the perichaetium is also very small, made up of 3–4 unistratose perichaetial leaves (Fig. 10.26C), which enclose one or two archegonia and a few, very small paraphyses.

*Buxbaumiales are commonly called **bug mosses**.

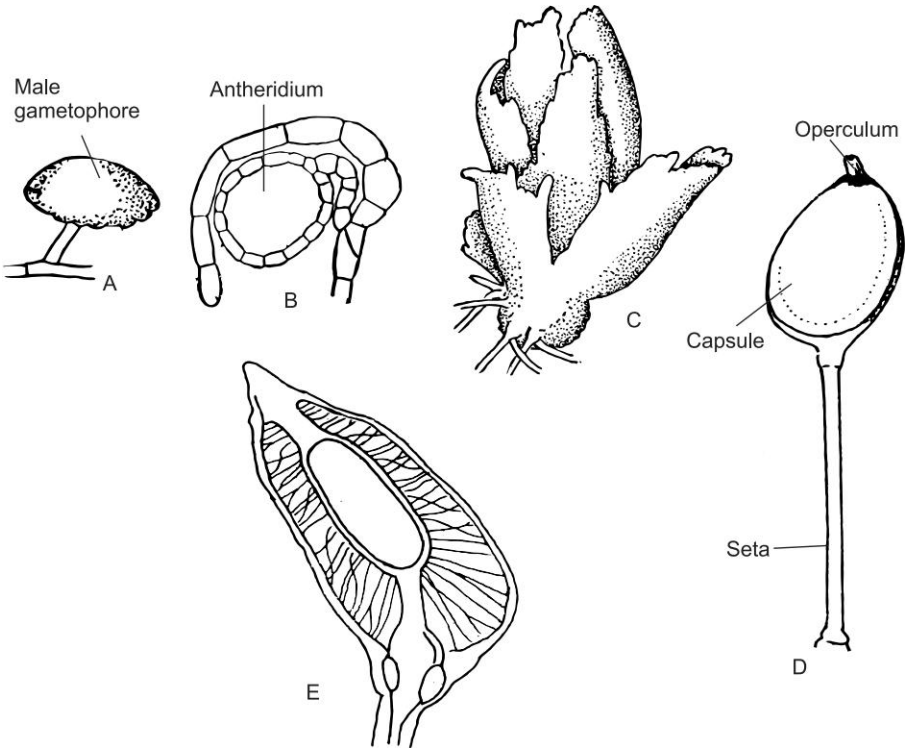


Fig. 10.26 A-E, *Buxbaumia aphyllla.* A, A male gametophyte; B, Vertical section of a male gametophore showing single antheridium; C, A female gametophyte of *B. aphylla;* D, Sporophyte; E, LS of capsule drawn diagrammatically

The **sporophyte** (Fig. 10.26D) comprises **foot**, **seta** and **capsule**. The **foot** is a bulbous body embedded within the upper part of the perichaetium. Ths sporophyte, when young, is a green body containing a small conical **calyptra** at the top of the seta. The **seta** is a papillose body containing red pigments in its outer thick-walled cells. A small conducting strand is present in the centre of the seta. It is as long as 1.5 cm. The **capsule** is oval in shape and contains a short conical operculum and a broad expanded apophysis (Fig. 10.26D). A characteristic feature of the capsule of *Buxbaumia* is that it is oriented obliquely at the apex of the seta in a way that one face appears a flattened structure. The capsule remains surrounded by a multistratose jacket. The stomata are present only in the region of apophysis. A well-developed cylinder of intercellular space is present in between the jacket and the sporogenous tissue. The mature capsule is a glossy, chestnut-coloured structure attaining a length of as much as 0.5 cm.

In *Buxbaumia*, the peristome consists of a most complex structure found among mosses. Each peristomial ring contains 32 teeth, and there may be as many as five concentric rings in the peristome. The teeth are shortest in the outermost ring and gradually become longer in each outer row. The outer teeth are termed **exostome**. Each tooth of the peristome is an individual and isolated body. In all species, there is present a central truncated core of fused peristomial teeth. It is termed as **endostome**.

The peristomial teeth in *Buxbaumia* are not hygroscopic, and due to this it is not confirmed whether or not they help in spore dispersal.

Germination of spore starts by producing a small germ tube made up of green cells representing **chloronema**. From the chloronema develops **caulonema**. A bud is produced on the caulonema, which can develop either into a female gametophyte or male gametophyte.

TETRAPHIS: A BOTANICAL NOTE  10.9

Systematic Position

Division—Bryophyta
Class—Bryopsida
Subclass—Bryidae
Cohort—Eubryiidae
Order—Tetraphidales
Family—Tetraphidaceae
Genus—*Tetraphis*

Tetraphis is one of the two genera of the family Tetraphidaceae. The another genus of the family is *Tetradontium*. *Tetraphis* is important because of some unique features of its sporophyte. Due to the presence of four teeth in its peristome, *Tetraphis* is known as **four-toothed moss**.

Tetraphis occurs commonly in coniferous forests distributed widely in the northern hemisphere. Plants are small-sized (less than 1 cm in length) and grow on peat banks, decomposing wood and other similar surroundings.

The gametophytic plant body remains attached to the substratum by means of uniseriate rhizoids. Leaves are very small on the lower side of the axis but large on its upper portion. They are ovate, costate and bright green in colour (Fig. 10.27A). At the top of the young gametophyte is present a cup-like cluster of short blunt leaves enclosing several gemmae (Fig. 10.27B). Each gemma is a multicellular, lens-shaped body with a long stalk (Fig. 10.27C). It serves as a major method of vegetative propagation in *Tetraphis*.

Anatomically, a single-layered epidermis surrounds a well-developed cortex, differentiated usually into an outer cortex of thick-walled cells and an inner cortex of broad thin-walled cells. A narrow strand of centrally-located, small-sized cells serves the purpose of conducting strands, which are known as **hydroids**.

Tetraphis is a monoecious moss. The sex organs (antheridia and archegonia) are present terminally on separate branches in groups of 8–10 or more, and remain surrounded by a cluster of elongate perichaetial or perigonial leaves, along with many filamentous paraphyses. After the formation of sex organs the growth of the plant stops.

The sporophyte is green and chlorophyllous when young. It consists of foot, seta and capsule. The **foot** is tapered, penetrates the apex of the gametophyte and serves the functions of anchorage and absorption. The **seta** is very long and contains a central conducting strand. It is quite rigid, and its rigidity is due to the presence of thick-walled **stereids** present outside the conducting strand. The jacket of the capsule in *Tetraphis* is derived from the amphithecium while the other remaining tissues of the capsule are derived from the endothecium. The columella is centrally-located in the capsule in the form

of a multicellular central cylinder. A sporogenous layer surrounds the columella. The apical portion of the jacket of the sporophyte develops into the operculum. The peristomial teeth are four in number (Fig. 10.27E), and each one is multicellular and wedge-shaped. The calyptra persists till the capsule is fully mature.

The jacket of the mature capsule contains elongate and thick-walled cells in its outermost layer, in which stomata are absent. At the time of dehiscence, the capsule dries. Due to dryness, the operculum is shed, the peristomial teeth are exposed and the spores are then dispersed. Twisting and untwisting of seta also help in spore dispersal. Resembling *Funaria*, the peristomial teeth in *Tetraphis* are also hygroscopic in nature. In moist conditions, they move inwards but they get apart in dry conditions. Dispersal of spores is checked in excessive moist weather.

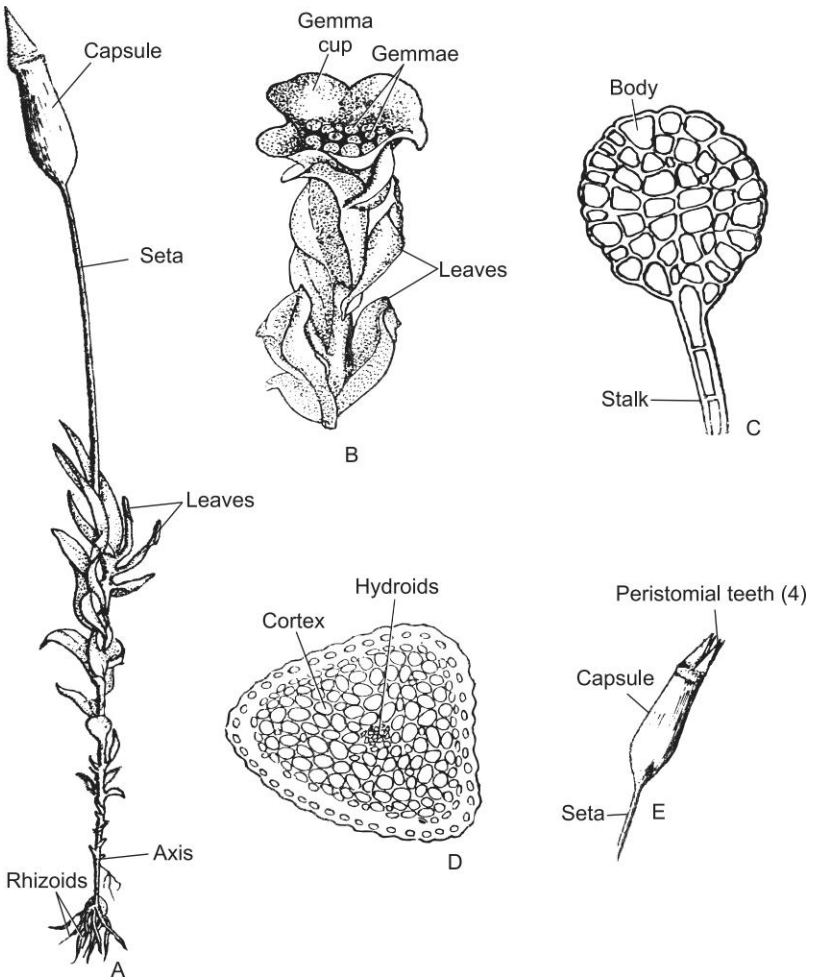


Fig. 10.27 *A-E* *Tetraphis pellucida.* A, An enlarged gametophyte of *T. pellucida* with a sporophyte; B, Upper part of a plant bearing gemma cup and gemmae; C, An enlarged gemma; D, T.S. stem of *T. pellucida;* E, A capsule with peristomial teeth

The spores are unicellular. They germinate by producing a well-branched and green filamentous protonema, called chloronema. It gives rise to perpendicular, green protonemal flaps, which are chlorophyllous, unistratose and strap-shaped bodies. Near the base of the protonemal flaps originate the shoot buds, from which **leafy gametophytes** are formed. *Tetraphis* resembles *Sphagnum* in possessing a flat, plate-like protonema.

ARCHIDIUM: A BOTANICAL NOTE 10.10

Archidium is the monotypic genus of the only family Archidiaceae of order Archidiales of Bryopsida. It is represented by more than 25 species, and due to the unusually large-sized spores, these mosses are commonly known as **large-spored mosses**.

Archidium is distributed widely in temperate regions of the globe. The gametophores (Fig. 10.28A) are very small-sized, attaining a height of about 2 mm to 2 cm. Plants usually occur on clay, sand or gravel and moist soils of somewhat disturbed habitats. The axis or stem is erect and remains attached to the substratum by many rhizoids. The leaves remain spirally arranged on the stem. The leaves are usually clasping and of varying shapes, but generally they are ovate to slightly lanceolate. All leaves are costate and the cells of multistratose costa are uniformly thick-walled. The plants are annual or perennial. Formation of innovations is quite common.

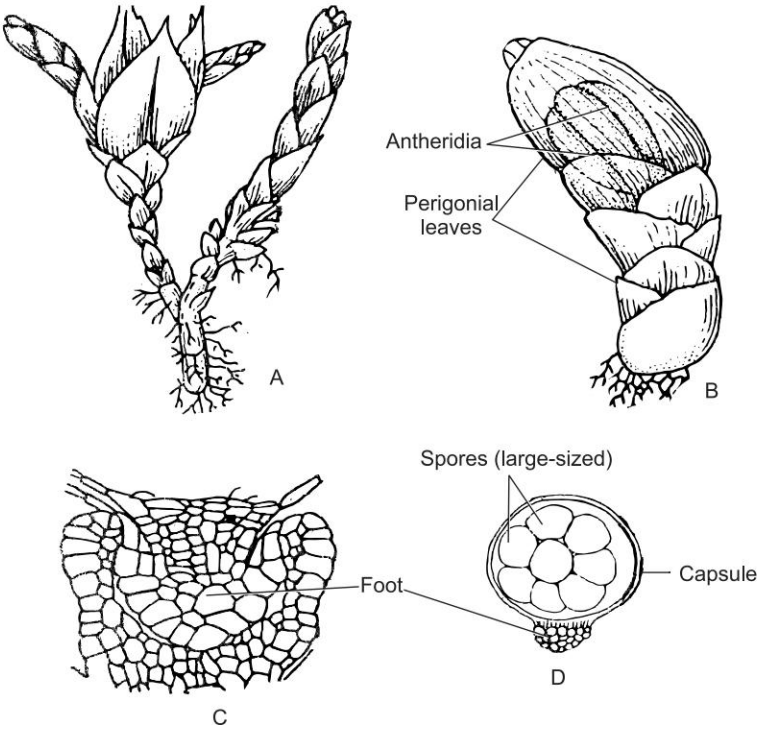


Fig. 10.28 *A-D, Archidium.* A, An enlarged gametophyte; B, A gametophyte bearing antheridia; C, Sporophyte with a massive foot and no seta; D, Sporophyte bearing large-sized spores

Anatomically, the axis comprises of mainly simple, large parenchymatous cells. The cells of the outer side are quite large and those of inner central regions are thin-walled and somewhat compact.

Archidium gametophytes are monoecious. The antheridia (Fig. 10.28B), produced at the apex of branches, remain enclosed by many perigonial leaves. Some filiform paraphyses are also present. The archegonia also develop at the tips of the branches and remain surrounded by few perichaetial leaves and ill-developed paraphyses.

The sporophyte of *Archidium* is quite unique among mosses. Columella is absent in the capsule, and the seta or stalk of the capsule is also absent or ill-developed. The differentiation of amphithecium is also unique in *Archidium*.

The zygote divides first by a transverse division into an epibasal and a hypobasal cell. The hypobasal cell divides several times to form a multicellular, massive **foot** (Fig. 10.28). The remaining parts of the sporophyte develop from the epibasal cell. Development of sporophyte is unique because in a developing embryo, the four cells of a quadrant are unequal in size. The periclinal divisions form the amphithecium and endothecium. A dome-shaped intercellular space develops between the amphithecium and endothecium. The sporogenous tissue is endothecial in origin. The number of spores in a capsule varies in different species. Sometimes, they are only four in a capsule but in many species their number reaches up to 60 in a capsule, and in *A. winteri*, up to 176 spores per capsule have been reported. The jacket surrounding the capsule is unistratose.

Unusually large-sized spores are present in the capsule of *Archidium*. They attain a diameter of 50 to 120 microns, and can be seen even with an unaided eye. The spore germination is also unique. A germinating spore forms a germ tube, developing into a protonema. A quadrant of unequal-sized cells are seen in this protonema. Of these, one starts forming an apical cell, which divides and redivides to form a new gametophyte.

POGONATUM: A BOTANICAL NOTE 10.11

Systematic Position (According to Holmes, 1986)

Division—Bryophyta
Class—Bryopsida
Subclass—Bryidae
Cohort—Polytrichiidae
Order—Polytrichales
Family—Polytrichaceae
Genus—*Pogonatum*

Plant body of *Pogonatum* is gametophytic, and each gametophore is differentiated into rhizoids, axis or stem and leaves (Fig. 10.29A-B). The lowermost rhizomatous part of the stem is stout, stiff and bears rhizoids. The rhizoids are thick-walled, multicellular and bear oblique septa. The axis is erect, aerial, well-developed, and bears many leaves. Leaves are well-developed and pale-coloured. Each leaf is sessile with a sheathing broad base. Its upper part gradually tapers towards the apex and bears a serrated margin. The leaf has a thick midrib. Parallel, longitudinal, plate-like structures, called lamellae (Fig. 10.29C) are present on the upper surface of the midrib of the leaves.

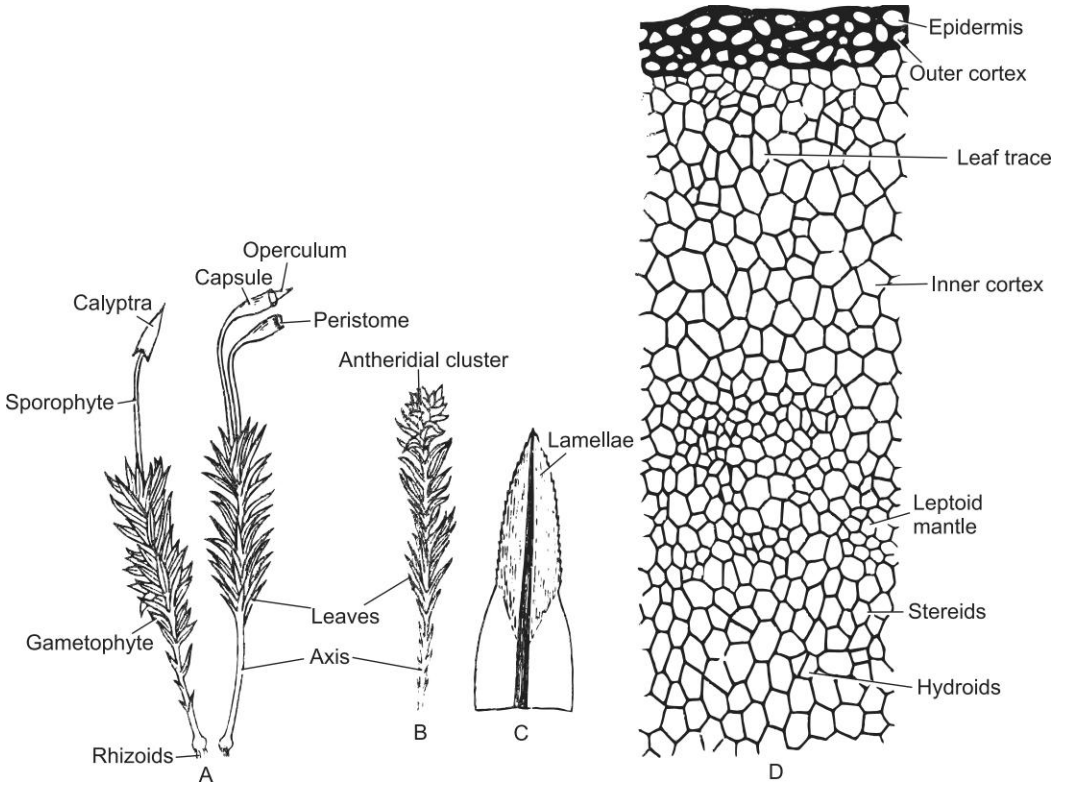


Fig. 10.29 A-D. *Pogonatum.* External features. A, Two female plants; B, A male plant; C, Upper part of leaf showing lamellae; D, A part cellular of TS axis

Anatomically, the axis (Fig. 10.29D) contains epidermis, cortex, leptoid mantle, stereids and hydroids. The epidermis is single-layered and consists of slightly thick-walled cells. A wide zone of cortex is present below the epidermis. The cortex is differentiated into deeply coloured and thick-walled outer cortex, and a very wide region of thin-walled and parenchymatous inner cortex. A few thick-walled leaf traces are also present in the thin-walled inner cortex. A well-developed zone of elongated cells having no starch represent the leptoid mantle inside the inner cortex. The cells of the leptoid mantle resemble sieve tubes and also contain sieve plate-like structures. These leptoid cells resemble the leptoid mantle of the axis. A hydrom cylinder is present in the centre of the axis. It is made up of two types of cells:(i) thick-walled, elongated cells with living contents, called **stereids**, and (ii) thick-walled elongated cells without living contents, called **hydroids**. The hydroids help in conduction of water.

The **male plant** (Fig. 10.29B) bears many antheridia in a cluster in its apical part. Antheridia remain surrounded by specialised leaves called perichaetial leaves. All these together constitute a flower-like antheridial head (Fig. 10.30A). Many long and multicellular, hair-like paraphyses are also present in the antheridial head along with a cluster of antheridia (Fig. 10.30B). Each antheridium is a shortly-stalked, club-shaped structure with multicellular antheridial stalk. A single-layered jacket surrounds each antheridium.

The **female plant** (Fig. 10.29 A,B) bears a cluster of archegonia at its tip (Fig. 10.30C). Along with multicellular, long, hair-like paraphyses and several perichaetial leaves, the group of archegonia constitutes the female head. Each archegonium is attached at the apex of the axis by a short multicellular stalk. It contains a neck and venter. The neck is made up of 6 vertical rows of cells, 2 cover cells and 6–12 or more neck canal cells. The venter consists of a venter canal cell and an egg.

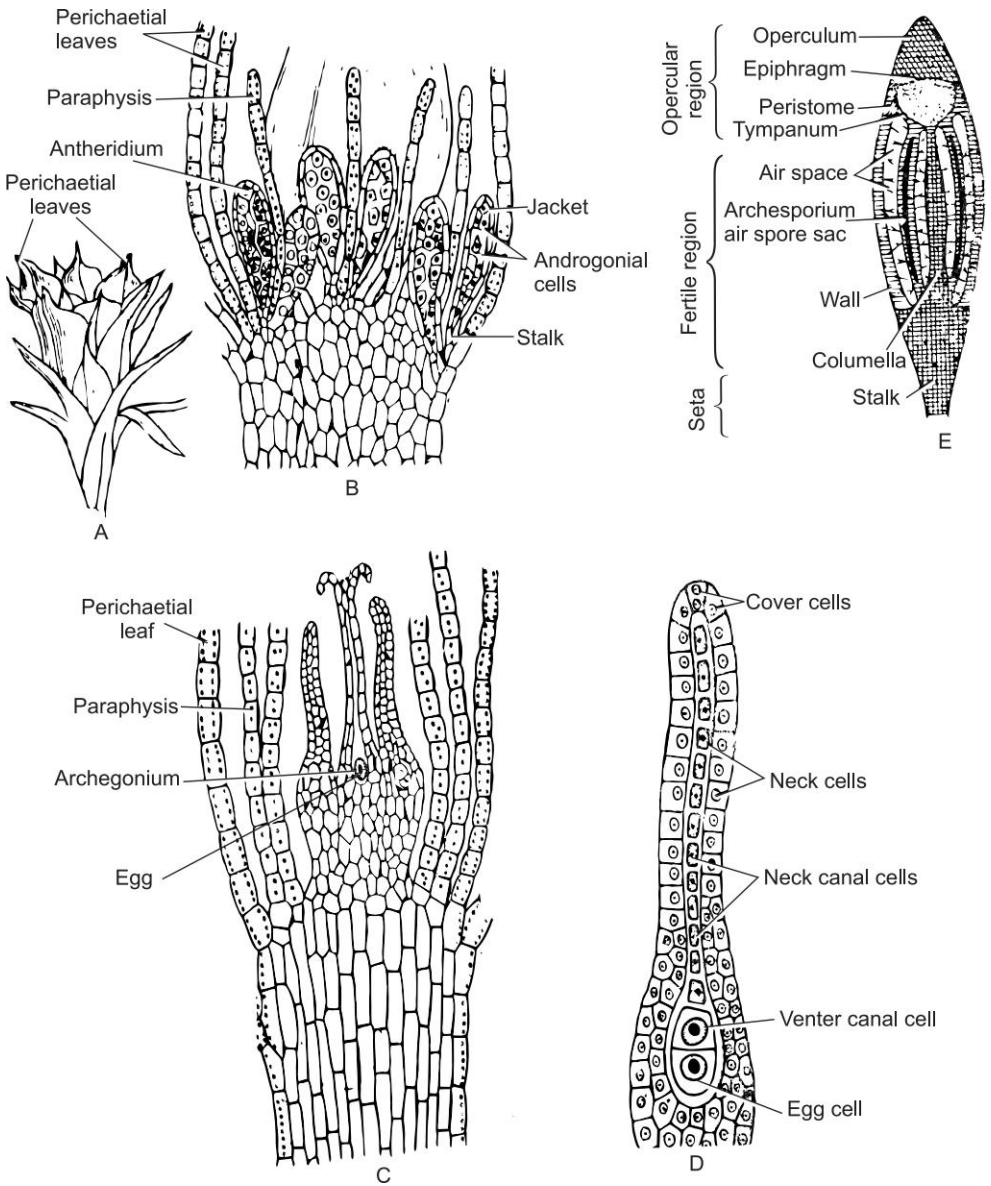


Fig. 10.30 A-E, *Pogonatum.* A, A detached antheridial head; B, LS antheridial head; C, LS of a female head; D, An archegonium; E, LS of sporophyte (diagrammatic)

The **sporophyte**, when mature, reveals that it is divisible into foot, seta and a calyptra-covered capsule (Figs. 10.29 A, 10-30E). The **foot** is bulbous and **seta** is very long. The **capsule** has a long well-developed lower stalk. It is divisible into a lower stalk, middle fertile region and the uppermost operculum (Fig. 10.30E). It lacks apophysis. The stalk is parenchymatous and remains surrounded by green, chlorophyll-filled cells. It appears to be merging with the columella of the capsule. The **fertile region of the capsule** shows the following structures:

1. A single-layered epidermis surrounds a many-layered, green region of chlorophyllous cells followed by a region of air spaces.
2. A region of air spaces surrounds the spore-sac cylinder.
3. The spore-sac cylinder contains archesporial tissue and remains surrounded by a bilayered spore-sac wall.
4. Archesporial tissue contains many spores at maturity.
5. Yet another air-space region is present inner to the inner spore wall.
6. The inner air space remains connected with a centrally-located parenchymatous columella.

Columella of the capsule passes into the region of operculum and swells in the form of the roof of capsule called **tympanum** or **epiphragm**. The **operculum** is a beak-shaped or conical structure above the **epiphragm**. It remains connected to the capsule by a ring-like diaphragm. A ring of 32 short **peristomial teeth** is present above the diaphragm. The peristomial teeth are hygroscopic in nature, and help in dispersal of spores.

POLYTRICHUM 10.12

10.12.1 Systematic Position (According to Holmes, 1986)

Division—Bryophyta
Class—Bryopsida
Subclass—Bryidae
Cohort—Polytrichiidae
Order—Polytrichales
Family—Polytrichaceae
Genus—*Polytrichum*

10.12.2 Distribution and Habitat

Represented by about 100 species, *Polytrichum* is a cosmopolitan genus, but occurs mainly in cool temperate and tropical regions of the world. It grows commonly along the margins of ponds, lakes, etc. as well as on sandy grounds, dry woods, damp soil, marshy surroundings, etc. *Polytrichum alpinum*, *P. commune*, *P. densifolium* and *P. juniperinum* are some of the common Indian species. *P. commune* is cosmopolitan in distribution.

10.12.3 External Features of Gametophyte

The gametophore of *Polytrichum* is foliose, moss-like, and differentiated into **rhizoids**, underground **rhizome**, an erect aerial **stem** and **leaves** (Fig. 10.31A). The plants attain a height of 20-35 cm or even more. The **rhizoids** are numerous, long, thick-walled, multicellular, and with oblique septa.

Innumerable rhizoids coil around one another to form a twisted or tufted strand and provide mechanical support to the plant. Water also passes upwards through these tufted strands of rhizoids by external capillarity. The **rhizome** is the underground rhizoid-bearing part of the stem. The aerial **stem** is erect, unbranched or sometimes branched, leaf-bearing part of the plant. The **leaves** are usually spirally arranged on the stem, and are green, brown or even colourless. On the upper part of the rhizome and on the middle transitional region of the stem, the leaves are arranged in three vertical rows, showing 1/3 type of phyllotaxy, while on the erect leafy shoot the leaves are arranged in a complicated spiral, showing 3/8 type of phyllotaxy. Each leaf (Fig. 10.31B) contains a membranous colourless sheathing base and narrows gradually towards the tip. It possesses a midrib and a coarsely toothed margin. The limb of each leaf is lanceolate to linear lanceolate. On the upper or adaxial surface of the midrib are present close-set rows of one-celled thick longitudinal plates of green tissue called **lamellae**. The midrib appears firm and dark green because of these lamellae.

10.12.4 Anatomy of Rhizome

It is circular or triangular in outline with rounded corners (Fig. 10.32A). The outermost layer is the epidermis or **piliferous layer**, some cells of which give rise to rhizoids. Below the epidermis are two to four layers of parenchymatous **cortex**. Three sclerenchymatous or parenchymatous **hypodermal strands** are present in the three corners of the cortex, dividing the latter into three parts. These hypodermal strands form the **radial strands** in the centre. The continuity of the **endodermis** is broken by these radial strands. The **pericycle** is 2–3 layered and discontinuous because of the radial strands. The **central cylinder** is a trilobed structure with three furrows, and consists of compact mass of thick-walled tissues. Elongated cells with very thick walls form the central mass of this cylinder. These cells are living with oblique end walls and a small amount of starch, and are called **stereids**. The stereids are collectively called **stereom**.

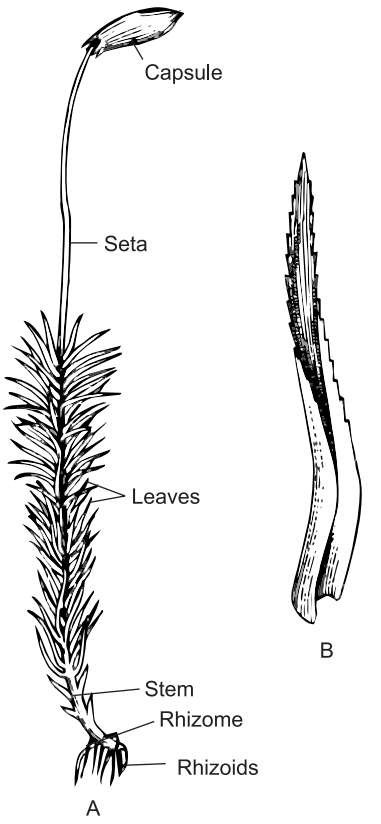


Fig. 10.31 A, A female plant of *Polytrichum commune* with a terminal sporophyte; B, An enlarged leaf

Along with the stereids are present certain other elements of the same diameter but of different nature. They often fuse together in the form of bands of two or three cells, separated from each other by delicate cellulose walls, and function as water-conducting tissue. These are individually called **hydroids** and collectively called **hydrom**. In the furrows of the interrupted pericycle are present 6 to 8 polygonal cells of proteinaceous nature. These cells are individually called **leptoids** and collectively called **leptom**. In

between the leptom and hydrom are present some starchy parenchymatous cells called **amylom**. The terms, such as stereom, hydrom, leptom and amylom, etc. have been proposed by Tansley and Chick (1901).

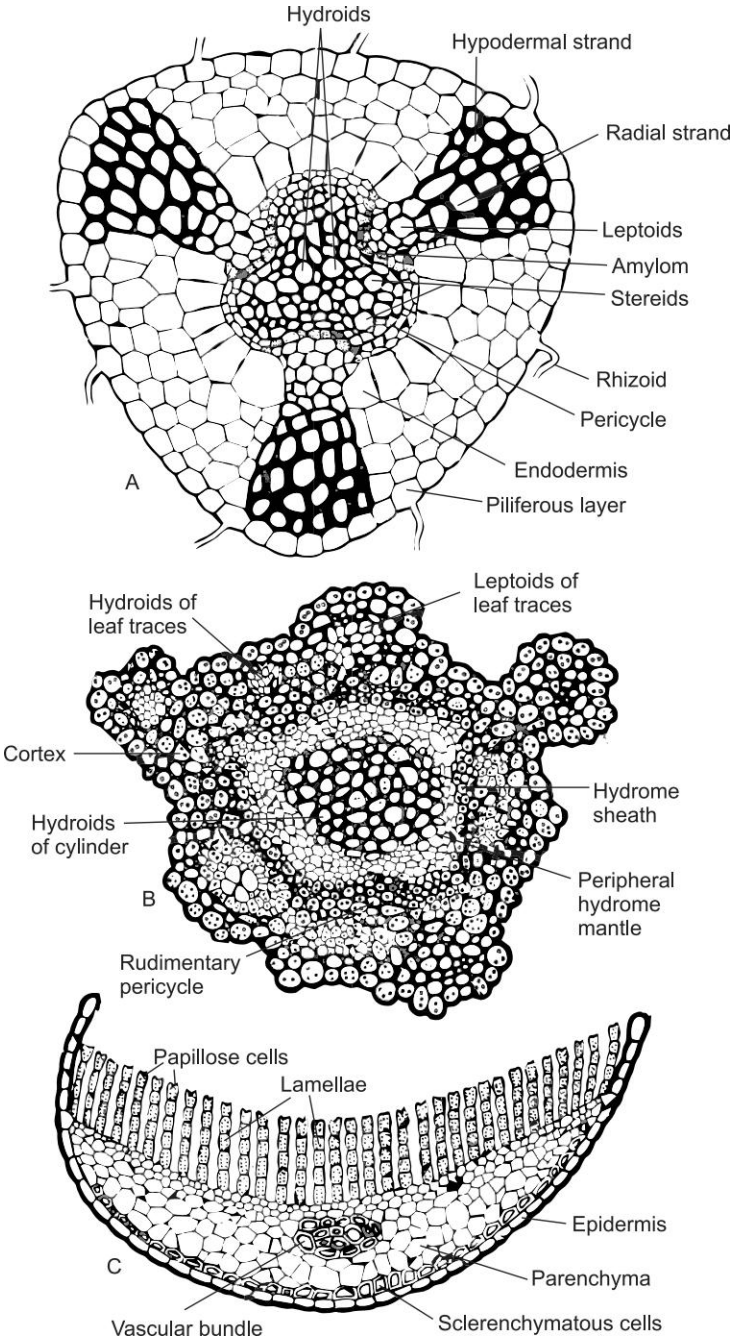


Fig. 10.32 Anatomy of *Polytrichum commune*. A, TS rhizome; B, TS aerial leafy stem; C, TS leaf

10.12.5 Anatomy of Aerial Leafy Stem

The aerial leafy stem is irregular in outline because of the attachment of leaves (Fig. 10.32 B). The epidermis is single-layered but not sharply defined. The cortex, present just inner to the epidermis, is irregular, and consists of compact, elongated and prosenchymatous cells, thus representing the outer cortex. The inner cortex cells are parenchymatous. Leaf traces are present at different locations of the cortex. The pericycle is rudimentary and discontinuous. Inner to the pericycle is the region of the **leptom mantle**, consisting of cells like that of "sieve tubes", and thus representing a region like that of the phloem of higher plants. **Amylom layer** is situated inner to the leptom mantle. Its cells are filled with starch. Inner to the amylom layer is the **hydrom mantle**, the cells of which are thin-walled. **Hydrom cylinder**, a region of thick-walled cells, is present in the centre of the stem. It is the water-conducting tissue of the aerial leafy stem.

10.12.6 Anatomy of Leaf

The leaf is a boat-shaped structure in TS (Fig. 10.32 C). A distinct epidermal layer is present on the lower or dorsal surface of the leaf. This layer is cuticularised. One or two layers of sclerenchymatous cells are present just inner to the epidermis. The midrib region is centrally-located and many-celled thick. The number of cells decreases towards both the sides, forming the wings. A major part of the leaf is filled by several large parenchymatous cells. Many vertical filaments (lamellae) of chlorophyll-containing cells are present on the ventral or upper surface of the leaf. Each filament is 5–8 or more cells in height and contains a papillose or bifurcated terminal cell. Lamellae are the main photosynthetic regions of the leaf.

10.12.7 Sexual Reproduction

Polytrichum plants are usually dioecious, i.e. male and female sex organs develop at the apex of separate plants.

10.12.8 Antheridial Head

The antheridia are present at the apex of the male gametophore along with several perichaetial leaves and form a clustrous structure. This clustrous structure looks like an open cup or a flower. Some of these perichaetial leaves form hair-like structures called **paraphyses** (Fig. 10.33 A-C). The tips of some of the paraphyses become a mass of one-celled thick multicellular body. The apical cell of the shoot is not utilised in the formation of an antheridium. Because of this, the growth of the antheridial head is not stopped by the development of antheridia. The **mature antheridium** (Fig. 10.33 C) is a short-stalked, club-shaped body consisting of several androgonial cells, surrounded by a single-layered sterile jacket.

10.12.9 Archegonial Head

Terminal clusters of archegonia (Fig. 10.34A-C) develop at the apex of the female gametophore and form the archegonial head. The archegonia are also surrounded by the perichaetial leaves. Along with the archegonia are also present many hair-like, multicellular structures. Unlike the antheridial head, the apical cell of the female gametophore develops into the archegonial initial, and due to this, the growth

of the archegonial head is stopped after the development of archegonia. Each **mature archegonium** is a stalked structure (Fig. 25-4C) with a long neck and globular venter. The neck contains several neck canal cells and remains surrounded by six vertical rows of cells. The venter is multicellular and contains a venter canal cell and an egg.

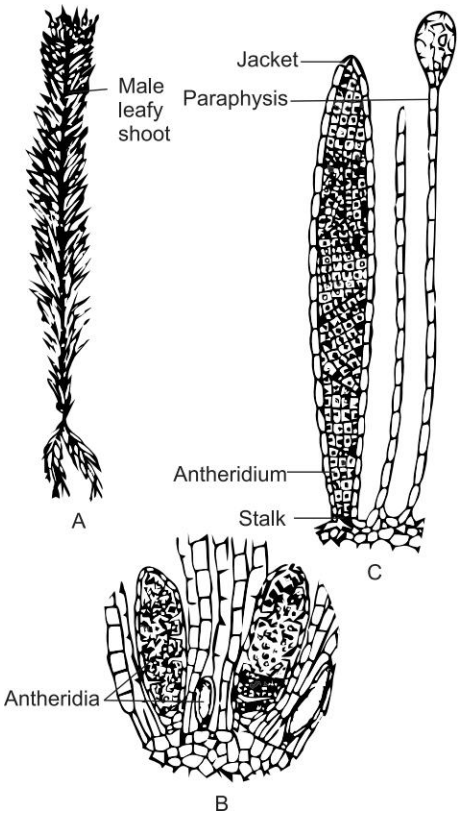


Fig. 10.33A-C Details of the antheridial head of *Polytrichum commune*. A, A male gametophore; B, A part of antheridial head; C, An antheridium along with paraphyses

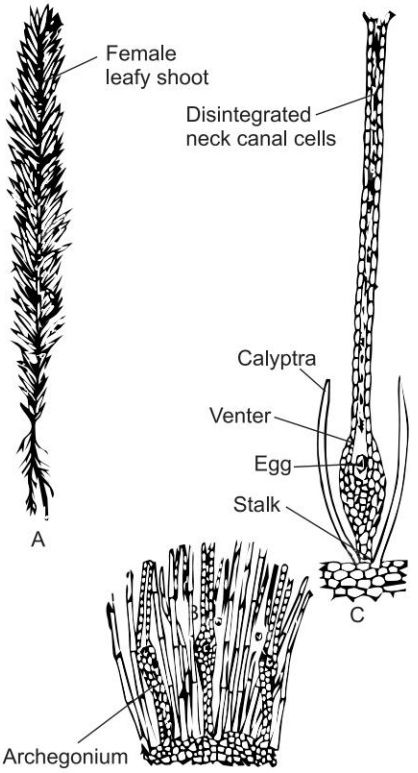


Fig. 10.34A-C Details of the archegonial head of *Polytrichum*. A, A female gametophore; B, A part of archegonial head; C, An archegnoium

During the fertilization process, the neck canal cells and venter canal cells disintegrate and form a mucilaginous liquid, which provides the way for the entry and union of antherozoid with the egg.

10.12.10 Sporophyte

It can be differentiated into foot, seta and capsule (Fig. 10.35A). The **foot** is bulbous, remains buried in between the leaves at the apex of the female gametophore, and consists of thin-walled parenchymatous cells. The **seta** is a very long and slender part of the sporogonium which pushes the capsule towards the upper side, and its function is elongation.

Anatomically, the **seta** consists of an outermost superficial layer of thick-walled cells, followed by one or a few layers of sclerenchymatous cells, which merge internally into parenchymatous, green and thin-walled cells, having some intercellular spaces. Some very simple centrally-located cells form the central strand of the seta.

The elongating seta enlarges at the base of the capsule in the form of a region called **apophysis** (Fig. 10.35B). In between the apophysis and the sporogenous region **(theca)** is present a groove. The stomata are present in the epidermis of the apophysis, specially in the region of the groove. Inner to the epidermis are present some chlorophyll-containing cells in the region of apophysis.

In the **theca region**, the capsule wall consists of an outermost layer of epidermis, followed by a few layers of chlorophyll-containing cells. Several air spaces traversed by chlorophyll-containing filaments are present on the outer (outer lacuna) as well as the inner (inner lacuna) sides of the spore sac. The spore sac, thus, separates the outer and inner lacunae. The inner air spaces thus remain in touch with the centrally-located columella. When young, the archesporium is only unilayered but, in the mature sporogonia, it is 4- to 6-layered. The archesporium or sporogenous cells develop into diploid spore mother cells. Each spore mother cell divides meiotically into four haploid spores.

The **operculum** is a lid-like structure present at the top of the capsule (Fig.10.35 B,C). It contains a conical beak or rostrum. Instead of annulus, a rim or diaphragm (Fig. 10.35C) is present. The epiphragm, present at the base of the operculum, is a transverse band of thin-walled and compressed cells with no intercellular spaces. The epiphragm actually closes the upper part of the capsule. The peristome is present in the form of thick, fibrous, crescent-shaped cells near the epiphragm. In the mature sporogonium, the peristome is represented by 32 or 64 peristomial teeth connecting the capsule wall and the epiphragm. The peristomial teeth help in the dispersal of spores.

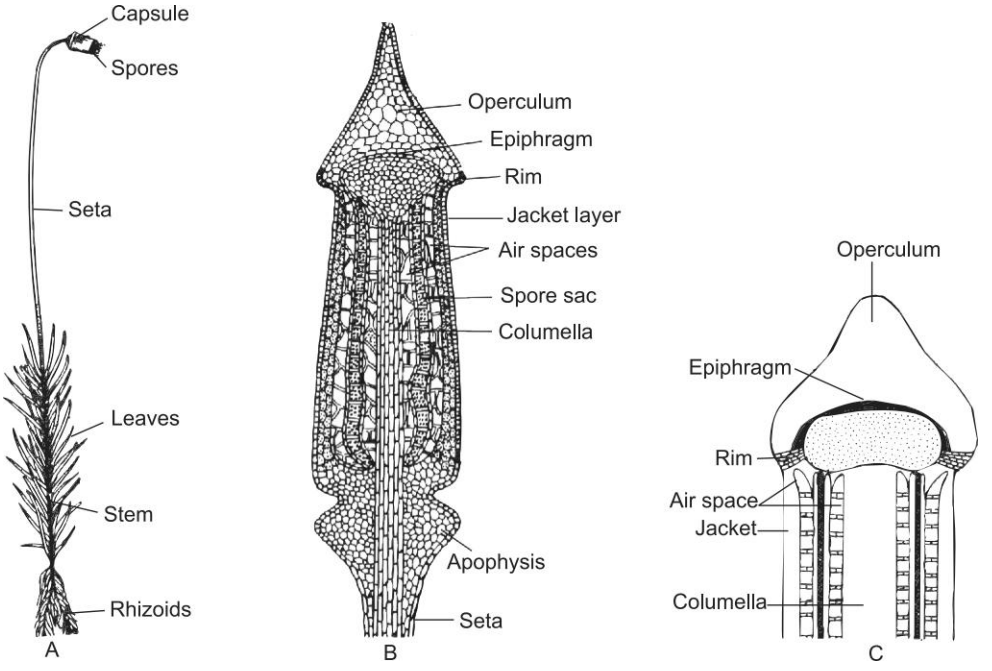


Fig. 10.35 A-C A, A female plant of *Polytrichum* commune bearing a mature sporogonium; B, LS of the capsule of same; C, LS upper part of the capsule of *P. commune* showing details of theca and operculum

10.12.11 Germination of Spore and Formation of Young Gametophyte

The spores are very large in number, but very small in size (0.005 to 0.01 mm in diameter), and remain viable for a long time. According to Wigglesworth (1947), the yellow-coloured spores, at the time of germination, become green due to the formation of chloroplast in *P. commune*. The endospore ruptures the outer exospore and comes out in the form of one or more germ tubes. Repeated transverse divisions in the germ tube result in a filamentous protonema. Some of these filaments penetrate into the substratum and develop oblique walls, while other filaments grow towards upper sides. Some buds develop from these upright filaments, which develop into young gametophores of *Polytrichum*.

TEST YOUR UNDERSTANDING

1. What do you mean by the following terms?
   (a) Bog (b) Peat
2. _____ are commonly known as bog mosses or peat mosses.
3. The most common bryophyte of bogs is_____.
4. Mention at least four points of differences between bog mosses and other mosses.
5. Sphagnales comprises of how many genera? Name one of them.
6. Is *Sphagnum* an annual moss or a perennial moss?
7. Why is *Sphagnum* also known as peat moss?
8. "*Sphagnum* is of great commercial importance". Comment in about 100 words.
9. With the help of suitable illustrations, describe the external features of mature gametophore of *Sphagnum*.
10. Define the terms "innovation" in reference to *Sphagnum*.
11. Describe anatomy of leaf and stem of *Sphagnum* with the help of suitable illustrations.
12. Explain following terms with reference to the anatomy of axis of *Sphagnum*:
    (a) Hadrom, (b) Retort cells.
13. How does *Sphagnum* reproduce vegetatively?
14. Describe in detail the sexual reproduction in *Sphagnum*.
15. What do you mean by "primary archegonium" and "secondary archegonium" in *Sphagnum*?
16. Give an illustrated account of development of sporophyte in *Sphagnum*.
17. In *Sphagnum*, the archesporium is _____ in origin.
18. Explain the following terms with reference to the mature sporophyte of *Sphagnum*:
    (a) Pseudopodium, (b) Vaginula
19. Explain explosive mechanism of dehiscence of capsule in *Sphagnum*.
20. Describe affinities of *Sphagnum*.
21. Mention at least six unique characteristics of *Sphagnum.*
22. The common name "lantern mosses" is given to which category of mosses?
23. Write any five characteristic features of Andreaeales.
24. Describe the life history of *Andreaea* in about 500 words giving suitable illustrations.
25. The name "granite moss" is given to which bryophyte?
26. Are structures like seta, operculum and peristome present or absent in the mature sporophyte of *Andreaea*?
27. In mature sporophyte of *Andreaea*, the function of seta is taken by a body of gametophytic tissue known as _____

28. Write at least seven general characteristics of Bryales.
29. The name "true mosses" is given to members of _____.
30. Give a brief illustrated account of the life history of *Funaria* in about 1000 words.
31. What is the most common species of *Funaria*, also available widely in India?
32. In "true mosses" (Bryales), is pseudopodium present?
33. Describe some methods of vegetative reproduction in *Funaria*.
34. How can you differentiate between a gemma and a bulbil in *Funaria*?
35. Explain development of sporophyte in *Funaria* with the help of suitable diagrams.
36. Describe the fate of amphithecium and endothecium in the development of capsule of *Funaria*.
37. Make well-labelled diagrams of the following parts of *Funaria*:
    (a) LS capsule, (b) TS seta, (c) Peristomial teeth.
38. Write a botanical note on *Buxbaumia* in about 250 words.
39. Regarding size of *Buxbaumia*, is it a macroscopic or microscopic moss?
40. How many teeth does *Tetraphis* contain in its peristome?
41. What is the common name of *Tetraphis*?
42. Write a botanical note on *Archidium* in about 200 words only.
43. The name "large-spored-moss" is given to _____.
44. Describe external features and sporophyte of *Pogonatum* in about 300 words.
45. What is *Polytrichum*? Describe its life history in about 500 words. Substantiate your answer with suitable diagrams.
46. In terms of rhizome anatomy of *Polytrichum*, explain the following terms:
    (a) Hydroids, (b) Leptoids, (c) Hydrom, (d) Amylom
47. Describe mature sporophyte of *Polytrichum* with the help of suitable illustrations.

11

Gametophyte of Bryophytes

WHAT IS A GAMETOPHYTE? 11.1

A **gametophyte** is technically the haploid generation in an alternation of generations. The gametophyte is the generation producing gametes. In bryophytes, the gametophyte is the main vegetative stage. In angiosperms, however, the gametophyte is very small, contained in the ovule and pollen grain.

On the other hand, **sporophyte** is the diploid generation in an alternation of generations, and it produces the spores. In bryophytes, the sporophyte grows directly from the archegonium of the gametophyte, and it thus depends on the gametophyte for its nutrition.

EXTERNAL FORM OF MATURE GAMETOPHYTE 11.2

The mature gametophyte of bryophytes shows a wide range in its structure and size. There are bryophytes in which the whole plant is very small and microscopic, i.e. *Zoopsis argentea*, while some bryophytes are very large and attain a size as much as 50 cm in height (e.g. *Dawsonia superba*) and 50 to 70 cm

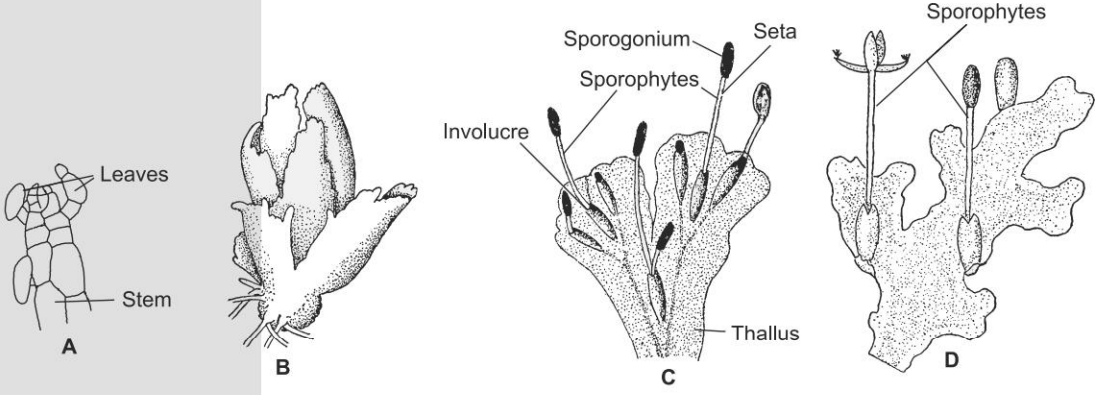


Fig. 11.1 A-D Gametophytes of some bryophytes. A, *Zoopsis argentes;* B, *Buxbaumia aphylla;* C, *Monoclea forsteri;* D, *Riccardia pinguis*

in length (e.g. *Fontinalis antipyretica*). *Buxbaumia aphylla* (Fig. 11.1 B) attains a length of only a few millimetres while *Carrpos sphaerocarpos* is spheroidal in shape and attains a diameter of 0.5 to 2 mm. *Monoclea foresteri* attains a width of 5 cm. and a length of as much as 20 cm (Fig. 11.1 C).

Structurally, the gametophytic plant body of bryophytes may be simple thallus-like, i.e. **thalloid**, or may bear leafy shoots, i.e. **foliose**.

THALLOID FORMS OF GAMETOPHYTE 11.3

A more or less undifferentiated plant body, without distinct roots, stem and leaves, is known as **thallus**. In thalloid liverworts, the gametophyte is a flat, more or less undifferentiated thallus. Thallus is found in members of Marchantiales, many anacrogynous Jungermanniales and Anthocerotopsida. It contains a distinct midrib, as in *Riccia*, *Marchantia* and *Dendroceros*. Midrib is, however, absent in many thalloid forms, such as *Monoclea* (Fig. 11.1C) and *Riccardia pinguis* (Fig. 11.1D). Thalloid bryophytes are usually dichotomously branched, e.g. *Riccia* and *Marchantia*. Closely developing dichotomous branches form rosette-shaped structures, as in *Riccia*.

Gametophytes of some bryophytes are neither typically thalloid nor typically leafy forms. They appear to be intermediate forms between thalloid and leafy forms, as in members of Metzgerineae (acrogynous Jungermanniales), e.g. *Treubia* and *Fossombronia*. In *Treubia insignis*, the plant body has a thick, fleshy prostrate axis bearing two rows of well-developed fleshy leaves. In *Fossombronia*, the plant body is also leafy with two rows of leaflike lobes borne on an axis (Fig. 11.2).

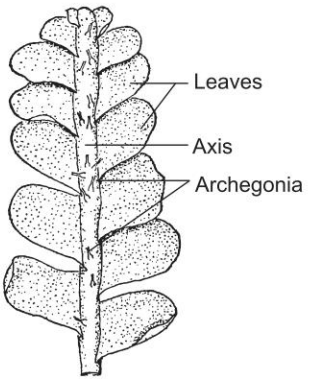


Fig. 11.2 Female gametophyte of *Fossombronia intestinealis* bearing archegonia

LEAFY FORMS OF GAMETOPHYTE 11.4

11.4.1 Leafy Forms of Hepaticopsida

1. Sphaerocarpales The gametophytic plant body of *Sphaerocarpos* and *Geothallus* consists of an axis containing two rows of alternately inserted lobe-like "leaves". In *Riella americana*, the gametophyte consists of a thick stem-like axis containing two rows of leaflike scales and a well-developed undulate wing or two wings (Fig. 11.3A).

2. Calobryales In *Calobryum blumei* and *Haplomitrium*, the gametophytic plant body consists of an underground rhizomatous region devoid of leaves and upright leafy shoots bearing three rows of flat and unlobed leaves (Fig. 11.3B).

3. Takakiales In *Takakia*, the gametophytic plant body is made up of branched underground rhizomatous portion whch lacks rhizoids, and erect axis with phyllids (Fig. 11.3C) or isophyllous leafy shoots. Phyllids do not show any definite arrangement.

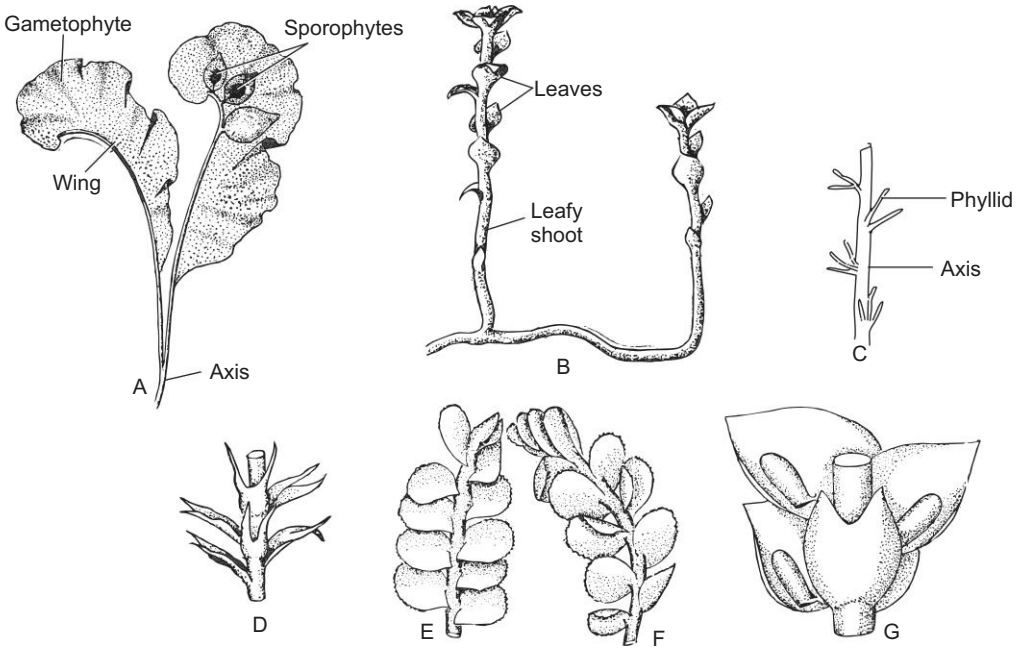


Fig. 11.3 A-G, Gametophytes of some leafy forms of Hepaticopsida. A, *Riella americana;* B, *Calobryum blumei;* C, *Takakia* showing portion of axis with phyllids; D, Ventral view of *Herbertia adunca;* E-F, Dorsal and ventral view of *Plagiochila asplenioides;* G, Ventral view of *Frullania armiliana* showing water sacs on lateral leaves

4. Jungermanniales In acrogynous Jungermanniales, the plant body usually consists of a prostrate to procumbent leafy axis bearing distichous leaves. In *Herbertia* (Fig. 11.3D) and a few more genera, the leafy shoot shows radial symmetry. It bears an erect axis bearing three rows of radially arranged leaves. Usually, two rows of these leaves are laterally placed and a third row of smaller leaves (amphigastria) are ventrally placed. In *Plagiochila asplenioides* (Fig. 11.3 E), the leaves are arranged only in two rows. The smaller ventrally-placed leaves (amphigastria) are absent.

As far as the form or shape of the leaves in acrogynous Jungermanniales is concerned, they may be entire (*Porella*), bilobed (*Herbertia*), trilobed (*Bazzania*), four-lobed (*Lepidozia*) or even highly divided. In *Frullania armiliana* (Fig. 11.3 G), lateral leaves contain water sacs.

Two main types of branching in acrogynous Jungermanniales are terminal or end branching (as in *Frullania*, *Porella*, *Microlepidozia* and *Radula*) and intercalary branching (as in *Herbertia*, *Plagiochila*, *Scapania* and *Cephaloziella*).

11.4.2 Leafy Forms of Bryopsida

Gametophytic plant body of mosses is usually differentiated into rhizoids, stem and leaves. The gametophores of different genera have different sizes, varying from very small and microscopic (e.g. *Ephemerum*) to very large reaching up to 50 to 70 cm (e.g. *Dawsonia*).

The axis may be radial (e.g. *Funaria*) to dorsivental (e.g. *Rhocopilum africans*, *Hylocomium splendens*).

The leaves are usually sessile and subulate to orbicular in outline in different species of mosses. They are never lobed. When young, the leaves are spirally arranged in three vertical rows on the axis. Each row of leaves corresponds to three cutting faces of the apical cell. In a few mosses, the leaves are arranged only in two rows on opposite side of the axis (e.g. *Distichium*, *Fissidens*). The mature leaves are spirally arranged with a divergence of 1/3 (*Fontinalis antipyretica*), 2/5 (*Sphagnum*), 3/8 (*Funaria*), 5/13 (*Polytrichum*), 4/11 (*Dicranum scoparium*) and 8/21 (*Leskea*).

Bryopsida members never show dichotomous type of branching. The branching is usually lateral, but not axillary. On the basis of the two major types of branching, the mosses may be divided into two groups, viz. acrocarpous and pleurocarpous. **Acrocarpous mosses** have an upright stem, with the reproductive organs at the apex. On the other hand, **pleurocarpous mosses** have a stem with many branches, spreading across the ground. The reproductive organs in pleurocarpous mosses are borne on short side branches. A dendroid habit is resulted due to brancing in some mosses, e.g. *Climacium dendroides*.

APPENDAGES FOUND ON THE GAMETOPHYTE 11.5

Rhizoids, scales, mucilage papillae (or hairs) and paraphyllia are some of the appendages found on the gametophyte of bryophytes.

11.5.1 Rhizoids

A **rhizoid** is a thread-like cell which grows from the lower surface or base of a bryophyte. Bryophytes lack roots. The rhizoids in bryophytes have the function of roots. Their combined functions include anchorage and absorption. In a majority of Hepaticopsida and Anthocerotopsida, the rhizoids are unicellular. But in Bryopsida or mosses, the rhizoids are multicellular, well-branched and contain oblique septa. The unicellular rhizoids are of two types, smooth-walled and tuberculate, as in *Marchantia*, *Riccia* (Fig. 7.2). In *Anthoceros* and some members of Jungermanniales and Sphaerocarpales, only smooth-walled rhizoids and present. In some members (e.g. *Riccia fluitans*, *Ricciocarpos natans*, *Takakia*), the rhizoids are absent. The bundles of rhizoids form anchoring discs in some members, e.g. *Lejeunea*. In some bryophytes, the rhizoids develop in very large quantity and form a red or dark-brown felt-like covering or tomentum over the stem, as in *Dicranum scoparium* and *Mnium punctatum*.

11.5.2 Scales

Multicellular, one-celled thick, purple-coloured structures found on the ventral surface of Marchantiales (e.g. *Riccia*, *Marchantia*; Fig. 7.17) are known as **scales**. Scales are absent in other members of Hepaticopsida, Anthocerotopsida and Bryopsida.

The scales usually protect the growing point of the thallus. They keep the growing points moist and thus protect them from the loss of water. The usual purplish colour of the scales is due to the presence of anthocyanin pigment. Small-sized chloroplasts are also present in the scales of many members, including *Asterella reticulata*, *Athalamia pusilla*, *Cryptomitrium himalayensis* and *Stephensoniella brevipedunculata*. Due to the presence of such chloroplasts, the scales are also assimilatory in function in these bryophytes. Scales are either simple and ligule-like, as in *Riccia*. But in *Marchantia*, scales are of two types, i.e. ligulate and appendiculate. They are either arranged in one row (e.g. *Riccia*), in two rows on either side of the midrib (e.g. *Oxymitra*), or in two to four rows on either side of the midrib (e.g. *Marchantia*). In some bryophytes, the scales are irregularly distributed, as in *Athalamia* and *Corsinia*.

11.5.3 Mucilaginous Hairs or Mucilage Papillae

Mucilaginous hairs or papillae secrete mucilage, which protect the growing points against drought. They are found in some Hepaticopsida, e.g. *Sphaerocarpos*, *Blasia*, *Metzgeria*, *Marchantia*, *Lunularia*, etc. Mucilage hairs are usually absent in Anthocerotopsida. In *Sphaerocarpos*, the mucilage hairs develop on the ventral surface of the thallus near the growing point. In *Blasia*, they are found on both the surfaces of the thallus. Mucilage hairs may be unicellular (as in some species of *Sphaerocarpos*) or multicellular (as in *Calobryum* and *Diplophyllum*). In *Takakia*, the mucilage hairs are of two types: (i) filamentous closed type, and (ii) beaked open type.

11.5.4 Paraphyllia

Paraphyllia are the delicate minute appendages of variable forms, found on the stem and sometimes on the leaf bases of some Hepaticopsida (e.g. *Trichocolea paraphyllina*) and Bryopsida (e.g. *Plagiothecium deplanatum*). These are made of chlorophyll-containing tissue, and found intermixed with normal leaves. In Bryopsida, the paraphyllia are also found in some species of *Ectropothecium*, *Helodium*, *Hylocomium* and *Thuidium*. Paraphyllia have the ability to absorb and retain water like a sponge, and also help in external capillary condition of water. Because of the presence of chlorophyll, they may also be helpful in photosynthetic activity of the plant.

INTERNAL FORM OF MATURE GAMETOPHYTE 11.6

11.6.1 Anatomy of Mature Gametophyte

Anatomy of thalloid forms of gametophyte of bryophytes is highly variable in different members.

In **very simple forms** (e.g. Anthocerotales, thalloid Jungermanniales and some Marchantiales), the thallus is made up of one to several layers of uniform, undifferentiated cells, with no differentiation of tissues. In *Pellia*, the cells of upper layer of the midrib and wings usually contain chloroplasts, which are usually absent in other cells of the thallus (Fig. 11.4).

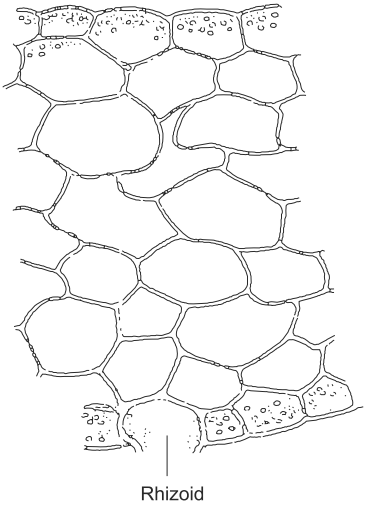


Fig. 11.4 Transverse section of the midrib region of the thallus of *Pellia fabbroniana*

In some thalloid Jungermanniales (e.g. *Hymenophytum, Makednothallus*, *Pallavicinia* and *Podomitrium*), the midrib is transversed by a centrally-located strand made up of narrow, elongate, thick-walled cells with pointed ends. These cells are densely pitted and usually lack protoplasmic content. The centrally-located strand of these genera functions as a water-conducting system. Smith (1964) compared this strand with the xylem of vascular plants. It, however, lacks tracheids and vessels, characteristic of xylem.

More anatomical differentiation of tissues is observed in a majority of Marchantiales. There is a clear anatomical differentiation of dorsal and ventral regions. In ventral region, the thallus contains large, parenchymatous cells containing starch. It functions as the storage region of the food reserves. Mucilaginous cells and oil bodies may also be present in the ventral region in genera like *Marchantia* and *Targionia*. The dorsal region is mainly photosynthetic in function because it consists of chlorophyll-containing cels. A network of large air chambers is present in the entire thallus of aquatic species such as *Riccia fluitans* (Fig. 7.1C) and *Ricciocarpos natans*.

In *Conocephalum*, *Lunularia*, *Marchantia* and *Targionia*, the dorsal region of the thallus contains a single horizontal layer of **air chambers**, just below the upper epidermis. Air chambers are separated by vertical partitions in these genera. In *Asterella* and *Reboulia*, the air chambers are in several rows, and they are separated by a single layer of chlorophyll-containing cells. Secondary partitions may also be present in these air chambers. The air chambers, when present in several rows, are always empty, and do not contain chlorophyll-containing cells.

Air chambers open on the dorsal surface of the thallus, and these openings are called **air pores**. In *Riccia*, the air pores are simple air spaces bounded by 4 to 6 or more cells. In many other thalloid bryophytes, the air pores may be simple or barrel-shaped or compound (e.g. *Marchantia*). In simple air pores, the pore is either surrounded (i) by a single ring of 5 to 8 cells and such pores appear star-shaped in surface view, as in *Peltolepis*; or (ii) by one or two rings of thin-walled cells, as in *Corsinia*; or (iii) by 3 to 8 concentric rings of cells, of which each ring is made up of 6 to 8 cells, as in *Plagiochasma*, *Reboulia*, etc. The compound air pores of *Marchantia* contain 4 to 5 superimposed concentric rings of cells, of which each ring consists of 4 to 8 cells.

11.6 2 Anatomy of Leafy Forms of Gametophyte

1. Hepaticopsida

Leafy forms of the gametophytes of Hepaticopsida consists of stem and leaves.

(a) Stem A well-differentiated conducting strand is absent in the leafy Hepaticopsida. They are able to absorb water through any of the external surface of the stem, and such members are called **ectohydric**.

In leafy forms of Hepaticopsida, the stem is usually composed of uniform cells with no differentiation of tissues. The size and thickness of the walls of **superficial** or **cortical cells** and **internal** or **medullary cells**, however, differ in different members, as exemplified by the following:

(i) In *Bazzania* and *Omphalanthus*, the cells of the cortical layer are smaller than that of the medullary cells. Almost all cells of the stem have more or less thickened walls.

(ii) In *Frullania*, *Plagiochila* and *Scapania*, the cortical cells are smaller and thick-walled while the medullary cells are usually larger and thin-walled.

(iii) The stem of *Acromastigum* contains 7 rows of large cortical cells.

(iv) The stem of *Zoopsis* contains 4 to 6 rows of cortical cells.
(v) The stem of *Lejeunea* contains 7 rows of cortical cells and as many as 10 to 20 rows of medullary cells.
(vi) The stems of *Drepanolejeunea* and *Leptolejeunea* contain 7 rows of cortical cells and only 3 rows of medullary cells.
(vii) In *Cololejeunea*, the stem contains 5 rows of cortial cells and only 1 row of medullary cells.
(viii) In *Calobryum*, the stem contains an outer zone of cells containing oil droplets and pale green plastids and a central zone of colourless elongated cells. A thin cuticle is also present on the outermost side.
(ix) In *Takakia*, the cortical cells are usually thick-walled while the medullary cells are thin-walled.

(b) Leaf Usually, the leaves are one layer of cells in thickness, as in *Calobryum* and *Haplomitrium*. The leaves of the basal part of the plant in these members are, however, two to four cells in thickness. The cells of the leaves are parenchymatous. Leaves of leafy Hepaticopsida usually lack a midrib. In some genera, the leaves are pluristratose as in *Chondrophyllum cucculatum*.

The shape of the cells of leaves is variable. It may be round (e.g. *Bazzania trilobata*), rectangular (e.g. *Blepharostoma trichophyllum*) or even polygonal (e.g. *Calypogeia trichomanis*). Numerous chloroplasts are present in each cell of the leaf.

2. Bryopsida

(a) Stem In Bryopsida (mosses), the stem is generally differentiated into an epidermis, cortex and central conducting strand. In several mosses, however, there is no well-differentiated conducting strand, e.g. *Drummondia*, *Hedwigia*, *Helodium*, *Neckera* and *Ulota*. Anatomically, the stem shows several variations, a few of which may be exemplified as under:

(i) In *Sphagnum*, the central cylinder is surrounded by cortex. The conducting strand is absent.
(ii) In *Andreaea*, the stem contains uniformly thick-walled cells without any differentiation of cortex and central conducting strand.
(iii) In *Polytrichum*, the rhizome contains an endodermis-like layer and a pericycle. Its central cylinder shows differentiation of tissues.
(iv) In *Dawsonia* also, there is a differentiation of tissues in the central cylinder, like *Polytrichum*. Both these genera also contain leaf traces which are loosely connected with the central cylinder.
(v) In *Bryum* and *Mnium*, a distinct conducting strand is present. Water in these mosses is absorbed by the rhizoids and conducted up to leaves through the stem. Such mosses are called **endohydric**.
(vi) In *Funaria* and several other mosses, the cortex of the stem contains **leaf traces**. Such traces end bindly in the cortex without reaching up to the central cylinder.

(b) Leaf The leaves of most of the mosses possess a midrib, as in many species of *Tetraphis*, *Fissidens*, *Phascum*, *Lepidopilum* and *Callicostella*. In several mosses, however, the midrib is absent, as in many species of *Sphagnum*, *Andreaea*, *Ephemerum*, *Fontinalis*, *Hedwigia* and *Nanomitrium*. The midrib, when present, is single in each leaf. But in *Lepidopilum* and *Callicostella*, each leaf possesses two midribs. In *Fissidens bryoides*, the midrib may extend up to the tip of the leaf.

The leaves of mosses is usually one-celled thick except the midrib region. The cells of this single-layered wing or laminate portion contain chloroplasts. In *Polytrichum*, the leaves show highest grade of development. In a majority of mosses, the apical cell of the leaf is wedge-shaped, and usually it cuts segments from two sides.

TEST YOUR UNDERSTANDING

1. Give an illustrated account of the external form of mature gametophyte of bryophytes.
2. Write an essay on gametophyte of bryophytes in about 1000 words.
3. In an alternation of generations, a gametophyte is technically a _____ generation.
4. In bryophytes, the _____ is the main vegetative stage.
5. _____ is the diploid generation in an alternation of generations, and it produces the _____.
6. Name a very small-sized, microscopic bryophyte.
7. The gametophytic plant body of bryophytes may be thalloid or _____.
8. Describe some leafy forms of the gametophyte of Hepaticopsida giving suitable illustrations.
9. Describe the appendages found on the gametophyte of bryophytes.
10. Write short notes on:
    (a) Paraphyllia, (b) Mucilage papillae, (c) Scales.
11. Describe the anatomy of mature gametophyte of bryophytes.
12. How can you differentiate between ectohydric and endohydric mosses?

12

Sporophyte of Bryophytes

WHAT IS A SPOROPHYTE AND A SPORE? 12.1

From the technical viewpoint, the **sporophyte** is the diploid generation in an alternation of generations. The sporophyte is the generation producing **spores**, which are haploid. In angiosperms, gymnosperms and pteridophytes, the sporophyte is the main vegetative stage. In bryophytes, on the other hand, the sporophyte grows directly from the archegonium of the gametophyte, and thus depends on the gametophyte for its nutrition.

Spore is a small round cell from which a whole new plant is produced. In bryophytes, the spores are haploid and are produced by the sporophyte. They are produced as a result of meiosis in the spore mother cells

In bryophytes, the sporophyte is usually made up of three parts, viz. foot, seta and capsule. **Foot** is the basal part which remains embedded within the gametophyte. It is basically an absorbing and anchoring structure. **Seta** is an elongated, stalk-like structure and bears the third most important part of the sporophyte, the **capsule**. Foot and seta are sterile structures while the capsule is the fertile structure of the sporophyte which produces the spores.

HOW IS THE SPOROPHYTE DIFFERENT FROM THE SPOROGONIUM? 12.2

Capsule is the spore-bearing structure of the sporophyte in bryophytes, and it has also been described as **sporogonium**. The terms like "sporogonium" and "sporangium" are used as synonyms of the capsule. Since, the sporangium is the spore-bearing structure in pteridophytes, its use in bryophytes should be abandoned or stopped. The term "sporogonium" is usually used as an alternative for a sporophyte in bryophytes. As mentioned in the ***Chambers Biology Dictionary***, the term "sporogonium" is the "same as the sporophyte in bryophytes". In ***Longman's Illustrated Dictionary of Botany***, sporogonium is "the sporophyte of a moss and a liverwort consisting of a foot, seta and capsule."

BRYOPHYTIC SPOROPHYTE: A BODY DEPENDENT ON GAMETOPHYTE 12.3

In bryophytes, the sporophyte is always dependent on the gametophyte, and due to this some bryologists even describe it as "a parasite on the gametophyte". However, since some cells of the wall of the capsule contain chloroplasts, the sporophyte is not fully dependent for nourishment on the gametophyte, and due to this it should not be described as a parasite on the gametophyte. In some bryophytes, the cells of the seta also contain chloroplasts. A few cells of the foot also contain some chloroplasts in a few bryophytes, such as *Sphaerocarpos*. In comparison to mosses, the chlorophyll content in the cells of seta and capsule is very low in liverworts. Due to the presence of chlorophyll in some cells, the sporophyte is not fully dependent on the gametophyte. It is partially dependent.

In *Anthoceros*, the sporophyte is highly organised, green throughout its life and even some of its epidermal cells contain functional stomata, helpful even in gaseous exchange. A well-organised region of mechanical support, also helpful in conduction, is present in the form of columella in the sporophyte of *Anthoceros*. Some intercalary meristematic cells are also present in the basal part of the sporophyte. All these make the *Anthoceros* sporophyte a highly organised and highly evolved body.

STRUCTURE OF SPOROPHYTE 12.4

As mentioned earlier, the sporophyte in most liverworts (e.g. *Marchantia*; Fig. 12.1A) and mosses is made up of foot, seta and capsule. A brief discussion of all these parts is mentioned below.

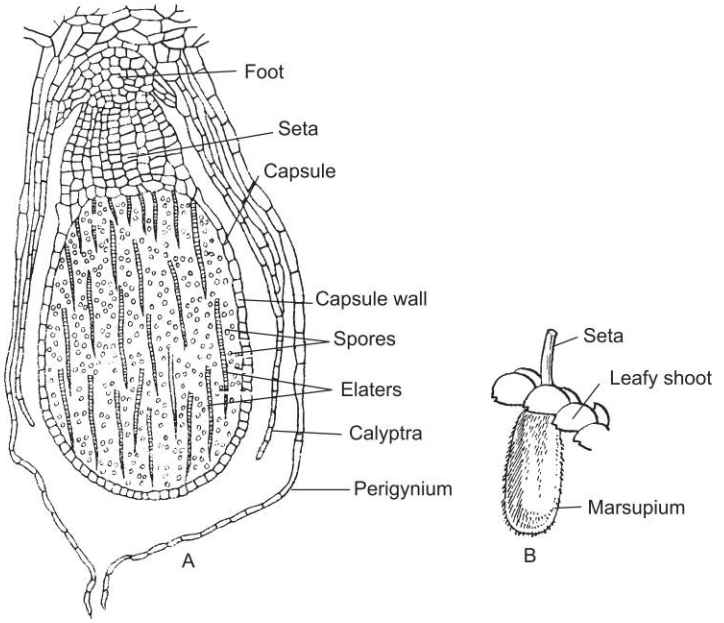


Fig. 12.1 A, A mature sporophyte of *Marchantia* showing foot, seta and capsule; B, A leafy shoot with sporophyte and enlarged marsupium

12.4.1 Foot

The base of the sporophyte of a bryophyte, which is the part that attaches it to the gametophyte, is known as **foot**. It functions for absorption and anchorage. Its size and shape are variable in different bryophytes. In some bryophytes, the foot is absent, e.g. *Riccia*. In most bryophytes, the foot is globose (e.g. *Conocephalum*, *Corsinia*, *Marchantia*, *Anthoceros*) to anchor-shaped (e.g. *Pellia*, *Porella*). In a majority of thalloid liverworts, the foot is large and massive, but in a few liverworts it is very small (e.g. *Trichocolea*). The foot is nearly spherical and bulbous in a few mosses (e.g. *Micromitrium*). In *Schistochila*, a foliose liverwort, some rhizoid-like extensions develop from the foot. *Marsupium*, a tuber-like outgrowth of the foot, is seen in *Calypogeia* (Fig. 12.1 B).

12.4.2 Seta

Seta is the stalk of the sporophyte of a bryophyte. When young, the seta is made up of elongate cells meant for conduction and support. Seta is absent in some bryophytes, e.g. *Riccia*, *Anthoceros* and *Notothylas*.

The seta usually elongates by elongation of its cells and not by division of its cells. Usually, the elongation of the seta is as fast as 1 mm per hour, when young. It attains a length of over 5 cm or more in some liverworts, e.g. *Pellia*, *Monoclea*, etc. In *Marchantia* (Fig. 12.1A), *Corsinia* and *Targionia*, the seta is not a very long structure. In *Pohlia natans*, seta reaches up to 7 cm in length, and in *Drepanocladus fluitans*, seta may attain a length up to 10 cm or even more. In genera such as *Phascum* and *Ephemerum* seta is a very minute body.

Seta is long but a delicate and ephemeral structure, made up of thin-walled cells. Transverse section of the seta of *Jubula* reveals that in circumference, it is only made up of a few cells (Fig. 12.2A). But it is made up of many cells in *Mylia* (Fig. 12.2 B). In *Caphaloziella*, seta consists of four small central cells surrounded by four larger cells (Fig. 12.2 C).

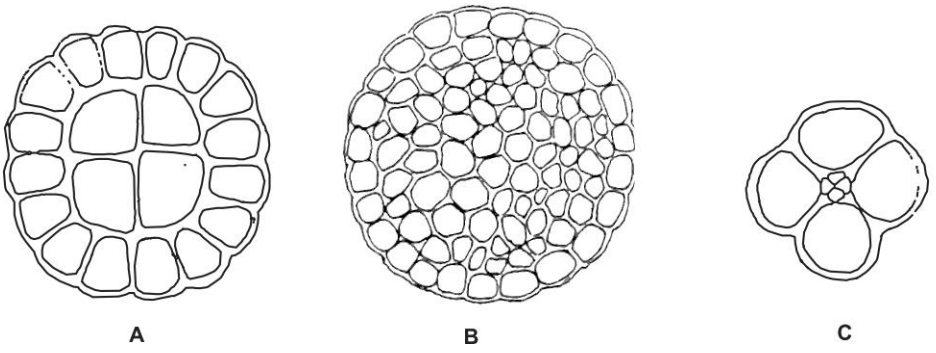


Fig. 12.2 Transverse sections of the seta of *Jubula* (A), *Mylia* (B) and *Cephaloziella* (C)

Some of the striking differences between seta of liverworts and mosses are listed in Table 12.1.

In several species of *Brachythecium* and *Dicranella*, the seta contains some specialised papillae-like structures. In *Brachythecium rutabulum*, papillae on the seta are quite large and can be seen even with the naked eye.

Table 12.1 *Differences between the seta of liverworts and mosses*

S No.	*Liverworts*	*Mosses*
1.	Seta is quite an elongate body much before the maturity of capsule.	Seta is a short structure prior to the maturity of capsule.
2.	Seta is not highly specialised for conduction.	Seta is a highly specialised structure for conduction.
3.	It does not provide that much support to the capsule as in mosses.	It provides more support to the capsule than in liverworts.
4.	It is more significant for dehiscence in liverworts.	It is not so significant for dehiscence in mosses as it is in liverworts.

12.4.3 Capsule

Capsule is the spore-producing organ of the sporophyte of a bryophyte, borne at the top of the seta. In liverworts, it varies in its form in different members. It may be cylindrical, ovoid, subspherical or even spherical. In *Riccia* (Fig. 7.10 J), *Sphaerocarpos* (Fig. 5.2 M), *Frullania*, *Porella* (Fig. 4.7), *Pellia* (Fig. 4.16 B), *Fossombronia*, *Lejeunea* and some other bryophytes, the capsule is nearly spherical in shape. Capsules are almost ovoid or ovoid-cylindrical in *Blasia* and *Riccardia* while they are elongated in *Haplomitrium* and *Monoclea*.

As far as the size is concerned, the capsules of mosses are usually larger than the capsules of liverworts. In Marchantiales, they attain a diameter of 1 to 1.25 mm but in Jungermanniales, the capsules are comparatively narrower and reach up to 0.6 to 1 mm in diameter. In *Riccardia* and *Pellia*, the capsule reaches up to 1.5 mm or more in diameter.

In mosses, the capsule is usually cylindrical and erect (*Funaria hygrometrica*), subglobose (e.g. *Bartramia*) or pyriform and pendulous (*Bryum*, *Pohlia*).

DEVELOPMENT AND DIFFERENTIATION OF DIFFERENT ORGANS OF SPOROPHYTE 12.5

Development and differentiation of different organs of the sporophyte in bryophytes may be studied in the form of five different stages, viz. embryogeny stage, protected stage, green stage, differentiation stage and, dehiscence and dispersal stage.

12.5.1 Embryogeny Stage

A plant at an early stage of development is known as **embryo**, and the processes leading to the formation of the embryo is known as **embryogeny**. So, early developments of the sporophyte of a bryophyte are included under the embryogeny stage.

Two main findings of the embryogeny stage in liverworts are (i) early embryo passed through the formation of an 8-celled octant stage (Marchantiales) or linear stage (Jungermanniales), and (ii) origin of sporogenous tissue. The young multicellular embryo divides periclinally to form the outer amphithecium and the inner endothecium, either of which form the sporogenous tsissue in different members. Endothecium is, however, responsible for the formation of sporogenous tissue in most liverworts.

In mosses, on the other hand, the early embryogeny (Fig. 12.3 A-H) is more uniform. Polarity is established in the initial stages, and elongation of the young sporophyte takes place by the activity of an apical cell. In the lower part of the young sporophyte, a second apical cell starts functioning. Soon, the ovoid embryo of the moss transforms into an ellipsoidal body and finally a narrow cylindrical body tapering at both ends is resulted. The central endothecium is soon demarcated from the peripheral amphithecium in this young multicellular cylindrical embryo. The archesporium originates from the endothecium. The external wall layers and central columella are differentiated when the young embryo is about 20 to 24 cells thick. Various mosses require different periods for the differentiation and development of various parts (i.e. foot, seta and capsule) of the sporophyte. For example, the processes from the time of fertilization up to the discharge of spores are completed within 2–3 weeks in *Phascum cuspidatum*, but in *Polytrichum* the period required for completion of all these processes is over one year.

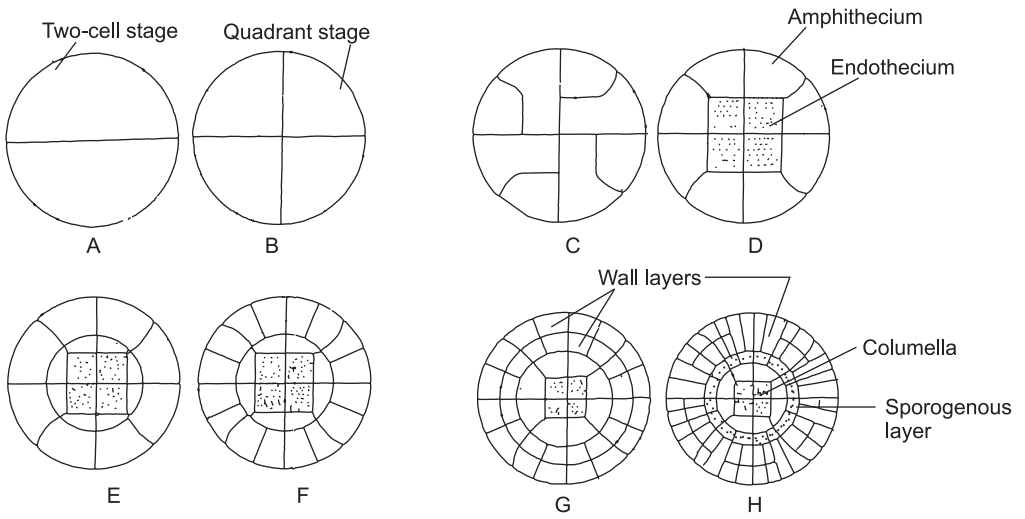


Fig. 12.3 A-H Diagrammatic representation of the early stages of embryogeny in a moss capsule. A, Two-celled stage; B, Quadrant stage; C-D, Differentiaion of amphithecium and endothecium; E-H, Differentiation of wall layers, sporogenous layer and columella

12.5.2 Protected Stage

Calyptra and positioning of foot are the two major ways which help in the protection of young developing sporophyte. Besides calyptra and foot, some **additional protective structures** are also present in some bryophytes. Involucre, green curtain of tissues and perianth are some such additional protective structures. Well-developed pear-shaped **involucres** are present as a protective body in *Sphaerocarpos*. Some **green curtain of tissues** develop amongst the archegonia in *Corsinia*. Some bryologists consider these tissues as forerunners of carpocephalum. Infoldings of scale-like structures develop as a protective tissue in the sporophytes of *Targionia.* A green involucre is present in *Pellia*. In *Marchantia*, the protective structures of sporophyte include calyptra, perianth and involucre. A Chinese-lantern-type additional protective covering is present in the sporophyte of *Fimbriaria*. *Riccardia* lacks any additional protective structure.

1. Calyptra

The calyptra is actually a hood of tissue produced from the wall of the archegonium, especially in mosses. It is also formed in liverworts. Calyptra protects the young sporophyte. The size and shape of the calyptra affect the shape and orientation of the capsule in mosses. The calyptra is highly variable in different bryophytes in its extent of covering the capsule. In bryophytes, in general, and mosses in particular, the shape of the calyptra serves as a useful tool of taxonomic importance. In *Eucalypta*, the calyptra is an elongate cone-like structure which covers the capsule all over. In a majority of other bryophytes, the calyptra is a small cap-like covering surrounding the basal part of the developing capsule. Due to very fine hairy calyptra in *Polytrichum*, the name **hair-cap-moss** is given to this genus.

2. Foot

The foot of the sporophyte of bryophytes remains housed in the green gametophytic tissue. It provides adequate nutrition to the sporophyte. In some leafy liverworts, the sporophyte is housed in a special pouch-like structure of gametophytic origin, known as **marsupium**. It is a multilayered pouch-like or tube-like structure made up of gametophytic tissue. In *Geobelobryum*, the marsupium is a well-developed, elongated, tube-like structure bearing rhizoids, which are sometimes seen even buried into the substratum like that of a root of higher plants.

In thalloid liverworts, the foot of the sporophyte is a globose mass of undifferentiated cells. In the foot of mosses, some differentiation may be observed in the form of outer haustorial cells, intermediate unspecialised cells and central cells. The central cells function like that of conducting cells. Intense enzymatic activity can be observed in the cells of the outer region of the foot of mosses. Chauhan (1988) reported cytochemical reactions for respiratory enzymes and phosphotases in the cells of the foot region of *Physcomitrium cyathicarpum*. The haustorial cells of the foot of the sporophyte function as the organs of absorption and transfer of nutrients, and due to these, they are named **transfer cells**. In *Physcomitrium cyathicarpum* and *Dendroceros*, the peripheral cells of the foot show some infoldings or invaginations, which form wall labyrinths. The characteristic feature of transfer cells is the presence of these wall labyrinths in this genus. The transfer cells of the foot, therefore, form the junction between sporophyte and gametophyte. Besides mosses and liverworts, transfer cells have also been reported in hornworts (e.g. *Anthoceros punctatus*) by Ligrone and Gamberdella (1988). Transfer cells are absent in the foot region of *Pellia* and *Sphagnum*.

12.5.3 Green Stage

Photosynthetic efficiency of the sporophyte represents its **green stage**. It is an important stage because it provides some independence to the sporophyte from the gametophyte. **In almost all liverworts**, the young sporophyte remains buried in the gametophytic tissue. In developing and nearly mature sporophytes, the capsule is pushed out of the gametophytic tissue due to the meristematic activity of seta and absorbing nature of foot. However, due to low chlorophyll content in seta and capsule, the sporophyte depends on the gametophyte for its requirements of inorganic and organic contents. In **mosses**, on the other hand, more amount of chlorophyll is present in different tissues and parts of the sporophyte. The sporophyte is, therefore, more photosynthetically efficient than liverworts. The long seta of the sporophyte of mosses is quite green, especially when young, and hence more efficient in terms of its photosynthetic activity. The seta, however, is more specialised for support and conduction.

In mosses (e.g. *Bartramia*, *Bryum*, *Funaria*), a well-developed green tissue is present in the wall of the capsule of the sporophyte. More photosynthetic activity is possible in the sporophytes of these

mosses. In *Torula* and some more mosses, the green tissue in the capsule region is less extensive, hence there is less amount of photosynthetic activity. In *Splachnum ampullaceum* and many other species of this genus, the apophysis region is most extensive amongst mosses.

Stomata are not found on the capsules of liverworts. In most mosses, they are present on the capsule, specially in the apophysis region. In *Pleuridium*, the number of stomata are only 3-5 on a capsule. But in some mosses (e.g. *Philonotis*), each capsule has as many as 200 or more stomata. Some mosses have no stomata on their capsules, e.g. *Fontinalis* and *Atrichum*.

12.5.4 Differentiation Stage

Differentiation stage of the sporophyte is the demarcation of tissues which results into the formation of sporogenous cells and spores in the sporophyte. The entire sporogenous tissue is endothecial in origin in Marchantiales (e.g. *Riccia*) and results in the formation of spores. In Jungermanniales, a part of the sporogenous tissue remains sterilised and forms the elaters. And, as we proceed further in mosses the capsule elaborates and only very little of its tissue is meant for production of spores. Moreover, the sterile structures like elaters are also not formed in capsules of mosses. A sterile region in the capsule of *Funaria* and other mosses is present in the form of columella, which provides mechanical support to the capsule and also helps in conduction. Columella is absent in liverworts. In *Anthoceros* and other hornworts, a well-developed columella is also present.

The sporogenous tissue develops into spores, and the number of spores per capsule per plant have been estimated in some bryophytic genera by bryologists. Some such findings are listed in Table 12.2.

Table 12.2 *Approximate number of spores per plant in some bryophytes*

S No.	*Genus*	*Number of spores/spore tetrads per plant per capsule (Approx.)*
1.	*Sphaerocarpos*	200 spore tetrads per capsule
2.	*Pellia*	4500 spores per capsule
3.	*Lophocolea cuspidata*	24,000 spores per capsule
4.	*Diplophyllum albicans*	40,00,00 spores per capsule
5.	*Eurhynchium*	700,000 spores per capsule
6.	*Scapania undulata*	10,00,000 spores per capsule
7.	*Marchantia polymorpha*	7000,000 spores per plant

12.5.5 Dehiscence and Dispersal Stage

Structure of the capsule wall is of utmost importance in the dehiscence of sporophyte in bryophytes. Marchantiales possess a unistratose capsule wall whereas in Jungermanniales the capsule wall is multistratose. The unistratose capsule wall of Marchantiales sometimes has transverse thickenings (e.g. *Peltolepis quadrata*, Fig. 12.4A). But in *Plagiochasma intermedium* (Fig. 12.4B), the cells of the jacket are thin-walled and do not bear any ornamentation. In *Asterella*, the capsule jacket is without an apparent thickening (Fig. 12.4 C). But in *Conocephalum*, the entire transverse wall is thickened (Fig. 12.4 D). The wall of *Norwallia* shows ornamentation in the longitudinal wall (Fig. 12.4 E) while the longitudinal wall shows thickenings (Fig. 12.4F). The epidermal cells shows ornamentation in case of *Frullania* (Fig. 12.4 G) but in *Radula* (Fig. 12.4H), the epidermal cells of the wall of the capsule show

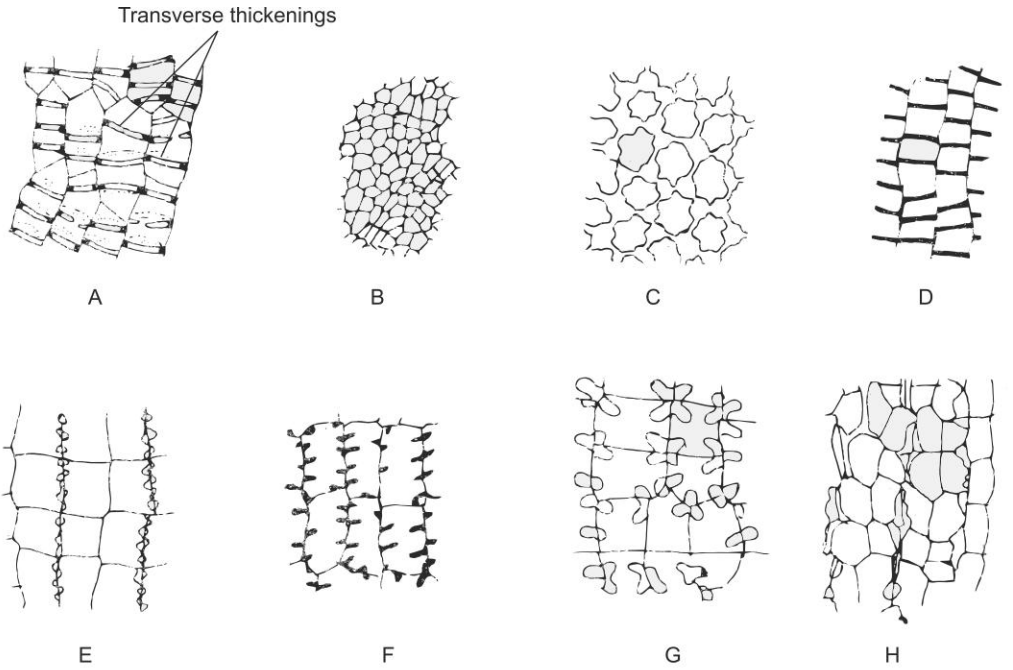


Fig 12.4 A-H Wall of capsule of *Peltolepis quadrata* (A) showing transverse thickenings; capsule walls of *Plagiochasma* (B), *Asterella* (C), *Conocephalum* (D), *Norwallia* (E), *Arnellia* (F), *Frullania* (G), and *Radula* (H)

thickenings. It has been observed in different members that the jacket of the capsule ruptures along four longitudinal lines resulting in the formation of four valves or flaps. Intact capsules of *Cephalozia*, before (Fig 12.5A) and after dispersal Fig. 12.5B) and in *Frullania* before (Fig. 12.5 C,D) and after dispersal (Fig. 12.5 E) are shown in Fig. 12.5.

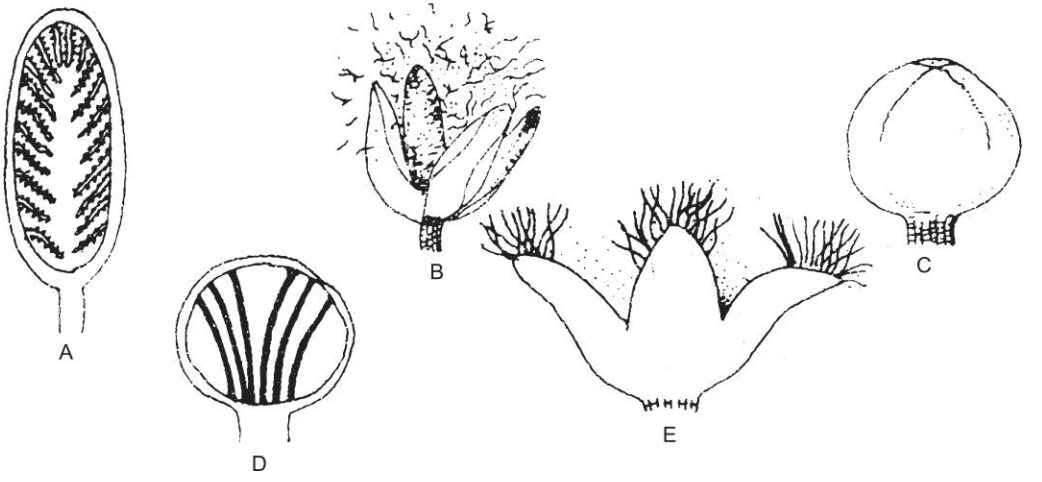


Fig. 12.5 A-B, Intact capsules before and after dispersal in Cephalozia; C-E, Intact capsules before and after dispersal in *Frullania*

In mosses, the jacket of the sporophyte is multistratose. The stomata are also present in its epidermal wall in most mosses. The stomata when present, are either exposed (e.g. *Funaria*) or immersed (e.g. *Orthotrichum*). Operculum, a cap-like structure, gets differentiated in the apical region of the jacket of the capsule. The operculum ruptures and this triggers the dehiscence of the capsule. The operculum is released by the annulus, which is made up of a ring of enlarged elastic cells. The shape and structure of the operculum help in the dehiscence and dispersal of spores.

1. Categories of Dehiscence of Capsule and Dispersal of Spores

Two categories of dehiscence of capsule and dispersal of spores may be as under:

(a) Passive Dehiscence and Passive Dispersal This takes place in those bryophytic genera (e.g. *Corsinia*, *Riccia*) in which the seta is absent in the sporophyte and dehiscence takes place by disintegration of jacket of the sporogonium. Because of the absence of elaters or any specialised structures, the dispersal is also passive.

(b) Active Dehiscence and Active or Passive Dispersal This takes place in those genera in which the sporogonium wall ruptures along four lines of dehiscence and elaters are present. The elaters help in the dispersal of spores.

2. Dehiscence and Dispersal in Liverworts

Dehiscence of capsule and dispersal of spores in liverworts mainly take place by three different mechanisms, described below:

(a) hygroscopic mechanism (e.g. *Pellia*, *Marchantia*, etc.),
(b) water-rupture mechanism (e.g. most of the foliose liverworts), and
(c) spiral-ring mechanism (e.g. *Frullania*).

Spores are dispersed slowly in hygroscopic mechanism but very fast and violently in water-rupture mechanism and spiral-ring mechanism.

In members showing hygroscopic mechanism, the spiral bands of elaters are weaker than those showing the other two mechanisms. On the other hand, in members showing water-rupture mechanism and spiral-ring mechanism, spiral bands of their elaters show great strength of bispiral thickenings, as in *Cephalozia* and *Lophocolea*. In dry conditions, the coils of bispiral thickenings contract sharply, resulting in extreme tension. This loosens the coils abruptly, untwists the elaters instantaneously and results in dehiscence and violent dispersal of spores.

In the liverworts showing hygroscopic mechanism resulting into slow dispersal of spores, the elaters bear weaker spiral bands. The spirals of bands of these elaters, of course, contract but this contraction is not sufficient to induce water rupture. The elaters simply twist in the available atmospheric humidity, and there is seen only gradual dispersal of spores.

The spiral-ring mechanism is characteristic of Frullaniaceae and Lejeuneaceae, and this is linked with unique internal organisation of the capsule. A series of elaters are present from roof to floor in the globose capsule of these members. Dehiscence mechanism in these members is also unique. It takes place by four valves of its jacket, which curve outwards rapidly, resulting into the discharge of spores.

3. Dehiscence and Dispersal in Mosses

Various types of dehiscence of capsules and dispersal of spores are observed in mosses. In *Andreaea* (Fig. 12.6A,B), the dehiscence of capsule is of great taxonomic significance. The jacket of the capsule

of this moss is thick-walled and possesses four or more lines of weakness which extend from the base towards the apex. The mature sporogonium starts drying out, shrinks, and the shrinkage leads to lines of weakness and finally yields into the dispersal of spores.

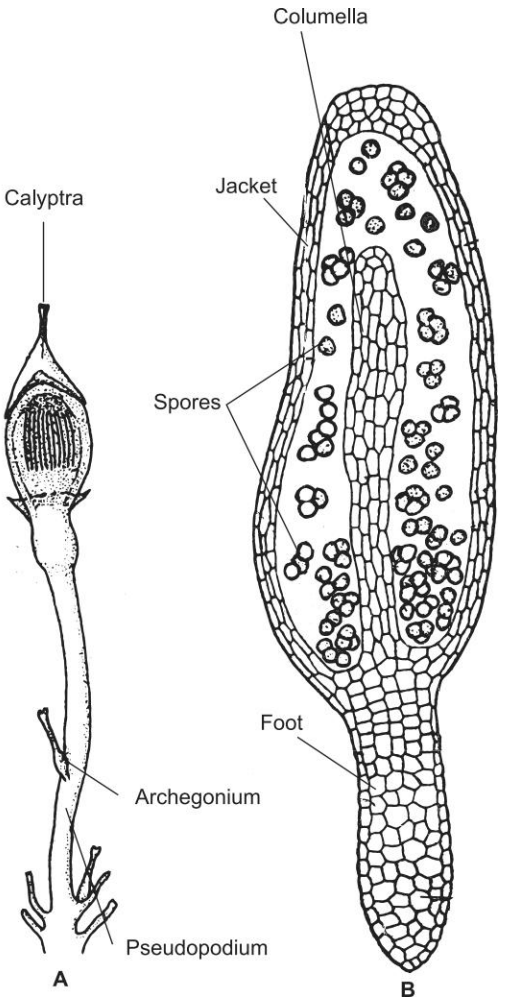


Fig. 12.6 *Andreaea rupestris* showing entire sporogonium (A) and LS (B) of the same

In *Ephemerum* and some species of *Physcomitrium*, the capsules are closed or **cleistocarpous**. They open in an irregular manner to disperse the spores. Peristome and a detachable operculum or lid are absent in such mosses. Seta is also ill-developed or even absent in these mosses. Only a few leaves present in the gametophyte of these mosses surround the sporophyte. In dry conditions, the entire plants of these mosses can be blown away by winds and are also transported far by humans and animals.

In **gymnostomous mosses** (e.g. *Pottia truncata*), the operculum may or may not be present in the capsules. They also lack peristome. Due to these characteristics, these mosses have no gradual or regulated mechanism of dispersal of spores. Dehiscence of the capsule takes place by blowing off of

the upper part of the capsule. The spores are dispersed by gravitational force because the capsule mouth is directed downwards in these mosses

According to Edwards (1980), weather plays an important role in the dehiscence of the capsule and dispersal of spores in aquatic mosses like *Scouleria* and *Wardia*. It is so because their capsules are not directed downwards and they also lack teeth. In dry weather, their lid opens but in wet weather, it remains intact, and spores are exposed due to wind.

Peristome is the major part to regulate the spore dispersal in the moss capsule, e.g. *Funaria hygrometrica*. Two well-defined rings of peristome are present in this moss. In some other species (e.g. *Funaria fascicularis*), however, the peristome is either missing or rudimentary. Similarly, two rings of peristome are present in *Encalypta streptocarpa* but only one ring of peristome is present in *E. rhabdocarpa*. Peristomate mosses thus fall in two categories, viz. **haplolepideae** (having single ring of peristome), and **diplolepideae** (having two rings of peristome). Usually, a single ring of peristome has 16 teeth. They form a close-fitting circle at the base and their apical parts taper to a point. Each tooth of the peristome is a barred structure, and the tooth bars are actually remnants of the cell wall. Thickenings, which are characteristic of outer teeth, are usually absent in the inner teeth. Usually, 16 teeth of the inner ring alternate with the 16 teeth of the outer ring. 16 thread-like cilia, in groups of 3 or 4, are also usually present on the same radii as that of the outer teeth. Dispersal of spores is actually regulated by the peristome.

Regarding variations in peristomial teeth (Fig. 12.7 A-F), solid type of 4 erect peristome teeth are present in *Tetraphis* (Fig. 12.7A), a ring of spirally twisted filliform teeth are present in *Barbula* (Fig. 12.7B), a ring of 16 barred slow-moving teeth are present in *Dicranella* (Fig. 12.7C) while double peristome quite active in spore dispersal, are present in *Hypnum* (Fig. 12.7D) and *Bryum* (Fig. 12.7 E). Peristome shows teeth curving over epiphragm in *Atrichum* (Fig. 12.7F).

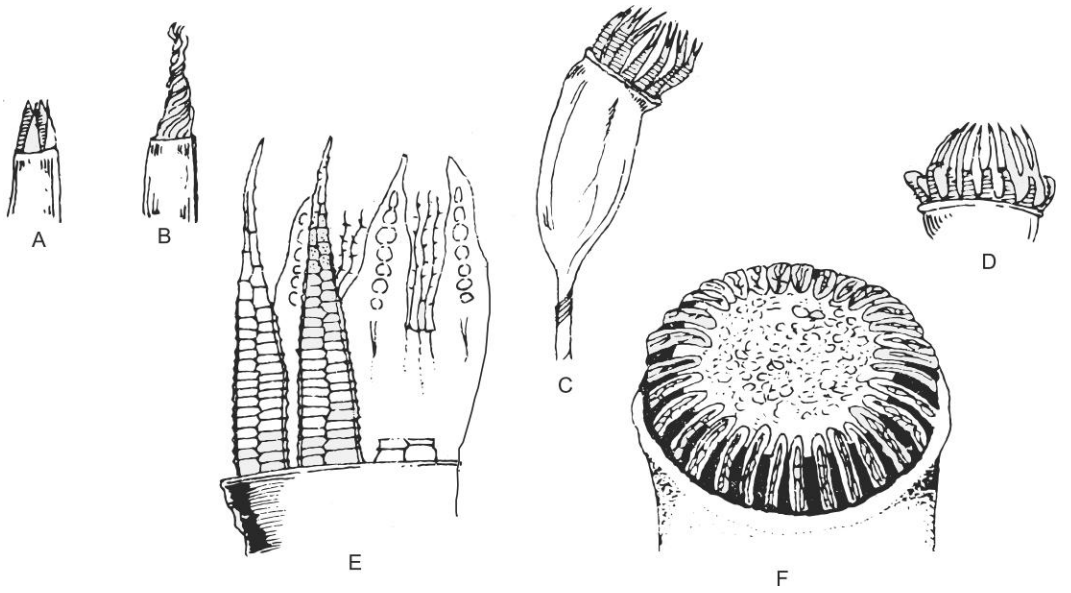


Fig. 12.7 A-F Showing variations in peristomial teeth in *Tetraphis* (A), *Barbula* (B), *Dicranella* (C), *Hypnum* (D), *Bryum* (E) and *Atrichum* (F)

The entire process of spore dispersal in mosses can be grouped in three broad categories, as under:

(a) Primitive Type In mosses like *Barbula* (Fig. 12.7B) and *Tortula*, teeth movements have very little or no active role in spore dispersal, and this is called primitive type. The peristome in such mosses serves only as a hygroscopic lid.

(b) Intermediate Type In *Dicranella* (Fig. 12.7(C) and some other mosses, the peristome has 16 forked and freely moving teeth. In these mosses, the spores accumulated under the capsule mouth are caught in between slowly moving teeth and get dispersed.

(c) Advanced Type Gradual discharge of spores is seen in the advanced type of mosses. Teeth play a more active role in this type of dispersal. A majority of the mosses, which fall under this category, have two rings of peristomial teeth. Advanced type is exemplified by mosses such as *Brachythecium*, *Bryum* (Fig. 12.7E), *Hypnum* (Fig. 12.7D) and *Mnium*. The spores are dispersed in dry conditions in these mosses by a process in which inner peristomial teeth stand up as a central cone and the tips of teeth of outer ring are inserted into the gaps present in between different inner structures. In moist conditions, the process of gradual discharge of spores depends on the ability of peristomial teeth to close the capsule mouth.

In *Atrichum* (Fig. 12.7(F), *Oligotrichum* and *Polytrichum*, the peristome is of complex type, and dispersal of spores takes place by **censor mechanism**. As many as 32 or 64 peristomial teeth of different structures, are present in these mosses. Each tooth consists of fibre-like cells of several layers of thickness, and this represents a solid construction. All these teeth unite at their tips to form a membranous structure called epiphragm. Dispersal of spores takes place through very fine holes present between the successive teeth, and this type of dispersal of spores is called censor mechanism. An unusual type of spore dispersal is observed in *Tetraphis* (fig. 12.7A). Its peristome contains four large teeth of solid construction, but it lacks epiphragm.

Sphagnum (Fig. 12.8A-D) shows **air-gun mechanism** of dehiscence of capsule and dispersal of spores. The mature sporogonium of this moss dries out, shrinks in diameter, and due to this, the columella collapses and a high air pressure is resulted inside the capsule. Due to this pressure, the operculum is thrown away and spores are shot away into the atmosphere. This violent process of dispersal of spores is known as air-gun mechanism.

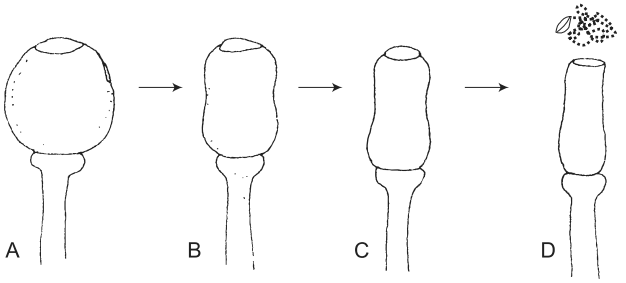


Fig. 12.8 A-D Dehiscence of capsule in Sphagnum showing air-gun mechanism of spore dispersal

TEST YOUR UNDERSTANDING

1. Write an essay on the sporophyte of bryophytes in about 1000 words.
2. Give precise definitions of sporophyte and spore with reference to bryophytes.
3. "Sporophyte in bryophytes is dependent on gametophyte". Comment in about 200 words.
4. Sporophyte is the _____ generation in an alternation of generations.
5. Sporophyte is the generation producing _____, which are haploid.
6. Sporophyte in bryophytes is usually made up of three parts, viz. _____, seta and capsule.
7. Describe the general structure of sporophyte of bryophytes in about 500 words.
8. Name a bryophyte which lacks foot and seta in its sporophyte.
9. How can you differentiate between seta of liverworts and mosses?
10. The spore-producing organ of the sporophyte of a bryophyte is called _____ .
11. Give an account of development and differentiation of different organs of sporophyte in bryophytes.
12. What is calyptra?
13. How will you differentiate between haplolepideae and diplolepideae in terms of peristome in bryophytes?
14. Process of spore dispersal in mosses can be grouped in three broad categories. Name them and explain them in about 200 words.

13 Spore Germination and Formation of Gametophyte

WHAT IS TECHNICALLY A SPORE? 13.1

As explained also earlier, a spore is a "small round cell with a thick wall from which a whole new plant is produced". In bryophytes, pteridophytes and spermatophytes, spores are haploid and are produced by the sporophyte. In bryophytes and pteridophytes, dispersal is achieved by spores. In angiosperms, the spores develop into small gametophytes in the pollen grains and ovules. In bryophytes and a majority of other plants, spores are produced as a result of meiosis.

In bryophytes, the spore formation represents the beginning of the gametophytic phase and end of the sporophytic phase of the life cycle. Because the spore develops due to meiosis in the diploid spore mother cells of the sporophyte, it is a haploid structure and carries new gene combinations. The gametophytic plant, produced by spore germination, therefore, has better adaption to the environment and are genetically uniform.

In brief, it can be mentioned that in bryophytes, the spore is the first cell of the gametophytic generation. It is a specialised unicellular body which is capable of developing into a new individual. In the initial stages of their formation, the spores remain in groups of four, thus showing tetrahedral arrangement. They later on separate into four constituent spores.

ARE BRYOPHYTES HOMOSPOROUS OR HETEROSPOROUS? 13.2

Plants whose spores are all the same, i.e. possess spores of the same size, are known as **homosporous**. On the other hand, plants which produce spores of two different sizes are known as **heterosporous**. All bryophytes are usually homosporous, except a few mosses (e.g. *Macromitrium salakanum* and *Schlotheimia grevillaena*) which are heterosporous. In *Macromitrium salakanum*, the large-sized spores produce female plants whereas small spores form the male gametophytic plants.

SIZE AND OUTPUT OF SPORES 13.3

The **size** of the spores is highly variable in different bryophytes. Some of the reported range in the size of the spores of selected genera, as mentioned by Parihar (1987), is from 5μ (*Dawsonia*) to 200μ (*Archidium*) in Bryopsida, 6 μ to 80 μ in foliose members of Jungermanniales, and 10 μ (*Marchantia polymorpha*) to 140 μ (*Corsinia*) in Marchantiales.

The number of spores in each capsule is also highly variable. It is as low as 4 to 28 in *Archidium* but as high as 300,000 in *Marchantia polymorpha*, 400,000 in *Diplophyllum albicans*, and 1,000,000 in *Scapania undulata*.

STRUCTURE OF SPORES OF BRYOPHYTES 13.4

A thin wall surrounds the young spore, but soon it becomes thick and bilayered. The inner layer consists of cellulose and called *intine* or *endosporium*, while the outer layer is usually sculpturous or contains ornamentations and called *exine* or *exosporium*. The exine ornamentations may be in the form of tubercles, spines, folds, ridges, grooves, etc. In many Hepaticopsida, a third spore wall (*outer exosporium* or *perinium*) is also seen. The spores are uninucleate and the nucleus remains surrounded by granular cytoplasm which contains oil bodies, starch grains, albuminous matter, etc. Chloroplasts are also present in the spores of several genera including *Andreaea*, *Monoclea*, *Riccardia*, leafy liverworts and mosses.

SPORE GERMINATION AND FORMATION OF GAMETOPHYTE IN LIVERWORTS (HEPATICOPSIDA) 13.5

13.5.1 Marchantiales

Spore germination and formation of the early stages of gametophyte in several members of Marchantiales has been studied and reviewed by Inoue (1960) and several other workers. On germination, the spore coat ruptures in many different ways by the enlargement and then emergence of the germ cell. Based on the polar axis of the spore, Inoue (1960) recognised four types of the spore-coat dehiscence in Marchantiales. These are (i) irregular, (ii) tangential, (iii) proximal, and (iv) distal. Usually the germ cell divides by a transverse wall to form a germ rhizoid and a germ tube. But in some genera (e.g. *Riccia*), there is no wall formation between the germ cell and germ tube. Seven different patterns of germ rhizoid formation have been reported in Marchantiales. These are (i) *Targionia*-type, (ii) *Marchantia*-type, (iii) *Neohodgsonia*-type, (iv) *Stephensoniella*-type, (v) *Reboulia*-type, (vi) *Mannia*-type, and (vii) *Conocephalum*-type by Inoue (1960).

The germ tube usually elongates and forms a short filament representing the future gametophyte. A few chloroplasts and some oil drops are present in the cells of the short filament. Soon, the terminal cell of the filament divides by two vertical divisions at right angles to one another, to form four cells at the apex of the filament. This represents the quadrant stage of the young gametophyte. Further vertical and tangential divisions result in the formation of a several-celled plate of the gametophyte. A distinct two-sided apical cell is soon differentiated in this multicellular plate. Then there is the differentiation of the apical cell with four cutting faces. Activity of this apical cell gives rise to a young thallus.

Inoue (1960) reported five types of the plate formation in Marchantiales. These are (i) *Asterella*-type, (ii) *Conocephalum*-type, (iii) *Marchantia*-type, (iv) *Reboulia*-type, and (v) *Stephensoniella*-type.

13.5.2 Sphaerocarpales

Spore germination of majority of the members of Sphaerocarpales, including *Geothallus*, *Riella* and *Sphaerocarpos*, has been studied in detail. A slender germ tube emerges and divides by a transverse division to form a basal cell and a terminal cell. The basal cell does not divide any further and develops into the first rhizoid. The terminal cell divides by few transverse divisions to form a young, fine filament, and from this stage onwards the further development of gametophyte is different in different genera.

In *Geothallus*, the few-celled young filament develops into an erect, unistratose, green, chlorophyll-containing, flap-like or loose juvenile plant of determinate growth. From the basal part of this juvenile plant develops the adult plant as a lateral outgrowth. The juvenile plant gives rise to only one adult plant.

Riella resembles *Geothallus* in producing a single erect, unistratose juvenile plant of determinate growth but it is comparatively larger than that of *Geothallus*. At the base of this juvenile plant, a series of cells remains embryonic and function as its intercalary meristem. This meristem first makes the juvenile plant more active by adding new cells. Lower and upper regions are soon differentiated in this young gametophyte due to the activity of this intercalary meristem. Soon the young gametophyte attains a size of 5 to 8 cm or more.

In *Sphaerocarpos*, the slender germ tube emerges, pushes through a slit on the outer face of the spore, divides transversely into a terminal cell and a basal cell, and a filament develops due to some transverse devisions in the terminal cell. Cells of this filament divide and form a germinal disc at right angles to a short multiseriate filamentous body. This multicellular germinal fisc transforms into a juvenile thallus. A lateral outgrowth develops from this juvenile thallus and changes into an adult plant of *Sphaerocarpos*.

13.5.3 Jungermanniales

The young plant, formed after the early divisions of spore in Jungermanniales, has been termed **sporeling**. The so-called sporeling (Fulford, 1956) includes all the stages of a young developing plant, such as (i) protonema, (ii) the shoot with primary leaves, and (iii) shoot with underleaves and juvenile stages.

The **protonema** stage, as explained by Fulford (1956) includes "all stages from the first division of the spore up to the formation of an apical cell with three cutting faces by which the leafy shoot is formed". He divided all Jungermanniales into the undermentioned two groups, which include ten different types of sporelings. Two types are included under **Group A** and the remaining eight types are included under **Group B**. In Group A, protonema develops outside the exospore, while in Group B, the protonema develops completely or at least partially, within the stretched exospore. In Group A, the juvenile leaves are with a deep sinus and spreading lobes, but in Group B, the juvenile leaves are large and saccate inflated.

Group A

(a) Cephalozia Type It contains a simple or branched filamentous protonema with stems at the tips of branches, e.g. *Cephalozia bicuspidata* (Fig. 13.1.A).

(b) Nardia Type It contains a globose, multicellualr protonemata, e.g. *Nardia scalaris* (Fig. 13.1B).

Group B

(a) Radula Type It contains a disciform protonema, e.g. *Radula complanata* (Fig. 13.1 C).

(b) Frullania Type It contains a multicellular (up to 50 or more cells), globose protonema within the exospore, e.g. *Frullania dilatata* (Fig. 13.1 D).

(c) Lopholejeunea Type It contains a globose protonema made up of only a few cells, e.g. *Archilejeunea* (Fig. 13.1 E).

(d) Leucolejeunea Type It contains elongate cylindrical protonema, as in *Leucolejeunea* (Fig. 13.1F).

(e) Lejeunea Type It contains a narrow, unistratose protonema which develops due to the activity of an apical cell with two cutting faces, as in *Lejeunea* (Fig. 13.1 G).

(f) Stictolejeunea Type It contains unistratose protonema which does not grow by an apical cell, as in *Stictolejeunea* (Fig. 13.1 H).

(g) Ceratolejeunea Type It contains a bifold protonema made up of two thalloid stages, as in *Ceratolejeunea* (Fig. 13.1 I).

(h) Unnamed type of bifold protonema with a multicellular primary protonema and a ribbonlike secondary protonema.

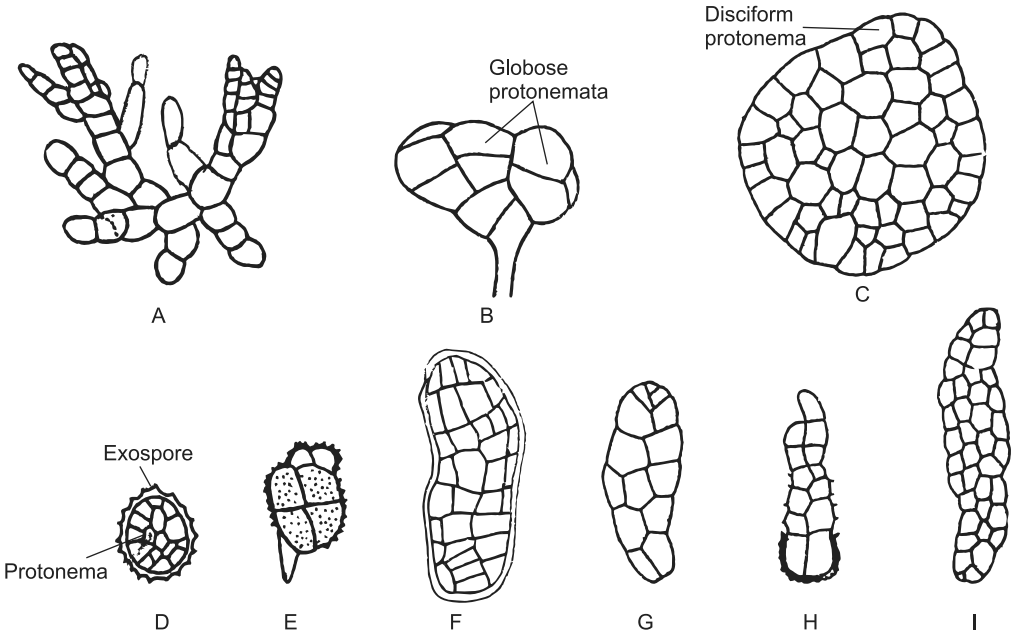


Fig. 13.1 A-I Various types of protonema of bryophytes. A, *Cephalozia;* B, *Nardia;* C, *Radula;* D, *Frullania;* E, *Lopholejeunea,* F, *Leucolejeunea;* G, *Lejeunea;* H, *Stictolejeunea,* I, *Ceratolejeunea*

SPORE GERMINATION AND FORMATION OF GAMETOPHYTE IN HORNWORTS (ANTHOCEROPSIDA) 13.6

Spore germination in *Anthoceros* (Fig. 8.9A-H) starts by rupturing of the exospore along the triradiate ridge, the endospore protrudes as a papilla and forms a germ tube. The plastid, oil globules and other food materials of the spore pass into the germ tube. Initial two divisions in the germ tube are transverse, forming a 3-celled short filament (Fig. 8.9 D, E). A cylindrical elongated young gametophyte is resulted soon. For more details, refer to Article 8.5.14 (Fig. 8.9 A-H).

In *Notothylas*, a spore germinates to form a mass of cells which is known as a germ disc. It is made up four or eight cells. One or two basal cells of the germ disc extend to form rhizoids. They are not separated by any wall. A marginal meristem soon differentiates and initiates the growth of the thallus.

SPORE GERMINATION AND FORMATION OF GAMETOPHYTE IN MOSSES (BRYOPSIDA) 13.7

Bryopsida usually possess a well-branched filamentous protonema, from which develop numerous buds (Fig. 13.2 A-G). Thalloid protonema is rarely seen amongst Bryopsida, except *Andreaea*, *Sphagnum*, *Tetraphis* and a few more members.

Each bud produced on the filamentous protonema shows differentiation of a tetrahedral apical cell. It divides and redivides to form a leafy shoot system of gametophore. Protonema of most mosses has a heterotrichous structure, of which the prostrate multicellular filaments creep on the substratum, and from these filaments develop lateral erect filaments.

13.7.1 Formation of Buds

A bud develops as a lateral protrusion from a cell of the parent filament. Usually, it develops just behind a septum. It first divides transversely to form one or two stalk cells and an upper cell. The upper cell swells, divides by three successive oblique divisions to form a future gametophore. Usually, a bud develops near the base of the parent filament of the aerial erect system, but variations occur commonly in different mosses. Both prostrate as well as erect green branches bear buds in many mosses including *Ceratodon*, *Mnium* and *Pohlia*.

13.7.2 Requirements for Bud Formation in Mosses

In the normal conditions, certain minimum light intensity and sugar requirements are essential for bud formation. It has been experimentally proved that kinetin "acts as an agent which creates centres of attraction in moss protonema" (Bopp, 1963). Adequate nutrients and certain growth substances are also the major requirements for bud formation in *Pohlia nutans*, *Tortella caespitosa* and some more mosses. It has been proved experimentally by various workers that there is a definite role of light for the germination of spores in bryophytes (Valanne, 1971; Cove et al. 1978, Schield, 1981). Low temperatures are helpful in germination of liverwort spores. For more details of the role of temperature in spore germination, consult Steiner (1964), and Chopra and Sood (1973).

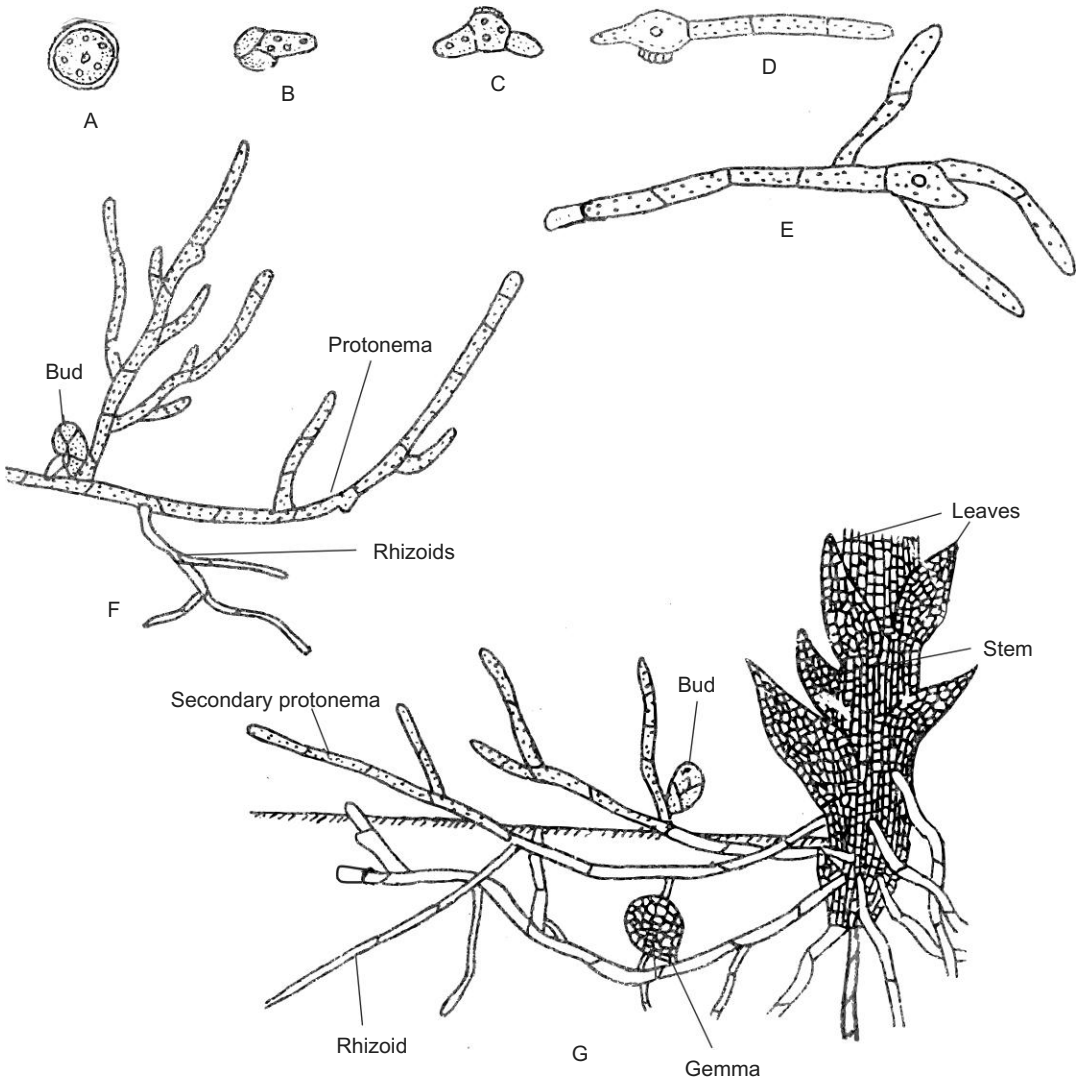


Fig. 13.2A-G Spore germination in *Funaria hygrometrica*

13.7.3 Protonema of Some More Mosses

In *Buxbaumia aphylla* (Fig. 13.3A), the protonema is persistent, green, filamentous and much branched. The leafy gametophores arising from it are small. Persistent protonema also develop in some more genera including *Pogonatum aloides*, *Nanobryum dummari* and *Schistostega pinnata*.

In *Ephemeropsis tjibodensis* (Fig. 13.3B), the protonema is quite extensive while the gametophore is very small. From the flanks of the main axis of this moss shoot out anchoring organs called **hapteres**. Well-branched forked green assimilatory short shoots develop from the dorsal surface.

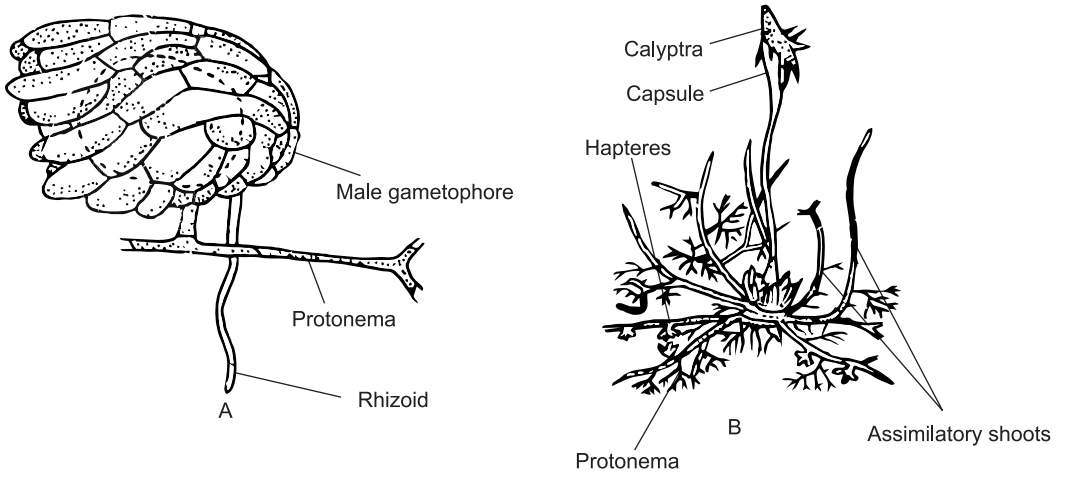


Fig. 13.3 Protonema of *Buxbaumia aphylla* (A) and *Ephemeropsis* (B)

SPORE VIABILITY 13.8

Spores of liverworts remain viable for a few weeks to a few months while that of mosses remain viable for several years. Amongst liverworts also, the foliose or leafy liverworts growing in mesic environment have a shorter period of viability while the thalloid liverworts, growing comparatively in xeric environment have a longer period of viability for many months. Looking over the mosses, the spores of *Sphagnum* remain viable from two to three years while that of *Funaria hygrometrica* remain viable for 10 to 12 years, and that of *Oedipodium* remain viable for as much as 20 years or even more.

POLARITY IN SPORE GERMINATION 13.9

Polarity means existence of a definite axis. Bryologists (Bentrup, 1968); Schulz, 1972; Olesen and Mogensen, 1978; Brown and Lemmon, 1980) have worked on polarity in bryophytes. It has been conclusively established that spore germination in bryophytes show polarity. Spores of Marchantiales and some other investigated thalloid bryophytes are polar structures. On the other hand, spores of mosses are apolar structures, and they generally do not show polarity in their spores. According to Brown and Lemmon (1980), however, the subcellular structure of moss spore shows an innate polarity. The term "*innate*" actually refers to behaviour which normally occurs in all members of a species despite natural variation in environmental influences.

TEST YOUR UNDERSTANDING

1. Give a precise definition of spore.
2. In bryophytes, pteridophytes and _____, the spores are haploid and are produced in the _____.
3. In bryophytes, the spores are produced as a result of which division: mitosis or meiosis?
4. The spore formation in bryophytes represents the beginning of _____ phase.
5. In bryophytes, the spores are always which type of structures: diploid or haploid?
6. What is the first cell of a gametophytic generation in bryophytes?
7. Write an essay on spore germination and formation of gametophyte in bryophytes in about 500 words.
8. Leaving aside only a few exceptions, are all bryophytes homosporous or heterosporous?
9. Write a brief scientific note on size and output of spores.
10. Size of the spore of which of the following bryophytes is smallest?
    (a) *Dawsonia,* (b) *Marchantia polymorpha,* (C) *Corsinia,* (d) *Archidium*
11. Give an account of spore germination and formation of gametophyte in liverworts.
12. What is protonema? Describe it with particular reference to Jungermanniales.
13. Describe spore germination and gametophyte formation in Bryopsida (mosses).
14. Write scientific notes in about 100 words each on the following:
    (a) Spore viability in bryophytes
    (b) Polarity in spore germination in bryophytes

14

Factors Affecting Sexuality in Bryophytes

MAJOR FACTORS AFFECTING SEXUALITY 14.1

Besides widespread occurrence of vegetative reproduction, the bryophytes also reproduce sexually, provided necessary climatic conditions are available in their surroundings. Sexual reproduction in any group of plants or animals is also necessary and essential because this is the only way for genetic variability, which is required for existence and evolution of the group.

In bryophytes, initiation of gametangia, their development and appearance of sporophytes are influenced by a variety of factors including (i) photoperiod, (ii) temperature, (iii) carbohydrates, (iv) nitrogenous substances, (iv) pH and hydration of medium, and (iv) growth regulators. All these factors affect sexuality in bryophytes, and are discussed briefly here in this chapter.

INFLUENCE OF PHOTOPERIOD ON SEXUALITY 14.2

"The number of hours of daylight needed by a plant before it will begin to flower" is called **photoperiod**, and this phenomenon of the "physiological responses of an organism to changes in the lengths of day and night is called **photoperiodism**". The photoperiodic control of sexuality in bryophytes was first studied by Wann (1925), and these details were published in the ***American Journal of Botany***. In several further studies of different workers, it was established that photoperiodic control of gametangial initiation is more prevalent amongst Hepaticopsida and Anthoceropsida than Bryopsida or mosses. As we see commonly among angiosperms, in bryophytes also there exist long-day plants, short-day plants and also day-neutral plants. Differing from angiosperms, however, the photoperiod in bryophytes refers to "hours of duration of light during 24-hour cycle" and it does not refer to length of the dark period, which is actually very critical for control of flowering in higher plants.

14.2.1 Long-day Bryophytes

Wann (1925) was the first to report *Marchantia polymorpha* as a long-day bryophyte. During long days, it grows more vigorously and becomes fertile by producing gametangia. During short days, only

a few or no gametangia are produced by this liverwort. Some other bryophytic taxa which have been reported by different workers as long-day plants are *Conocephalum conicum*, *Diplophyllum albicans*, *Lophocolea cuspidata*, *Pellia epiphylla* and *Riccardia multifida*. All these produce gametangia only when they receive 16–18 hours of light per day.

Proskauer (1967) confirmed experimentally that a hornwort (*Phaeoceros laevis*) from western Himalayas is a long-day bryophyte. It grows luxuriantly and produces gametangia only during long days.

Amongst the long-day bryophytes, temperature also plays a definite role besides light intensity for initiation of gametangia. *Pellia epiphylla*, a long-day bryophyte, produces more gametangia at higher temperatures. *Marchantia polymorpha* becomes more fertile during long days when the temperature is above 20°C, and it produces only a few or no gametangia during long days when the temperature is below 10°C. Dua et al. (1982) proved *Riccia gangetica*, a common liverwort of Indo-Gangetic plains, to be a long-day bryophyte.

Plagiomnium undulatum, a moss of Britain, is a long-day plant and produces male and female gametangia only during high intensity of daylight of 15 to 18 hours per day. Some other mosses which fall under the category of long-day plants are *Barbula gregaria*, *Bryum argenteum* and *Bartramidula bartramioides*.

14.2.2 Short-day Bryophytes

Asterella tenella and *Targionia hypophylla* of Hepaticopsida; *Anthoceros laevis*, *Notothylas orbicularis* and *Phaeoceros laevis* of Anthoceropsida; and *Sphagnum subnitens* of Bryopsida are some examples of short-day bryophytes. According to Bapna et al. (1984), *Targionia hypophylla* produced archegoniophores only under cool short-day conditions. Mosses are seldom short-day plants, except a few, e.g. *Sphagnum subnitens*.

14.2.3 Day-Neutral Bryophytes

A majority of mosses and only a few liverworts are day-neutral bryophyte, and in all such genera, the gametangial initiation is independent of the length of the day. Amongst the mosses, common day-neutral members are *Funaria hygrometrica*, *Laptobryum pyreforme*, *Physcomitrium pyriforme* and *Polytrichum aloides*. *Cryptothallus mirabilis* of Metzgeriales (Hepaticopsida) is a day-neutral bryophyte, in which initiation of gametangia is independent of the length of the day. In this member of Metzgeriales, the initial requirements of the initiation of gametangia are cold environment and then rise in temperature up to 21°C and there is not much role of the day length.

INFLUENCE OF TEMPERATURE ON SEXUALITY 14.3

As mentioned earlier also under Article 14.2, besides photoperiod, temperature also influences and controls the initiation and development of sexuality in bryophytes. There are, however, many bryophytes which are not sensitive to temperature and form sex organs in a wide range of temperature from very low to very high.

On the basis of the influence of temperature on sexuality, all bryophytes may be grouped under the following five categories:

1. A cold-conditioning of some of the bryophytes is a prior condition for the gametangial initiation.
2. Formation of gametangia in some bryophytes is possible only at low temperature. Higher temperatue in such bryophytes inhibits gametangial formation.
3. Formation of gametangia in some bryophytes is possible ony at fairly high temperature.
4. Formation of gametangia in some bryophytes is inhibited at low temperature and possible only at temperatures above 21°C.
5. Formation of gametangia takes place over a wide range of temperatures, i.e. these bryophytes are insensitive to temperature.

In *Cryptothallus mirabilis* and *Lunularia cruciata*, gametangia are formed at 20–21°C but both these liverworts have an obligate requirement of cold-conditioning of their thalli at 4–10°C as a stimulus. In *Funaria hygrometrica*, gametangia are formed when day and night temperatures are maintained at 10°C and 7°C, respectively. Plants of this common moss remain sterile when day and night temperatures are at 5°C and 3°C and also 17°C and 15°C, respectively. According to Benson-Evans (1964), *Riccia glauca* in Britain is a short-day bryophyte and forms gametangia when day and night temperatures are 18°C and 10°C, respectively. Its plants remain sterile at 21°C. However, Chopra and Sood (1973) reported that gametangia formation in *Riccia crystallina* in India is at its peak at a temperature range of 8 to 15°C. Kumra and Chopra (1984) also demonstrated the temperature requirements for initiation of gametangia as 20°C in *Philonotis turneriana*. In *Leptobryum pyreforme*, the plants remain sterile at 25°C, but at 20°C only a few plants become fertile. Early gametangial initiation in very large number of plants in *L. pyreforme* is observed when the temperature is as low as approximately 10°C. It shows protrandrous condition also, i.e. antheridia develop first and archegonia later on. Benson-Evans (1964) demonstrated that the moss *Polytrichum aloides* and two liverworts (*Marchantia polymorpha* and *Conocephalum conicum*) show their specific temperature requirements of gametangial initiation as 21°C. All these three bryophytes remain sterile at low temperatures. Some mosses (e.g. *Barbula gregaria*, *Bartramidula bartramoides* and *Bryum argentatum*) and liverworts (e.g. *Pellia epiphylla*) develop gametangia under a wide range of temperature.

INFLUENCE OF CARBOHYDRATES ON SEXUALITY 14.4

Wann (1925), while studying sexuality in bryophytes, observed that in *Marchantia polymorpha* the sex-organ initiation takes place at a higher carbohydrate/nitrogen ratio. Rao and Das (1968) also confirmed this finding in some other bryophytes including *Plagiochasma articulatum*, *Reboulia hemispherica* and *Fimbriaria angusta*.

Excess of sugar shows inhibitory effect on sexuality in several Hepaticopsida members including *Athalamia pusilla*, *Fossombronia himalayensis*, *Riccia crystallina* and *R. frostii*. Even in the absence of carbohydrate supply, the gametangial formation takes place in some mosses, e.g. *Barbula gregaria* and *Bryum argenteum*. However, Dua et al. (1982) opined that sucrose is more effective for initiation of sexuality in *Riccia gangetica* and *R. crystallina*.

INFLUENCE OF NITROGENOUS SUBSTANCES ON SEXUALITY 14.5

It has been proved experimentally that in liverworts, inorganic nitrogen proves inhibitory for gametangial formation while organic nitrogen favours it. Sood (1974) proved experimentally in *Riccia crystallina* that if organic nitrogen is supplied in the form of either urea, casein hydrolysate or yeast extract, it favours formation of archegonia. Almost similar results were seen in *Riccia frostii* and *Pohlia nutans* by other workers. Antheridial formation, however, is not affected by the supply of these nitrogenous substances. Woodfin (1976) proved that in several species of *Riccia*, including *R. flutians*, the gametangial formation stops if concentration of ammonium nitrate is reduced to half.

INFLUENCE OF pH AND HYDRATION OF MEDIUM ON SEXUALITY 14.6

pH is actually the negative of the logarithms of hydrogen-ion concentration in aqueous solution. Low pH is acid while high pH is alkaline. pH of 7 is neutral. pH and hydration of medium show definite effect on sexuality in bryophytes. A few such examples are listed below:

1. In *Sphaerocarpos donnellii*, male plants grow well in alkaline medium or near-neutral medium whereas female plants grow well in low pH.

2. Dua (1983) observed that in *Riccia gangetica*, the maximum antheridial formation is seen at a pH of 4.5 while initiation of archegonia is optimum in alkaline pH of 7.5

3. Rahbar and Chopra (1982) observed that in *Bartramidula bartramioides*, a moss, the optimum negative growth takes place at a pH of 4.5, and as the pH increases, the vegetative growth declines. The optimum initiation and development of gametangia in this moss is seen at a pH of 7.5.

4. Sood (1974) observed in *Riccia crystallina* that level of mineral elements and hydration of medium affect the initiation of gametangia in this common Hepaticopsid. If level of mineral elements and hydration of medium is reduced, it favours maleness. On th the other hand, higher levels favour femaleness.

5. Vashistha (1985) observed that female thalli of *Riccia frostii* remain sterile in liquid medium while they start producing archegonia in agar cultures.

6. Differing from this trend of *R. frostii*, Kumar (1981) observed that in mosses (e.g. *Barbula gregaria*), the initiation of gametangia is delayed in the presence of agar, and an increased response of gametangial initiation is observed in liquid medium.

INFLUENCE OF GROWTH REGULATORS ON SEXUALITY 14.7

Almost all categories of hormones (auxins, gibberellins, cytokinin) have been reported to promote initiation of sexuality in bryophytes. They are effective individually as well as in combination.

14.7.1 Auxin

"**Auxin**" is actually a general name for an important group of plant hormones. Indole Acetic Acid (IAA) is the most common auxin. Auxins have been reported to favour femaleness in liverworts. If IAA is applied on the vegetative thalli of *Marchantia polymorpha*, it results into the formation of structures similar to the receptacles. Almost similar results are seen if the auxin 2, 4-D (2, 4-Dichlorophenoxyacetic acid) is applied. (2, 4-D is a "synthetic auxin used as a selective herbicide and in media for tissue culture"). Rao and Das (1968) observed initiation of archegonia by increasing the level of IAA in several bryophytes including *Asterella angusta*, *Pallavicinia canarus*, *Plagiochasma articulatum* and *Reboulia hemispherica*. Chopra and Sood (1973), Kumra and Chopra (1984), and Vashistha (1985) observed that auxins favour femaleness in several species of *Riccia*, including *R. crystallina*, *R. frostii* and *R. gangetica*. Much work has not been done on the role of auxins in the initiation of sexuality in bryophytes. Chopra and Kumra (1983) observed that IAA stimulates the formation of antheridia in two mosses, viz. *Barbula gregaria* and *Bryum argenteum*.

14.7.2 Gibberellins

Gibberellins are a group of chemically complex plant hormones, important in control of tropisms, the lengthening of cells during growth, germination and other processes. Gibberellins promote maleness in liverworts as well as in mosses. Chopra and Kumra (1983), and Sarla (1986) reported antheridial induction at very low level of gibberellic acid in *Philonotis turneriana* and *Riccia discolor*, respectively. In basal medium, both these bryophytes remain sterile. Chopra and Sood (1973) reported that in monoecious *Riccia crystallina*, gibberellic acid enhanced antheridial formation remarkably. Chopra and Kumra (1986) reported that the number of antheridia increased at all levels of GA_3 in *R. gangetica*. In yet another study, Chopra and Gupta (1992) observed that gibberellin suppresses formation of archegonia in female clones of *Riccia discolor*.

14.7.3 Cytokinins

Cytokinins are a group of plant hormones (e.g. kinetin), which control cell division. They support femaleness in some hepaticopsids and mosses. Chopra and Sood (1973) observed that in monoecious *Riccia crystallina*, kinetin increased the archegonia production without showing any effect on the number of antheridia. Kumra and Chopra (1984) also observed almost the same results in *Riccia gangetica*. Vashistha (1987) reported in *Riccia frostii* that application of cytokinins also promotes formation of archegonia in female plants. Chopra and Rawat (1977) studied that cytokinins show no effect on formation of sex organs in monoecious species of the moss *Leptobryum pyriforme*. Chopra and Kumra (1983) reported that cytokinins are ineffective on male clones of mosses, such as *Bryum coronatum* and *Barbula gregaria*. As reported by Chopra and Mehta (1987), cytokinin increased the frequency of fertile gametophytes in male clones of *Microdus brasiliensis*. In mosses, such as *Bryum argenteum*, a mixture of auxin and cytokinin promotes formation of both male and female gametangia.

TEST YOUR UNDERSTANDING

1. Make a list of at least five factors which affect sexuality in bryophytes.
2. Describe influence of different factors affecting sexuality in bryophytes.
3. Define the term 'photoperiod' and describe its role on sexuality in bryophytes.
4. Name at least three long-day bryophytes.
5. State whether a majority of mosses are day-neutral bryophytes or long-day bryophytes?
6. "Mosses are seldom short-day plants". Is it true or false?
7. Write a detailed note on the influence of temperature on sexuality in bryophytes.
8. Is pH of 7 acidic, alkaline or neutral?
9. Describe in detail the role of growth regulators on sexuality in bryophytes in about 200 words.

15 Alternation of Generations

WHAT IS ALTERNATION OF GENERATIONS? 15.1

"The life cycle of bryophytes, pteridophytes and spermatophytes, which consists of a haploid **gametophyte** producing gametes followed by a diploid **sporophyte** producing spores" is known as **alternation of generations**. It is actually the regular alternation of two types of individuals in the life history of plants or animals. Typically, in plants, there is alternation of a diploid sporophyte and a haploid gametophyte. If the two generations (i.e. sporophyte and gametophyte) are morphologically similar, it is known as **isomorphic alternation of generations**, but if two generations are morphologically different, then it is known as **heteromorphic alternation of generations**.

In bryophytes, the dominant generation is the gametophyte (Fig. 15.1), and it is markedly different from the sporophyte, and hence these plants show **heteromorphic alternation of generations**. The gametophyte or gamete-producing generation has a single set of genomes while the sporophyte or

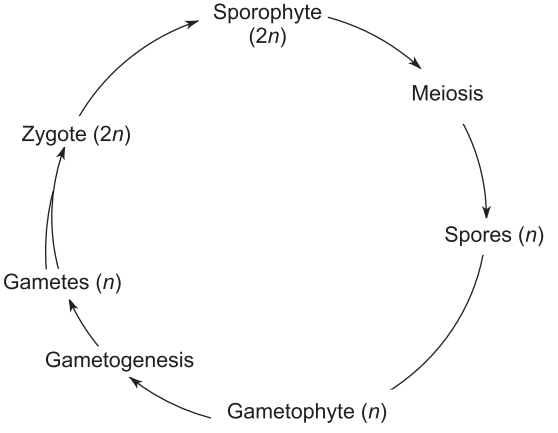


Fig. 15.1 *Diagrammatic representation of alternation of generations*

spore-producing generation is morphologically different from the gametophyte and is diploid. The sporophyte undergoes meiosis to form haploid spores which germinate to produce haploid gametophytes (n). The gametophyte undergoes gametogenesis and produces haploid male and female gametes (antherozoids and egg) that fuse sexually to form a diploid zygote, from which develops the diploid sporophyte.

WHO DISCOVERED ALTERNATION OF GENERATIONS IN ARCHEGONIATAE? 15.2

"**Archegoniatae**" includes the plants having archegonia, applied to bryophytes, pteridophytes and gymnosperms. Technically speaking, an "archegonium" is the female sex organ of bryophytes, pteridophytes and gymnosperms, containing the egg inside a cellular jacket. W. Hofmeister (1851) was the first to show that life cycle of members of Archegoniatae includes two distinct and well-marked generations: (i) the **gametophyte**, which contains gamete-producing sex organs, i.e. archegonia and antheridia, and (ii) the **sporophyte**, which produces the asexual spores; and both these generations (i.e. gametophyte and sporophyte) appear one after another in regular alternation succession to complete the life-cycle, and this entire cycle represents **alternation of generations**. Hofmeister's 1851 findings were published in the book ***Vergleichende Untersuchungen***.

WHAT ARE ANTITHETIC ALTERNATION AND HOMOLOGOUS ALTERNATION OF GENERATIONS? 15.3

It was L. Celakovsky (1874) who coined these two terms (**antithetic** and **homologous**) in connection with alternation of generations, and explained them as under

1. **Antithetic** means heteromorphic. The term describes the life cycle in which the alternating generations are morphologically and physiologically distinct, as in bryophytes and pteridophytes. Celakovsky (1874) explained it as "antithetic alternation of two generations phylogenetically distinct, i.e. where a new stage (sporophyte) has been interpolated between pre-existing generations (gametophytes)". According to him, this type of alternation might have probably developed" independently in several different groups, but was most evident in Archegoniatae" (Celakovsky, 1874).
2. **Homologous** means isomorphic. The term describes the life cycle in which alternating generations are morphologically identical, as commonly occurs in algae (e.g. *Dictyota*) and fungi. Individuals may be identified as sporophyte or gametophyte by observation of the reproductive process. Such life cycles are seldom seen in archegoniate plants. Celakovsky (1874) explained it as "homologous alternation of two or more generations phylogenetically similar to one another, but differing in the presence or absence of sexual organs."

PHENOMENA OF APOGAMY AND APOSPORY 15.4

In connection with nature of alternation of generations and origin of sporophytes, two phenomena were later on recognised. These were termed *apogamy* and *apospory*.

1. Apogamy Apogamy was first discovered by Farlow in 1874 but the name (apogamy) to this phenomenon was given by De Bary in 1874. *Apogamy* is a phenomenon of asexual reproduction in which embryos and propagules are produced without the occurrence of meiosis. Thus, the sporophyte might develop vegetatively from the gametophytic tissue without the process of fertilization.

2. Apospory Apospory was first discovered by Pringsheim in 1876. *Apospory* is a phenomenon of production of a diploid gametophyte from the vegetative cells of the sporophyte, i.e. without the production of spores.

ANTITHETIC THEORY 15.5

It is also called **interpolation theory** or **intercalation theory**. As mentioned earlier also, the antithetic theory was first proposed by Celakovsky in 1874. According to this theory, the "gametophyte (or sexual) generation is original or historically a prior generation, while the sporophyte (or spore-producing) generation" is completely a new phase. This new sporophytic phase is "derived from the progressive elaboration of the zygote of some algal ancestor". This phase is also intercalated or interpolated into the life cycle, during the course of evolution, "between the successive events of fertilization and meiosis, and is therefore different in structure from the gametophyte from its very inception" or right from the very beginning.

FO Bower (1935) has been the main supporter of **antithetic theory** of Celakovsky (1874) besides many others, including E Strasburger (1894), F Cavers (1911) and DH Campbell (1940). According to this theory of alternation of generations, the sporophyte originated from the zygote (or unicellular sporophyte) of some ancestor of filamentous green algae, e.g. *Oedogonium*. From this simple unicellular sporophyte or zygote, the complex sporophyte evolved gradually by progressive elaboration, of course, through several undermentioned stages:

1. First Stage The life cycle in the earliest hypothetical land plants would be resembling to that of many filamentous green algae, e.g. *Oedogonium* (Fig. 15.2A), in which the sporophyte would be represented by unicellular diploid zygote. It divided meiotically to form four haploid zoospores, also called zoomeiospores (Fig. 15.2B-E).

2. Second Stage *Coleochaete*-like (Fig. 15.3) green algal members represented this stage, in which the zygote increases greatly in size and divides meiotically to form 16–32 biflagellate swarmers or zoospores. Reduction division in this genus takes place in the first dividion of the diploid zygote, and thus the contrasting type of *Coleochaete* individual, formed from the zygote, is haploid in nature.

3. Third Stage (Simplest Sporophyte) In this next stage, the zygote is retained within the archegonium and did not divide meiotically. It first divided mitotically to form a diploid multicellular body of spore-producing cells. Each such spore-producing cell is diploid, divided meiotically to form four haploid spores. Although hypothetical, but this would have been the **simplest type of multicellular sporophyte of plants** possessing multicellular embryo (i.e. **Embryophyta**, which includes bryophytes, pteridophytes and spermatophytes). In such a sporophyte, all the cells were sporogenous. However, it differs in structure from the gametophyte.

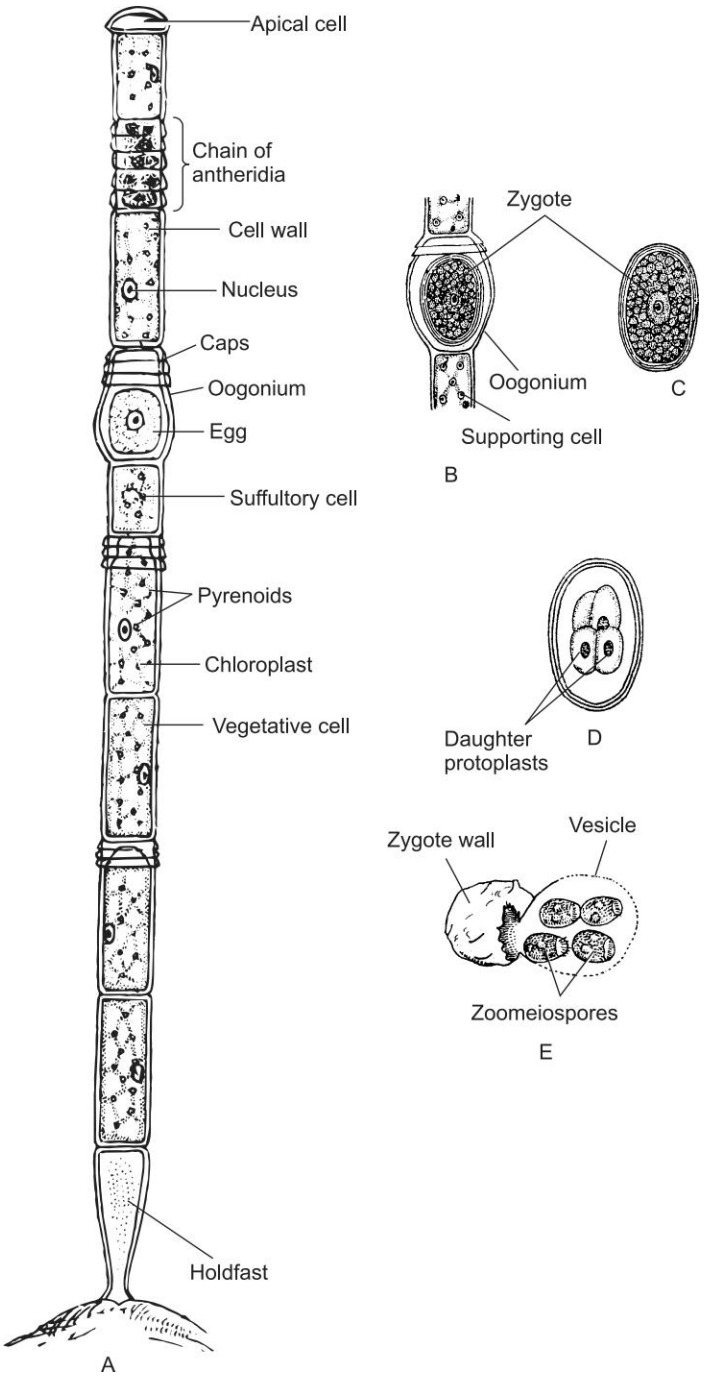


Fig. 15.2 A-E *Oedogonium. A,* A filament of monoecious species; B-C, Zygotes present inside and outside the oogonium; D, Showing four daughter protoplasts formed after meiosis; E, Showing haploid zoomeiospores

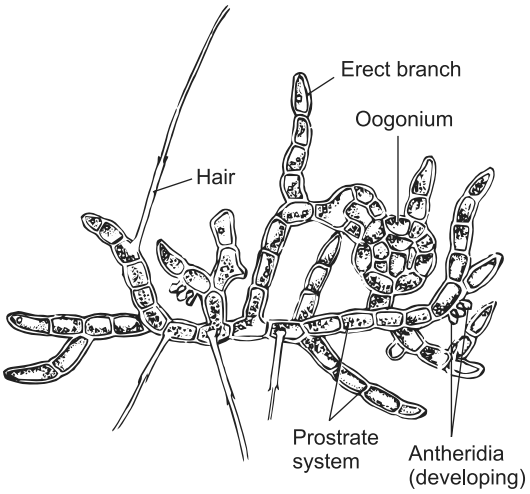


Fig. 15.3 *Coleochaete divergens*

4. Fourth Stage This stage is seen in *Riccia* (Fig. 15.4 A) in which the diploid zygote divided and redivided to form a multicellular, spherical diploid body, of which the outermost layer became sterile and formed the jacket while the inner central mass remained sporogenous and diploid in nature. Now, reduction division took place in each cell of the diploid sporogenous tissue to form four haploid spores. There was no differentiation of the foot, seta and capsule in this simple stage of sporophyte. Its growth was also limited, and it remained surrounded by a single-layered jacket. A very large part is thus capable to form the spores.

According to F O Bower, it was this above-mentioned type of **simple sporophyte of *Riccia***, from which evolved the more complex types of sporophytes of Embryophyta (i.e. bryophytes, pteridophytes and spermatophytes), and all this happened by "progressive sterilization of potentially sporogenous tissue". **A series** can be traced amongst different members of bryophytes which shows (i) ever-increasing sterilization of sporogenous tissue, and (ii) such a sterilized tissue shows its regular diversion to somatic functions. From simple sporophyte of *Riccia* developed most complex type of sporophytes of mosses, e.g. *Funaria* and *Polytrichum*, via a series of different other members of bryophytes.

5. Fifth Stage In *Riccia crystallina* and *Oxymitra*, a stage slightly ahead of *Riccia* is seen of "progressive sterilization of potentially sporogenous tissue." Both these contain a simple sporophyte made up of a single-layered sterile jacket which encloses a mass of sporogenous tissue. But some of the potential spore mother cells remain unable to produce spores. They instead form absorptive **nutritive cells**. These cells have been considered forerunners of true elaters.

6. Sixth Stage It is seen in genera such as *Sphaerocarpos* (Fig. 15.4 B) and *Corsinia*. The entire basal part of the sporophyte gets sterilised in these members in the form of a small sterile foot made of only a few cells in *Corsinia*, or a small bulbous foot and a 2-cells broad, narrow seta in *Sphaerocarpos*. A single-layered sterile jacket also surrounds the capsule in both *Corsinia* and *Sphaerocarpos*, as in the fourth and fifth stages described above. Sterile nurse cells are also present in the *Corsinia* capsule.

These nurse cells are homologous with elaters but lack their characteristic thickenings. Presence of capsule at the apex and a foot at the base shows the existence of polarity amongst both *Corsinia* and *Sphaerocarpos*.

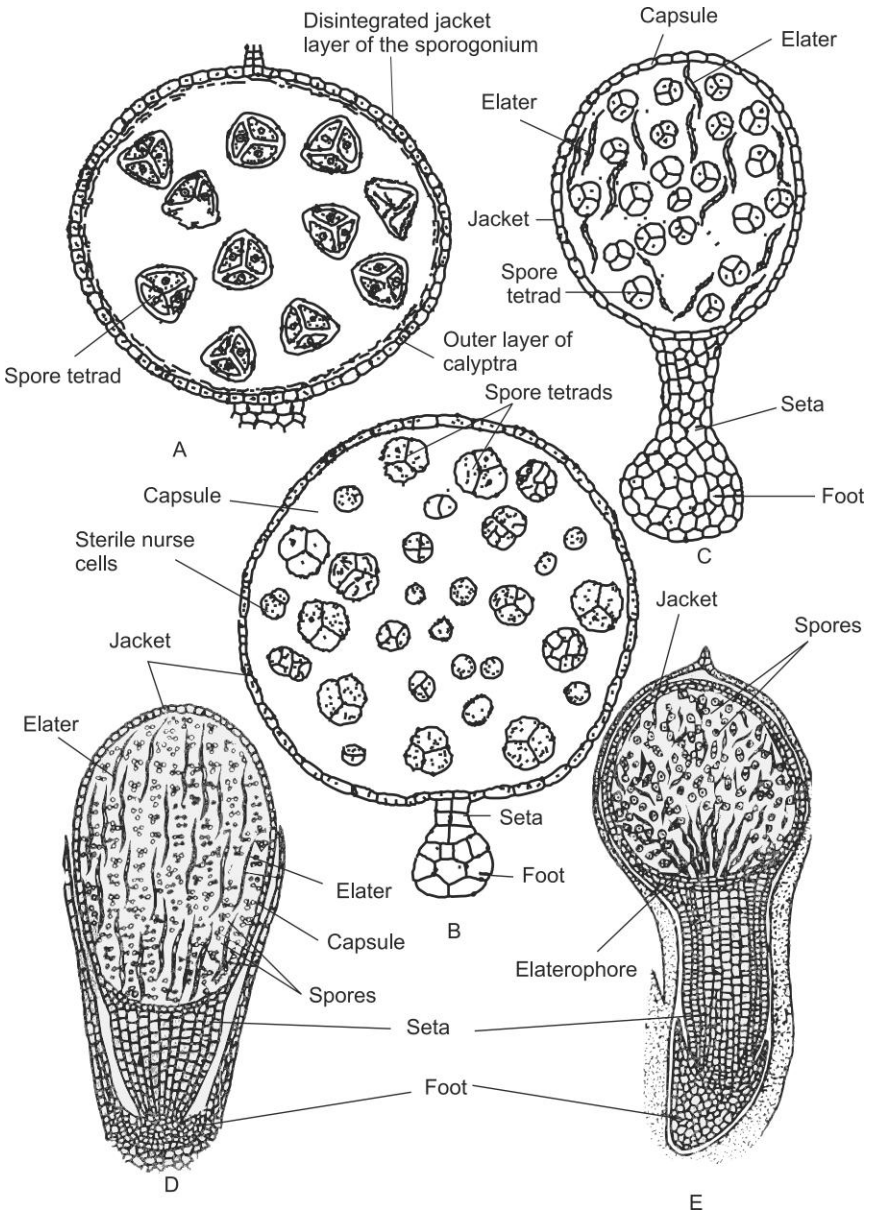


Fig. 15.4 Evolutionary series of sporophytes in bryophytes. A, *Riccia;* B, *Sphaerocarpos stipitatus;* C, *Targionia hypophylla;* D, *Marchantia polymorpha;* E, *Pellia epiphylla*

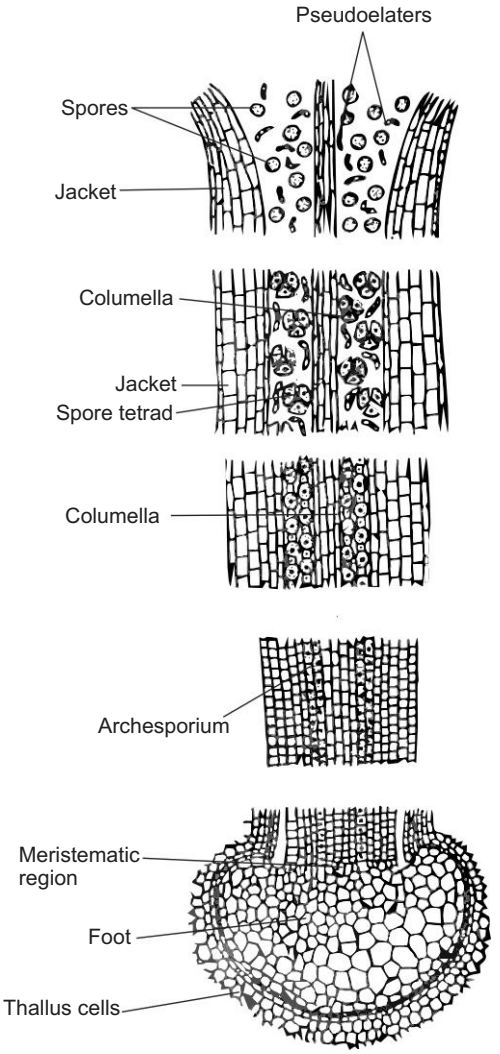


Fig. 15.5 Longitudinal sections of different stages of sporophyte of *Anthoceros*

7. Seventh Stage *Targionia* (Fig. 15.4C) shows this next stage of evolutionary series of sporophytes, in which more sterile region is present than in the sixth stage. The sterile region includes a broader foot, a more developed and long seta, a single sterile jacket layer of jacket of the capsule and about half of the sporogenous cells becoming sterile in the form of several elaters, each with 2 or 3 spiral thickenings.

8. Eighth Stage *Marchantia polymorpha* (Fig. 15.4D) shows the next stage of evolution among sporophytes of bryophytes, in which more sterile tissue is present in the form of (i) broad foot, (ii) more developed, long and thick seta, (iii) single-layered sterile jacket of capsule, (iv) sterile cells in the form of cap at the apex of the capsule, and (iv) long and well-developed large number of spirally thickened elaters.

9. Ninth Stage In *Pellia epiphylla* (Fig. 15.4E) and *Riccardia*, sterilization of potentially sporogenous tissue is more developed than the above-mentioned eighth stage of *Marchantia*. In both these genera, the sterile tissue consists of a large foot, more developed seta, two to many-layered sterile jacket around the capsule, diffused elaters and a sterile mass of cells in the form of elaterophore, either at the basal end of the capsule (*Pellia*, Fig. 15.3E) or at the apical end of the capsule (*Riccardia*). Only a very small percentage of actual sporogenous tissue is present in the sporophyte in the form of spores.

10. Tenth Stage More sterilization of potential sporogenous tissue is seen in this stage, exemplified by *Anthoceros* (Fig. 15.5). The sterile tissue in the sporophyte includes (i) a massive foot, (ii) a 4 to 6-layered capsule wall, (iii) a central column of elongated cells in the form of columella, and (iv) pseudoelaters. The sporophyte in Anthocerotoes becomes more independent due to the presence of chlorophyllous tissue, an epidermal layer and presence of stomata in the epidermis.

11. Eleventh Stage In *Funaria hygrometrica* (Fig. 15.6), *Polytrichum* and some other higher bryopsida, there is seen the height of the sterilization of the potentially sporogenous tissue. The sterile tissue is present in the form of a large foot, very long seta, apophysis, multilayered capsule wall, per-

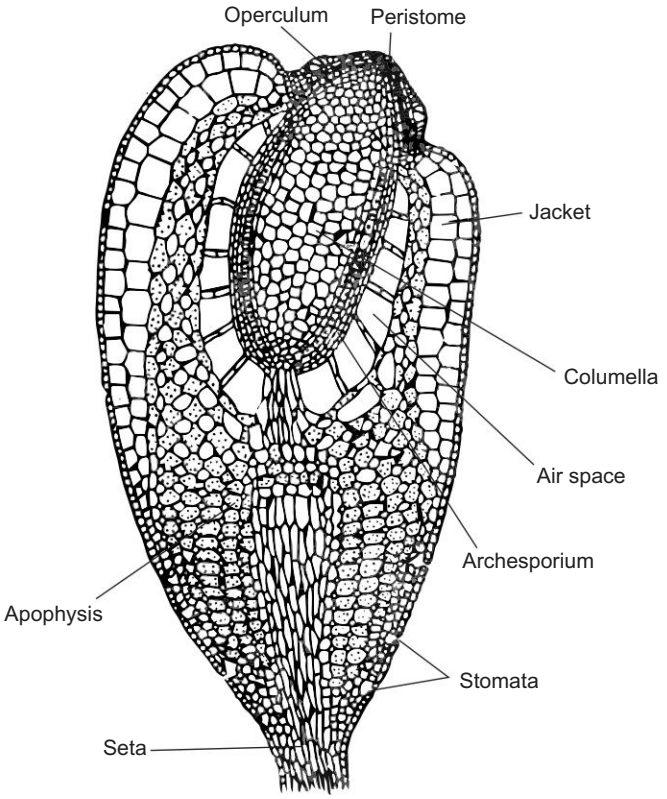


Fig. 15.6 Longitudinal section of the capsule of *Funaria hygrometrica*

istome, operculum, a well-developed columella and also aerenchyma and wall around the spore sac. The potential sporogenous tissue is present only in the form of spores in the spore sac.

During course of time there was seen more elaboration of the sterile vegetative structure of the sporophyte, and due to the development of roots and leaves, the sporophyte became independent and achieved a dominant phase of the life cycle. Bower put forward the view that origin of alternation of generations is also related with a change in habit from aquatic to subaerial life or terrestrial life.

FINAL PICTURE ABOUT NATURE AND EVOLUTION OF PRIMITIVE SPOROPHYTE 15.6

15.6.1 View of Bower and his Supporters

Botanists such as Bower (1908), Cavers (1910), Campbell (1940) and several of their supporters believe that the most primitive sporophyte is the simplest sporophyte of *Riccia*, and from this simplest sporophyte evolved the more advanced type of sporophytes by progressive sterilization of potentially sporogenous tissue. This all happened through various stages discussed above under "Antithetic Theory" (Article 15.5).

15.6.2 View of Kashyap and his Supporters

Shiv Ram Kashyap (1919) and his supporters (Church, 1919; Evans, 1939 and others) believe differently, and opined that "the simplest sporophyte of *Riccia* is not a primitive type, but it is a reduced type evolved as a result of **descending or regressive evolution**", to which they called "**progressive simplification**". It was AH Church (1919), who proposed his theory that "the hypothetical ancestral sporophyte of Bryophyta was an erect leafy shoot, which was independent." During the process of descending or regressive evolution, this erect leafy sporophyte passed through the following changes:

1. It attached permanently to the gametophyte.
2. Its leaves lost because of desiccation and intense isolation.
3. It became more dependent on the gametophyte because of the disappearance of air spaces in its photosynthetic system.
4. Its chlorophyll-containing tissue became reduced.
5. Its stomata became functionless (e.g. *Sphagnum*).
6. After becoming functionless, the stomata disappeared completely (e.g. Marchantiales).

Church (1919) thus opined that sporophytes of Bryopsida (e.g. *Funaria*, *Polytrichum*) and Anthocerotopsida (e.g. *Anthoceros*) are (i) "primitive and nearer to the ancestral type", (ii) "markedly reduced and simplified", as that of Marchantiales (e.g. *Marchantia*), and (iii) "highly reduced", as in *Riccia*.

HOMOLOGOUS THEORY 15.7

15.7.1 What is Homologous Theory?

It is also called "**modification theory**" or "**transformation theory**", and it was N Pringsheim (1876, 1878) who proposed this theory. According to this theory, "the sporophyte and gametophyte generations are fundamentally similar in nature and the sporophyte is a direct modification of the gametophyte and is not a new structural type" (Pringsheim, 1876, 1878). The homologous theory of Pringsheim got support from several eminent botanists, including Zimmermann (1930), Bold (1938) and Fritsch (1945).

15.7.2 Some Evidences to Support Homologous Theory

Listed under are the evidences which support the homologous theory of alternation of generations:

1. Existence of isomorphic alternation of generations in a large number of algae belonging to Cladophorales, Chaetophorales, Ulvales, Dictyotales and Ectocarpales.
2. Existence of photosynthetic tissue in sporophytes of several members of Bryopsida (e.g. *Funaria*), Anthoceropsida (e.g. *Anthoceros*), etc., which shows the nature of self-sufficiency of both gametophyte and sporophyte of these members.
3. Similarity in structure between the primitive gametophytes (e.g. *Psilotum*, *Tmesipteris*) and primitive sporophytes (e.g. *Rhynia*, *Psilotum*) of many members of pteridophyta.
4. Similarity in a large number of bryophytes and pteridophytes in the occurrence and type of phenomena like apogamy and apospory.

GENETICAL AND ONTOGENETIC VIEWS ON ALTERNATION OF GENERATIONS 15.8

Stebbins (1950), while working on variation and evolution of plants, studied some genetic aspects of alternation of generations, and proposed that "homologous theory seems more agreeable than antithetic theory".

Regarding the ontogenetic view of alternation of generations, W H Lang (1909) was the first to work on this aspect. Lang opined that "the differences in the two generations are the result of different environmental conditions on equivalent germ cells. The spore and the fertilized egg, when first formed, are conceived to be in perfect neutral condition, without any tendency to form either sporophyte or gametophyte". Lang further elaborated that in different environmental conditions (i.e. spore in the open atmosphere and damp soil, and fertilized egg inside the protected environment of archegonium), both of them start developing differently. One develops into a sporophyte while the other develops into a gametophyte. Some later workers, however, gave different views on alternation of generations.

TEST YOUR UNDERSTANDING

1. Describe various aspects of alternation of generations in bryophytes and limit your answer in approximately 500 words.
2. What do you mean by alternation of generations?
3. Explain heteromorphic alternation of generations in one sentence only.
4. Bryophytes show _____ alternation of generations.
5. 'Archegoniatae' includes plants having _____, and the term is applied to pteridophytes, gymnosperms and _____.
6. Draw a diagrammatic representation of alternation of generations.
7. Who discovered alternation of generations in Archegoniatae?
8. Explain the terms "antithetic" and "homologous" with reference to alternation of generations.
9. How will you differentiate between apospory and apogamy?
10. Who was the first to discover apogamy?
11. The term 'apospory' was coined by whom and when?
12. Write a detailed account of antithetic theory.
13. Who was the first to propose antithetic theory?
14. In bryophytes, the complex sporophyte evolved from a simple unicellular zygote gradually by progressive elaboration through about a dozen stages. Explain these various stages.
15. Who was the first to give some ontogenetic views on alternation of generations in bryophytes?
16. What is homologous theory of alternation of generations? Give some evidences which support this theory.

16 Phylogeny of Bryophytes: Role of Genosystematics

CURRENT STATUS OF MOLECULAR STUDIES ON BRYOPHYTE PHYLOGENY 16.1

Molecular studies of the recent past have made a definite impact on bryophyte phylogeny. Molecular data have contributed greatly to develop a phylogeny and modern classification of bryophytes. Widely known and still used traditional systems of classification of bryophytes in many parts of the world were based mainly on morphological data, and these have been now significantly revised. Scientists like Jonathan Shaw and Karen Renzaglia (2004) of USA and AV Troitsky and his team of collaborators (2007) of Moscow, Russia, have made significant contributions on phylogeny and diversification of bryophytes with particular emphasis on the role of genosystematics. Several results have been obtained "from nucleotide sequence data of the nuclear DNA internal transcribed spacers ITS1-21 and the trnL-F region of the chloroplast genome" (Troitsky et al., 2007).

Shaw and Renzaglia (2004) opined that "the bryophytes comprise three phyla of embryophytes, that are well-established to occupy the first nodes among extant lineages in the land-plant tree of life. The three bryophyte groups (hornworts, liverworts, mosses) may not form a monophyletic clade, but they share life-history features including dominant free-living gametophytes and matrotrophic monosporangiate sporophytes. Because of their unique vegetative and reproductive innovations, and their critical position in embryophyte phylogeny, studies of bryophytes are crucial to understanding the evolution of land-plant morphology and genomes". These workers have focused also on phylogenetic relationships within each of the three divisions of bryophytes and relates morphological diversity to new insights about those relationships. Their "multilocus, multigenome studies have been successful at resolving deep relationships within the mosses and liverworts, whereas single-gene analysis have advanced understanding of hornwort evolution" (Shaw and Renzaglia, 2004)."

BRYOPHYTES AND GENOSYSTEMATICS STUDIES 16.2

Bryophytes are a group of most simply organised embryophytes (embryo-containing plants, i.e. bryophytes and vascular plants) having a dominant gametophyte and lacking a developed vascular

system. The diploid sporophyte is spore-producing and dependent on the autotrophic gametophyte. Many bryophytes are often pioneers in extreme habitats and played vital biota-forming roles in the land settlement by plants.

On the basis of existing catalogues and databases, M S Ignatov (2003) of Russian Academy of Sciences estimated that three main phyla of modern bryophytes include about 100 (hornworts), 5000(liverworts) and 10,000 (mosses) species. According to Meyen (1987), "the time of origin of bryophytes and their phyla is into well-determined from paleontological data", mainly due to bad preservation of these plants in sediments. However, Sanderson (2003) opined that age of fossil spores of bryophytes "is 440–450 million years, which is in good agreement with the most reliable molecular-genetic chronology of the origin of land plants (425–490 million ago)".

Many studies of bryophytes and genosystematics are still not available, and a majority of the studies have been done only in the last few decades. Some studies have appeared in the second half of the 1990s, and over half a dozen papers, concerning various bryophyte groups appeared in ***Bryologist*** in 2000. Some of the recent studies have been done in 2004 by B Goffinet, V Hollowell and R Magill; and in 2007 by A E Newton, R S Tagney, K S Renzaglia and J G Duckett. As mentioned also earlier elsewhere, up to "September 2007, there are 337 entries for hornworts, 5517 for liverworts, and 17,412 for mosses in the GeneBank Database" (Troitsky et al. 2007).

MACROSYSTEMATICS AND ORIGIN OF BRYOPHYTES 16.3

Prior to the researches of molecular phylogenetics, bryophytes were usually divided into two classes, viz. Bryopsida (mosses) and Hepaticopsida (liverworts). Later on, Anthocerotopsida (hornworts) were separated from thalloid bryophytes or liverworts. In modern classifications, these three groups have the rank of divisions, namely **Bryophyta, Marchantiophyta** and **Anthocerotophyta** (Kenrick and Crane, 1997). Several hypotheses of origin of bryophytes have already been proposed, and they were thought to derive from green, brown, or red algae as "an independent lineage of land-plant evolution, considered as an intermediate group of evolution from Charales to tracheophytes (vascular plants), or supposesd to be a result of reduced organisation of more advanced embryophytes" (Kenrick and Crane, 1997).

Cladistic analysis of ultrastructure and ontogenesis of male gametes of several bryophytes has suggested monophyly rather than paraphyly of bryophytes, which are, "together with *Selaginella* (lycophytes), sister to other Lycophytes and other vascular plants" according to Garbary et al. (1993). Hori et al. (1985) and Van de Peer et al. (1990) were amongst the first to apply molecular data (short sequences of 5 SrRNA) to phenetic analysis of four species of bryophytes that revealed monophyly of this group. Waters et al. (1992), however, studied and compared longer sequences (18 S and 26 S rRNA) of eight species of bryophytes and has shown a "paraphyly of bryophytes, with liverworts in the basal group and mosses and hornworts sister to vascular plants". Manhart (1994) made phylogenetic analysis of the chloroplast rbcL gene sequence of six species of bryophytes and concluded the "polyphyly of both bryophytes and vascular plants". Later on, Nickrent et al. (2000) made phylogenetic analysis of several bryophytes and suggested Anthocerotopsida (hornworts) "as a basal group of embryophytes and moss-liverwort clade as sister to vascular plants". All these molecular studies of evolution, thus give conflicting results on the relationships between three groups of bryophytes (liverworts, hornworts and mosses) and tracheophytes.

Nashiyama et al. (2004) concluded on the monophyly of bryophytes and made phylogenetic trees on the basis of their studies of "51 gene sequences from whole chloroplast genomes of 20 higher plants

and algal species". Goremykin (2005) also established the monophyly of bryophytes with hornworts as the most primitive ones, on the basis of his studies of chloroplast genomes from 17 plant species, including one species each of liverworts, hornworts and mosses.

Samigullin et al. (2002) and Troitsky et al. (2007) constructed phylogenetic trees for 38 species of bryophytes, 7 species of lycophytes and 2 species of algae "from sequences of inner transcribed spacers of chloroplast rRNA genes: ITS2, 3, and 4 using three different methods." According to the phylogenetic reconstruction of these workers, "hornworts are sister to vascular plants, liverworts comprise a basal group of land plants, whereas mosses occupy an intermediate position".

Duff et al (2007) made detailed studies published in Vol. 110 of ***Bryologist***. They have mentioned that "in a phylogenetic tree of 37 hornwort, 6 liverwort and 4 moss species reconstructed from sequence analysis of rbcL, nad 5, and 18S rRNA genes, hornworts are the most ancient, and mosses and liverworts form a clade sister to tracheophytes".

MARCHANTIOPHYTA OR LIVERWORTS 16.4

Earlier bryologists divided liverworts into two major groups dealing with (i) marchantioid or thalloid liverworts, and (ii) jungermannioid liverworts including simple thalloid and leafy taxa. Workers, like Frey and Stech (2005), Crandall-Stotter et al. (2005) and Forrest et al. (2006) developed new systems on the basis of their detailed genosystematic studies. In these studies, the data-sets used for phylogenetic reconstructions, included sequences from all major genetic compartments of the cell, viz. (i) chloroplast trnL-F, rps 4, rbcL, atp B, and psb A, (ii) mitochondrial nad5, and (iii) nuclear rRNA genes. As many as 173 liverwort species were used in these studies, and phylogenetic systems were reconstructed. Basic findings of all these findings are almost the same. A "backbone" tree of liverwort phylogeny (Fig. 16.1) was constructed by Forrest et al. (2006) published in ***Bryologist***. In this phylogenetic tree, the basal position was given to Haplomitriaceae (*Haplomitrium*) and Treubiaceae (*Treubia*). Basal position of these two families is also supported by the anatomical studies of these two genera by Renzaglia et al. (2007).

On the basis of the recent molecular studies, *Blasia*, which was earlier included under Jungermannioids, has now been included under marchantioid liverworts. An independent order (Blasiales) has been assigned to *Blasia* under an independent subclass Blasiidae of class Marchantiopsida (Article 2.3.1).

On the basis of phylogenetic studies, He-Nygren (2006) suggested a new system of liverwort classification, outlined already in Chapter 2. In this system, liverworts have been divided into three classes, viz. Treubiopsida, Marchantiopsida, and Jungermanniopsida.

ANTHOCEROTOPSIDA OR HORNWORTS 16.5

Represented by only about 100 species, Anthocerotopsida are relatively still unexplored. Genosystematic studies of Anthocerotopsida have been made by Duff et al. (2004, 2007). A new system has been proposed. A phylogenetic tree has been reconstructed from sequences of genes like rbcL, nad5, and 18SrRNA. According to these studies, *Anthoceros*, *Folioceros* and *Sphaerosporoceros* "form a separate clade (subclass Anthocerotidae) sister to most other hornworts affiliated to the subclass Notothylatidae." They have also proposed that "*Notothylas* is closer to the widespread genus *Phaeoceros*, than the latter is to the second widespread genus *Anthoceros*".

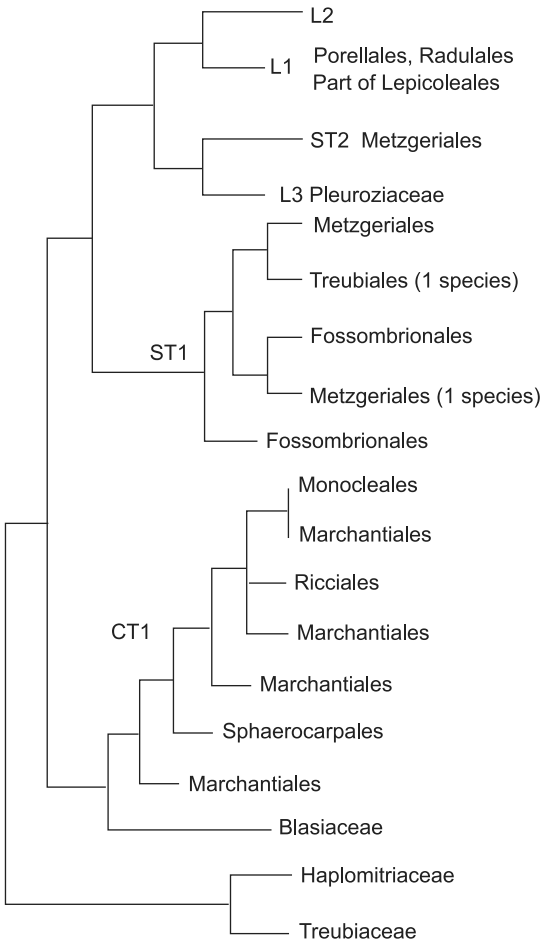


Fig. 16.1 *Phylogenetic tree of liverworts suggested by Forrest et al. 2006 (L1, L2 and L3 are leafy liverworts; ST1 and ST2 are simple thalloids, and CT1 are complex thalloids)*

Lieosporoceros, a small hornwort from Central America deserves special mention. It has a peculiarity of low-level RNA editing. Duff et al. (2007) analysed the phylogenetic relationship of this genus and compared it with other hornworts. "Based on molecular data and effect of character of RNA editing on conclusions is reported" by these workers.

BRYOPHYTA OR MOSSES 16.6

According to the modern classification proposed by Kenrick and Crane (1997), Bryophyta is now treated as a **division** along with two other divisions—Marchantiophyta and Anthocerotophyta. It includes mosses (Bryopsida). In all moss families and majority of the genera of mosses, various DNA regions have now been determined. In the latest system incorporating genosystematics data, all mosses have now been divided into eight classes, viz. Takakiopsida, Sphagnopsida, Andreaeopsida, Andreaeobryopsida, Oedipodiopsida, Polytrichopsida, Tetraphidopsida and Bryopsida (Goffinet and Buck, 2004). Five classes occupying basal positions on the phylogenetic trees are Takakiopsida,

Sphagnopsida, Andreaeopsida, Andreaeobryopsida and Oedipodiopsida. Mosses belonging to other three classes (viz. Polytrichopsida, Tetraphidopsida and Bryopsida) have peristome. It controls the dispersal of spores from the capsule of the sporophyte.

According to Troitsky et al. (2007), the position and relationship of many taxa has been drastically changed in the new system as evident from Fig. 16.2. On the basis of the conclusions made by molecular phylogenetics, these workers have suggested the following.

"Although the general idea on primitiveness of sphagnous and andreaeid mosses has been confirmed, some disagreement with systems adopted in both centuries are found, concerning, (i) two or three basal groups, (ii) inter-relation of main groups distinguished for structure of peristome, and (iii) pleurocarpous mosses, for which the former system turned out to be absolutely inadequate to new concepts." The evolutionary relationships amongst various groups of mosses on phylogenetic trees, reconstructed from analysis of various genes or their sets, are shown in Article 2.3.2 as opined by these workers (Troitsky et al 2007).

16.6.1 Importance of Peristome Architecture

In mosses, the main groups are distinguished by their peristome architecture. In very primitive groups of mosses, the peristome is made up of entire cells, whereas more complexly built ones of coalescent remnants of cell walls, which allow them to execute multivarious hygroscopic movements (Troitsky et al., 2007). Molecular data have confirmed such a general evolutionary trend." Molecular data given by Ignatova and Ignatova (2003), and Goffinet and Buck (2004) suggest that "more primitive is a double peristome with opposite elements, and both the double alternate and single peristomes are its derivatives".

16.6.2 Pleurocarpous Mosses

The mosses which have a stem with many branches, spreading across the ground are called **pleurocarpous mosses**. The reproductive organs in these mosses are borne on short side branches. Approximately 50% of the present-day moss species are pleurocarpous mosses. The mosses which have an upright stem, with the reproductive organs at the apex are called **acrocarpous mosses**. Pleurocarpous mosses form rapidly extensive coverings on trees, rocks, or soils. It is difficult to classify pleurocarpous mosses because of ecological diversity of their habitats.

On the basis of the analysis of distinct regions of chloroplast genome and also of mitochondrial genes, Troitsky et al. (2007) concluded that "diversification of pleurocarpous mosses occurred very rapidly." On the basis of such studies, Shaw et al. (2003) opined that "any construction of their reliable supported phylogeny is impossible". Troitsky et al. (2007) constructed "phylogenetic trees for 218 samples of pleurocarpous mosses reconstructed in their works from the analysis of nuclear ITS 1-2 sequences and trnL-F of chloroplast genome."

In determining the phylogeny of mosses, "the choice of genome loci used for the analysis plays an important role as well" (Troitsky et al. 2007). The set of sequences applicable for these aims is, however, very limited at present. In plant genosystematics, the nuclear genome ITSs are most variable in bryophytes among popular loci. In bryophytes, these sequences are used most frequently for studies at the species level, and can also be successfully employed at higher taxonomic level. Troitsky et al. (2007) opined further that in revealing of phylogenetic interrelations, "not only construction of trees by sequences, but also analysis of structural genome rearrangements and localisation of introns may play very important roles".

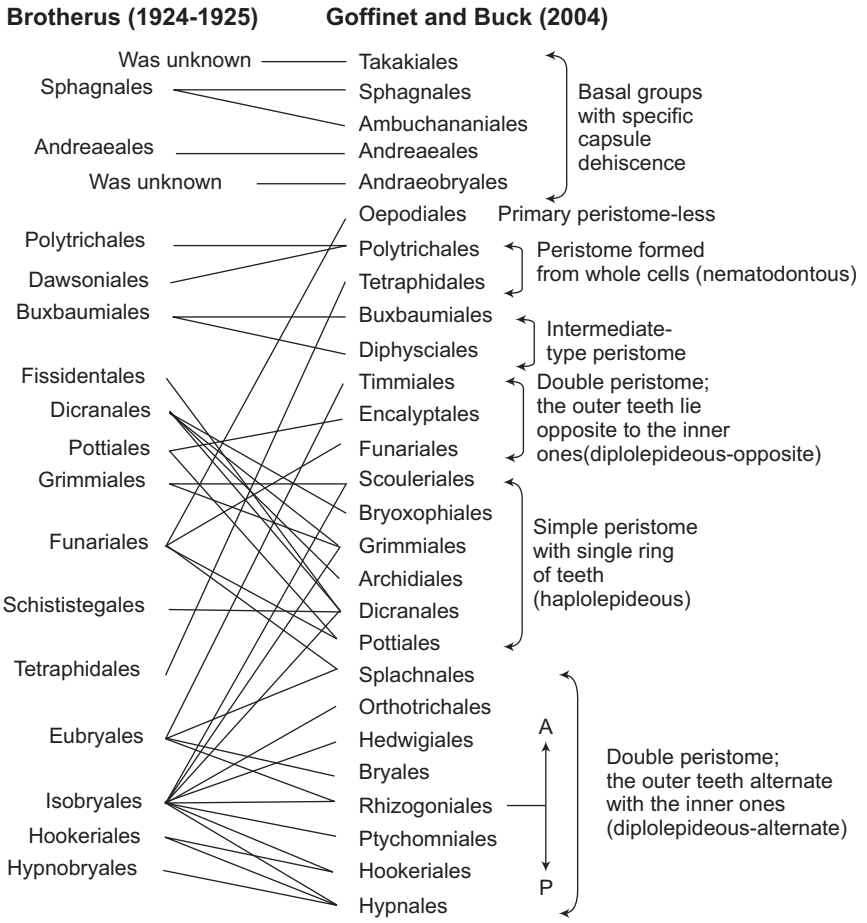


Fig. 16.2 Interrelationships between the systems of mosses suggested by Brotherus (1925) and Goffinet and Buck (2004) as also illustrated by Troitsky et al. (2007) (A, Apocarpous mosses; P, Pleurocarpous mosses)

MAJOR ROLES OF MOLECULAR PHYLOGENETICS 16.7

In solving several taxonomic problems, particularly in bryophytes, molecular phylogenetics has several major roles to play. Of these, some are listed below:

1. It has "introduced a determining contribution to the solution of phylogenetic and systematic problems in bryophytes".
2. It "opened wide perspectives for populational and micro-evolutional studies" in bryophytes.
3. Molecular phylogenetics "has provided strong impulse to the search for new morphological and anatomical markers of phylogenesis" and to provide new concepts of "morphological evolution pathways".
4. It has revealed "key groups in evolution", which has "put forward new tasks for comparative anatomy."

5. Molecular phylogenetics has a definite role in determining "the tasks for investigations on evolution of distinct systems: genetic, biochemical, physiological, anatomical and morphological".

TEST YOUR UNDERSTANDING

1. Write an essay on phylogeny of bryophytes with particular reference to role of genosystematics.
2. The evolutionary history of an organism or taxonomic group of organisms is known as _____
3. _____ is the genetic material on the sets of chromosomes in a cell.
4. Embryophytes are embryo-containing plants, i.e. all vascular plants and_____.
5. Major studies on bryophytes and genosystematics have been done during last ____ decades.
6. Give an account of macrosystematics and origin of bryophytes.
7. Hornworts include members of the class _____
8. A method of classification in which the relationships between organisms are represented by a diagram, or cladogram, based on selected shared characteristics is known as _____
9. Make a phylogenetic tree of liverworts as suggested by Forrest et al. (2006).
10. Genosystematic studies of which of the following are still least explored?
    (a) Marchantiophyta, (b) Anthocerotopsida, (c) Bryophyta
11. According to modern classification, Bryophyta is treated as a division along with two more divisions, namely Anthocerotophyta and _____.
12. Differentiate between pleurocarpous mosses and acrocarpous mosses in about 100 words.
13. Enumerate some major roles of molecular phylogenetics.

17

Morphogenesis

WHAT IS MORPHOGENESIS? 17.1

Morphogenesis is "the development of shape and structure of organs and tissues". Or, it may also be defined as "the developmental changes that give rise to the adult form from the zygote".

LIMITS OF MORPHOGENETIC STUDIES IN BRYOPHYTES 17.2

Morphogenesis is such a vast subject that it is not possible to specify its limits in one chapter of a book of this nature. The studies made on the subject during the last fifty years are so enormous that even a brief mention of all of them is neither possible nor within the scope of this book. Only certain selected undermentioned aspects are listed and discussed, in general, here briefly:

1. Germination of spore
2. Initiation of bud and its growth into gametophyte
3. Physiology of sex expression
4. Growth of diploid sporophyte
5. Vegetative propagation
6. Metabolism
7. Senescence
8. Physiology of rhizoid formation

GERMINATION OF SPORE 17.3

Stephen (1928), Mohr (1956) and many others observed that there is an absolute requirement of light for spore germination. But, workers like Kessler (1914), Meyer (1948) and many others reported that spores of some mosses also germinate in darkness on inorganic media. Besides light, some other factors responsible for germination of spores in bryophytes are (i) temperature (optimum temperature 16–25°C), (ii) moisture (in the form of liquid water or large amount of air humidity), (iii) pH (optimum

pH is more on the acid side but sometimes it is neutral or slightly on the alkaline side), and (iv) more amount of oxygen, etc.

Several studies have confirmed that sucrose accelerates the germination of spores in bryophytes (Benson-Evans, 1953; Hoffman, 1964; Valanne 1966).

Growth substances (e.g. IAA) have a marked effect on the polarity of spores. Gibberellic acid and kinetin induce germination in darkness. Vaarama and Taran (1963) observed that there was a clear promotion of germination by gibberellic acid. Valanne(1966) reported that low concentrations of gibberellin have been found to promote germination in *Ceratodon purpureus*.

17.3.1 Liverworts

In Hepaticopsida, the spores do not germinate in dark, even if sugar is present, and according to Inoue (1960), blue light plays an important role in spore germination in many taxa. Mohr (1963) observed that spore germination can be induced by both blue and far-red radiations in *Sphaerocarpos donnellii*. Steiner (1964) studied the spore-germination aspect further and observed that it can be controlled by phytochrome as well as high-energy reaction, and while functioning, there exists an interaction between phytochrome and high-energy reaction.

It has also been established in some liverworts that spore germination in blue and green light can be promoted if there is a simultaneous irradiation of these two lights. On the other hand, germination inhibits in far-red light. Regarding spore germination and quality of light, Steiner (1964) also proved that red light is more effective at the beginning of day and far-red at the end of the day. Doyle (1963) observed that red, far-red, green and blue lights are equally effective in promoting spore germination in *Sphaerocarpos cristatus.*

17.3.2 Mosses

In mosses, spore germination passes through two phases: (i) the first phase results into an increase in volume due to absorption and uptake of water, and (ii) the second phase starts by rupturing of the exospore and intensive greening of plastids due to light. Rhizoid initiation also takes place in the second phase.

It has also been proved that requirement of light in the germination of spores in mosses is associated with the phytochrome system. Valanne (1966) detected phytochrome system in *Ceratodon purpureus* and a few more mosses, while Egunyomi (1979) detected it in *Octoblepharum albidum*. The phytochrome system has, however, not been detected in *Funaria hygrometrica*. According to Krupa (1967), blue and far-red lights prove quite effective in inducing spore germination in *Funaria hygrometrica*. Different studies suggest that mosses, in general, differ in their response to different spectra of light. Red light (640 to 680 nm) is more effective in including spore germination in *Physcomitrella patens*. It has also been proved by Kass and Paolillo (1977) that in *Polytrichum*, the chloroplasts of germinating spores replicate more in light than in darkness.

INITIATION OF BUD AND ITS GROWTH INTO GAMETOPHYTE 17.4

17.4.1 Conditions Determining Bud Initiation

The major conditions which determine the initiation of buds, specially in mosses, include (i) effect of light, (ii) effect of temperature, (iii) effect of carbohydrates, and (iv) effect of growth regulators.

Effect of light on initiation of buds in mosses has been studied by many different workers, and it has been finally established that moss protonema, when reared under high light intensities, readily forms buds. Besides intensity, the quality of light is also important in bud initiation.

Effect of temperature on bud initiation has also been studied in several mosses including *Funaria hygrometrica*, *Phascum cuspidatum* and *Physcomitrium turbinatum*. It has been established that a majority of mosses have a certain temperature range during which the buds are formed.

Regarding the **effect of carbohydrates**, it can be generalised that an attainment of a certain minimum concentration of sugar in the moss protonema is a necessary prerequisite for initiation of buds.

Growth regulators (IAA, GA, kinetin, etc.) have a definite effect on formation of buds in mosses. Higher concentrations of auxins have a marked inhibitory effect on the formation of shoot buds on the protonema. Kinetin very strongly stimulates the process of bud initiation in mosses.

17.4.2 Growth of Gametophyte of Some Liverworts, Hornworts and Mosses

Consult Chapter 13 (Articles 13.5, 13.6 and 13.7).

PHYSIOLOGY OF SEX EXPRESSION[1] 17.5

Sex in several bryophytes is determined genotypically, but in many others, it is determined phenotypically, i.e. under environmental control. Wettstein (1924) believed that phenotypic determination of sex in mosses is an interesting process. Androgynous mosses, which are protrandrous, show "tissue differentiation as male and female organs have bisexual potentialities, i.e. plants regenerated from this tissue again produce both sexes in a genetically determined sequence". Several mosses show genotypic sex expression, e.g. *Bryum argenteum.* In such cases, some spores give rise to female gametophytes and others to male gametophytes. Differing from this, the diploid gametophytes, regenerated from the sporogonium, possess both male and female sex organs.

In *Sphaerocarpos donnellii*, out of the four spores produced by a tetrad, two produce male and two the female gametophytes. The females have a very large chromosome, perhaps X-chromosome, and the males have a much smaller homologue, perhaps Y-chromosome. Similar pairs of sex chromosomes are present in many other dioecious liverworts and mosses.

It was observed by Bauer (1959) that "diploid gametophytes, regenerated from the sporogonium of dioecious *Splachnum luteum*, formed archegonia but failed to form antheridia if they were transferred at frequent intervals." Three main points are observed in the stabilisation of the male sexual tendency in Splachnaceae, according to Bauer (1961, 1963).

[1]Also refer Chapter 14.

(i) "Protonema, regenerated from the sporogonium, is at first potentially male;
(ii) Sex-expression determination is at first liable for the effect can be reversed by rejuvenation, and
(iii) After the male sex organs attain maturity, the maleness of the strain becomes stabilised". Bauer (1963) also studied and confirmed that in *Splachnum rubrum*, "the male sexual characters appear on a genotypically determined female plant". Lorbeer (1936) and Heitz (1942) are some of the workers who opined that in Hepaticopsida, the transformation of genotypically determined females has been successfully obtained several times by giving X-ray treatment, i.e. by means of mutation. In *Splachnum ampulaceum*, *S. luteum* and *S. rubrum*, the male plants are formed from the females in the same fashion irrespective of whether they are of phenotypic or genotypic sex determination.

GROWTH OF DIPLOID SPOROPHYTE 17.6

Light plays a definite role in the growth and expansion of sporophyte in mosses. In *Funaria hygrometrica*, it was observed as early as 1886 by Haberlandt that light is required for proper development of its capsules. The spore sac failed to expand in darkness in *Funaria* even if the gametophyte and seta were exposed to light. Paolillo and Bazaz (1968) also observed the role of light in controlling expansion of capsule in *Polytrichum* and opined that "it appears to be morphogenetic rather than photosynthetic". In capsule expansion, the red light is more effective than white, blue, or green light of equal energy. Krisko and Paolillo (1972) opined that in *Polytrichum,* comparatively low irradiations are needed for expansion of capsules, and French and Paolillo (1976) also proved the same in *Funaria hygrometrica.*

The phenomena of **apogamy** (asexual reproduction in which embryos and propagules are produced without meiosis occurring) and **apospory** (production of a diploid gametophyte from vegetative cells of the sporophyte, that is, without the production of spores) are also of importance from evolutionary and morphogenetic point of views. For more details of these two phenomena, consult Chapter 20.

VEGETATIVE PROPAGATION[2] 17.7

17.7.1 Hepaticopsida (Liverworts)

An important role is played by light in the vegetative propagation by promoting the formation of gemmae and other types of propagules in liverworts. **Gemma** is a small group of cells in the form of a bud that will give rise to a new individual. Gemmae are produced in cup-shaped structures on the surface of thalloid liverworts.

In liverworts, the vegetative propagation through gemmae is a light-controlled response. It is so because gemmae do not germinate in dark. In *Marchantia polymorpha*, the rhizoid formation and further growth of gemmae is controlled by the phytochrome system. According to Otto and Halbsguth (1976), red light is essential for the rhizoid formation on gemmae in *M. polymorpha*. Kaul and Kaul (1974) observed that germination of gemmae in *Marchantia nepalensis* takes place only in red, orange

[2]Also refer Chapter 18.

or green light. Also in *Lunularia cruciata*, the formation of rhizoids on gemma is very sensitively controlled by red or far-red light system. If given for a very short period, the far-red light inhibits rhizoid formation completely in *L. cruciata*.

17.7.2 Bryopsida (Mosses)

Phytochrome is a pigment which controls many of the physiological responses of plants to light. This actually absorbs red and far-red wavelenghts of light. In *Mnium affine*, regeneration of protonema from the cells of its isolated leaves is under the control for its phytochrome-mediated system. Giles and von Moltzahn (1967) observed that action of blue light is similar to that of red light in *M. affine*, and this action is reversible by far-red light. Both these researchers also isolated phytochrome from *M. hornum* and *M. undulatum*. Demkiv (1971) studied regeneration in cells of protonema in *Funaria hygrometrica* and concluded that it occurs in red and blue light, and is probably influenced by phytochrome. In *Aulacomnium palustre* and *Tetraphis pellucida,* the germination of propagules is controlled by phytochrome.

Kumra (1977) reported that red light promotes maximum gemmae production in *Bryum klinggraeffii*, and blue light and green light are next in order of effectiveness. In yet another study, Jenkins and Cove (1983) observed the light requirements for regeneration of protoplasts of *Physcomitrella patens*. A simple regeneration sequence is followed by this moss, which include (i) synthesis of cell wall, (ii) formation of an asymmetric wall, (iii) division of this asymmetric wall, and (iv) further extension and division to produce a new chloronemal filament. Except that of cell-wall formation, all these processes require light for their completion. For cell division, red light is more effective than blue or far-red light.

METABOLISM 17.8

The sum of the chemical reactions which occur in an organism or a cell is known as **metabolism**. It involves the breakdown of organic compounds, and releasing energy that is used in the synthesis of other compounds. In bryophytes, it is the quality of light that controls and affects, directly of indirectly, the growth and development, which actually take place by synthesis of many endogenous morpho-regulatory substances.

Several experiments have so far been performed on metabolism in different members of bryophytes. A few such examples are mentioned here:

1. In the vegetative thalli of *Marchantia polymorpha*, Melstrom et al. (1974) detected three endogenous gibberellin-like substances. If the photoperiod is increased from 12 to 18 hours, it resulted in the quantitative difference in the activity of these gibberellin-like substances, and the result is observed in the form of increase in growth and elongation of thallus.
2. A compound (lunularic acid), which controls growth and drought resistance, has been isolated from *Lunularia cruciata*. Growth of gemmae, while they are still within gemma cups, is checked by lunularic acid.
3. Phytochrome regulates the synthesis of acetylcholine in the moss callus, regenerated from the seta of hybrid sporophyte of *Funaria hygrometrica* and *Physcomitrium pyreforme*. In these hybrid sporophytes, red light promotes synthesis of acetylcholine while far-red inhibits its synthesis.

4. In *Ceratodon purpureus*, light induces the synthesis of a cellular division factor by the cells of its protonema.
5. According to Chopra and Kumra (1978), a morphoregulatory substance, produced by the protonema of *Bryum klingraeffii*, controls the formation of gemma in this moss.

SENESCENCE 17.9

The process of growing old before death is known as **senescence**. The quality of light controls senescence in *Marchantia polymorpha*. It has been shown in this liverwort that its thalli remain green if a daily one hour photoperiod of white light is given. Its tissues, however, start showing bleaching symptoms when daily one-hour photoperiod is terminated with a brief irradiation of far-red light. While bleaching its chlorophyll is lost and there is simultaneous breakdown of its cell organelles and cytoplasm. There is a clear implication of phytochrome in the control of senescence by light.

PHYSIOLOGY OF RHIZOID FORMATION 17.10

Experiments of LaRue (1942) and others have proved that auxins stimulate the rhizoid production in bryophytes. Inhibition of rhizoid production induced by darkness in gemmae of *Marchantia polymorpha* was overcome by applying IAA at a concentration of 0.1–0.01 ppm. It was shown by LaRue (1942) that rhizoid formation gets stimulated by applying IAA and IBA in lanolin on leaves and sporophytes of several mosses and also on thalli of *Conocephalum conicum*.

The effect of indole-acetic-acid on the regenerative behaviour of the isolated tissue of the rhizoids of *Riella helicophylla* was studied by Stange (1958). Initially, a majority of the cells underwent regenerative cell division. IAA did not cause rhizoid formation after isolation of individual cells or a small group of cells by plasmolysis. Stange (1958) observed that IAA influences or promotes rhizoid production in *Riella helicophylla*.

Morphogenetic responses of several growth substances (e.g. IAA, IBA, 2, 4-D, etc.) on the thallus of *Marchantia* was studied by Kaul et al. (1962). They observed that if a concentration of 1 ppm or more of growth substances is applied, it stimulated rhizoid formation, but thallus growth was inhibited. Major rhizoid-inducing growth substances according to these workers are NOA (Naphthalene Oxyacetic Acid), NAA, (Napthalene Acetic Acid) and TCPA (Trichlorophenoxy Acetic Acid). They induced rhizoid formation not only on ventral but also on dorsal surface of the thalli of *Marchantia*. 0.1 ppm of NAA stimulates the production of rhizoids but not of the thallus. According to Allsopp et al. (1968) also, auxins have a pronounced effect on rhizoid formation in *Marchantia polymorpha*. They (IAA, NAA and 2, 4-D) not only induced production of an increased number of rhizoids but also their formation from both upper and lower surfaces of the gemma in this liverwort.

TEST YOUR UNDERSTANDING

1. Give an overview of morphogenesis in bryophytes in about 1000 words.
2. Define the following terms:
   (a) Morphogenesis (b) Apogamy
   (c) Apospory (d) Phytochrome
   (e) Metabolism (f) Senescence
3. Explain germination of spore in bryophytes, keeping in mind the phenomenon of morphogenesis.
4. What are the major conditions which determine initiation of bud in mosses?
5. Describe physiology of sex expression in bryophytes in about 250 words.
6. Is it true that light plays a definite role in the growth and expansion of sporophyte in mosses?
7. The pigment which controls many of the physiological responses of plants to light is named as _____.
8. The sum of chemical reactions, which occur in an organism or a cell, is known as _____.
9. The process of growing old before death is known as _____.
10. Elaborate the abbreviations NAA and TCPA.

18 Vegetative Reproduction and Regeneration in Bryophytes

DIFFERENCE BETWEEN VEGETATIVE REPRODUCTION AND REGENERATION 18.1

Vegetative reproduction may be defined as a type of asexual reproduction in which a whole new plant is produced from an organ, e.g. a tuber, which is not involved in sexual reproduction. In the absence of mutation, the offspring of the vegetative reproduction will be genetically identical to the parent plant.

Regeneration is (i) the growth of new tissue on a part of a plant that has been damaged; or (ii) the growth of new plants from perennating organs, e.g. rhizome. It may also be defined as regrowth of tissues or organs; or the formation of new plants from cultured tissues.

METHODS OF VEGETATIVE REPRODUCTION IN BRYOPHYTES 18.2

Bryophytes reproduce vegetatively by various means. In several of their dioecious species, the plants reproduce mainly by vegetative methods, and some such species have even ceased to reproduce sexually. C Correns (1899), a famous bryologist, was the first to summarise various methods of vegetative reproduction in bryophytes with main emphasis on mosses (Bryopsida), while F Cavers (1903) was the first to give an authentic and detailed account of various methods of vegetative reproduction in liverworts (Hepaticopsida) in his two articles "on asexual reproduction and regeneration in Hepaticae", published in the journal ***New Phytologist***. The detailed studies of both these bryologists on vegetative reproduction in bryophytes have been beautifully summarised by the well-known Indian author N S Parihar (1987), and an outline of the same is presented here in this account.

1. Death and Decay of Older Parts In a majority of Hepaticopsida and Anthocerotopsida, the younger branches of dichotomously dividing thallus get isolated due to progressive death and decay of the older posterior parts. Such isolated parts start functioning as new thalli (Fig. 18.1 A-C) on return of favourable conditions. This is the most common method of vegetative reproduction in thalloid bryophytes, particularly in liverworts and hornworts. This is also seen in those mosses (Bryopsida) which have prostrate rhizomes bearing erect branches.

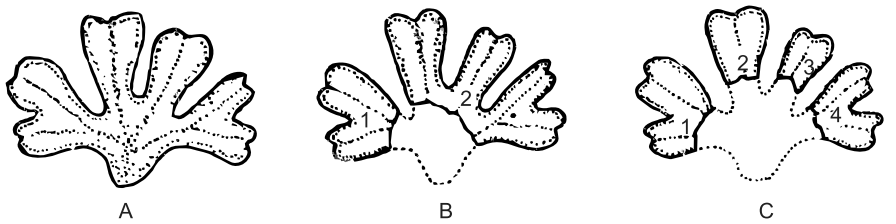


Fig. 18.1 A-C Isolation of younger dichotomies due to death and decay

2. Adventitious Branches The term 'adventitious' is applied to a plant part developed out of the usual order or in an unusual position. In thalloid bryophytes, adventitious branches usually develop from the underside of the midrib. Upon separation from the parent plant, the adventitious branch develops into a new plant, e.g. *Anthoceros laevis*, *Asterella*, *Blasia*, *Corsinia*, *Dumortiera*, *Marchantia*, *Pellia*, *Reboulia*, *Riccia fluitans*, *Sphaerocarpos*, *Targionia*, etc.

3. Innovations A young offshoot from the stem is known as **innovation**. On being separated, and falling on the suitable substratum, the innovations develop into new plants, e.g. *Sphagnum* and many acrogynous Jungermanniales. In *Sphagnum*, the innovation grows more vigorously than the other branches, continues its upward growth, and takes all the characteristics of the main axis. It is an effective method of multiplication in *Sphagnum*.

4. Leaf Cladia A small detachable branch originating from the individual cells of the leaf is known as **leaf cladia**. On being detached, leaf cladia develop into new plants, e.g. *Frullania fragilifolia*, *Plagiochila*, etc.

5. Stem Cladia It is a small detachable branch which originates from the individual cells of the stem. It occupies almost the same position on the stem as the sex-organ bearing branch. **Stem cladia** develop on the stem in several leafy liverworts and mosses, e.g. *Bryopteris fruticulosa*, *Drepanolejeunea*, etc.

6. Whole Shoots All and complete shoots get separated from the parent plant, and on getting suitable water and other requirements develop into new plants, e.g. *Pohlia nutans*.

7. Shoot Tips In *Campylopus*, *Polytrichium* and some other mosses, tips of the shoots get separated and develop into new plants.

8. Modified Branch of Budlike Form In some species of *Bryum* and many species of *Pohlia* and some more mosses, the organ shed is a modified branch of bud-like form. This type of organ is

strictly a deciduous branchlet and quite capable of developing into a new plant. In some taxonomic works of bryophytes, such organs have also been termed as **bulbil** or **gemma**.

9. Tubers Technically, a **tuber** is a "thick underground stem in which food is stored", or, "a swollen underground stem acting as a storage and perennating organ". Some define tuber as a "swollen part of a stem or root, usually modified for storage". In bryophytes, tubers develop in several species of liverworts as well as mosses. Some of the common tuber-forming species are *Riccia billardieri, R. discolor, Geothallus tuberosus, Asterella angusta, Aitchisoniella himalayensis, Conocephalum conicum, Fossombronia tuberifera, Sewardiella tuberifera, Anthoceros himalayensis* and *A. laevis* (Fig. 18.2 A-B).

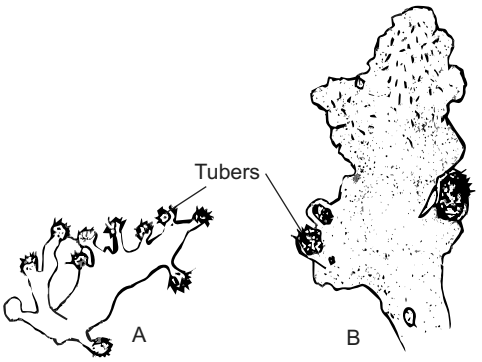


Fig. 18.2 A-B Tubers on the thallus of *Anthoceros himalayensis* (A) and. *A. laevis* (B)

10. Gemmae *Gemmae* (singular: gemma) are "small groups of green cells, produced in cup-shaped structures on the surface of thalloid liverworts." Gemmae are usually dispersed by splashes of rain. Some define gemmae as "a bud that will give rise to a new individual, e.g. the multicellular structure in algae, pteridophytes and specially bryophytes". These are the means of vegetative propagation and form abundantly in liverworts (Hepaticopsida), to some extent in hornworts (Anthocerotopsida) and to a lesser extent in mosses (Bryopsida). Gemmae are not formed in Sphagnales. Gemmae reported in different groups of bryophytes are listed below.

(a) Gemmae of Liverworts (Hepaticopsida) Many types of gemmae are produced in Hepaticopsida. Of these, some are listed below:

(i) **One to three-celled gemmae** developing on the stem apex, e.g. *Cephalozia bicuspidata*, *Lophozia heterocolpa.*

(ii) **One- to three-celled gemmae** developing on the leaves, e.g. *Cephalozia francisci, Lophozia barbata*.

(iii) **Two-celled endogenous gemmae** developing within any external cell of the thallus, e.g. *Riccardia multifida* (Fig. 18.3A), *Haplozia caespiticia*.

(iv) **Three- to four-celled gemmae** developing in the axils of the leaves, e.g. *Treubia*.

(v) **Stalked, multicellular, discoid gemmae** formed on the dorsal surface of the thallus inside gemma cups, e.g. *Marchantia* (Fig. 18.3 B), *Lunularia*.

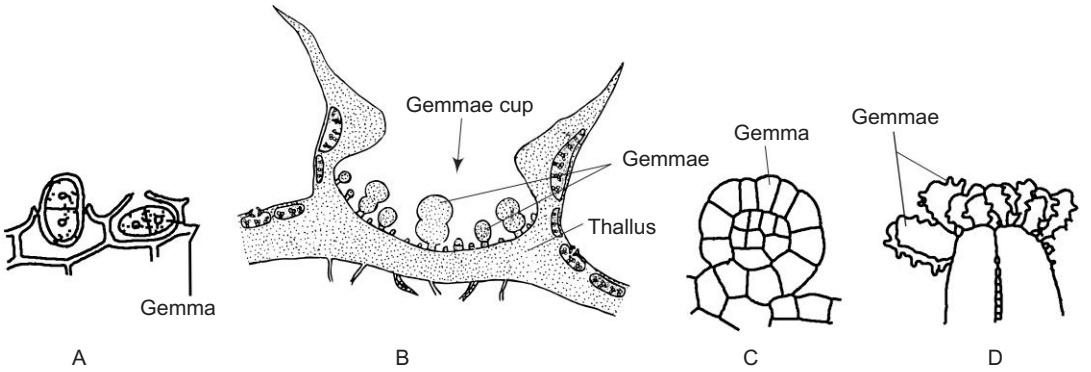


Fig. 18.3A-D Gemmae of some bryophytes. A, *Riccardia multifida*; B, Vertical section of the thallus of *Marchantia polymorpha* through gemma cup; C, *Radula complanata*; D, *Metzgeria uncigera*

(vi) **Subspherical gemmae** produced in large number in flask-shaped gemma receptacles e.g. *Blasia*.

(vii) **Star-shaped gemmae** developing on the dorsal surface of the thallus, e.g. some species of *Blasia*.

(viii) **Discoid, multicellular gemmae** developing on leaves, e.g. *Rudula complanata* (Fig. 18.3C), *Leptocolea*.

(ix) **Discoid multicellular gemmae** developing on erect gemmiferous branches, e.g. *Metzgeria uncigera* (Fig. 18.3D).

(b) Gemmae of Hornworts (Anthocerotopsida) Some *Anthoceros* species bear gemmae. In *A. glandulosus,* several gemmae develop along the margin of the thallus, and a few also develop on the dorsal surface. Gemmae have also been reported in some more species, such as *A. formosae* and *A. propaguliferus.*

(c) Gemmae of Mosses (Bryopsida) Six types of gemmae developing on different plant parts of mosses are listed as under:

(i) ***On Rhizoids of Leafy Shoots*** These are the multicellular gemmae developing on the rhizoids of leafy shoots, e.g. *Barbula convoluta*, *Bryum erythrocarpum*, etc.

(ii) ***At the Base of Stem*** In *Bryum erythrocarpum* (Fig. 18.4A) and *B. rubens,* multicellular and globular gemmae develop at the base of the stem.

(iii) ***At the End of Leafless Stalks*** In *Aulacomnium androgynum* (Fig. 18.4 B), stalked fusiform gemmae develop at the end of leafless stalks.

(iv) ***At the Tip of the Shoot*** In *Tetraphis pellucida* (Fig. 18.4 C), green, stalked, multicellular and lenticular gemmae develop at the tip of the shoot. Widened leaves form a cup-like structure around such gemmae.

(v) ***On the Stem and Branches*** In *Pterygynandrum filiforme*, smooth, golden-brown gemmae develop on the stems and branches. Such gemmae are ovoid and stalked bodies. These are bicelled structures and develop on colourless stalk made of three or more cells.

(vi) ***On the Leaves*** In *Torula papillosa*, *Ulota phyllantha* (Fig. 18.4D) and some more bryophytes, multicellular, articulate gemmae develop on the leaves.

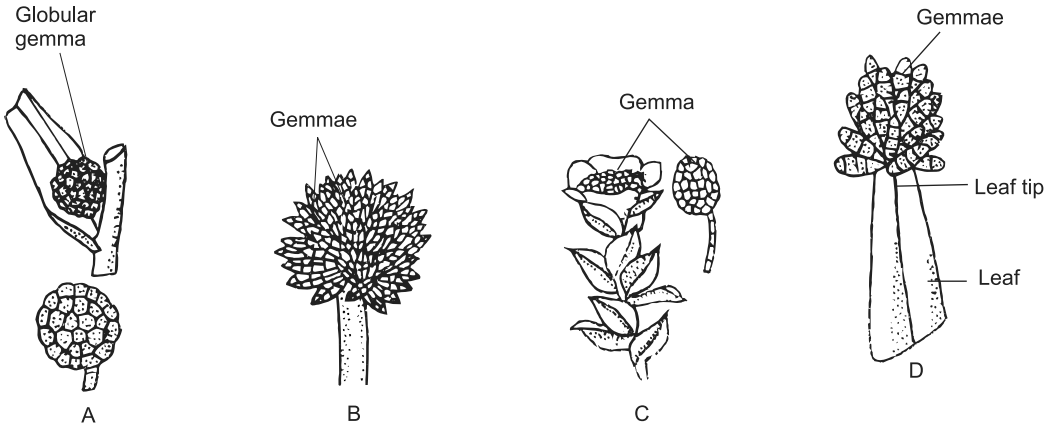


Fig. 18.4 Gemmae found in some bryopsida. A, *Bryum erythrocarpum*; B, *Aulacomnium androgynum*; C, *Tetraphis pellucida*; D, *Ulota phyllantha*

11. Primary Protonema In almost all mosses, the spore germinates into a young filamentous and branched gametophyte, known as **primary protonema**. It usually breaks into smaller parts or fragments, and each such fragment is capable of developing into a new protonema and forms gametophyte initials.

12. Secondary Protonema A protonema-like structure, developing by other methods than from the germination of spores is known as **secondary protonema**. It is also a means of vegetative reproduction in Bryopsida (e.g. *Funaria hygrometrica*). Secondary protonema develops (i) either from the rhizoids of a leafy gametophore when exposed to light, or (ii) from almost any separated living part of the moss plant such as stem, leaves, sex organs, or even paraphysis and sterile cells of seta and capsule.

BOTANICAL NOTE ON REGENERATION IN BRYOPHYTES 18.3

As mentioned earlier also, **regeneration** is technically "the growth of new tissue on a part of a plant that has been damaged, or it is the growth of new plants from the perennating organs, e.g. rhizomes". Fulford (1956) defined "regeneration" as a process in which a new plant is formed from a presumably adult cell which has undergone differentiation back to an activated condition." Regeneration actually means the capacity of an organ, tissue or cell to give rise to the entire organism. According to Wilmot-Dear (1980), regeneration of differentiated cells follows injury or isolation from the meristem, and the isolation may be physical or physiological.

Generally, bryophytes possess enormous potentialities for regeneration. Regeneration of the physiologically isolated parts of both sporophytic and gametophytic generations takes place readily in an artificial medium. Regeneration in nature may be caused because of the attacks of fungi, insects, from mechanical injuries of many sorts or even from unfavourable conditions which impede the function of plant parts. According to Stange(1964), regeneration does not include "normal physiological processes in which new growth is initiated as normal vegetative reproduction or formation of secondary meristems or meristemoids in plants".

Liverworts regenerate with particular readiness among bryophytes. For example, in *Sphaerocarpos*, regeneration occurs from single cells or a group of adjacent cells from almost anywhere on the thallus. They first form a globular, cylindrical or ribbon-like body, which soon develops into a new typical thallus, as is formed from a germinating spore of *Sphaerocarpos*. Among Jungermanniales (e.g. *Fossombronia*) also, plantlets develop frequently from single cells in the leaves and their development is almost in the similar fashion as that of a spore. Mehra and Pahwa (1971) observed in thalli of *Fossombronia himalayensis* that they regenerate from rhizoids of starved cultures.

Many Bryopsida (mosses) also have excellent power of regeneration. Several studies have been made in India by many different workers, including Kachroo (1954) on *Physcomitrium pyreforme,* Chopra and Sharma (1956) on *Pogonatum,* and Banerji and Sen (1957) on *Barbula indica*. Different mosses show different regenerative capacity from many of the body parts such as leaves, antheridia, archegonia or as protonemal outgrowths from different parts of the sporophyte. In mosses, the regeneration from the leaves occurs only if they are detached from the axis, as shown by many workers including Gemmell (1953) in *Atrichum* and Meyer (1942) in *Physcomitrium turbinatum*. Several Japanese workers have made extensive contribution on the regeneration of detached leaves in mosses, and, in general, have opined that "the manner of regeneration of leaves is similar to that of the germination of spores in mosses" (Noguchi and Mizuno, 1959). Chopra and Kumar (1961) generalised that "the percentage of regeneration increases with the advance of age in different species of *Atrichum*", a moss. They have shown that "lower percentage of regeneration of the younger organs is due to scanty food reserves as they are actively used by these organs in their growth and other activities".

Chopra and Kumra (1988) have compiled a list of "some specific examples of regeneration from organs other than thallus, protonema, stem, leaf, and seta". Some of these specific examples are listed below:

1. Antheridial stalk—*Bryum cellulare* (Narayanaswami and Lal, 1957)
2. Archegonial neck—*Mnium* (Wettstein, 1924)
3. Archegonial stalk—*Rhodobryum* (Narayanaswami and Lal, 1957)
4. Archegonial venter – *Funaria* (Correns, 1899)
5. Calyptra – *Barbula indica* (Narayanaswami and Lal, 1957; Fig. 18.5 A)
6. Jacket of capsule—*Funaria* (Kumra and Chopra, 1980)
7. Perianth—*Fossombronia* (Mehra, 1976)
8. Perichaetial leaves—*Octoblepharum* (Egunyomi et al., 1980)
9. Rhizoids—*Physcomitrium coorgense* (Narayanaswami and Lal, 1957)
10. Vaginula—*Barbula indica* (Fig. 18.5B; Narayanaswami and Lal, 1957)

Major factors which affect regeneration are light, radiation, pH, humidity, season, temperature, reserve food material, wounding, location of the plant, size of the fragment and age.

For more details of regeneration in bryophytes, readers may consult ***Biology of Bryophytes*** by Chopra and Kumra (1988).

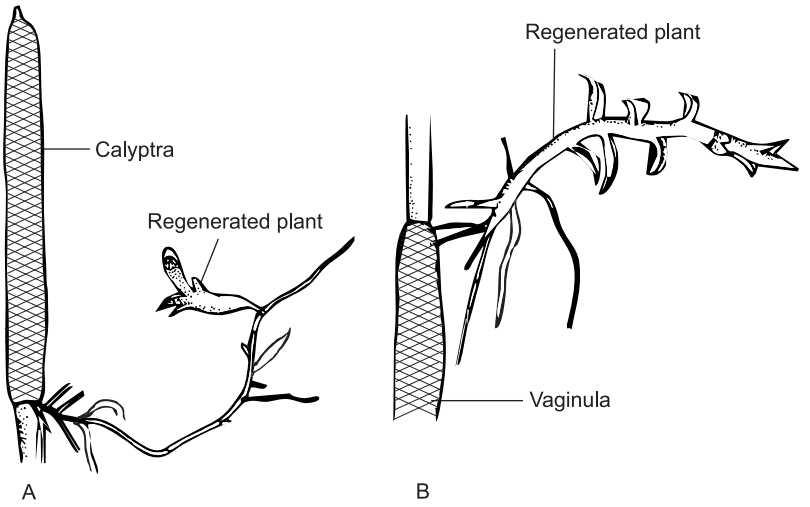


Fig. 18.5 *Barbula indica* showing regeneration from calyptra (A) and vaginula (B)

TEST YOUR UNDERSTANDING

1. How can you define the two terms? (i) Vegetative reproduction, (ii) Regeneration.
2. Write an essay on various methods of vegetative reproduction in bryophytes.
3. A thick underground stem in which food is stored is known as _____.
4. Is the word “gemmae” singular or plural?
5. Give a detailed account of gemmae in bryophytes.
6. “Gemmae are formed in all the three major groups of bryophytes”. Comment.
7. Give a brief illustrated account of gemmae of Hepaticopsida.
8. How do mosses reproduce by protonema?
9. Write a brief scientific note on regeneration in bryophytes in about 200 words.
10. Define regeneration.
11. Besides thallus, protonema, stem and leaves, mosses exhibit the phenomenon of regeneration also from almost all parts of their body. Justify giving suitable examples.
12. Innumerate major factors which affect regeneration in bryophytes.

19 Origin and Fate of Archesporium in Bryophytes

WHAT IS ARCHESPORIUM? 19.1

The tissue that gives rise to spore mother cells is known as **archesporium**. The archesporium is actually the first cell generation of the sporogenous tissue. In almost all bryophytes, it appears as a continuous tract of tissue, which occupies (i) usually a central position, as in majority of liverworts (Hepaticopsida), or (ii) a more or less superficial position between the wall and the columella, as in majority of hornworts (Anthocerotopsida) and mosses (Bryopsida). The cells of the archesporium divide and redivide several times to form a large number of sporogenous cells.

PRODUCTS OF ARCHESPORIUM 19.2

Sporogenous tissue, produced from the archesporium, develops into several types of cells in different bryophytic genera, as shown below:

1. Sporocytes These are produced in all bryophytes and are also called **spore mother cells**. They are diploid in nature, divide by meiosis and produce haploid **spores**.

2. Abortive Nurse Cells These are produced along with sporocytes in some species of *Riccia*. They abort soon and form a nutritive fluid for the developing spore mother cells.

3. Persistent Nurse Cells In the sporogonium of some genera, such as *Geothallus*, *Riella* and *Sphaerocarpos*, some cells persist for quite some time along with spore mother cells. These are called persistent nurse cells.

4. Elaters Elaters are a bunch of long, thin cells in the capsule of the sporophyte of several liverworts, e.g. many members of Marchantiales (e.g. *Marchantia*) and Jungermanniales. Elaters have spiral thickenings of the cell wall. They alter their position with changes in humidity, and help in the dispersal of spores from the capsule.

5. Apical Cap of Sterile Cells These are the cells present in the form of a cap on the apical side of the capsule of the sporophyte of some bryophytic genera, as in some Marchantiales (e.g. *Marchantia*).

6. Elaterophore In some Jungermanniales (e.g. *Pellia*, *Riccardia),* some large-sized sterile cells are present in the capsule either at the base (e.g. *Pellia*, Fig. 19.1 A) or at the top (e.g. *Riccardia*, Fig. 19.1 B). These cells develop spiral thickenings on their walls and form a somewhat compact structure called **elaterophore**. Some elaters also get attached on this, making it a thick and more distinct structure inside the capsule.

7. Pseudoelaters In Anthocerotopsida (e.g. *Anthoceros*, Fig. 8.7 M) the sporogenous tissue gives rise to sporocytes and some elaters or pseudoelaters.

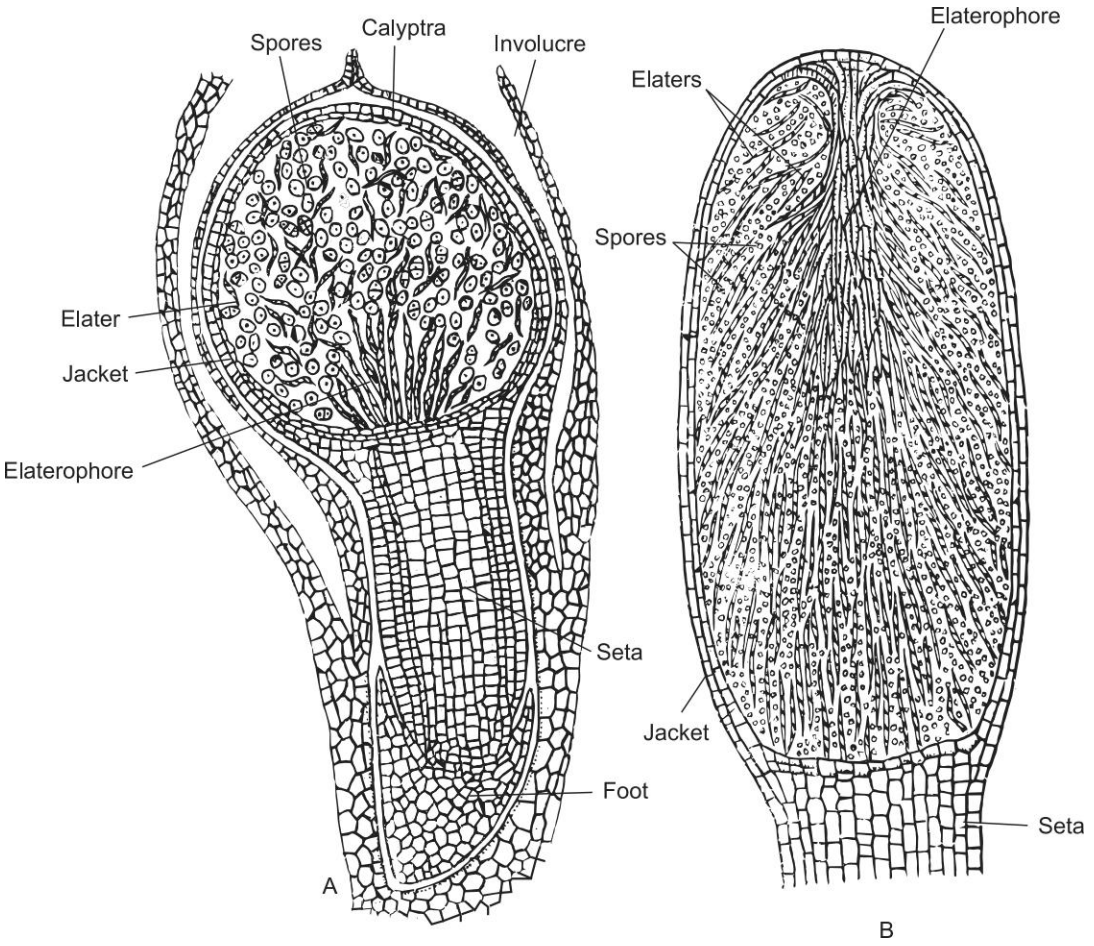


Fig. 19.1 Elaterophore at the base of capsule in *Pellia epiphyla* (A), and at the top of the capsule in *Riccardia pinguis* (B)

FUNDAMENTAL EMBRYONIC LAYERS OF CAPSULE 19.3

The **amphithecium** and **endothecium** are the two fundamental embryonic layers of capsule in bryophytes. Usually, the diploid zygote divides and redivides to form a multicellular, more or less spherical mass of 20 to 40 cells. They divide by a periclinal division to form an outer layer, called **amphithecium** and an inner central mass of cells, called **endothecium** (e.g. *Riccia*). The archesporium (the first cell generation of sporogenous tissue) is amphithecial in origin in some bryophytes (e.g. *Anthoceros)*, while in others it is endothecial in origin (e.g. *Marchantia*).

ORIGIN, POSITION AND FATE OF ARCHESPORIUM IN SOME SELECTED GENERA 19.4

The origin, position and fate of the archesporium in majority of the genera of Hepaticopsida, Anthocerotopsida and Bryopsida, discussed earlier in Chapters 4 to 10, have already been described. A brief summary of some of the selected genera is given in Table 19.1.

Table 19.1 *Origin, position and fate of archesporium in some common genera of bryophytes*

No.	*Name of genus*	*Origin*	*Position*	*Fate*
1.	*Riccia*	Endothecial; entire endothecium functions as archesporium and forms sporogenous tissue.	Centrally-located; forms entire sporophyte except single-layered wall.	Almost all sporogenous cells start functioning as **spore mother cells**, which divide reductionally to form haploid spores; a few peripheral cells, called **nurse cells**, however, degenerate and form nutritive fluid.
2.	*Marchantia*	Endothecial; entire endothecium functions as archesporium, divides and redivides several times and forms sporogenous tissue.	Entire cavity of capsule remains filled with sporogenous tissue surrounded by single-layered wall of the capsule.	Half of the sporogenous tissue forms **spore mother cells** and remaining half forms **elaters**. Some cells at the top remain sterile and form the **apical cap**.
3.	*Porella*	Endothecial; entire endothecium functions as archesporium, which divides and redivides to form sporogenous tissue.	Entire cavity of capsule remains filled with sporogenous tissue, which remains surrounded by two or more-layered wall of the capsule.	Entire sporogenous tissue forms **spore mother cells** and **elaters**. Elaterophore is absent.
4.	*Pellia*	Same as in *Porella.*	Same as in *Porella.*	Some sporogenous tissue forms basal elaterophore (Fig. 19.1A); remaining sporogenous tissue forms **spore mother cells** and **elaters**.

Contd.

5.	*Riccardia*	Same as in *Pellia* and *Porella.*	Same as in *Pellia* and *Porella.*	Same as in *Pellia* except that the elaterophore is at the top of the capsule (Fig. 19.1 B).
6.	*Anthoceros*	Amphithecial; archesporium originates from the **innermost layer of amphithecium**. It divides to form 1 to 4-layered sporogenous tissue, which is one cell in thickness in *A. erectus*, two-layered in *A. pearsonii*, and 2 to 4 cells in thickness in *A. hallii.* The entire endothecium forms the central axis in the form of columella.	Located more superficially than Hepaticopsida; when young, the archesporium overarches the columella; its position is in between several-layered thick capsule wall and the centrally located columella.	Regarding the fate of the archesporium, it gets differentiated into **spore mother cells** and **pseudoelaters**. The pseudoelaters are sterile, more slender, elliptical cells with smaller nuclei.
7.	*Sphagnum*	Amphithecial; archesporium originates from inner layer of amphithecium, which divides and forms a 4-layered thick sporogenous tissue.	In position, it is superficial, as in *Anthoceros*; when young, it is dome-shaped and present in the upper part of the capsule, overarching the tip of the centrally-located massive columella within the wall of the capsule.	Fate of the archesporium is that entire sporogenous tissue develops into **spores**. Inside the capsule, this tissue thus forms a coherent tract of fertile cells.
8.	*Funaria*	Endothecial; archesporium originates from the outermost layer of endothecium; a two-cells thick sporogenous tissue is resulted.	Position of archesporium is superficial, which surrounds the centrally-located columella like a barrel.	Fate of archesporium is that all sporogenous cells are fertile and form spores; similar to *Sphagnum*, the sporogenous tissue forms a coherent tract of fertile cells.

1. Amphithecium The amphithecium either gives rise to (i) capsule wall, as in Hepaticopsida, Bryopsida and a few species of *Notothylas* and also *Andreaea*, or it gives rise to (ii) archesporium and capsule wall, as in majority of Anthocerotopsida and *Sphagnum*.

2. Endothecium The endothecium gives rise either to (i) archesporium, as in Hepaticopsida and a few species of *Notothylas*, or to (ii) columella, as in most species of Anthocerotopsida and Sphagnidae, or to (iii) archesporium and columella, as in some Bryopsida and *Andreaea.*

A NOTE ON THE ORIGIN OF ELATERS 19.5

As mentioned earlier also, elaters are long, thin, sterile cells in the capsule of the sporophyte of a liverwort. They have spiral thickenings of the cell wall, and have the ability to change their position with changes in humidity. Elaters help in the dispersal of spores from the capsule.

Regarding the origin of elaters, some bryologists believe that in Hepaticopsida, certain cells in the young sporogonium become sporocytes or spore mother cells while others form elaters, and both of them arise independently from the undifferentiated sporogenous tissue. Other bryologists, however, opined differently and believe that in some Hepaticopsida (e.g. *Pellia*, *Plagiochasma*, etc.) and Anthocerotopsida (e.g. *Notothylas*), each undifferentiated cell divides into two daughter cells, of which one gives rise to one or more spore mother cells and the other develops into one or more elaters. This later view is supported by Goebel (1927), who also advocated that such a "spore-elater division" of fertile and sterile cells is true in all elater-containing Hepaticopsida. This is not seen in members where the sterile cells or elaters are not found, as in *Riccia* and *Sphaerocarpos*.

In genera like *Targionia* and *Reboulia*, the spore mother cells and elaters may be the members of the same cell generation or there may exist a difference of 3 to 5 or more generations between the two. Parihar (1987) mentioned that in *Marchantia polymorpha,* "the elaters are differentiated five generations before spore mother cells". In some other genera, however, elaters are differentiated 3 to 5 generations later than that of the generation of spore mother cells, e.g. *Stephensoniella.*

TEST YOUR UNDERSTANDING

1. The first cell generation of the sporogenous tissue in bryophytes is known as _____.
2. How can you define the term archesporium?
3. What is archesporium? Describe its origin and fate in bryophytes giving suitable examples. Your description should not exceed 500 words
4. Make a list of at least five products of archesporium.
5. What are elaters? How do they differ from elaterophore?
6. Name a bryophytic genus in which the elaterophore is present at the base of the capsule.
7. In which bryophytic genus is the elaterophore present at the top of the capsule?
8. Two fundamental embryonic layers of the capsule in bryophytes are _____ and _____.
9. Make a table of comparison giving details of origin, position and fate of archesporium in *Riccia, Marchantia, Anthoceros* and *Funaria.*
10. The archesporium is _____ in origin in *Marchantia*.
11. In *Anthoceros*, the archesporium is _____ in origin.
12. Write a botanical note on the origin of elaters in bryophytes in about 100 words.

20 Apogamy and Apospory in Bryophytes

APOGAMY AND APOSPORY: TWO ALTERNATIVE PATHWAYS OF LIFE CYCLE 20.1

As mentioned earlier also under Article 15.4, **apogamy** is the phenomenon of the development of a sporophyte directly from a cell of gametophyte without fusion of gametes so that the resulting sporophyte has the same chromosome number as the parent gametophyte. On the other hand, **apospory** is the phenomenon of the development of a gametophyte directly from a sporophyte cell without meiosis and the formation of spores. The resulting gametophyte has the same chromosome number as the parent sporophyte. Some major aspects of the two phenomena (apogamy and apospory), we shall discuss here in this chapter

All bryophytes exhibit a well-defined heteromorphic alternation of generations, in which the gametophytic generation is predominant and present in the form of a well-defined thalloid or foliose gametophore, while the sporophytic generation is dependent on gametophyte and present on it in the form of sporophyte, usually made up of foot, seta and capsule.

The phenomena of apogamy and apospory, defined above in the first paragraph, are, therefore, two alternative pathways of life seen in some bryophytes. In nature, however, both these phenomena are rare, hence their significance in the usual life-cycle process is meagre.

WHY ARE THE PHENOMENA OF APOGAMY AND APOSPORY OF CONSIDERABLE INTEREST? 20.2

In spite of the rare occurrence of apogamy and apospory in nature, these are of considerable interest for bryologists because of the following reasons:

1. We can observe and study differentiational processes at the cellular level from the very beginning because of the studies of apogamy and apospory.
2. We can obtain, preserve and study tissues with haploid and diploid compliments and can use them in several other experimental studies.

3. We can study more details of the normal phenomenon of alternation of generations due to the studies of apogamy and apospory.
4. **Callus** (a tissue consisting of large, thin-walled, parenchymatous cells developing as a result of injury, as in wound healing) is usually formed at the beginning of apogamy and apospory. By modifying the cultural conditions, controlled differentiation of callus into gametophytes or sporophytes can be achieved and studied.
5. While studying phenomena of apogamy and/or apospory, the role of external factors regulating or effecting differentiation can be studied more specifically.
6. By maintaining homogenous cell clumps, formed during experimentations of apogamy and apospory, we can find and develop suitable materials for the production of secondary metabolites.
7. Biosynthetic problems relating to several compounds can be studied and solved while studying apogamy and apospory phenomena in bryophytes.

APOGAMY 20.3

20.3.1 Apogamy Occurrence During Diploid and Haploid Phases

Few details of the occurrence of apogamy in diplophase and haplophase are listed below:

1. Springer (1935) was the first to report occurrence of apogamy in sporophytes of mosses. He reported apogamous sporophytes on the leaf tips of naturally occurring diploid gametophytes of *Phascum cuspidatum*. This is the only reported example of apogamy **in vivo** (*in vivo* means biological processes occurring within the living organism or cell). Two alternative paths of differentiation were shown by the swellings on the leaf tips of *P. cuspidatum*. When plenty of moisture was available, protonema was produced in this moss. But in dry conditions or if increased amount of salt is added in the nutritive medium, these swellings of the leaf tips developed into apogamous sporogonia.
2. Bauer (1956) reported in *Georgia pellucida* "that differentiation of apogamous sporophytes is to a great extent favoured by relative dryness of the nutritive medium".
3. Bauer (1957) observed in *Physcomitrium pyreforme* that, instead of protonema, young sporophytes regenerated to form new sporophytes in this species.
4. In yet another study, Bauer(1959) obtained apogamous sporophytes from the diploid protonema, regenerated from the intergeneric hybrid sporophyte of *Physcomitrium pyreforme* and *Funaria hygrometrica*.

Apogamy in haplophase has been reported in many mosses including *Desmatodon randii* by Lazarenko et al. (1961), *Funaria hygrometrica* by Chopra and Rashid (1967), *Tetraphis pellucida* by Hughes (1969) and *Physcomitrium pyreforme* by Menon (1974). Lazarenko (1965) reported coexistence of apogamous sporophytes with normal sporophytes on the haploid plants of *Desmatodon randii*.

Apogamy in diplophase has been reported in many mosses including *Phascum cuspidatum* by Springer (1935), *Physcomitrium pyreforme* by Bauer (1957, 1959), *Desmatodon ucrainicus* and *D. randii* (Fig. 20.1 A, B) by Lazarenko (1960), *Grimmia pulvinata* by Hughes (1969) and *Funaria hygrometrica* by Kumra and Chopra (1980).

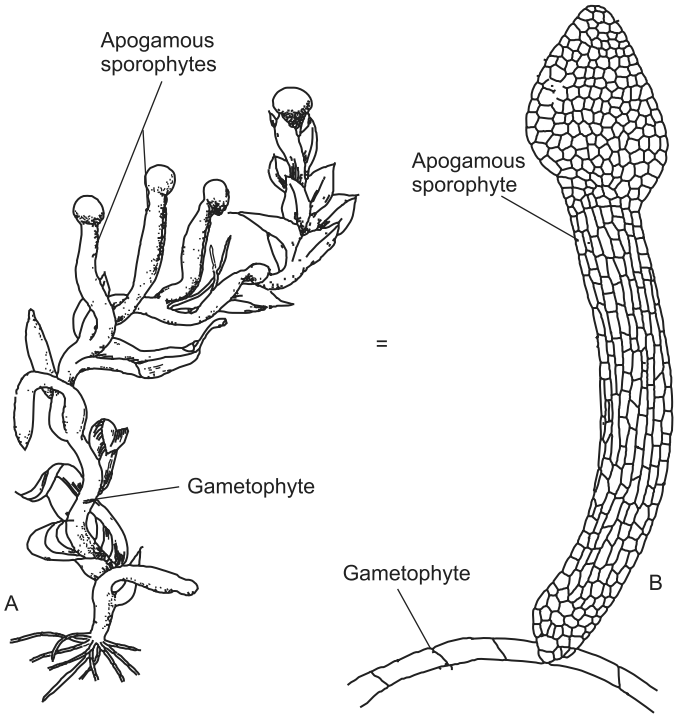


Fig. 20.1 Apogamous sporogonia in diplophase of *Desmatodon ucrainicus* (A) and *D. randii* (B) (After Lazarenko, 1960)

20.3.2 Production of Viable Spores by Apogamous Sporophytes

Apogamous sporophytes of only a few mosses produce the viable spores in haplophase, and one such case was reported by Lal (1961) in *Physcomitrium coorgense*. However, many reports are available of apogamous sporophytes producing viable spores in diplophase in mosses, and some such investigated species include *Phascum cuspidatum* by Springer (1935), *Physcomitrium pyreforme* by Bauer (1959), *Desmatodon randii* and *D. ucrainicus* by Lazarenko (1960), *Brachythecium campestre* by Lazarenko (1961) and *Pottia intermedia* and *Splachnum ovatum* by Lazarenko (1965).

20.3.3 Production of Apogamous Sporophytes from Callus

Several workers, while working on apogamy in bryophytes, have worked on differentiation of apogamous sporophytes from the callus in different genera including *Physcomitrium pyreforme* (Bauer 1957, 1961), *P. coorgense* (Lal, 1961, 1963) and *Funaria hygrometrica* (Kumra, 1981).

Bauer (1957, 1961) observed that "besides producing protonema, the sporophytes of *Physcomitrium pyreforme*, *Funaria hygrometrica*, and their hybrid sporophytes form calli which later on differentiate into daughter sporophytes".

Lal (1961, 1963) observed that the callus obtained from the haploid gametophytic axis and archegonia of *Physcomitrium coorgense* also differentiate into apogamous sporophytes. In similar fashion, Kumra

(1981) observed that the callus obtained from the haploid protonema of *Funaria hygrometrica* produced apogamous sporophytes or gametophytes in different environmental conditions.

20.3.4 Factors Responsible for Differentiation of Apogamous Sporophytes

Some major factors which control differentiation of apogamous sporophytes include light, hydration, sugars, growth hormones, inorganic nutrients, and several endogenous factors (e.g. sporogon factor, age of tissue, and genetic constitution).

1. Light Diffuse light promotes production of sporophytes and gametophytes from the gametophytic callus of *Physcomitrium coorgense* while in darkness, only apogamous sporophytes get differentiated in this species. Lal (1963) opined that light plays a positive and definite role in establishing the behaviour of the apical cell. Hughes (1969) observed that in daylight, the frequency of apogamy in the diploid protonema of *Phascum cuspidatum* is very low, but it is exceptionally increased in yellow filtered fluorescent light.

2. Hydration Springer (1935), the first bryologist to work on apogamy, observed and suggested that reduced hydration of the medium favours apogamy in *Phascum cuspidatum*. Observations of Springer were later on confirmed in some other bryophytes, such as *Georgia pellucida* (Bauer, 1956), *Desmatodon ucrainicus* (Lazarenko, 1960) and *Splachnum ovatum* (Lazarenko, 1961). Chopra and Rashid (1967) reported that drying of medium induces apogamy in *Funaria hygrometrica*.

3. Sugars It has been observed in some mosses (e.g. *Physcomitrium coorgense*) that sucrose, and also glucose to some extent, influences the induction of apogamous sporophytes. Rashid and Chopra (1969) studied and suggested that in *Funaria hygrometrica*, an enhancement in sucrose concentration in the medium promotes initiation of apogamous sporophytes from the axis. Kumra and Chopra (1980) also reported in *F. hygrometrica* that a 2% addition of sucrose in the medium favours induction of protonema as well as apogamous sporophytes.

4. Growth Hormones Several such studies have been made on the effect of growth hormones on apogamy in bryophytes, of which two are on *Georgia pellucida* and *Funaria hygrometrica.*

In *Georgia pellucida*, Bauer (1956) observed that the number of sporogonia per unit area of protonema increases by adding low concentrations of indole-acetic-acid.

In *Funaria hygrometrica*, Rashid and Chopra (1969) observed that the "capacity of gametophytes to produce sporophytes is influenced to varying degrees by growth substances". If low concentrations of GA_3, IAA, kinetin and a mixture of kinetin and IAA is applied, it "appreciably increases the number of sporophytes per culture". If higher concentrations of kinetin is applied, it proves "inhibitory for gametophyte as well as sporophyte differentiation, but GA_3 and IAA inhibit sporophyte formation" without showing any effect on the growth of gametophyte.

In *Physcomitrium pyriforme,* Menon (1974) observed that abscisic acid is inhibitory for growth of protonema and also for the differentiation of apogamous sporophytes".

5. Inorganic Nutrients Varied types of influences of inorganic salts have been observed on the induction of apogamous sporophytes in bryophytes. A few such examples are listed below:

(a) Bauer (1959) observed that nitrogen promotes apogamy in *Splachnum luteum*.
(b) Lal (1964) observed that higher concentrations of salts inhibit the formation of apogamous sporophytes in *Physcomitrium coorgense.*
(c) Menon (1974) observed no change in the incidence of apogamy in *Physcomitrium pyriforme* if there is a "change in nitrogen source or doubling of the nitrate and chloride concentration".

6. Endogenous Factors

(a) Sporogon Factor Bauer (1959) was the first to suggest the presence of a factor called **sporogon factor**, which emanates from the diploid sporophyte and is translocated into the aposporous protonema. This factor multiplies in the tissue and is inherited during vegetative propagation. The sporogon factor appears to be of hormonal nature and may be a mixture of hormones. Application of one such factor (**bryokinin**) enhances apogamy in *Splachnum ovatum* (Bauer, 1966).

(b) Age of Tissue Bauer (1963) suggested that apogamy seems to depend on age of the tissue. He observed that when sporogonia attain ageing, they regenerate only protonema, irrespective of the zone.

(c) Genetic Nature It has been observed that chromosome number appears to play an important role in apogamy. But it also appears that polyploidization is an important factor is apogamy.

20.3.5 Differentiation of Gametophore and Sporophyte

In mosses, usually an apical cell with three cutting faces is established prior to the differentiation of gametophores, while differentiation of sporophytes is preceded by establishment of an apical cell with two cutting faces. Apical cell, if present in the protonemal phase, usually contains only one cutting face. Parihar (1972) and others believe that an apical cell with three cutting faces usually passes through a stage bearing only two cutting faces. If conditions suitable for apogamy are existing, the apical cell with two cutting faces gets stabilised and thus develops the sporophyte. On the other hand, if conditions for its further development into an apical cell with three cutting faces are available, this results into the differentiation of gametophores.

20.3.6 Role of Calyptra in the Development of Sporophyte

Calyptra is a hood of tissue produced from the wall of the archegonium, especially in mosses. Calyptra protects the young capsule or sporophyte till the latter is nearly mature. It is usually a membranous, cap-like body formed after fertilization. Studies of Hughes (1969) and others suggest that "gametophyte exerts a controlling influence on the developing sporophyte mainly through calyptra". Rashid and Chopra (1969) have also proved the significance of the role of calyptra in their studies of apogamous sporophytes.

APOSPORY 20.4

20.4.1 Apospory and Who Discovered it in Bryophytes?

Apospory (production of diploid gametophyte from vegetative cells of sporophyte without the production of spores) was discovered by Pringsheim (1876) in *Bryum caespitosum*, *Hypnum cupressiforme* and

H. serpens and Stahl (1876) in *Ceratodon purpureus*. Wettstein (1925) developed the technique of seta regeneration for obtaining diploid gametophytes for genetic studies in *Funaria hygrometrica*, *Physcomitrium pyriforme* and some other bryophytic genera.

20.4.2 Apospory in Mosses

Besides the studies of apospory in mosses mentioned above, P Kachroo (1954) studied apospory in *Physcomitrium pyriforme*, Narayanaswami and Lal (1957) studied this phenomenon of the regeneration from the capsule wall in *Physcomitrium cyathicarpum*, and Kumra and Chopra (1980) studied the same aspect of seta regeneration in *Funaria hygrometrica*. It has been observed that the protonema regenerated from the seta of *F. hygrometrica* possesses aposporous gametophytes. Kumra and Chopra (1980) observed that these diploid gametophytes grow very slowly and are much smaller than that of haploid gametophytes.

20.4.3 Apospory in Liverworts and Hornworts

Many reports of apospory in liverworts and hornworts are, however, not available, but some of these reports are listed below:

1. Burgeff (1943) studied apospory in *Marchantia polymorpha.* He developed diploid thalli aposporously in this liverwort.
2. Matzke and Raudzens (1968) studied apospory in yet another liverwort, *Blasia pusilla* and observed almost the same details like that of *Marchantia polymorpha.*
3. Matzke and Raudzens (1969) reported apospory in two more liverworts (*Pellia epiphylla* and *Pallavicinia lyellii).*
4. Simone (1966) reported apospory in some Jungermanniales, such as *Jungermannia lanceolata*, *Porella pinnata, Rudula complanata* and *Lophocolea heterophylla*.
5. Aposporous, diploid gametophytes have been obtained from the setae of *Athalamia pusilla*, a member of Marchantiales (Mehra and Pental, 1976).
6. Borenhagen (1926) observed aposporous growth in *Anthoceros*, a hornwort.

TEST YOUR UNDERSTANDING

1. Write an essay on apogamy and apospory in bryophytes in about 500 words.
2. In bryophytes, two alternative pathways of life cycle are _____ and _____.
3. Define the terms ‘apogamy’ and ‘apospory’ in about 50 words.
4. Are the phenomena of apogamy and apospory rare in nature?
5. Apospory and apogamy are of considerable interest for bryologists. Why?
6. What is callus?
7. Give an account of apogamy in bryophytes in about 500 words only.
8. Describe some major factors responsible for differentiation of apogamous sporophytes.
9. What is calyptra? Describe its role in the development of sporophyte in about 50 words only.
10. Who discovered apospory in bryophytes?
11. Give an account of apospory in bryophytes in about 200 words.

21

Physiology of Bryophytes

Physiology of an entire, well-established group of plant kingdom and limit of a few pages in a textbook of this nature, as it is, is not possible, even to summarise. A very elementary account of some of the selected physiological processes is given here, just to give a very preliminary idea of the physiology of bryophytes to the readers.

WATER RELATIONS 21.1

In the field of water relations, some attention has been given to **absorption** and **conduction** of water and solutes in the gametophyte and sporophyte of bryophytes. Some work has also been done on the aspect of remarkable **resistance to drought** shown by the spores and vegetative cells of the members of this group. With reference to water relations, bryophytes are very specific because they have very limited power of withdrawing water from the substrate, they remain attached with. Most of the water they require for their physiological processes is derived (i) either from the water falling on them, or (ii) from the water flowing over them.

21.1.1 Absorption of Water

Haberlandt (1886) studied rapid movement of dye solutions in the central strands of the axis of *Plagiomnium undulatum* and *Polytrichum juniperinum*. It was shown that there is an upward movement of water from the base of the axis to the leaves, and it can be compared with the transpiration stream of higher plants. Bowen (1933) observed that "all bryophytes are capable of absorbing water over the entire surface of thalli or leafy shoot. On the basis of his studies of absorption and conduction of water, Buch (1947) concluded that bryophytes have two major physiological groups, viz. *endohydric* and *ectohydric*. A third group of '*myxohydric*' mosses is also present.

1. Endohydric These are the mosses which have a well-developed conducting strand, e.g. *Bryum capillare*. *Polytrichum commune* and *Mnium undulatum* have the ability to absorb water by their rhizoids present at the base and transfer the water from the base up to the actively photosynthesising leaves at the tip. A transpiration stream is present in such mosses. Majority of the endohydric mosses

are *tuft-forming*. They have well-developed basal rhizoidal system. They usually do not grow on rocks or tree barks, but occur frequently on loose substrata, such as soil or humus.

2. Ectohydric These are the bryophytes which lack well-developed conducting strands. Ectohydric includes all the leafy liverworts and majority of mosses, such as *Cryphaea, Orthotrichum, Rhacomitrium* and *Ulota*. They have the ability to absorb water and dissolved substances through any part of their external surface (thallus or shoot). They lack regular internal movement of water within their body parts. Absorption of dew is also very important as a source of water to enable photosynthesis in these bryophytes.

In ectohydric bryophytes, the leaves often revive within a few seconds while in endohydric bryophytes, the air-dry leaves become turgid very slowly.

3. Myxohydric In this group of bryophytes, features of both endohydric and ectohydric bryophytes are present, e.g. *Funaria hygrometrica.* Such mosses show both external and internal conduction of water. They occur mainly on moist, porous and nutrient-rich substrata.

21.1.2 Conduction of Water

For details, refer Chapter 28 (Conduction in Bryophytes).

GROWTH FORMS IN BRYOPHYTES 21.2

Bryophytes have special structural features, due to which their ability to hold capillary water is increased. They possess specialised growth forms. Some have aggregated shoots and are thus gregarious while others are solitary and have separated shoots, and many are **hanging bryophytes** in which the secondary branches are long and pendulous. A **growth-form classification** for tropical forest bryophytes has been proposed by P W Richards (1983). An outline of the same is given here as under:

Table 21.1 *Growth-form classification for tropical forest bryophytes, as proposed by Richards (1983)*

(A) Social Forms Aggregated leafy shoots or thallus branches.
(i) **Cushions,** in which shoots are mainly erect and radiating to aggregated, cushion-like dome-shaped structures.
(a) Large cushions, e.g. *Leucobryum* (b) Small cushions, e.g. *Octoblepharum*
(ii) **Turfs**, in which shoots are upright or somewhat parallel.
(a) **Tall turfs with mostly erect branches**, e.g. *Leucoloma*. (b) **Tall turfs with divergent or creeping branches**, e.g. *Sphagnum, Macromitrium* (c) **Short turfs** less than 2 cm in height, e.g. *Diphyscium* (d) **Open turfs**, e.g. *Drepanophyllum*
(iii) **Mats**, in which stems usually creeping over the substratum, forming closely interwoven mats.
(a) Rough mats, e.g. *Sematophyllum* **(b) Smooth mats**, e.g. *Radula, Frullania* **(c) Thread-like mats**, e.g. *Lejeunea* **(d) Thallose mats**, e.g. *Dumortiera*

(B) Solitary Forms Leafy shoots or thallus branches not aggregated
(i) **Protonemal bryophytes**, e.g. *Ephemeropsis*
(ii) **Unbranched dendroid forms**, e.g. *Pogonatum, Dawsonia*
(iii) **Branched dendroid forms**, e.g. *Protothanium*
(iv) **Feather forms**, e.g. *Bryopteris*
(v) **Bracket mosses**, e.g. *Spiridens*
(vi) **Hanging bryophytes**, e.g. *Plagiochila, Frullania*

WATER-HOLDING CAPACITY OF BRYOPHYTES 21.3

In *Sphagnum* and some oher mosses, the water-holding capacity perhaps depends on the morphological construction of the shoots. Many bryophytes grow very slowly, and this important factor affects *competetion* between them and other surrounding plants, specially higher plants. Temperature and moisture are also important factors in determining the growth rate and water-holding capacity of bryophytes.

PHOTOSYNTHESIS 21.4

Haberlandt (1886) was the first to establish that in mosses "all cells of protonema contain enough chloroplast to be able to assimilate CO_2 in the manner of thalli of liverworts and leaves of the green higher plants". It has also been observed and suggested that moss leaves and thalli of Marchantiales and a few other liverworts are better adapted for photosynthesis than many leaves of higher plants. There appears no major difference in the mode of photosynthesis in bryophytes and higher plants. In most of the bryophytes, formation of the starch can be observed easily. Instead of starch, some species of *Frullania* and *Andreaea*, however, produce other types of carbohydrates. Starch grains of bryophytes may contain a large amount of other carbohydrates, including glycogen. Cell walls of many bryophytes contain hemicellulose and pectin.

Bryophytes require optimum light and temperature for photosynthesis, as required by higher plants. Coloured substances, found in the cell walls of some liverworts and other bryophytes, are mainly due to strong light combined with high temperature.

Some **major factors,** which affect photosynthesis in bryophytes, are availability of water, temperature and light intensity.

1. Water Content In *Hypnum triquetrum*, photosynthesis activity increases with increase of water content up to as much as 300%. When water is supplied to this moss, photosynthesis begins within 5–10 minutes, attains a suitable higher rate within 25 minutes to utilise CO_2 produced by respiration, and within 30-40 minutes it reaches an equilibrium. In *Rhacomitrium*, very high rate of photosynthesis occurs in suitable light intensity, when water content is 200–300% of the dry weight and temperature in the surrounding environment is 12–15°C.

2. Temperature In *Rhacomitrium*, a moss, the balance between respiration and photosynthesis is markedly effected by temperature. Photosynthesis rate declines appreciably after a temperature

of 13–15°C. In *Bryum sandberghii*, yet another moss, the optimum temperature for photosynthesis is between 24–30°C but its gametophytes have the capacity to respire and photosynthesise even at –5°C, as observed by Rastorfer and Higinbothom (1968). According to Atanasiu (1971), the lowest temperature for photosynthesis in *Brachythecium geheebii* and *Camtothecium philippeanum* is –9°C, and for *Isothecium viviparum* is –8°C, and all these three are mosses.

3. Light Intensity In epiphytic mosses, the intensity of light plays a definite role on the rate of photosynthesis. It has been proved that the upper limit of vertical distribution of these mosses on trees of forests is restricted primarily by water but their lower limit is restricted by light intensity. The chlorophyll content and photosynthetic efficiency of epiphytic mosses resembles those of higher green plants. It has been shown by Hahn and Miller (1966) in *Polytrichum commune* that chloroplast replication in this moss takes place "in continuous white light and red light of 15 minutes/6 hours. In continuous darkness and in far-red light of 15 minutes/6 hours, the size of chloroplasts increased" but there is no effect on their number.

NITROGEN METABOLISM 21.5

Schuler et al. (1955), Diller (1966) and Montagne et al. (1969) are some of the workers who have worked on nitrogen metabolism in bryophytes. Montagne et al. have studied the enzymatic transamination by *Sphaerocarpos texanus* cultivated **in vitro**. Their studies show similarity between the transaminase system of this liverwort (*S. texanus*) and that of angiosperms.

RESPIRATION 21.6

Although much work has not been done on respiration in bryophytes, two major workers who have reviewed this aspect of bryophytes are A J M Garjeanne (1932) and W Stiles (1960). Instead of respiration, most researchers have focused on the capacity of the bryophytes to survive severe desiccation, and also on the relationship between respiration and water content. However, it has been established that there is no difference between the mode of respiration in bryophytes and that of higher plants. The rate and intensity of respiration in bryophytes is also affected by all the factors in almost all the same ways as that of higher plants. These **factors** include light, temperature, amount of available oxygen, the amount of carbohydrates in the cells, amount of CO_2 in the surrounding atmosphere, concentration of salts in the soil, etc.

It has been observed in *Sphagnum* and some other mosses that weak solutions of nutritive salts increase the intensity of respiration. The respiration process diminishes constantly in *Sphagnum*, if kept in distilled water. Solutions containing calcium salts first show an increase in rate of respiration but later on they show negative effect because its pH becomes unfavourable for the process.

Thalli, or leafy parts of several bryophytes, live in close contact with the soil. Air in such surroundings is relatively rich in CO_2 and water, and O_2 is in lower amounts. Several microorganisms, like algae, fungi, bacteria, protozoa, etc. occur freely in such surroundings. In such environment, the respiration of bryophytes is lowered. However, the process of respiration goes on regularly.

RQ (Respiratory Quotient the ratio of moles CO_2 evolved to moles O_2 absorbed in respiration) of many mosses including *Polytrichum juniperum*, *Hypnum triquetrum*, etc. have been studied by

Bastit (1891) and Plantefol (1927) and it was suggested that RQ. is that of a carbohydrate substrate irrespective of whether the plants are turgid or in a state of partial desiccation.

Studies have proved that effect of temperature on the respiration in mosses is almost the same as that in higher plants. In the germinating spores of *Polytrichum juniperum*, it has been shown by Paolillo and Jagels (1969) that respiration is limited by hydration rising to a maximum after 10 minutes. In some mosses, it has been shown that respiration and photosynthesis are increased in autumn but decreased in winter and reach their lowest level in February and again increase in the coming spring season (Atanasiu, 1971).

ENZYMES 21.7

Enzymes are usually large, complex protein molecules which, in very small quantities catalyse and control the natural chemical reactions of metabolism. In bryophytes, Udar and Chandra (1960) detected in male and female plants of *Riccia discolor* several enzymes, including aldolase, amylase, butyrase, catalase, deaminase, invertase, lipase, maltase, phosphatase, phosphorylase, ribonuclease and urease. In yet another study in 1960, these two Indian bryologists reported several enzymes in four other liverworts and opined that "metabolic processes in hepatics may closely correspond to those obtained in green tissues".

Maravolo et al. (1967) studied biochemical changes during sexual development in *Marchantia polymorpha* and reported phosphatases, esterases and peroxidases from the extracts of different parts of its thalli, including antheridiophores and archegoniophores.

Rao et al. (1969) studied the behaviour of oxidising enzymes of the thalli of *Riccia plana* by subjecting the plants to different periods of light and darkness. It was noticed that the activity of ascorbic acid oxidase is higher in plants grown in darkness. On the basis of their studies, these workers suggested that "light has an inhibitory effect on the activity of the enzymes."

Taylor et al. (1970) separated many forms of formic dehydrogenase, glutamic dehydrogenase, lactic dehydrogenese and malic dehydrogenase from 20 species of bryophytes.

ORGANIC ACIDS 21.8

Allsopp (1951) was the first to make a chromatographic survey of eight liverworts but he could not detect any acids in them. Ten years later, VSR Das in 1961 reported large quantities of aconitic acid in *Riccia*. Das and Rao (1966) detected mannuronic acid in the cell wall of *Riccardia*. Detection of organic acids in bryophytes still needs much work to be done.

MOVEMENTS 21.9

Responses to stimuli of the bryophytes awaits a lot of work still to be done. Garjeanne (1932) published a brief account of such studies in bryophytes in Fr. Verdoorn's ***Manual of Bryology***. A detailed account of tropisms and other movement, specially geotropic responses of *Marchantia*, has been given by Miller and Voth (1962), published in Volume 65 of ***Bryologist***.

Spermatozoids of bryophytes show movement, and this is a specific property of many of them. **Chemotropism** (growth of plant organ in response to a chemical stimulus) and **hydrotropism** (growth in response to the stimulus of moisture) is shown by spermatozoids of bryophytes. Researches have shown that chloroplasts of bryophytes exhibit phototactic responses. It was Rawitscher (1932) who reviewed the researches regarding the effect of gravity, light and other factors on the thallus and tissues of *Marchantia*. Kohlenbach (1957) performed several experiments on geotropic response of the gemmae in *Marchantia.*

TEST YOUR UNDERSTANDING

1. Give a brief account of some major events of physiology of bryophytes in about 500 words.
2. How can you differentiate between endohydric, ectohydric and myxohydric bryophytes?
3. The bryophytes which lack well-developed conducting strands are known as _____.
4. Give an example of a myxohydric moss.
5. Enumerate some major types of growth forms in bryophytes.
6. Give an example for protonemal bryophyte.
7. What are hanging bryophytes?
8. Give an example of a hanging bryophyte.
9. Describe some developments in the field of photosynthesis in bryophytes in about 250 words.
10. Write a brief scientific note on respiration in bryophytes.
11. What are enzymes? Write a brief note on enzymes of bryophytes.

22 Chemical Constituents of Bryophytes

Bryologists from different parts of the globe have reported several organic compounds from bryophytes in the recent past. These include antibiotics, terpenoids, lignins, flavonoids, lipids, sterols and growth substances. In several cases, these have also been utilised in taxonomic categorisation of bryophytes.

ANTIBIOTICS 22.1

Antitumor elements have been reported from the extracts of *Marchantia polymorpha*, *M. stellata* and *Polytrichum commune* by Hartwell (1971). Antimicrobial activity is shown by several bryophytes. *Dumortiera hirsuta* and *Conocephalum conicum* are active against the fungus *Candida albicans* while *Sphagnum strictum* inhibits the growth of several bacteria including *Pseudomonas aeruginosa* and *Staphylococcus aureus*. *Sphagnum* inhibits the growth of bacterium *Sarcinia lutea* (Ramaut, 1959). Mosses, such as *Anomodon rostratus* and *Orthotrichum rupestre* inhibit the growth of several species of bacteria like *Micrococcus* and *Streptococcus*. A pronounced effect over the activity against several bacteria is shown by several mosses including *Sphagnum, Polytrichum* and *Atrichum* (McCleary and Walkington, 1966). Gupta and Singh (1971) reported antibacterial activity of petroleum ether extracts of *Barbula* and *Timmiella* against 33 species belonging to both Gram +ve and Gram –ve bacteria. Antibacterial activities of 52 species of bryophytes have been reported by Banerjee and Sen (1979). According to these workers, however, none of the 52 investigated species of bryophytes possessed antifungal property. They also opined that antibiotic activity of bryophytes varies from species to species and it also depends on the age of the plant, season of collection and ecological niche. Some species of *Marchantia* and *Plagiochasma* also have antibiotic activity and cause inhibition of several bacteria such as *Bacillus subtilis, Vibrio cholerae*, *Sarcina lutea* and *Staphylococcus aureus*. Chopra and Kumra (1988) have mentioned that the "taxa *Campylopus laetus, Asterella sanguinea, Plagiochasma appendiculatum* and *Reboulia hemispherica* were moderately active against the Gram –ve bacteria, *Salmonella typhi* and *Vibrio cholerae"*. Several bryophytes have antifungal property, e.g. *Sphagnum portoricense* and *Dumortiera hirsuta* (McCleary et al., 1960). Wolters (1964) also studied antifungal activity of two Jungermanniales and 16 mosses.

GROWTH SUBSTANCES 22.2

Five major groups of growth substances include auxins, gibberellins, cytokinins, abscisic acid and ethylene, of which the first three are generally growth promoters while the last two are generally growth inhibitors.

1. Auxins Chromatographic and some other studies of Narayanaswami and LaRue (1955) suggest the production of indole-acetic-acid, an auxin, in the apical parts of the thallus of some liverworts, e.g. *Lunularia cruciata*. Schneider et al. (1967) and Maravolo (1981) reported the occurrence of IAA in *Marchantia polymorpha* and some other bryophytes. Presence of IAA in the gametophytes of *Physcomitrella patens* has also been reported by Ashton et al. (1985).

2. Gibberellins Gibberellin-like substances have been reported in some bryophytes like *Polytrichum commune* (Muromtsev et al., 1969) and *Marchantia polymorpha* (Melstrom et al. 1974).

3. Cytokinins **Bryokinin**, an endogenous cytokinin has been isolated from the callus cells of the hybrid sporophyte (*Funaria hygrometrica* X *Physcomitrium pyriforme*) by Bauer (1966). This cytokinin is physiologically active at several stages of the development in mosses. It promotes activities like bud formation, archegonium differentiation and formation of apogamous sporogonium in *Splachnum ovatum.*

4. Abscisic Acid and Lunularic Acid Most of the liverworts lack abscisic acid. It has been reported that the same growth regulating functions, as of abscisic acid, are fulfilled by lunularic acid in most of the liverworts.

5. Ethylene DeGreef et al. (1981) and Thomas et al. (1983) reported production of ethylene in *Marchantia*. It has also been reported in *Funaria hygrometrica* by Rohwer and Bopp(1985). In mosses, ethylene works as a senescence hormone.

LIPIDS 22.3

Lipids are a group of chemical compounds which contain glycerol and fatty acids. They are insoluble in water and soluble in organic solvents. Triglycerides, wax, steryl esters, phospholipids and glycolipids are some lipids. Of these, considerable amounts of triglycerides, wax, esters and steryls have been reported in green moss protonema, shoots and spores by several workers including Lilgenberg and Karunen (1978), and Karunen and Mikola (1980).

ALKANES 22.4

Alkanes are saturated hydrocarbons, i.e. compounds containing carbon and hydrogen. Bryophytes contain a wide range of alkanes. A detailed list of major alkanes found within several members of Hepaticopsida and mosses is given by Chopra and Kumra (1988).

FATTY ACIDS

22.5

A **fatty acid** is an organic acid with the general formula $C_nH_{2n}O_2$. Fatty acids have been reported in several members of Hepaticae including *Pellia* (Matsuo et al., 1971), *Marchantia polymorpha* (Gellerman et al., 1972), *Asterella* (Caldicott and Eglinton, 1976) and *Conocephalum* (Matsuo et al., 1980). Huneck (1983) isolated fatty acids from about 30 genera of mosses including *Distichum, Fontinalis, Hedwigia, Hypnum, Polytrichum*, *Sphagnum* and *Tortula*. Lipid content of three species of *Sphagnum*, at different ages of 1–5 years, have been studied by Karunen et al. (1979).

TERPENOIDS

22.6

The compounds made up of two or more isoprene molecules, i.e. $CH_2 = C(CH_3) – CH = CH_2$ are called **terpenoids**. On the basis of such C_5 units present in them, these are classified into various categories like **monoterpenoids** containing C_5 units (reported only in a few bryophytes, e.g. *Radula complanata* and *Conocephalum conicum*), **sesquiterpenoids** containing C_{15} units (e.g. *Bazzania trilobata*), **diterpenoids** containing C_{20} units (e.g. *Jungermannia infusca*), **triterpenoids** and **sterols** containing C_{30} units (e.g. *Thamnium alopecurum*), etc. As many as 14 **steroids** have been isolated from bryophytes as mentioned by Chopra and Kumra (1988), mostly from mosses (e.g. *Polytrichum* and *Sphagnum*; Marsili et al., 1972), hornworts and liverworts (e.g. *Anthoceros* and *Marchantia*; Asakawa et al., 1981). Chopra and Kumra (1988) have given a list of ninety-nine bryophytes containing steroids.

FLAVONOIDS

22.7

Flavonoids are natural phenolic products found in several groups of green plants, including bryophytes. Flavonoids in the form of anthocyanin-like pigments have been reported in several species of *Sphagnum*. Three rare flavonoids have been reported in *Bryum cryophilum*, a moss, by Benz et al. (1962). Markham et al. (1969) reported flavonoids from *Hymenophyton flabellatum*. Flavonoids seem to be more frequent in Hepaticae than in Musci, and "nearly all investigated species of Marchantiales possess flavonoids" (Chopra and Kumra, 1988).

Flavones are the predominant type of flavonoids found in bryophytes, e.g. *Marchantia polymorpha, Plagiochila asplenioides*, etc. Other flavonoids reported from bryophytes include **isoflavones** (e.g. *Bryum capillare*), **flavonols** (e.g. *Reboulia hemisphaerica*), **dihydroflavones** (e.g. *Riccia crystallina*), **aurones** (e.g. in antheridiophores of *Marchantia polymorpha*), **chalcones** (e.g. *Plagiochasma rupestre*, *P. tenue*; Schier, 1974), **anthocyanins** (e.g. *Bryum cryophilum*) and **sphagnorubins** (e.g. *Sphagnum magellanicum*).

LIGNINS

22.8

Lignin is a complex aromatic compound which is deposited in the cellulose cell walls of the xylem and sclerenchyma during the process of secondary thickening. Wood is made mostly of lignin. In

bryophytes, Siegel (1962) found evidence for the presence of traces of lignin-like materials in peristomial teeth tissues of *Polytrichum* and also in the gametophyte axes of giant mosses like *Dawsonia* and *Dendroligotrichum*. Presence of lignin, built mainly of *p*-hydroxyphenyl units, has been shown by Bland et al. (1968) in *Sphagnum*. However, the presence of true lignin in bryophytes is still doubtful and needs further investigations.

CAROTENOIDS 22.9

Using paper chromatography methods, Douin (1956, 1958) investigated the carotenoids of 20 species of Marchatiales and Jungermanniales and 40 species of Bryales as well as some species of Andreaeales and Sphagnales, and concluded that α-carotene, β-carotene and lutein are present in almost all these taxa. Along with these carotenoids, some others like violaxanthin and zeaxanthin have also been reported in some species of mosses by Freeland (1957). As many as ten carotenoids have been isolated from *Fontinalis antipyretica* by Benz et al. (1968). In spores of *Polytrichum commune*, Karunen and Ihantola (1977)) reported the presence of carotenes, violaxanthin, lutein, neoxanthin and zeaxanthin. Chopra and Kumra (1988) have given a detailed list of carotenoids found in 9 genera of liverworts and 15 genera of mosses.

CARBOHYDRATES 22.10

Several types of carbohydrates have been reported from the bryophytes including glucose, fructose and sucrose, as in *Sphagnum*. As many as 40 genera of liverworts and 6 genera of mosses have been investigated for this purpose. Some major carbohydrates met within some common genera of liverworts include **raffinose** (e.g., *Diplophyllum*), **sucrose** (*Fossombronia*), **amidon** and **hexitol** (*Marchantia),* **inuline** (*Monoclea*), **amidon** and **maltose** (*Pellia*), **mannuronic acid** (*Plagiochasma*), and **glucose** and **fructose** (e.g. *Porella, Reboulia*). Amongst the mosses, glucose, maltose and sucrose, along with small amounts of mannose, melibiose and deoxyribose have been reported in *Torula, Rhyncostegium, Platyhyphidium* and *Homalothecium* (Margaris and Kalaitzakis, 1974).

ORGANIC ACIDS 22.11

Much work has still not been done on organic acids in bryophytes. Das and Rao (1963) have shown the presence of transaconitic acid and malic acids in *Riccia, Plagiochasma* and *Riccardia*. The latter two genera also contain mannuronic acid. Citric acid, fumaric acid, malic acid and succinic acid have been reported in *Sphagnum* by Maass and Craigie (1964). Derivatives of cinnamic acid have been reported to occur in several bryophytes including *Sphagnum magellanicum* (Tutschek et al., 1973) and *Anthoceros* (Mendez and Sanz-Cabanilles, 1979). Some other organic acids have also been reported from some bryophytes like **cis-aconitic acid** (*Riccia*), **glycolic acid** (*Plagiochila*), and **shikimic acid** (*Pellia conocephalum*).

ENZYMES 22.12

Enzymes have been reported to occur in several bryophytes. Amongst the liverworts, Udar and Chandra (1960) reported amylase, butyrase, catalase, invertase, laccase, lipase, maltase and urease from *Asterella* and *Plagiochasma. Marchantia* contains esterase, urease and phosphatase, according to Jones et al. (1973) while *Lophocolea* and *Frullania* contain urease and oxalic acid oxidase, respectively. Amongst mosses, enzymes have been reported in over 30 genera, of which major ones include *Dawsonia, Fontinalis, Funaria, Hypnum*, *Pogonatum, Polytrichum*, *Sphagnum* and *Tortula* (Chopra and Kumra, 1988).

AMINO ACIDS 22.13

Amino acids within bryophytes have been investigated in only a few members. Amongst the Hepaticae, they have been investigated in *Marchantia* (Schneider et al., 1967), *Pellia, Plagiochila* and *Diplophyllum* (Touffet and Villeret, 1958). Some amino acids reported from these genera include tryptophan, allantoin, alanine, aspartic acid, glycine, glutamic acid, lysine, proline, valine, etc. Amongst the mosses, they have been investigated in *Funaria hygrometrica* and some species of *Sphagnum* (Hartmannn and Geissler, 1973; Black et al., 1955). Some of the amino acids reported from these mosses include allantoine, allantoic acid, arginine, glycine, histidine, leucine, lysine, proline and tyrosine.

ALLERGENIC AND ANTI-TUMOUR ACTIVITIES 22.14

Liverworts like *Radula* and *Frullania* cause skin allergies, and the active allergenic principle in some species of these genera is **sesquiterpene lactone frullanolide** according to Perold et al. (1972). Potential allergenic agents have been reported from some members, such as (i) germacranolide from species of *Frullania* and *Porella*, and (ii) eudesmanolides from *Diplophyllum.*

In the treatment of Sarcoma-37, a type of malignant tumour of connective-tissue origin, ethanolic extract of *Polytrichum juniperum* has proved to be effective (Belkin et al., 1953). A compound **diplophyllin** has been isolated from *Diplophyllum*. This is effective against human epidermoid carcinoma according to Ohta et al. (1977).

TEST YOUR UNDERSTANDING

1. Write an account of the chemical constituents of bryophytes in about 500 words.
2. Name any five bryophytic genera which have antimicrobial activity.
3. Write a note on growth substances in bryophytes in about 200 words
4. Name a member of Marchantiales, from which at least three growth substances have been reported.
5. Name two bryophytes from which fatty acids have been reported.
6. What are flavonoids? Give an account of flavonoids from bryophytes.
7. "Some bryophytes have allergenic and anti-tumour activities". Comment in about 100 words.
8. *Marchantia* is the most important genus from the point of view of chemical constituents. Elaborate.

23 Bryophytes as Indicators of Environmental Conditions and Pollution

Most people, in general, think that bryophytes are of no use to mankind. However, besides their several economic and ethnic uses (discussed in detail in Chapter 32), bryophytes are of definite ecological uses, and they are of particular utility as indicators of environmental conditions and pollution. In bryophytes, pollutants (i) inhibit sexual reproduction, (ii) reduce photosynthesis, and (iii) reduce growth of plants and may eventually cause their death. Increased pollution has made some species of bryophytes "rare" and others have even become "extinct". In general, however, "rough mats, tall turfs, large cushions, and leafy liverworts are least resistant to pollutants" (Gilbert, 1970). From the point of view of indicators of pollution, there are two types of bryophytes. The **first** are extremely sensitive to pollution and show clear visible symptoms of injury even in the presence of very little quantities of pollutants. Such bryophytes serve as good bioindicators of the degree of pollution. The **second** type of bryophytes have the capacity to absorb and retain pollutants in quantities much higher than those absorbed by members of other plant groups growing in the same habitat.

INDICATOR SPECIES OF BRYOPHYTES 23.1

Many bryophytes are good indicators of environmental conditions. Terrestrial bryophytes in several countries, including Finland, are widely used as indicators of specific forest types. Importance of bryophytes as indicators of several minerals was established in the middle of the 20th century, and it was R R Brooks (1972) who recommended bryophytes as guides to mineralisation. D C Smith (1976) worked on indicator species of bryophytes with reference to minerals and proved that "bryophytes could solve several difficulties that are often associated with stream sediment sampling". Copper mosses (e.g.

Scopelophila, Mielichhoferia elongata and *M. mielichhoferi),* grow almost exclusively in areas high in copper, particularly in copper sulphate" (Shacklette, 1984).

According to Glime and Keen (1984), presence of *Fontinalis* and *Brachythecium rivulare* indicate the presence of iron oxide in the area. It has been proved by Shiikawa (1962) that *Jungermannia volcanicola*, *Polytrichum* and *Sphagnum* "play active roles in deposition of iron ore" in any area. Dierssen (1973) established that presence of *Sphagnum* is a reliable indicator of acidic conditions in the surrounding.

Mentioned below are some examples of bryophytes which are indicators of environmental conditions and pollution:

1. *Ceratodon purpureus* indicates good drainage and high amounts of nitrogen.
2. *Pleurozium schreberi* and *Pogonatum alpinium* are indicators of less nitrogen.
3. *Funaria hygrometrica* and *Pohlia cruda* in an area indicate good base saturation.
4. *Psilopilum laevigatum* is an indicator of poor physical soil condition and poor base saturation.
5. Absorption of rain and atmospheric water by bryophytes make some of them as pH indicators, e.g. *Polytrichum* is a good acid indicator.
6. Presence of *Leucobryum* in a region is an indicator of acidic soil combined with dry, infertile and deep humus.
7. J A Janssens (1988) and others have used bryophytes (e.g. *Sphagnum*) as indicators to identify past climates. Such studies enhance our information about the bryophytic flora of the past.

EROSION CONTROL BY BRYOPHYTES 23.2

Conard (1935) suggested and proved that "sowing spores and vegetative fragments of bryophytes on bare areas could help to prevent erosion". He opined that bryophytes (e.g. *Barbula, Bryum* and *Weissia*) are major "pioneers on new roadbanks, helping to control erosion" prior to the large-sized plants getting established there. Ando (1957) worked on erosion control by bryophytes and suggested that in Japan, the bryophytes (e.g. *Atrichum, Blasia, Nardia, Pogonatum* and *Pohlia*) "play a role in preventing erosion of banks" of the rivers, streams and other water reservoirs. Oechel and Sveinbjornsson (1978), on the other hand, suggested that "when bryophytes such as *Sphagnum* reach saturation, they can suddenly release a great load of water at unexpected times. Because of its tremendous water-holding capacity, *Sphagnum* along with *Calliergon sarmentosum*, controls water during spring runoff in the Arctic".

NITROGEN FIXATION 23.3

Usually, the nitrogen is a limiting nutrient for plant growth, in general, and agriculture in particular. Because of the presence of nitrogen-fixing blue-green algae (e.g. *Anabaena, Nostoc*) in many bryophytes (e.g. *Anthoceros*), they can contribute significant soil nitrogen, particularly to dry range land soils. The blue-green algae present in *Anthoceros* behave symbiotically, take nitrogen from the atmosphere and convert it to ammonia and amino acids. The extra amount of nitrogen is released to the substrate where it is usually used by other organisms. The bryophyte crusts provide homes for nitrogen-fixing organisms, according to Harper and Marble (1988).

Some bryophytes (e.g. communities of *Sphagnum*) show very high nitrogen-fixing rates. In this way, bryophytes function as substrate for nitrogen-fixing organisms, and are thus very important to the forestry industry. According to Granhall and Hofston (1976), following three types of nitrogen-fixing associations exist in *Sphagnum* and other taxa:

1. Epiphytic Cyanobacteria,
2. Intracellular Cyanobacteria, and
3. Nitrogen-fixing bacteria.

Rao and Burns (1990) opined that "nitrogen-fixing Cyanobacteria of bryophyte species also provide growth enhancement for oilseed rape."

BRYOMETER OR MOSS BAG 23.4

It is now an established fact that bryophytes have played a major role in maintaining changes in the atmosphere of the earth. For monitoring these changes, scientists in Japan have developed an instrument called *bryometer*. The **bryometer**, developed by H Taoda of Japan in 1976, is "a bag of mosses that responds in predictable ways to various levels of air pollution". Taoda (1976) exposed a variety of mosses to various levels of SO_2 and confirmed that most species of mosses "are injured by 10–40 hours of exposure at 0.8 ppm SO_2, or at 0.4 ppm after 20–80 hours."

Bryometers are now used throughout the world to monitor changes in the atmosphere. In many European countries, the bryometer is now used so commonly that it is now named a **moss bag**. Monitoring of heavy metals around coal-fired plants in Finland is done by moss bags made of *Hylocomium splendens.*

SO_2 AND ACID RAIN 23.5

Mosses are not widely used as reliable indicators of environmental conditions. *Grimmia pulvinata* and several other bryophytes are used as indicators of SO_2 in England and several countries of Europe and North America. H Taoda (1972) of Japan used several epiphytic species of bryophytes to assess pollution impact in the city of Tokyo, and "divided the city into five zones, based on pollution intensity". He listed four groups of bryophytes "in order of increasing sensitivity to SO_2". In 1980, Taoda used three bryophytes (*Conocephalum supradecompositum, Lunularia cruciata* and *Marchantia polymorpha*) "to assess the degree of urbanization in Chiba city near Tokyo".

SO_2 fumigation affects mosses and shows reduction in their coverage. It is, however, very difficult to estimate whether the damage to mosses is directly due to SO_2 or if it is the result of the ultimate formation of sulphuric acid, formed due to acid rain. According to the researches of Raeymaekers (1987), "acid rain, resulting from SO_2 emissions, can actually improve conditions for *Pleurozium schreberi* in some jackpine (*Pinus banksiana*) forests. *P. schreberi* grew faster and increased in cover when sprayed with water acidified to pH 4.5". "However, at pH 3.5, its growth and chlorophyll content were reduced and capsule production decreased". It has also been established that " a pH as low as 3.5 is not uncommon in acid fog. While acid rain may favour some bryophytes, acid fog can be more damaging."'

According to Winner et al. (1978), bryophytes can not only serve as warning systems, but can also "protect the nutrients and roots beneath them. By intercepting sulphate ions, bryophytes prevent formation of sulphuric acid that contributes to leaching valuable nutrients from soil".

BRYOPHYTES AS BIOINDICATORS OF HEAVY METALS IN AIR POLLUTION 23.6

Gilbert (1969) was the first to strongly recommend the "use of cryptogamic epiphytes as biological pollution indicators". Since then, the "bryophytes have been used to monitor airborne pollution caused by emissions from factories". Scientists in different parts of the world have now strongly correlated the absence of epiphytic mosses, lichens, and majority of liverworts from urban areas with air pollution. Rao and Le Blanc (1967), Le Blanc (1969), Rao et al. (1977), Ferguson and Lee (1978), Rao (1982) and others have now conclusively proved that air pollutants, especially heavy metals, affect growth and reproduction of bryophytes and lichens.

Bryophytes, particularly mosses and liverworts, suit well as bioindicators and biomonitors because of their characteristics such as (i) lack of significant cuticle, (ii) lack of significant epidermis, (iii) lack of well-organised leaves, (iv) "leaves" being only one cell thick, and (v) absence of a well-developed conduction system. Due to all these characteristics, bryophytes absorb both nutrients and pollutants directly from the atmosphere.

Scientists have now proved that bryophytes easily "absorb heavy metals without the regulation characteristic of their nutrient absorption". This ability of many bryophytes to separate or set apart "heavy metals while remaining unharmed makes them good biomonitors" or bioindicators. For example, "*Marchantia polymorpha* accumulates lead" (Briggs, 1972) and "*Calymperes delessertii* is a good monitor for aerial lead and to a less extent, copper" (Low et al., 1985). Nash (1972) has proved that *Pottia truncata*, *Polytrichum ohioensse, Dicranella heteromella* and *Bryum argenteum* are very tolerant of high tissue levels of cadmium (610 ppm), copper (2700 ppm), and zinc (55,000 ppm). Thomas (1983) opined that "*Hypnum cupressiforme* accumulates three times as much zinc, copper and cadmium as do lichens or seed plants".

Satake et al. (1989) investigated that bryophytes have a variety of means by which they can separate or set apart "substances that are toxic to many higher plants and animals".

LeBlanc and Rao (1973) proved that in many countries, including Germany and Canada, "bryophytes have been transplanted from pollution-free areas to areas suspected of pollution damage".

Studies suggest that heavy metals constitute a very important class of pollutants. The most significant among these are (i) lead, (ii) cadmium, (iii) zinc, and (iv) mercury. A few examples to prove this are mentioned below:

1. Lead The most toxic metal known is lead. It tends to accumulate more in ectohydric mosses like *Dicranella varia*. These mosses lack cuticle and are, therefore, able to absorb water from their entire body surface. In *Grimmia deniana*, lead is ionically bound to the cell wall, and thus prevents its toxic amount from penetrating the cell wall. Studies of Briggs(1972) in *Marchantia polymorpha* proved that lead tolerance can play a major role in natural selection

2. Cadmium Mosses are able to take up airborne cadmium. They can also absorb cadmium from the substrate. Bryophytes show sensitivity to cadmium at very low concentrations, and even as

low as 10^{-8} M. The indications of damage to the bryophytes (e.g. *Sphagnum*) are noticeable in the pigmentation and growth rate. Cadmium at 1 ppm can significantly enhance the elongation of germ tubes in *Funaria hygrometrica.* At higher concentrations (e.g. 10 ppm), however, it can significantly reduce spore germination in this moss.

3. Zinc According to Shimwell and Laurie (1972), zinc uptake is related to the water economy of mosses, e.g. *Dicranella varia*. In *Funaria hygrometrica* and *Marchantia polymorpha*, zinc concentrations more than 50 ppm result in complete inhibition of spore germination and extension of germ tube.

4. Mercury Bryophytes collect mercury through rainwater or dust particles. Mosses have the ability to tolerate high concentrations of mercury, and have, therefore, been widely used as indicators of atmospheric mercury. Mondano and Smith (1974) recorded 4.34ppm mercury in *Dicranella heteromella* in urban regions, but only 0.24 ppm mercury in rural areas. Mercury values in mosses and some other plants indicate that bryophytes give a more reliable indication of mercury fall-out.

COPPER MOSSES AS INDICATORS OF COPPER CONCENTRATION 23.7

Some species of mosses serve as indicators of high copper concentration in the substrate, and these are known as **copper mosses**, e.g. *Dryptodon stratus*, *Merceya ligulata*, *Mielichhoferia elongata*, *M. macrocarpa* and *M. mielichhoferi*. Some liverworts whose principal substrata are copper ores are *Cephaloziella phyllacantha* and *Gymnocoba acutiloba*. According to Warncke (1968), *Marchantia alpestris* in Scandinavia "is generally restricted to copper-rich areas," and it should be added to the list. According to Shacklette (1967), many copper mosses grow on substrata low in sulphur, and others on substrata with relatively high pH.

Copper mosses occur on soil rich in copper but they cannot be used as plant indicators in determining the presence of copper in the region. It is so because (i) these mosses are very rare, and (ii) it is very difficult to identify them.

BRYOPHYTES AS BIOINDICATORS OF SOME OTHER AIR POLLUTANTS 23.8

Besides heavy metals, SO_2 and acid rain, discussed already in the earlier part of this chapter, bryophytes are also useful indicators for other types of air pollution, e.g. hydrogen fluoride and ozone. A bryophyte sensitive to hydrogen fluoride is *Orthotrichum obtusifolium*. On the other hand, some bryophytes, tolerant of fluoride fumes, are *Rhacomitrium*, *Polytrichum commune* and *P. strictum*. According to Gagnon and Karnosky (1992), some species of *Sphagnum* are especially susceptible to ozone. They show characteristics such as (i) reduced photosynthesis, (ii) reduced growth, (iii) loss of colour, and (iv) symptoms of desiccation. Lee at al. (1998) proved that well-hydrated bryophytes are not generally sensitive to ozone at concentrations likely to occur in the atmosphere.

BRYOPHYTES AS INDICATORS OF UV-B RADIATION 23.9

According to Hedenas (1991), *Bryum argenteum*, a moss, is now being used widely "to monitor the thickness of the ozone layer over Antarctica. As the ozone layer decreased, increased exposure to UV-B (280–315 nm or UV-Medium) radiation stimulated production of flavonoids" in *B. argenteum.* However, in *Sphagnum magellanicum*, there were no noteworthy differences in chlorophyll or carotenoid concentrations following UV-B exposure, as observed by Searles et al. (2002). Wilson et al. (1998) reported earlier that "in the presence of adequate water, growth of *Hylocomium splendens* in Norway was strongly stimulated by UV-B equivalent to 15% reduction in ozone." A decrease in concentration of UV-B-absorbing compounds is also shown by *Polytrichum commune* after the third year of its growth.

BRYOPHYTES AS INDICATORS OF RADIOACTIVITY 23.10

Bryophytes have the ability to sequester minerals, and then also they remain unharmed. It is this ability of bryophytes which makes them "good indicators of accumulated radioactivity" according to researchers like Whitehead and Brooks (1969), Beckett et al. (1982) and Summerling (1984). Due to the cation exchange activity of several species of *Sphagnum*, they "could be used to decontaminate water containing radioactive materials" (Fischer, et al. 1968). It has been proved by Kulikov et al. (1976) that "the uptake of radioisotopes by epigean mosses occurs not so much from substrates as directly from atmospheric fall-out."

BRYOPHYTES AS INDICATORS IN AQUATIC HABITATS 23.11

Several bryophytes are of specific importance as indicators in aquatic habitats. One of their major advantage is their ability to integrate pollution over time and keep a record that cannot be achieved through testing of water chemistry. It is so because their contaminant content is more consistent than that of the sediments. Bryophytes are used as aquatic bioindicators because (i) they are easy to collect, (ii) they are easy to transplant, (iii) they can be harvested any time of the year, and (iv) their samples can be kept for many years for further analysis. Some such suitable bryophytes include species of *Fontinalis, Leptodictyum, Platyhypnidium* and *Scapania. Scapania undulata* can survive at a low pH of 3.9, and it is a very useful accumulator for zinc, lead and cadmium in nutrient-poor water (Satake et al, 1989).

In *Pohlia ludwigii*, a moss, it has been reported by Soma et al. (1988) that "aluminium, manganese, copper, zinc and lead were in higher concentrations 1–3 cm below growing stem tips than at tips, but sodium, phosphorus, calcium and iron differed little between the 1 cm tip portion and lower parts." This study proves that accumulations differ in different parts of mosses.

Mosses prove to be of great advantage for us because of their ability to help in the clean up of some contaminants. If phenol is present in low concentrations in water, *Fontinalis antipyretica* can decompose this phenol up to 32–43%, and *Platyhypnidium ripariodes* can decompose them up to 20–27%. According to Mouvet et al. (1985), *Cinclidotus danubicus*, an aquatic bryophyte, is a good

accumulator of polychlorinated biphenyls. Mouvet et al. (1986) proved further that *Fontinalis* and some other aquatic mosses "could be used to monitor both cadmium and polychlorinated biphenyls because of their high accumulation ability."

Takaki (1977) proved that "in some cases, pollution actually increases the cover of bryophytes." Bowden et al. (1994) studied that water bodies rich in phosphorus show an extensive growth of *Hygrohypnum alpestre* and *H. ochraceum.*

BRYOPHYTES AS CLEANING AGENTS OF TOXIC WASTE 23.12

Some bryophytes, e.g. *Sphagnum*, show great promise to function as cleaning agents of toxic waste. Rozmej and Kwiatkowski (1976) have opined that "even microorganisms have been cleaned up by *Sphagnum*, perhaps due to the antibiotic properties of peat". *Calymperes delessertii*, a moss, is also an efficient adsorbent for dyes. According to Crum (1988), peat moss (*Sphagnum*) is "especially effective at removing nitrogen (96%) and phosphorus (97%) applied from sewage or eutrophic river water". Peat has also been used to clean wastewater containing oil. In some countries, like Finland and Canada, peat is also used "as a filter agent for oily waste in vegetable oil factories" (Ruel et al., 1977). According to Viraraghavan and Tanjore (1994), the "highly toxic pentachlorophenol (PCP) is readily adsorbed by *Sphagnum* peat." Such an adsorption is irreversible, and this makes *Sphagnum* peat "an effective and inexpensive means of removing such toxicants." In some countries, including Poland, *Sphagnum* is now being widely sold for reclaiming strip-mined land. Some scientists have also suggested that peat is "a possible material for filtering water for reuse in space travel" (Crum, 1988).

TEST YOUR UNDERSTANDING

1. Give a brief account of "bryophytes as indicators of environmental conditions and pollution" in about 500 words.
2. Discuss "ecological uses of bryophytes" in about 500 words.
3. Do pollutants in bryophytes inhibit sexual reproduction?
4. Giving suitable examples, give an account of indicator species of bryophytes in about 200 words.
5. "Bryophytes control erosion". Comment in about 100 words.
6. Write a brief scientific note on bryometer or moss bag.
7. An apparatus used to monitor changes in the atmosphere of bryophytes is named _____
8. Why do mosses and liverworts suit well as bioindicators? Write at least three such characteristics of bryophytes.
9. Explain in brief the role of "bryophytes as bioindicators of heavy metals in air pollution."
10. What are copper mosses?
11. Comment on "bryophytes as indicators of radioactivity".
12. Explain the following in about 100 words each:
    (a) Bryophytes as cleaning agents of toxic waste
    (b) Bryophytes as indicators in aquatic habitats

24 Biologically Active Compounds from Bryophytes

WHAT ARE BIOLOGICALLY ACTIVE COMPOUNDS? 24.1

A great variety of **terpenoids**, **aromatic compounds** and **acetogenins** have been isolated from bryophytes. Many of these have characteristic **scents**, **pungency** and **bitterness**, and show extraordinary bioactivities as well as medicinal properties. These terpenoids, aromatic compounds and acetogenins are included under biologically active compounds.[1]

SOME BIOLOGICALLY ACTIVE COMPOUNDS EXTRACTED FROM BRYOPHYTES 24.2

Amongst bryophytes, members of Hepaticae contain cellular oil bodies which are extracted easily with organic solvents, while members of Musci and Anthocerotae do not possess such cellular oil bodies. A large number of bryophytes have been used as medicinal plants in China and many other countries, specially to cure burns, bruises, external wounds, dermatitis, etc. Most of the Hepaticae (liverworts) "contain mainly lipophilic mono-, sesqui-, and diterpenoids, aromatic compounds (bibenzyls, bis-bibenzyls, benzoates, cinnamates, long-chain alkyl phenols, naphthalenes, phthalides, isocoumarins) and acetogenins which constitute the oil bodies" (Asakawa, 2007). Y. Asakawa of Japan made elaborate studies on this aspect and has isolated over 400 new compounds from bryophytes (Asakawa, 1990, 1993, 1995, 2007).

Some mosses and liverworts of medicinal importance and possessing biological activity are listed in Table 24.1.

[1] For details, consult article of Yoshinori Asakawa (2007) of Japan, published in ***Pure Applied Chem***. Vol. 79, No. 4, pp. 557–580.

Table 24.1 *Biological activity and effects of some liverworts and mosses of medicinal importance*

No.	*Plants*	*Biological activity and effects*
(A)	**Liverworts (Hepaticae)**	
1.	*Conocephalum conicum*	Antifungal, antimicrobial, antipyretic and antidotal activity; used to cure burns, cuts, fractures, snakebites, and swollen tissues.
2.	*Frullania tamarisci*	Antiseptic activity.
3.	*Marchantia polymorpha*	Antihepatic, antidotal, antipyretic, diuretic activity; used to cure burns, scalds, open wounds, poisonous snakebites, cuts, etc.
(B)	**Mosses (Musci)**	
1.	*Bryum argenteum*	Antidotal, antipyretic, antirhinitic activity.
2.	*Ditrichium pallidum*	For convulsions in infants.
3.	*Funaria hygrometrica*	For pulmonary tuberculosis, bruises, dermatomycosis.
4.	*Haplocladium catillatum*	Antidotal and antipyretic activities; pharyngitis, mastitis, uropathy, pneumonia, tymphanitis and urocystitis.
5.	*Plagiopus oederi*	As sedative; used for epilepsy and cardiopathy.
6.	*Polytrichum commune*	Antidotal and antipyretic; cuts, hemostasis, bleeding from gingivae, tuberculosis of lungs.
7.	*Rhodobryum roseum*	As sedative, used also for cardiopathy and neurasthenia.

CHARACTERISTICS OF BIOLOGICALLY ACTIVE COMPOUNDS ISOLATED FROM BRYOPHYTES 24.3

Yoshinori Asakawa (2007) listed the following characteristics of the biologically active compounds (terpenoids and aromatic compounds) isolated from liverworts:

1. Characteristic scents
2. Pungency and bitterness
3. Dermatitis
4. Cytotoxic, anti-HIV, and DNA polymerase β-inhibitory
5. Antifungal and antimicrobial activity
6. Insect antifeedant activity, mortality and nematocidal activity
7. Superoxide anion radical release inhibitory activity
8. Enzymes and NO production inhibitory activity
9. Piscidal and plant growth inhibitory activity
10. Neurotrophic activity
11. Muscle-relaxing activity
12. Inhibitory activity against osteoporosis and allergy
13. Cardiotonic and vasopressin antagonist activity
14. Anti-obesity activity
15. Synthesis of bioactive compounds from constituents of liverworts

Some brief aspects of all these characteristics of the biologically active compounds isolated from bryophytes are discussed below.

CHARACTERISTIC SCENTS 24.4

Several simple aromatic compounds or volatile terpenoids are emitted by many members of Hepaticae. These compounds are responsible for several **scents**, which are sweet-woody, sweet-mossy, carrot-like, mushroomy or seaweed-like. Some such Hepaticae members, possessing characteristic odours or scents (Asakawa, 2007), are listed below:

1. *Asterella* species produce indole- or skatole-like odour.
2. *Conocephalum conicum* produces strong mushroomy or camphor-like odour.
3. *Frullania davulica* produces mossy odour.
4. *Jungermannia obovata* produces carrot-like odour.
5. *Lophozia bicrenata* produces pleasant cedar-oil-like odour.
6. *Pellia endiviifolia* produces dried seaweed-like odour.
7. *Porella gracillima* produces woody-earthy odour.
8. *Takakia lepidozioides* produces mixed smell of cinnamon and burnt wheat powder.
9. *Targionia hypophylla* produces sweet terpentine-like odour.

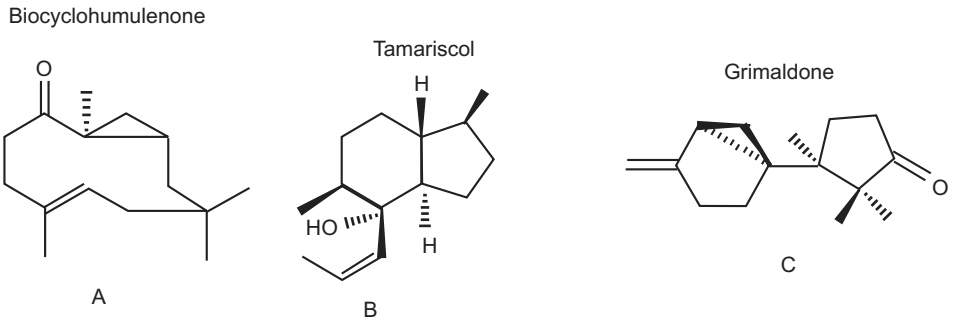


Fig. 24.1A-C Characteristic odorants from some liverworts. A, Biocyclohumulenone; B, Tamariscol; C, Grimaldone (after Asakawa, 2007)

Mushroom-like smell of almost all liverworts is due to the compound OCT-1-en-3-01 and its acetate. **Bicyclohumulenone** (Fig. 24.1A) has been isolated from *Plagiochila sciophila* while **tamariscol** (Fig. 24.1B) has been isolated from *Frullania davulica*. Both these compounds of commenre are used as "perfumes as such or as perfume components of powdery floral-, oriental bouquet-, fantastic chypre-, fancy violet-, and white rose-types in various cosmetics" (Asakawa, 2007). The "sweet terpentine-like odour of *Targionia hypophylla* is due to a mixture of *cis*- and *trans*- pionocarveyl acetates" (Asakawa, 2007). The compound **grimaldone** (Fig. 24.1 C) is responsible for the strong sweet-mossy smell of *Mannia fragrans*.

PUNGENCY AND BITTERNESS 24.5

Very intense pungent and bitter substances, which show interesting biological activities, are produced by some liverworts. *Porella vernicosa* and some other species of this liverwort contain potent pungent substances. Its strong, hot and pungent taste is due to the compound (–) -polygodial (Fig. 24.2A).

Several compounds possessing an intense pungent taste have been isolated by Asakawa (2007) and his co-workers from *Plagiochila, Pellia* and *Trichocoleopsis*. Sacculatal and 1 β-hydroxysacculatal (Fig. 24.2B) have been reported from the ether extract of *Pellia endiviifolia*. When one chews a whole plant of *Plagiochila asplenioides* and some of its other species, one feels a potent hot taste slowly. This is due to the compound plagiochiline-A (Fig. 24.2C).

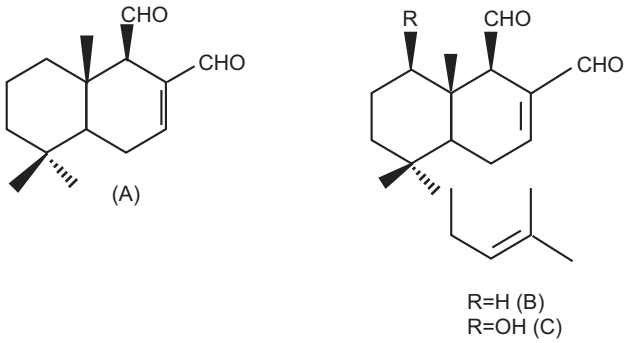


Fig. 24.2 Characteristic pungent and bitter substance e.g. polygodial (A), sacculatal and 1β- hydroxysacculatal (B) and plagiochiline (C) from some liverworts

DERMATITIS 24.6

Very intense allergenic contact dermatitis is caused by some liverworts including *Frullania* species. The substances responsible for inducing allergy include sesquiterpene lactones, **(+) – frullanolide** (Fig. 24.3A) and **(–) –frullanolide** (Fig. 24.3B). Allergenic contact dermatitis is also caused by *Marchantia polymorpha* and *Metzgeria furcata*.

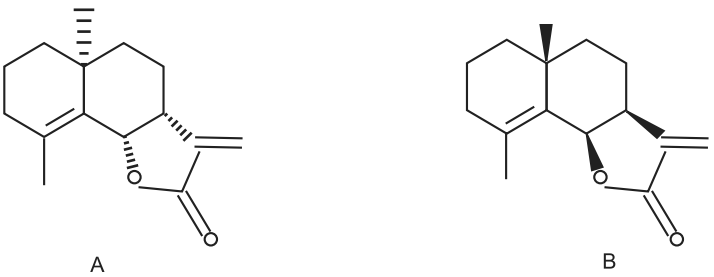


Fig. 24.3 Some allergy-inducing compounds isolated from *Frullania* sp.; A, (+) - Frullanolide; B, (–) - Frullanolide

CYTOTOXIC, ANTI-HIV-1, AND DNA POLYMERASE β-INHIBITORY ACTIVITY 24.7

Cytotoxic activity against lymphocytic leukemia is shown by some Hepaticae including *Bazzania pompeana*, *Porella japonica*, and *Radula perrottetii*. Marsupellone and acetoxymarsupellone isolated

from *Marsupella emarginata* also showed cytotoxicity against certain types of lymphocytic leukemia. Riccardin-A and Riccardin-B from *Riccardia multifida* inhibited KB cells. *Plagiochila* species also show similar characteristics. *Marchantia polymorpha*, which can cause allergenic contact dermatitis, shows inhibitory activity against Gram-positive bacteria. It also has diuretic activity. Marchantin-A isolated from *M. polymorpha*, also shows cytotoxicity against lymphocytic leukemia.

ANTIFUNGAL AND ANTIMICROBIAL ACTIVITY 24.8

Antimicrobial activity is shown by several liverworts including the species of *Bazzania, Dumortiera, Marchantia*, *Plagiochila* and *Radula.* Liverworts, which show antifungal activity include *Lunularia cruciata, Marchantia polymorpha* and *Plagiochila vernicosa*, besides many others. Antibacterial activity against *Bacillus cereus*, *Cryptococcus neoformans*, *Escherichia coli, Pseudomonas aeruginosa* and *Salmonella typhimurium* is shown by the compound Marchantin-A obtained from several species of *Marchantia,* including *M. polymorpha, M. plicata* and *M. tosana* (Asakawa, 2007). Marchantin-A also has antifungal activities against fungi such as *Alternaria kikuchiana*, *Aspergillus fumigatus*, *A. niger*, *Candida albicans, Penicillium chrysogenus* and *Trichophyton rubrum.* Strong antibacterial activity is shown against *Streptococcus mutans* (dental caries) by the compound **sacculatal** (Fig. 24.2) isolated from *Pellia endeviifolia*.

INSECT ANTIFEEDANT, MORTALITY AND NEMATOCIDAL ACTIVITY 24.9

Species of *Plagiochila* contain plagiochiline-A (Fig. 24.2 C), which is a strong insect antifeedant, specially against the worm *Spodoptera exempta*. Plagiochiline-A also shows nematocidal activity against the nematode *Caenorphabdiitis elegans.* Succulatal (Fig. 24.2 B), a compound obtained from several bryophytes (e.g. *Trichocoleopsis*), kills tick species (e.g. *Panonychus citri*). Insect antifeedant activity is also shown by several species belonging to *Chiloscyphus, Gymnocolea* and *Plagiochila.*

SUPEROXIDE ANION RADICAL RELEASE INHIBITORY ACTIVITY 24.10

Angiopathies are serious heart-related problems, such as cardiac infarction and arterial sclerosis. These may be caused by excess superoxide anion radical (O_2^-) in organisms. Plagiochilal-B (Fig. 24.4A) obtained from species of *Plagiochila*, norpinguisone methyl ether from *Porella elegantula* and radulalin–K (Fig. 24.4 B) from *Radula javanica* are examples of some of the compounds which inhibit the release of superoxide anion radical from guinea pigs.

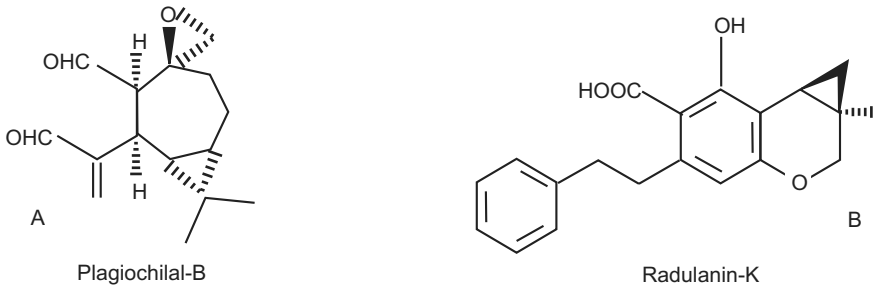


Fig. 24.4 A, Plagiochilal-B; B, Radunalin-K

ENZYMES AND NITRIC OXIDE PRODUCTION INHIBITORY ACTIVITY 24.11

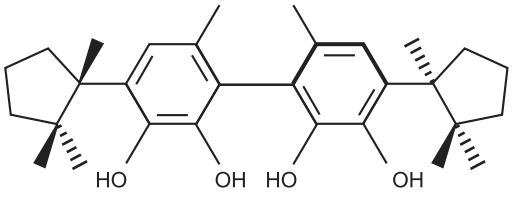
Production of several enzymes is inhibited by the activity of several compounds produced by many liverworts. The enzymes include 5-lipoxygenase, hyaluronidase, cyclooxygenase, etc., and compounds include marchantin-A, marchantin-B, marchantin-E from *Marchantia*, radulanin-H from *Radula*, and riccardin-C from *Riccardia*. Lunularic acid, found in almost all liverworts, as a minor component, has antihyaluronidase activity. In several liverworts "overproduction of NO is involved in inflammatory response-induced tissue injury and the formation of carcinogenic N-nitrosamines. Large amounts of NO were expressed and generated by iduced iNOS on stimulation of endotoxins or cytotoxins involved in pathological response. Thus, inhibition of iNOS is very important to control inflammatory disease" (Asakawa, 2007).

PESTICIDAL AND PLANT-GROWTH INHIBITORY ACTIVITY 24.12

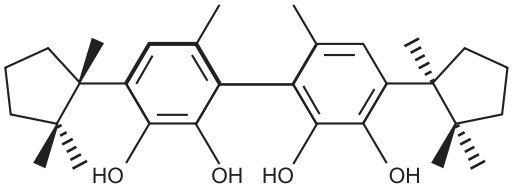
Porella vernicosa and several other species of this liverwort produce (–)-polygodial (Fig. 24.2), which is a pungent and very strong pesticide. Sacculatal (Fig. 24.2), obtained from some other species of *Porella* (e.g. *P. endiviifolia*) also possesses similar pesticidal properties. Both polygodial and sacculatal can kill certain kinds of fishes within two hours. "Almost all crude extracts from liverworts which contain bitter or pungent substances show phytotoxic activity". Polygodial also promotes root elongation in rice dramatically.

NEUROTROPHIC ACTIVITY 24.13

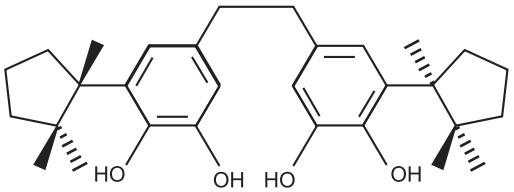
Compounds like mastigophorenes A, B and D (Fig. 24.5), obtained from *Mastigophora diclados* show neurotrophic properties in fetal rat hemisphere according to Fukuyama and Asakawa (1991). Acceleration of neurotic sprouting of neuronal cell culture of fetal rat cerebral hemisphere is also seen in the compounds obtained from *Plagiochila fruticosa*.



Mastigophorene-A



Mastigophorene-B



Mastigophorene-D

Fig. 24.5 Mastigophorene A, B and D obtained from *Mastigophora diclados*

MUSCLE-RELAXING ACTIVITY 24.14

Marchantin-A, obtained from *Marchantia polymorpha* and some other species (e.g. *M. paleacea*) of this genus, is a pharmacologically important compound because of its muscle-relaxing activity. Marchantin-A, along with its trimethyl ether, shows surprising muscle-relaxing activity.

INHIBITORY ACTIVITY AGAINST OSTEOPOROSIS AND ALLERGY 24.15

Matsunaga et al. (1993) and Katsunuma (1997) have established the role of some liverworts (e.g. *Porella japonica* in inhibitory activity against osteoporosis and allergy. Scientists in Japan are working to develop chemopreventive drugs for these diseases from some liverworts.

CARDIOTONIC AND VASOPRESSIN ANTAGONIST ACTIVITY 24.16

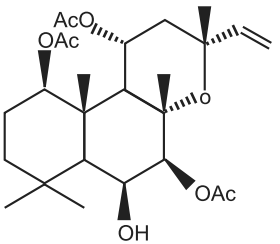
According to Asakawa (1990), marchantin-A, obtained from *Marchantia polymorpha*, shows cardiotonic activity because it increases coronary blood flow. Prenyl bibenzyl, a compound obtained from *Radula perrottetii*, shows vasopressin antagonist activity.

ANTIOBESITY ACTIVITY 24.17

Compounds, such as riccardin-C and ricccardin-F, have been isolated from some bryophytes (e.g. *Reboulia hemispherica* and *Blasia pusilla*). They function as liver-X-receptors (LXR) ∝- antagonist and liver-X-receptor β-antagonist. Riccardin-C also increases cholesterol efflux from some cells, and is used in the development of some drugs having antiobesity activity.

SYNTHESIS OF SOME BIOACTIVE COMPOUNDS FROM CONSTITUENTS OF LIVERWORTS 24.18

Mastigophora diclados produces herbertane dimers, such as mastigophorene-A and mastigophorene-B (Fig. 24.5) which possess neurotrophic activity. Ptychantin-A (Fig. 24.6), produced from the liverwort *Ptychantus striatus* of family Lejeuneaceae has properties of treating several disorders such as blood pressure, glaucoma, congestive heart failure and bronchial asthma, according to detailed studies of Hagihara et al. (2003, 2006).



Ptychantin-A

Fig. 24.6 Ptychantin-A produced from *Ptychantus striatus*

TEST YOUR UNDERSTANDING

1. What are biologically active compounds? Write a note on some biologically active compounds in about 200 words.
2. Write an essay on biologically active compounds found in bryophytes.
3. Y Asakawa of Japan isolated approximately how many biologically active compounds from bryophytes?
4. Make a list of at least seven characteristics of the biologically active compounds isolated from bryophytes. Elaborate at least one of them in about 100 words.
5. Give a brief account of biological activities and effects of *Marchantia polymorpha, Funaria hygrometrica* and *Polytrichum commune*.
6. Explain in brief the role of bryophytes in treating dermatitis, fungal and other microbial infections.
7. Name a bryophyte from which a compound obtained shows cytotoxicity against lymphocytic leukemia.
8. Compounds obtained from which bryophyte have antiobesity activity?

25 Bryophytes and Their Role in Carbon and Nitrogen Cycling

ROLE OF PLANTS IN REGULATING BIOGEOCHEMICAL CYCLES 25.1

Plants play critical and definite roles in regulating biogeochemical cycles. Growth of plants controls the exchange of gases that support life in our biosphere. Growth of plants also affects soil development. Plants are our primary producers, and due to this, they also influence the distribution of energy for higher trophic levels.

DO BRYOPHYTES HAVE THE SAME ROLE AS VASCULAR PLANTS IN REGULATING BIOGEOCHEMICAL CYCLES? 25.2

Bryophytes do not have the same role as vascular plants in regulating biogeochemical cycles. It is because of their unique physiology and ecology in which bryophytes differ from vascular plants in influencing cycles of elements (e.g. C, N), energy and water. For example, an effective water-relation system is present in bryophytes. Two phenomena, which allow bryophytes to tolerate longer periods of water stress than vascular plants and also allow them to recover quickly with rehydration, are **poikilohydry** and **desiccation tolerance**. (**Poikilohydry** is a phenomenon of lacking structures or mechanisms to regulate water loss and, hence, having water content determined rapidly by the water potential of the environment, as in algae, bryophytes).

Due to poorly-developed conduction systems, water and solutes are taken up over the entire plant surface in bryophytes. Characters such as lack of (i) effective gametophyte stomata, and (ii) effective cuticle in many species of bryophytes, allow free exchange of gases and solutions across cell surfaces. Because of such characters, bryophytes often serve as effective traps for water and nutrients. In

comparison to vascular plants, this quality of bryophytes also makes them more sensitive to atmospheric chemical deposition.

HOW DO BRYOPHYTES INFLUENCE ECOSYSTEM FUNCTIONS? 25.3

According to Turetsky (2003), bryophytes influence ecosystem functions due to the characters related to their specific physiology and life history by

1. Producing organic matter,
2. Stabilising soils or debris,
3. Trapping sediment and water, and
4. Providing food and habitat for algae, fungi, invertebrates and amphibians.

There exist several mechanisms by which bryophytes influence carbon (C) and nitrogen (N) cycles, and some such mechanisms are detailed in this chapter.

MAJOR ROLES OF BRYOPHYTES IN C- AND N-CYCLING 25.4

Mentioned below are some of the major roles of bryophytes in carbon and nitrogen cycling, as also pointed out by M R Turetsky (2003) in an article published in the ***Bryologist***:

Generally, the bryophytes

1. Fix C and N from atmospheric pools,
2. Reduce N availability for vascular plants and microbes,
3. Release dissolved compounds that are immobilised by soil microbes and lost via runoff, and
4. Transform C and N into recalcitrant organic matter.

ABILITY OF BRYOPHYTES TO INFLUENCE LOCAL SOIL CLIMATES 25.5

Bryophytes have definite impact on local soil climates. They influence local soil climates by

1. Increasing soil moistures,
2. Decreasing soil temperature, and
3. Changing the density of soil organic matter.

The roles and influences mentioned above under Articles 25.4 and 25.5 confirm that bryophytes influence the share of "C and N ecosystem inputs, and indirectly influence the rate at which these elements are lost from ecosystems through litter decay, fire, and herbivory" (Fig. 25.1; Turetsky, 2003).

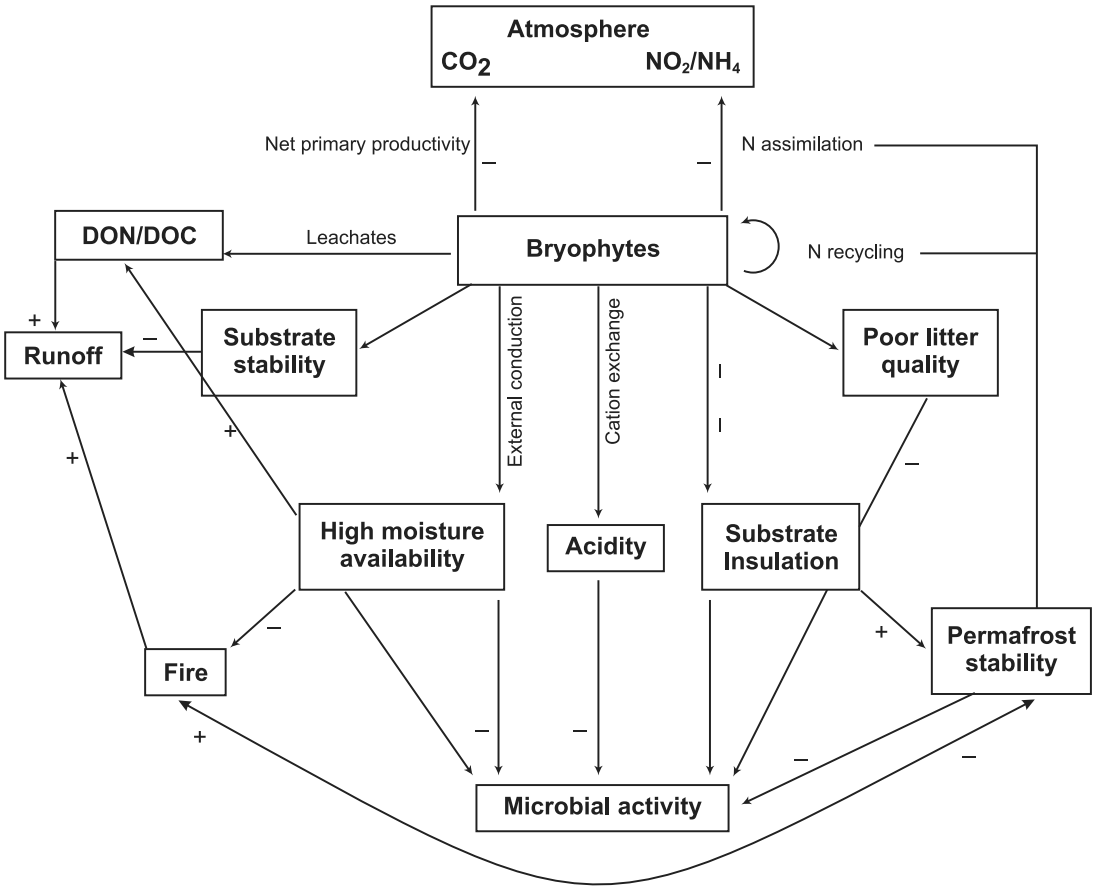


Fig. 25.1 Scheme summarizing the influences of bryophytes on carbon and nitrogen cycling in terrestrial ecosystems, including positive (+) and negative (–) influences on the microbial activity, fire and runoff (adapted from Turetsky, 2003)

ROLE OF BRYOPHYTES IN CARBON CYCLING 25.6

25.6.1 Carbon Fixation by Bryophytes

Houghton et al. (2001) opined that one of the largest flow or continuous change in the global C cycle is between atmospheric CO_2 and land vegetation. The carbon derived from autotrophic fixation through the process of photosynthesis makes a very large amount and comprises about half of all organic matter. It has been established that bryophytes directly influence the flow of C into "ecosystems through their metabolism and growth rates. While estimates of bryophyte biomass have been characterised in various ecosystems, annual accumulations of C in plant material are more useful for studies of the C cycle." Carbon gains through net primary production (NPP) can be determined through net exchange of CO_2 (Tuba et al., 1998) or annual production of biomass (Swanson and Flanagan, 2001; Ilyashuk, 2002).

(**NPP** represents the difference between gross primary production and primary respiratory losses. Gross primary production represents total amount of organic matter produced per unit time).

In comparison to tropical bryophytes, the production rates of temperate and polar bryophytes have been relatively well studied. From this point of view, worth-mentioning studies have been made on *Polytrichum alpestre* and *Chorisodontium aciphyllum* by Fenton (1980), and on *Sphagnum* by Schofield (2001) and Vitt et al. (2003).

Clarke et al. (1998) reported growth of tropical epiphytic bryophytes ranging from 122–203 g biomass m^{-2} yr^{-1}. The growth of the canopy and gap species may be higher than that of understorey bryophytes, as estimated by workers like Losch et al. (1994) end Zotz et al. (1997).

Sand-Jenson et al. (1999) opined that aquatic bryophytes often dominate vegetation in lakes, and bryophyte NPP can exceed that of algae. Bryophytes exploited from this point of view by various bryologists include *Sphagnum* (Lannergren and Ovstedal, 1983), *Jungermannia vulcanicola* (Miyazaki and Satake, 1985) and *Fontinalis hypoides* (Ilyashuck, 2002).

25.6.2 Control on Growth of Bryophytes

Mentioned below are some of the factors which internally control the photosynthetic efficiency in bryophytes:

1. Rate of photosystem electron transport.
2. Morphology of plant, in general, and 'leaf', in particular.
3. Environmental factors such as light and water. In species of *Sphagnum*, water limitation "decreases resistance to C uptake" according to Rice (2000).
4. Availability of nutrients also strongly influence C fixation by many bryophytes, especially terrestrial species.
5. Growth of temperate species of *Sphagnum* is promoted by increasing photoperiod length.
6. Increase in the radiation flow also helps in promoting the growth of temperate species of *Sphagnum.*
7. Factors, such as declining photoperiod length and declining night temperature, induce dormancy in mosses.
8. Both high and low water contents limit C uptake in bryophytes. Photosynthetic enzyme activity is inhibited in conditions of low water availability.
9. Effect of water stresses varies among different species of bryophytes. Higher water content was most stressful for *Leucobryum antillarum*, while growth of many tropical bryophytes (e.g. *Frullania mirabilis*, *Phyllogonium fulgens*) was more limited by low water availability according to Zotz et al. (1997).
10. Growth of bryophytes is also influenced substantially by "altered moisture availability" (Turetsky, 2003).
11. According to Vitt et al. (2003) and many other workers, "as N is thought to limit plant growth in many terrestrial systems, bryophyte productivity commonly increases following N or combined N and phosphorus (P) additions".
12. Arscott et al. (1998) have correlated high phosphorus inputs to high bryophyte productivity.

25.6.3 Impact of Dissolved Organic Carbon

According to Moore and Dalva (2001), "carbon can be leached from plant biomass as dissolved organic carbon". A major part of this dissolved organic carbon can be readily utilised by microbes, and its remaining part "can be comprised of highly refractory compounds with complex structures" (Turetsky, 2003). In this way, the dissolved organic carbon can either be "utilised by microbes or can be lost from terrestrial ecosystems via runoff". It is this terrestrial dissolved organic carbon which is transported to aquatic bodies like lakes, estuaries or oceans, where it represents an important transfer of energy and carbon from terrestrial to aquatic systems. This dissolved organic carbon is very important and has the ability to change the production in greenhouse gases, trace metal speciation, acid-base chemistry and N and P availability according to workers like Gergel et al. (1999).

In general, it has been proved that plants influence the leaching of dissolved organic carbon through production of soluble organic compounds. As far as bryophytes are concerned, the "species common to boreal peatlands differ in water-soluble carbohydrates, phenolics, and soluble non-polar compounds", according to Turetsky (2003). In *Frullania atrata*, the concentrations of soluble sugars and polyols comprised up to 17% of dry weight in the upper canopy of forests, while in *Phyllogonium fulgens*, it is equivalent to only 6% of dry weight in lower canopy, according to Coxson et al. (1992). In mosses, the "greater amounts of soluble proteins and carbohydrates are associated with higher metabolic activity" (Pakarinen and Vitt, 1974).

According to Coxson et al. (1992), the release of soluble sugars from epiphytic bryophytes in tropical forests is equivalent to 122 kg $ha^{-1}yr^{-1}$. Carleton and Read (1991) estimated leakage of carbohydrates from *Pleurozium schreberi* after the extended summers and concluded that "these carbohydrate-rich leachates are capable of supporting mycorrhizal fungal growth."

According to Charman et al. (1999) and Chasar et al. (2000), some amount of dissolved organic carbon in peatlands reaches downwards into the peat and is used by microbes. Fraser et al. (2001) opined that export of dissolved oxygen-carbon can be a significant loss of carbon from the terrestrial ecosystem.

In spite of all these above-mentioned studies, Turetsky (2003) mentioned that "more research is needed to understand the long-term fate of bryophyte-derived dissolved oxygen-carbon in terrestrial and aquatic ecosystems".

25.6.4 Decomposition and Implications for Soil Carbon

After the death of plants, carbon in their organic matter is degraded through the action of bacteria and fungi. The rate of decomposition is affected also by various factors such as temperature, moisture, etc. According to Merrifield and Ingham (1998), bryophytes "may influence microbial activity by providing microhabitat for invertebrates". Tsuneda et al. (2001) opined that "bryophytes can also harbour microfungi that decompose organic carbon". Eckstein (2000) suggested that "bryophytes also influence decay by reducing soil temperature and/or increasing soil moisture. Since bryophytes have low thermal conductance, they can increase water availability through external capillary action" (Turetsky, 2003).

Litter with poor organic-matter quality is produced by bryophytes. At the same time, bryophytes are also not able to synthesize lignin. Due to the absence of lignin, bryophyte litter would decay more rapidly than vascular material of higher plants. Organic matter produced by bryophytes generally decomposes very slowly. In *Sphagnum*, the slow rate of decomposition may be because of low N concentrations. Decay is also inhibited in bryophytes due to the presence of large concentrations of

phenolics and nonpolar compounds. Verhoeven and Liefveld (1997) have identified polyphenolic networks in mosses resembling vascular lignins and tannins. These compounds can mask cellulose and also inhibit microbial breakdown, and can also make cell walls impenetrable to hyphae of fungi.

Verhoeven and Toth (1995) have worded on antimicrobial properties of bryophytes, such as *Sphagnum*. Basile et al. (1999) have shown that flavonoids isolated from mosses have antibacterial properties. Banerjee and Sen (1979) have focused in detail on the antibiotic activity of 52 species of bryophytes.

Rate of decomposition, however, differs widely among different species of bryophytes, e.g. decay process is very slow in species of *Sphagnum* than other mosses (Belyea, 1996).

ROLE OF BRYOPHYTES IN NITROGEN CYCLING 25.7

25.7.1 Biological Fixation of Nitrogen

The largest global pool of nitrogen is the atmosphere. Plants need nitrogen for the production of chlorophyll and RUBISCO (Ribulose 1, 5- biphosphate carboxylase oxygense) and also for the construction of proteins and nucleic acids. This nitrogen comes from biological fixation, atmospheric deposition and weathering. In many ecosystems, the largest source of nitrogen is by biological fixation. Many prokaryotic microorganisms (e.g. Cyanobacteria) use the nitrogenase enzyme to break the triple bonds of atmospheric nitrogen and fix it into more soluble forms. Large amount of energy is spent in this nitrogen-fixation process. Symbiosis occurs between nitrogen-fixing Cyanobacteria and hosts (e.g. algae, fungi, bryophytes and many vascular plants). In this way, bryophytes also influence biological nitrogen fixation. These Cyanobacteria may be epiphytic or endophytic, e.g. *Nostoc* in the thalli of *Anthoceros*. Meeks et al. (1983) proved that "ammonium (NH_4^+) is the initial product of N fixation by symbiotic *Nostoc* associated with the hornwort *Anthoceros punctatus.* A small portion of N_2-derived ammonium (~10%) is assimilated by *Nostoc* and the remaining product is transferred efficiently to host tissue and utilised as amino acids."

Vitousek (1994) concluded that "liverworts are important to N fixation in Hawaiian forests." Sheridan (1991) estimated that "*Hapalosiphon flexosus–Sphagnum erythrocolyx* associations contribute about 400 mg N m^{-2} yr^{-1} on a tropical volcanic dome." Basilier (1980) reported that "N fixation in coniferous forests occurred only with *Sphagnum* plants."

Devey and Marchant (1983) and some other workers investigated that availability of moisture "appears to be important to N fixation", specially in plants like *Andreaea, Ditrichum strictum* and *Jamesoniella colorata*. Temperature is also a strong control on N fixation in bryophytes of polar regions (Davey and Marchant, 1983). Sheridan (1991) observed that "wind or volcanic disturbance increases fixation by tropical *Hapalosiphon flexosus–Sphagnum erythrocolyx*.

25.7.2 Assimilation of Nitrogen by Bryophytes

Bryophytes have access to inorganic N in the form of ammonia and nitrates and/or organic N, according to Lipson and Nasholm (2001). Nitrates (NO_3^-) and nitrites (NO_2^-) are reduced after assimilation. According to Brown (1992), "bryophytes generally assimilate NH_4^+ more readily than NO_3^-." Miyazaki and Satake (1985) concluded that "liverworts such as *Jungermannia vulcanicola* and *Scapania undulata* used NH_4^+ as their major N source". According to Rudolph et al. (1993), low pH usually inhibits NO_3^-

assimilation. Glime (1992), however, opined that "acid-tolerant aquatic species such as *Sphagnum* and *Drepanocladus* rely heavily on NH_4^+ for N requirements." Brown (1992) mentioned further that "bryophytes are able to take up organic N such as amino acids or dipeptides." Studies of Kielland (1997) illustrate that organic N is an important source of nitrogen for bryophytes such as *Cetraria richardsonii* and *Sphagnum rubellum*. Turetsky (2003) opined that "bryophytes generally are very efficient in assimilating N, and appear to rely mainly on atmospheric deposition." Tracer studies of Li and Vitt (1997) and Lamontagne et al. (2000) using ^{15}N highlight the mechanisms of N uptake and retention by plants. Svensson (1995) concluded that "bryophytes are competitive scavengers of N and reduce N availability for higher plants." Species of *Sphagnum* are extremely efficient in capturing N because the entire plant is able to absorb nutrients according to Rudolph et al. (1993). Turetsky (2003) stated that "epiphytic bryophytes play an important role in N cycling within canopies, though less is known about their N-use efficiency."

25.7.3 Loading of Nitrogen and Bryophyte Assimilation

Loading of nitrogen can generally change plant productivity and patterns of N retention. It "can also influence community composition by favouring nitrophilous species" (Turetsky, 2003). Nordin and Gunnarsson (2000) reported that ammonium nitrate ($NH_4^+NO_3^-$) applications increased amino acid concentrations in *Sphagnum* but NH_4^+ alone decreased organic acid concentrations in other bryophytes according to Soares and Pearson (1997).

Pitcairn et al. (2002) opined that bryophytes are often used in determining programmes as indicators of N pollution in ecosystems. Several studies (Penuelas and Filella, 2001) are available which prove that mosses have been used for temporal assessment of N deposition.

25.7.4 Transformations and Losses of Nitrogen

Uptake of nitrogen by plants and microorganisms is very rapid, and due to this, the majority of soil N occurs in organic forms. Nitrogen from organic matter is released by activity of microbes. This loss of organic N from ecosystems is reduced by processes such as (i) decreasing decomposition, (ii) herbivory, and (iii) combustion. Studies suggest that bryophytes may enhance N availability for higher plants if N slowly released from the breakdown of bryophyte litter can be taken up more efficiently. It has also been proved that dissolved organic nitrogen is released from organic matter of the plants through processes like (i) microbial breakdown, and (ii) leaching. Willimas et al. (1999) studied this aspect of dissolved organic nitrogen in *Sphagnum recurvum* and *S. capillifolium*. In case the dissolved organic nitrogen is not immediately immobilised, it can be exported from terrestrial ecosystems via runoff.

WHAT MORE CAN BE DONE IN UNDERSTANDING ROLE OF BRYOPHYTES IN C AND N CYCLING? 25.8

Some of the knowledge gaps still inhibiting our understanding of the role of bryophytes in C and N cycling are listed below:

1. Major researches in this aspect have only been done on mosses. Much more is still to be done on liverworts and hornworts.

2. A majority of the tropical bryophytes have not been investigated so far from the point of view of role of bryophytes in C and N cycling.
3. The role of bryophytes in biogeochemical cycling should be investigated not as a single functional group but it should also be investigated along with plants of other groups.
4. Due emphasis should be given to understand the mechanisms controlling bryophyte chemistry while studying the role of bryophytes in C and N cycling.
5. Usually, bryophyte material is of poor litter quality. It should also, therefore, be investigated in detail that how this poor quality litter influences C and N cycling.
6. Bryophyte productivity should also be measured properly prior to estimating their role of C and N cycling.
7. It should also be estimated thoroughly that "how will changes in species diversity influence ecosystem processes or controls on ecosystem processes" (Turetsky, 2003).
8. Whether genetic diversity of bryophytes is also an important factor in C and N cycling should also be studied in detail.
9. Tolerance levels of various species of bryophytes to N deposition should also be investigated while studying their role in C and N cycling.
10. It should also be observed whether species disappear in response to N pollution.
11. Whether deposition of N changes bryophyte biochemistry should also be worked out while studying the role of bryophytes in C and N cycling.
12. Will global warming influence bryophyte chemistry should also be studied properly?

TEST YOUR UNDERSTANDING

1. Write an essay on bryophytes and their role in carbon and nitrogen cycling.
2. Do bryophytes have the same role as vascular plants in regulating biogeochemical cycles? Comment only in about 100 words.
3. What is poikilohydry?
4. How do bryophytes influence functions of the ecosystem?
5. Describe the role of bryophytes in carbon cycling.
6. Write at least five factors which internally control the photosynthetic efficiency in bryophytes.
7. Discuss in brief the role of bryophytes in the nitrogen cycle.
8. What do you mean by biological fixation of nitrogen, with particular reference to bryophytes?
9. What is the full form of RUBISCO?

26 Evolution of the Gametophyte in Bryophytes

VIEWS ON THE EVOLUTION OF THE GAMETOPHYTE IN BRYOPHYTES 26.1

Two broad types of views have been put forward by bryologists to explain the process of the evolution of gametophyte in bryophytes. Some bryologists are of the opinion that the simple thallus of Marchantiales is the result of **retrogressive evolution** while the other group of bryologists believe that the Marchantiaceous thallus is simple because of **progressive evolution**.

Some aspects of the mechanisms of both retrogressive as well as progressive types of evolution are briefly discussed below:

MECHANISM OF RETROGRESSIVE EVOLUTION 26.2

This theory has been supported by Wettstein (1903–1908), Goebel (1906), Kashyap (1919), Evans (1939), Mehra (1953, 1957), Zimmermann (1966) and Udar (1970). These workers believe that the primitive gametophyte was an erect leafy shoot of Bryopsida showing radial symmetry. A reduction in the leaf development in such a primitive bryophytic member of Bryopsida resulted in the evolution of the dorsiventral thalli in acrogynous Jungermanniales, Marchantiales and Anthocerotales.

According to Wettstein (1903–1908), a hypothetical primitive ancestor may be traced in the leafy gametophytes of Calobryales and several true mosses, such as *Fontinalis, Polytrichum* and *Bryum.* The possible approach to such a hypothetical primitive ancestor may also be traced in the sexual branches of some prostrate forms of thalloid and leafy Hepaticopsida. Ultimately, the dorsiventral thalli of several Hepaticopsida and Anthoceropsida developed from such ancestors by the mechanism of retrogressive evolution, i.e. progressive reduction.

Evans (1939) was an active supporter of the mechanism of retrogressive evolution and had provided several examples to explain the evolution of the thalloid bryophytes from the erect, radial leafy shoots of foliose members. As the dorsiventral bilaterality of the leafy shoot progressed, a gradual reduction in the size of the ventral leaves took place, as seen in genera such as *Lepidozia* and *Lejeunea.* The process of

reduction in the size of the leaves ultimately reached such an extent that they appeared in the form of mucilaginous papillae, as in *Plagiochila,* and finally they disappeared in *Radula.*

Along with this character of gradual reduction and ultimate disappearance of ventral leaves, there was also a flattening of the axis as well as a gradual decrease in the size of lateral leaves either in the form of a few cells or slime papillae. Sometimes even their complete disappearance was noticed as in *Pellia,* Marchantiales and Anthocerotales. Some intermediate stages of the members, such as *Pellia,* may be seen in genera, such as *Zoopsi*s and *Schiffneria*—in which the leaves are more or less reduced and the axis is flat. However, in several such examples (e.g. *Marchantia),* the reproductive shoots (i.e. antheridiophores and archegoniophores) remain radial, erect and somewhat leafy in nature, and this indicates that the thalloid state is one of secondary origin. On the basis of his studies of genus *Monoselenium* of Marchantiales, Goebel (1906) had also favoured the mechanism of retrogressive evolution of gametophytes in bryophytes.

Shiv Ram Kashyap (1919), the noted Indian bryologist, made extensive studies on Indian liverworts, noted several examples of reduction series in genera belonging to Marchantiales, and became a strong supporter of the mechanism of retrogressive evolution. Three main points of this reduction series suggested by Kashyap (1919) are given below:

1. The Loss of Assimilatory Filaments in Air Chambers The stages of the gradual reduction in the assimilatory filaments can be observed in four different genera of bryophytes as under:

1. In *Preissia quadrata* (Fig. 26.1A), a species occurring on moist soil, all the structures of the higher forms (i.e. air chambers, air pores and assimilatory filaments) are present.
2. In *Conocephalum conicum* and other genera growing in more moist places, the assimilatory filaments are short (Fig. 26.1B) and pointed.
3. In *Weisnerella denudata* (Fig. 26.1C), growing near or under water, the air chambers contain only papillate cells.
4. In *Dumortiera* (Fig. 26.1D), growing under water, the air chambers are either absent completely or present only at the growing points. The air pores are rudimentary, and the assimilatory filaments are absent.

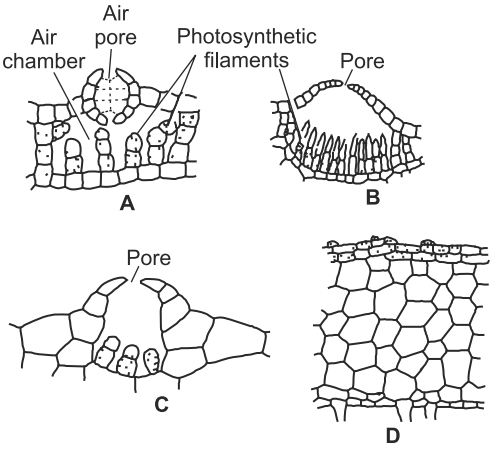


Fig. 26.1A-D Gradual reduction of the assimilatory filaments in Marchantiales (A, *Preissia quadrata*; B, *Conocephalum conicum*; C, *Wiesnerella denudata*; D, *Dumortiera hirsuta*)

2. Simplification of Air Pores The air pores are barrel-shaped on both thallus as well as on discs of antheridiophores and archegoniophores in *Marchantia;* they are barrel-shaped on the discs but simple on the thallus in *Conocephalum;* they are simple on both, thallus as well as discs in *Exormotheca;* and the air pores are not well-developed at all in *Riccia.*

3. Gradual Shifting of the Erect Branches bearing Sex Organs to the Dorsal Position due to the Continued Growth of the Thallus and Gradual Elimination of the Stalk In *Marchantia*, the two sex organs, i.e. antheridia and archegonia, develop on special erect branches called 'antheridiophores' and 'archegoniophores', respectively, and both these are usually terminal in position. In *Plagiochasma articulatum* and some other genera, the stalk is initially terminal in position but soon becomes dorsal because of the continued growth of the thallus. In *Corsinia,* the reduction trend reaches a step further as the female receptacle becomes sessile due to the gradual elimination of the stalk.

On the basis of his studies on a fossil Hepaticopsida—*Naiadita,* Harris (1939) also opined that "at a certain stage, the primitive Hepaticae had an erect leafy shoot with spirally arranged leaves as in moss."

Genetical studies of Burgeff (1943) also supported the theory of retrogressive evolution. Burgeff evolved numerous mutations of *Marchantia* and correlated several of them with the phyletic reduction series.

Mehra (1957) proposed the **condensation theory**, according to which the Marchantiaceous thallus has been derived from foliose Jungermanniales through the processes of compaction and condensation. Mehra suggested that the type of the thallus represented by *Stephensoniella brevipedunculata* and *Asterella reticulata* is the most primitive in Marchantiales and is very near to the ancestral type. "This, in turn, seems to be developed from foliose forms by the processes of compaction, condensation and fusion of leaves" (Mehra, 1957).

THEORY OF PROGRESSIVE EVOLUTION 26.3

This theory has been supported by bryologists such as Cavers (1910), Campbell (1918, 1936, 1940), Smith (1955), etc. According to this theory, the primitive gametophyte was a dorsiventral and prostrate thallus which was simple in its morphological as well as anatomical characters.

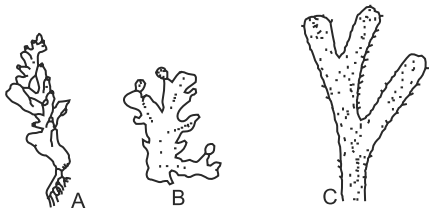


Fig. 26.2A-C Thalli of *Sphaerocarpos stipitatus* (A), *Riccardia indica* (B), and *Metzgeria pubescens* (C)

Cavers (1910), the main supporter of this theory, opined that the thallus of the present-day genus *Sphaerocarpos* (Fig. 26.2A) resembles the simplest primitive gametophyte. However, Campbell (1918, 1936, 1940) believed that the nearest approach to the simplest primitive gametophyte is to be seen in the thalli of the living genera *Riccardia* and *Metzgeria* (Fig. 26.2B,C). Therefore, the simple and ''primitive type of thalli according to this theory are of *Sphaerocarpos, Riccardia* and *Metzgeria*. The evolutionary advance in such simple thalli progressed in two different lines:

1. One line of the evolutionary advance resulted in the formation of the thalli of Marchantiales (e.g. *Marchantia)* by the gradual formation of structures, such as epidermis with air pores, air chambers, assimilatory filaments, and separate reproductive branches, i.e. antheridiophores and archegoniophores.
2. The second line of evolutionary advance resulted in the formation of the gametophytes of Jungermanniales and Calobryales, in which the internal structures remained simple, due to the absence of air pores and air chambers, but the external structures of the gametophyte elaborated finally into a foliose or leafy shoot.

TEST YOUR UNDERSTANDING

1. Give an account of the evolution of the gametophyte in bryophytes in about 500 words.
2. Descrive the mechanism of retrogressive evolution of gametophyte in bryophytes.
3. Who have been the two main Indian advocates of mechanism of retrogressive evolution of gametophytes in bryophytes?
4. Enumerate three main points of reduction series in evolution of gametophyte suggested by Shiv Ram Kashyap.
5. Describe the theory of progressive evolution of gametophyte in bryophytes in about 200 words.

27 Origin and Evolution of Sporophyte in Bryophytes

WHAT IS EVOLUTION OF THE SPOROPHYTE IN BRYOPHYTES? 27.1

The zygote is the first cell of the sporophytic generation. It divides and redivides to form the sporophyte, which is never an independent body in bryophytes. It is always dependent on the gametophyte, either completely or partially. The function of the sporophyte is the production of spores.

Two different theories have been put forward by the bryologists to explain the evolution of the sporophyte in bryophytes. These are (i) theory of the progressive sterilization of the potentially sporogenous tissue, and (ii) theory of progressive simplification or reduction theory.

THEORY OF PROGRESSIVE STERILIZATION OF POTENTIALLY SPOROGENOUS TISSUE 27.2

This theory, also called the **theory of sterilization**, has been proposed by Bower (1908), and supported by Cavers (1910) and Campbell (1918, 1940). According to this theory, *Riccia* possesses the simplest and the most primitive sporophyte, and from such a sporophyte of *Riccia* have evolved more advanced sporophytes, through the process of progressive sterilization of potentially sporogenous tissue. A definite series of such an evolution of the sporophyte from *Riccia* may be traced in the sporophytes of *Sphaerocarpos, Targionia, Marchantia, Pellia, Anthoceros* and *Funaria.* A brief discussion of all these stages from *Riccia* to *Funaria* follows:

1. First Stage The first stage is seen in *Riccia* (Figs. 27.1, 7.10) in which the zygote divides several times to form a multicellular diploid structure, of which the outermost layer develops into a sterile jacket while all the central mass remains sporogenous in nature. Each cell of this sporogenous tissue

divides meiotically to form four haploid spores. Thus, the only sterile part of this simple sporophyte is the sterile jacket, while the entire remaining tissue is fertile. Also, there is no differentiation of organs, such as foot, seta and capsule, and, therefore, the sporophyte of *Riccia* is the simplest and the most primitive (Bower, 1908).

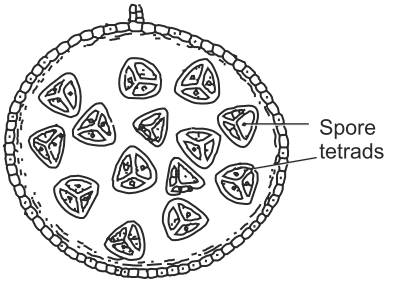


Fig. 27.1 Sporophyte of *Riccia*

2. Second Stage In *Riccia crystallina* and *Oxymitra,* the sporophyte, of course, consists of a single-layered jacket enclosing the central mass of the sporogenous tissue like that of other species of *Riccia* discussed above. But some potential spore mother cells remain unable to form the spores and form the sterile or abortive nutritive cells. Thus, the sterile tissue in the sporophyte is a little more in amount than that of the first stage, i.e. other species of *Riccia.*

3. Third Stage In both *Corsinia* and *Sphaerocarpos* (Figs. 27.2, 5.2), more amount of potentially sporogenous tissue becomes sterilised than that of *Riccia crystallina* and *Oxymitra.* In *Corsinia,* the whole of the basal part of the sporophyte gets sterilised to form the foot, made up of a few cells. And in *Sphaerocarpos* (Fig. 27.2), the basal part of the sporophyte is sterilised into a bulbous foot and a narrow two-cells broad seta. In both *Corsinia* and *Sphaerocarpos,* a single-layered sterile jacket surrounds the sporogenous tissue in the capsule. A few sterile **nurse cells** are also present in both along with the fertile spores. The nurse cells, however, lack the characteristic spiral thickenings of the elaters.

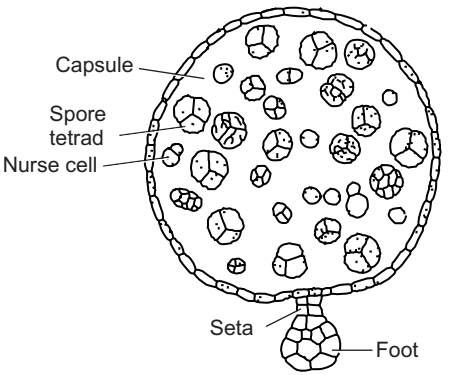


Fig. 27.2 Sporophyte of *Sphaerocarpos stipitatus*

4. Fourth Stage In *Targionia* (Fig. 27.3), the sporophyte contains still larger amount of the sterile region in the form of a bulbous foot, narrow seta, single-layered jacket of the capsule, and several elaters, containing spiral thickenings. Sterile elaters present along with the fertile spores, constitute about half of the number of the sporogenous cells of the capsule.

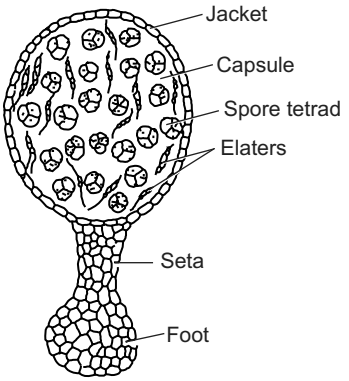


Fig. 27.3 Sporophyte of *Targionia hypophylla*

5. Fifth Stage In *Marchantia* (Figs. 27.4, 7.32), the sterile tissue in the sporophyte is slightly more in amount than that of *Targionia,* and consists of a broad and bulbous foot, elongated and more developed seta, single-layered sterile jacket of the capsule, a few sterile cells at the apex of the capsule in the form of a small apical cap, and a large number of long elaters containing the spiral thickenings, along with the fertile spores in the capsule.

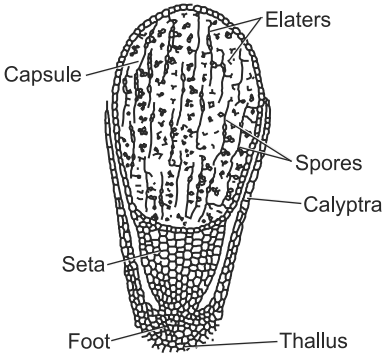


Fig. 27.4 Sporophyte of *Marchantia polymorpha*

6. Sixth Stage In *Pellia* (Figs. 27.5, 4.16F), *Riccardia* and other Jungermanniales, still larger percentage of the part of the total sporophyte is sterilised. The sterilised tissue consists of an elaborate foot, well-developed seta, two to many-layered sterile jacket of the capsule, several elaters, and a mass of sterile cells in the form of **elaterophore**. The elaterophore is either basal *(Pellia)* or at the apex *(Riccardia)* of the capsule. Only a small percentage of the sporogenous tissue actually remains fertile and forms spores.

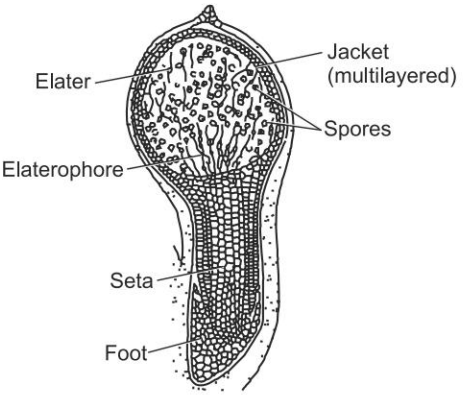


Fig. 27.5 Sporophyte of *Pellia epiphylla*

7. Seventh Stage Highly reduced sporogenous tissue is present in *Anthoceros* (Figs. 27.6, 8.7 I-M) on account of further sterilisation. The sterile tissue of the sporophyte consists of massive foot, small meristematic zone, 4- to 6-layered wall of the capsule, 4- to 16-celled thick columella and a large number of pseudoelaters. Further, the sporophyte of *Anthoceros* shows a greater degree of independence since its capsule wall possesses a well-defined epidermis, several stomata and chlorophyll-containing cells.

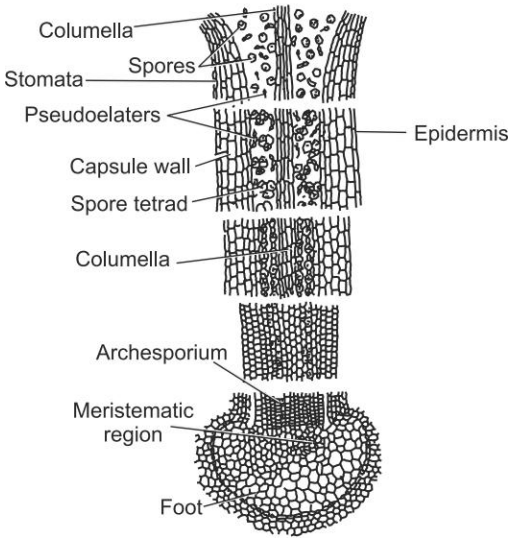


Fig. 27.6 Sporophyte of *Anthoceros*

8. Eighth Stage The process of the progressive sterilisation of potentially sporogenous tissue reaches at its peak in some higher members of Bryopsida, e.g. *Funaria* (Figs. 27.7, 10.22 B) and *Polytrichum.* In *Funaria*, the sterile tissue of the sporophyte consists of foot, seta, entire region of the

apophysis of capsule, many-layered capsule wall, spore sac wall, columella, peristome and operculum. The only fertile region is in the form of two spore sacs in the theca region of the capsule. Due to the presence of stomata, very long seta, well-developed capsule wall, and large number of chlorophyll-containing cells in the capsule, the sporophyte in these bryophytes shows still greater degree of independence. According to the **theory of progressive sterilisation of potentially sporogenous tissue** of Bower (1908), the sporophyte of *Funaria,* therefore, is the most advanced and highly evolved.

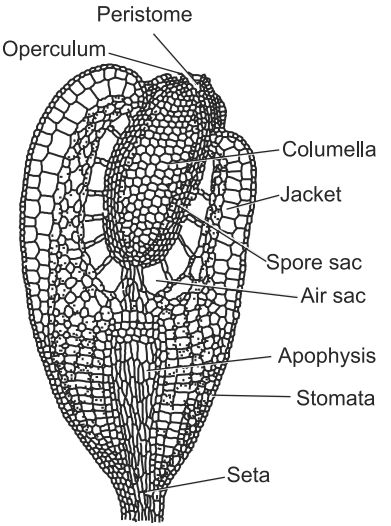


Fig. 27.7 Sporophyte of *Funaria hygrometrica*

THEORY OF PROGRESSIVE SIMPLIFICATION 27.3

This theory, also called the **reduction theory**, has been proposed by Church (1919) and supported by Kashyap (1919), Goebel (1930) and Evans (1939). According to these bryologists, the simplest sporophyte of *Riccia* is not a primitive type of the sporophyte. On the other hand, they believe that the *Riccia* sporophyte is a reduced type evolved by a process of descending or regressive evolution or "progressive simplification".

According to the reduction theory of Church (1919), the ancestral sporophyte of Bryophyta was an erect, foliose (leafy), and independent shoot like that of mosses. During the descending course of evolution, such an erect leafy sporophyte passed through the following changes:

(i) It became attached to the gametophyte on the permanent basis, (ii) its leaves were lost due to the prolonged isolation and desiccation, (iii) because of its greater dependence on the gametophyte, the intercellular spaces of its photosynthetic system disappeared, (iv) in the later stages its assimilatory tissue also became reduced, (v) the stomata of its epidermis first reduced into simple pores and became functionless, as in *Sphagnum,* and then they completely disappeared, as in *Marchantia* and *Riccia.*

Church (1919), followed by Goebel (1930) and Evans (1939), hence, believed that the complex and well-developed sporophytes of *Funaria* and *Anthoceros,* having intercellular spaces in their assimilatory tissue and stomata in their epidermis, are primitive and nearer to the ancestral type. On the other hand,

the sporophytes of *Pellia, Marchantia, Targionia* and *Sphaerocarpos* are reduced and simplified, and this series of reduction reached at its peak in the sporophyte of *Riccia.*

TEST YOUR UNDERSTANDING

1. Give an illustrated account of evolution of sporophyte in bryophytes.
2. What is the first cell of a sporophytic generation?
3. In bryophytes, the sporophyte is never an ……. body.
4. In bryophytes, the sporophyte is always dependent on ……., completely or partially.
5. The main function of sporophyte in bryophytes is the production of ……. .
6. What are the two major theories which have been put forward to explain evolution of sporophyte in bryophytes?
7. Explain in detail the "theory of sterilisation" given to explain origin and evolution of sporophyte in bryophytes.
8. According to the theory of sterilisation, which of the bryophytic genus possesses simplest and most primitive sporophyte?
9. In the undermentioned series of evolution of sporophyte, what is missing?
   Riccia → *Sphaerocarpos* → *Targionia* → *Marchantia* → *Pellia* → *Anthoceros* → ---------.
10. Draw labelled diagrams of the sporophytes of
    (a) *Anthoceros*
    (b) *Riccia*
    (c) *Pellia*
    (d) *Funaria*
11. With reference to the evolution of sporophyte in bryophytes, what is the theory of progressive simplification?
12. Theory of progressive simplification is also called ----------.

28

Conduction in Bryophytes

HOW DO BRYOPHYTES MAINTAIN POOR INTERNAL CONDUCTING STRANDS? 28.1

Being terrestrial, most bryophytes lack well-organised internal conducting strands. This deficiency of bryophytes is, however, overcome by some characteristics, of which some are mentioned below:

1. Usually, bryophytes grow in moist shady places, with abundant humidity.
2. The gametophytic plant body of bryophytes absorbs water from all over the surface.
3. Most of the thalloid bryophytes lie prostrate, i.e. parallel to the ground. Due to this, the area of contact, with the substrate or ground, increases.
4. The gametophytic plant body of such bryophytes, which are not prostrate but erect, is generally small. This reduces the distance through which the water has to actually move inside the plant body.
5. Plants show many adaptations which enhance or encourage external conduction.

EXTERNAL CONDUCTION AND ITS SIGNIFICANCE 28.2

28.2.1 External Conduction in Gametophytes

Several structures on the gametophytic plant body of bryophytes are responsible for external conduction of water, e.g. closely-placed branches on the main axis or leaves on the stem (e.g. *Polytrichum*) help in external conduction. Leaves possessing sheathing leaf bases (e.g. *Polytrichum*) also facilitate external conduction. Some mosses (e.g. members of Dawsoniaceae and Polytrichaceae) have **lamellae** on the leaves, and these lamellae help in external conduction. Extensive growth of **paraphyllia** on the stem of some mosses help in conduction of water.

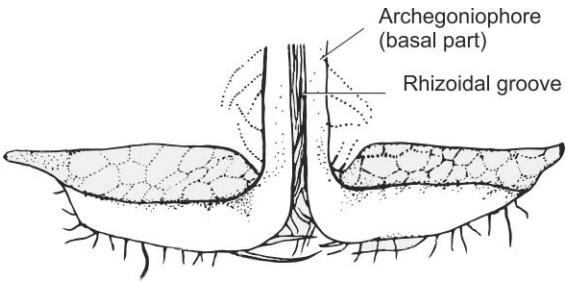


Fig. 28.1 Vertical section of thallus and basal part of archegoniophore of *Fimbriaria bleumeana* showing rhizoidal groove (after Bowen, 1935)

Some mosses show growth of their gametophytes in very close tufts, forming compact cushion-like structures with effective capillaries between the gametophytes, as in **pin-cushion moss** (*Leucobryum glaucum*). External conduction takes place through these capillaries. Several **appendages** develop on the stem of some mosses. These appendages produce capillary channels. Water moves through these channels in such gametophytes.

Pegged rhizoids and overlapping **scales** of many members of Marchantiales (e.g. *Marchantia*) also help in external conduction. Such structures make channels for effective water transport.

Rhizoidal grooves in the archegoniophore of *Marchantia* and *Fimbriaria* (Fig. 28.1) also serve the purpose of external conduction. Efficient capillary channels are also formed by twining together of rhizoids in some bryophytes, e.g. *Pogonatum.*

28.2.2 External Conduction in Sporophytes

External conduction in sporophytes in bryophytes is quite different from their gametophytes because of some definite reasons, as under:

1. Appendages are absent in sporophytes, and therefore, there are no capillaries for external conduction.
2. Mature sporophytes of mosses have seta and capsule bearing a thick cutinised epidermis followed by a thick-walled hypodermis. Both of them prevent direct absorption of water from their surrounding atmosphere. Some external absorption, however, occurs when the sporophyte is very young.
3. In liverworts, the seta of the sporophytes elongates only at maturity followed by quick dispersal of spores. So, the conduction is not needed at all.

28.2.3 Significance of External Conduction

Because of the absence of a well-developed conducting tissue in the gametophytes of most of the bryophytes, the external conduction of water by capillary action is of definite significance in these plants. The role played by external conduction of water mainly depends on the morphology and anatomy of the particular species of bryophyte. Environmental conditions (e.g. relative humidity) also plays a definite role in external conduction. Bopp and Stehl (1957) have experimentally proved that external conduction is more efficient than internal conduction in *Funaria hygrometrica*. Deloire et al. (1979) determined experimentally the rate of external conduction in some more mosses and also in liverworts

by employing fluorescent dye. Eosin due was used by Clee (1937) to study external conduction in *Plagiochila* and *Pellia*. In *Conocephalum*, McConaha (1939) proved experimentally that "conduction of water along the entire length of the thallus takes about 20 to 30 seconds". In the later years, the same author studied the rate of external conduction in some more bryophytes including *Reboulia* (0.5 mm/s), *Lunularia* (0.5 mm/s) and *Preissia* (1 mm/s). In *Polytrichum*, it has been proved by Magdefrau (1936) that "external conduction is sufficient to maintain turgidity at 90% relative humidity, but at 70%, both internal and external conduction are necessary".

INTERNAL CONDUCTION AND ITS SIGNIFICANCE 28.3

Cells Involved in Internal Conduction

In the gametophytic plant body, all the cells, to some extent, are capable of some degree of conduction. But the function of conduction in the cells is related to several characteristics including (i) increase in the length and breadth of cells, (ii) development of structures like plasmodesmata, small pores, etc., and (iii) thickening of the side walls of the cells, which provide support to the plant body. Wide variety in the structure of cells, with reference to the conduction of water, is shown by bryophytes. It has, however, been observed that poorly-developed conducting strands are seen when plants are very young, and also when they grow under high humidity in their surroundings.

(a) Cells Involved in Conduction in Liverworts and Hornworts Ordinary **parenchyma** cells in the ventral region of the thallus are mainly responsible for conduction in a majority of the liverworts and hornworts. According to Proskauer (1961), prominent **primary pit fields** are present in the walls of these cells, as in *Dendroceros crispus* (Fig. 28.2). In the centre of the stem of many leafy liverworts and also in the midrib region of thalloid bryophytes, some cells are elongated and possess plasmodesmata in their walls. Such cells are called **conducting parenchyma**, as in *Conocephalum*. Empty and dead cells form clear **conducting strands** in several liverworts including *Hymenophyton, Haplomitrium* and *Takakia* (Fig. 28.3). According to Hebant (1977), the end walls of these mature dead and empty cells in *Takakia* have small plasmodesmata-derived pores (Fig. 28.4 A, B), More advanced type of conducting cells are present in the midrib region in *Pallavicinia lyellii* (Fig. 28.5).

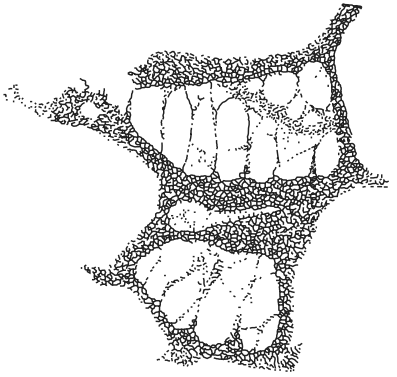


Fig. 28.2 Cells from the thallus of Dendroceros crispus showing well-developed primary pit fields

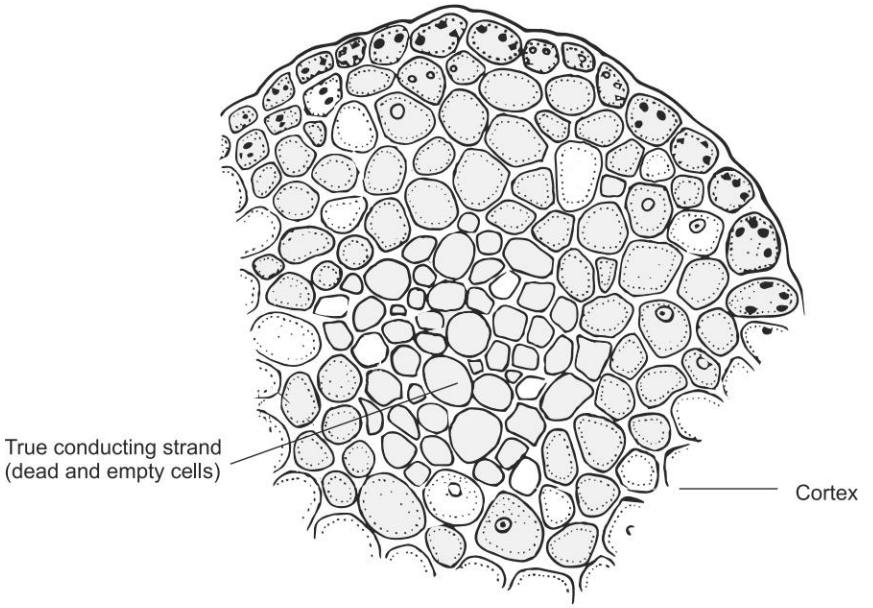


Fig. 28.3 Transverse section of a part of the stem of *Takakia* showing true conducting strand (after Hebant, 1977)

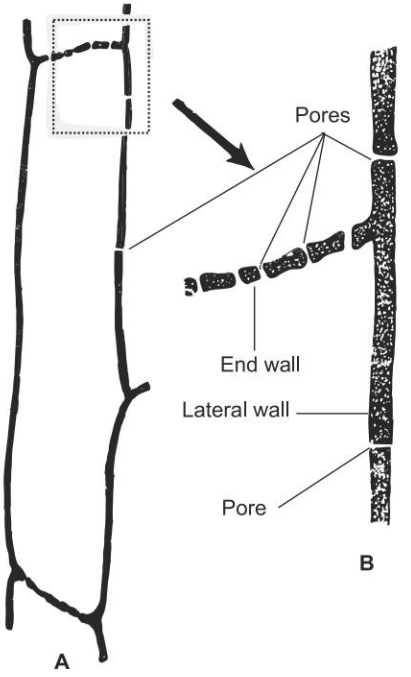


Fig. 28.4 A, Diagrammatic representation of the conducting cells from the stem of *Takakia* showing small plasmodesmata-derived pores in their end walls; B, Some part of 'A' (highly enlarged) showing details of end wall (after Hebant, 1977)

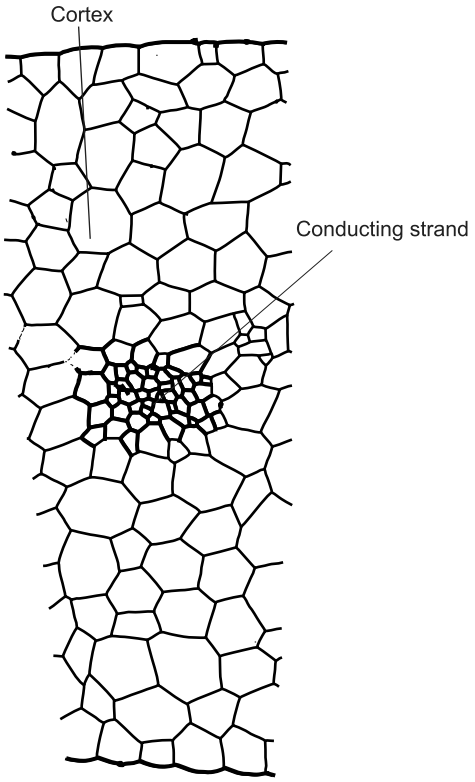


Fig. 28.5 Cross section (a part) of the midrib portion of the thallus of *Pallavicinia lyellii* showing conducting strand (after Smith, 1966)

(b) Cells Involved in Conduction in Mosses Conducting parenchyma, hydroids, leptoids and stereids are some major types of cells involved in conduction in mosses.

- **(i)** **Conducting parenchyma** occurs commonly in mosses in their stem, leaves and sporophyte. Plasmodesmata and pits derived from them are present in these cells.
- **(ii)** **Hydroids** are the water-conducting cells of mosses, e.g. *Polytrichum* (Fig. 28.6). They are found in stem and leaf of gametophyte and seta of sporophyte. The hydroids collectively constitute the **hydrom.**
- **(iii)** **Leptoids** are the food-conducting cells found in some mosses e.g. *Polytrichum* (Fig. 28.6). Along with the accompanying parenchyma, leptoids are collectively called **leptom.**
- **(iv)** The midrib region of the leaves and axis of the stem in some mosses contain some thick-walled elongated cells along with hydroids and leptoids. These are known as **stereids**, as in *Polytrichum* (Fig. 28.6). The stereids are collectively called **stereome**.

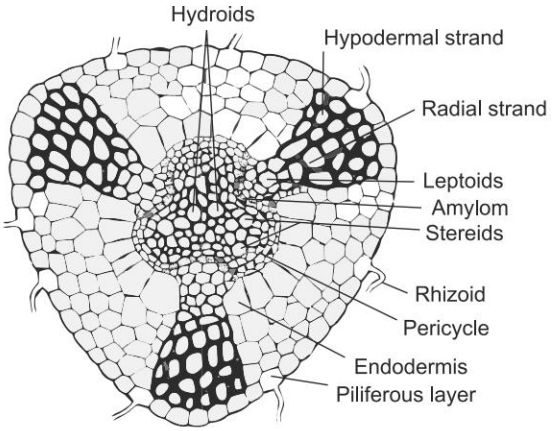


Fig. 28.6 TS Rhizome of *Polytrichum commune* showing hydroids, leptoids and stereids

According to Hebant (1977), hydroids and leptoids are present in both gametophytes as well as sporophytes (seta) in *Polytrichum*. In *Funaria*, hydroids are present in gametophyte (stem) as well as sporophyte (seta) whereas leptoids are present in seta and absent in the stem. In *Buxbaumia*, hydroids are present in the seta only, while they are absent in gametophytes (stem). Leptoids are absent in both stem as well as seta of *Buxbaumia*. Both hydroids and leptoids are absent in both gametophytes (stem) as well as sporophyte (seta) in *Orthotrichum* (Hebant, 1977). Members of Polytrichales are, therefore, the only bryophytes, the gametophytic generation of which possess leptoids (i.e. food-conducting cells).

ANATOMY OF MIDRIB AND LEAF TRACES 28.4

28.4.1 Midrib

The following three types of cells (Fig. 28.7) are found in the most complex midribs of leaves of mosses:

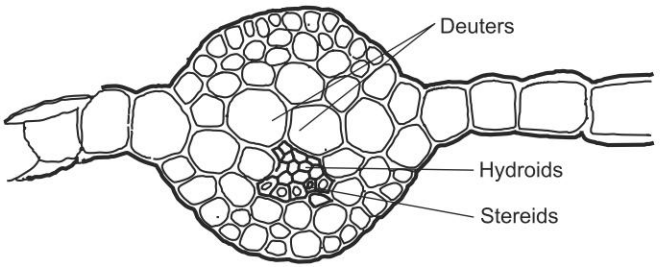


Fig. 28.7 Vertical section of the leaf of *Mnium undulatum* showing three types of cells

1. Deuters These are the large-sized, living cells which conduct food. They have plasmodesmata in their end walls.

2. Hydroids These are the cells responsible for conduction of water.

3. Stereids These are thick-walled cells which serve as supporting cells in the midrib.

28.4.2 Leaf Traces

Leaf traces, if present, are not as complex as the midribs. The midrib may or may not be connected to the central strands of the axis. The leaf traces may be true or false. If a leaf trace joins with the central strand, it is called true. But if it does not come in contact with the central strand, it is called a false leaf trace.

SIMILARITIES AND DIFFERENCES BETWEEN HYDROIDS OF BRYOPHYTES AND TRACHEARY ELEMENTS OF PRIMITIVE VASCULAR PLANTS 28.5

28.5.1 Similarities

Hydroids of bryophytes resemble tracheary elements of primitive vascular plants in the main events of their development. Some such events are:

1. Increase in length and other parameters of dimensions
2. Obliqueness of end walls
3. Thick lateral walls
4. Degeneration of their protoplasts, making the cells empty and finally dead
5. End walls getting partially hydrolysed,

All these characteristics make hydroids the preferential pathways for water conduction, as is also seen in primitive vascular plants.

28.5.2 Differences

1. Secondary thickenings in the form of spirals, rings or reticulum are absent in hydroids while present in tracheary elements of primitive vascular plants.
2. Nature of perforations in the end walls of hydroids is also different from that of tracheary elements of primitive vascular plants.

SIMILARITIES AND DIFFERENCES BETWEEN LEPTOIDS OF POLYTRICHALES AND SIEVE ELEMENTS OF VASCULAR PLANTS 28.6

28.6.1 Similarities

Typical leptoids are sieve-element-like cells. Some features, in which leptoids of Polytrichaceae resemble closely with the sieve elements of vascular plants, are listed below:

1. Lengthening and broadening of their extremities
2. Oblique placement of their end walls
3. Presence of well-developed plasmodesmata in their end walls
4. Thickened lateral walls
5. Presence of at least some amount of callose in their end walls
6. Presence of refractive spherules in the leptoids similar to that of phloem of pteridophytes
7. Similar to that of phloem, leptoids start translocation of food even when they are still not fully mature.

28.6.2 Differences

Leptoids differ from the phloem of vascular plants in some of the following characteristics:

1. Organisation of pores in their end walls
2. Persistence of degenerated nucleus
3. Absence of p-protein.

INTERNAL CONDUCTION OF WATER BY GAMETOPHYTE 28.7

Internal conduction of water in mosses (e.g. *Mnium* and *Polytrichum*) takes place by hydroids in the stem, and the same was demonstrated by Haberlandt (1886) using eosin and lithium sulphate solutions. Hebant (1974) also confirmed the same. The rate of conduction is 120 cm/h in *Mnium* and 200 cm/h in *Polytrichum*.

True conducting strands are rarely present in liverworts. Smith (1966) demonstrated that "eosin solution travelled up to 1.5 cm in 4 to 5 minutes in the conducting strand of *Symphyogyna circinata"*. The K-fluorescein solution, however, travelled slightly rapidly in *Takakia lepidozioides* according to Hebant (1972). Some studies suggest that water travels along the cell walls of all tissues of gametophytes of mosses.

INTERNAL CONDUCTION OF WATER BY SPOROPHYTE 28.8

Sporophytes of bryophytes lack capillaries on their surface, and they also do not show appreciable direct absorption of water. Therefore, the entire water required by the capsule of the sporophyte is supplied internally. Seta of the sporophyte has well-developed conducting tissues, whether the conducting strands are present or absent in the gametophyte. Bryologists have demonstrated the internal conduction in the seta of *Polytrichum, Funaria* and some more mosses using eosin solution and fluorescent dyes.

CONDUCTION OF ORGANIC COMPOUNDS IN BRYOPHYTES 28.9

With the help of ^{14}C-bicarbonate (a labelled compound), it has been shown by Eschrich and Steiner (1967) that in the stem of *Polytrichum*, the organic compounds are conducted at the rate of 32 cm/h. Conduction of organic compounds (assimilates, exogenously applied sucrose and ionic solutes such as

lead and sulphate) in the stem of *Polytrichum* takes place through leptom, according to Trachtenberg and Zamski (1978). In the seta of the sporophyte of *Polytrichum*, translocation of organic compounds takes place at the rate of 50 cm/h, as demonstrated by Eschrich (1975) using ^{14}C-sucrose. It has now been finally proved that in *Polytrichum*, the organic compounds travel through leptoids in both gametophytic and sporophytic generations.

Bopp and Knoop (1974) demonstrated the internal conduction of organic substances in the protonema of mosses while Rota and Maravolo (1975) studied conduction of labelled sucrose in the thalli of *Marchantia*. Rose and Bopp (1983) demonstrated internal transport of indole-acetic-acid in the rhizoids of *Funaria hygrometrica.*

TEST YOUR UNDERSTANDING

1. Explain conduction in bryophytes with the help of suitable diagrams.
2. Bryophytes have poorly developed conducting strands. How do they maintain their this characteristic? Explain in about 100 words.
3. Describe external conduction and its significance in bryophytes.
4. "Pin-cushion moss" is _____ _____.
5. In *Marchantia*, structures like overlapping scales and pegged rhizoids help in _____ _____.
6. Write a note on significance of external conduction in bryophytes.
7. Give a brief description of internal conduction in bryophytes.
8. Which of the following are the cells involved in conduction in mosses?
   (a) Hydroids (b) Leptoids (c) Stereids (d) All of these.
9. With the help of only one sentence about each of them, differentiate between the following with reference to their involvement in conduction in mosses:
   (a) Conducting parenchyma, (b) Hydroids, (c) Leptoids, (d) Stereides.
10. In *Polytrichum*, which of the following means of conduction is/are found?
    (a) Stereides, (b) Leptoids, (c) Hydroids, (d) All of these.
11. Name the only single order of bryophytes, the gametophytic generation of which possess leptoids.
12. What are deuters?
13. Leptoids are the _____ conducting cells of bryophytes.
14. Make a list of some similarities and differences between hydroids of bryophytes and tracheary elements of primitive vascular plants.
15. What are the similarities between leptoids of Polytrichales and sieve elements of vascular plants?
16. Write a note on conduction of organic compounds in bryophytes in about 100 words.

29 Elementary Cytogenetics and Cytotaxonomy of Bryophytes

Cytogenetics has been such a field of research during the last few decades that a very vast literature is available in the form of voluminous books and research publications. To give a glimpse of all aspects of **cytogenetics** of bryophytes within few pages of a chapter is neither possible nor within the scope of this book. Hence, only some selected preliminary aspects of this modern branch of bryophytes have been dealt with here.

In the **cytology**, the aspects briefly discussed include (i) basic techniques, (ii) mitosis, (iii) meiosis, (iv) heterochromatin, (v) chromosome number, and (v) extra chromosomes, including sex-associated chromosomes.

In the **genetical studies**, some aspects discussed are (i) hybridization, and (ii) polyploidy.

Some details of **cytotaxonomy** have also been discussed at the end of the chapter.

Important initial contributions on the cytology of bryophytes have been made by Mahabale (1942), Lowry (1954), Steere (1954), Bryan (1956), Vaarama (1956), Khanna (1960), Gangulee and Chatterjee (1960), and Mehra and Khanna (1961).

SOME BASIC TECHNIQUES OF CYTOGENETICS 29.1

Rapid **acetocarmine** squash method is the first and most suitable karyological technique. It enabled us to determine the chromosome number of several mosses. This technique was modified by Heitz (1926). In place of **orcein dyes** (1.5 g of orcein mixed in 100 cc of 45% acetic acid in a flask), **carmine** was largely replaced as a staining agent for studying bryological materials by Lowry (1948) and Vaarama (1949). Cytology of many bryophytes has also been studied by **Feulgen staining techniques** by workers, namely Darlington and La Cour (1950, Lewis (1957) and Vaarama (1964).

For studying fresh material of bryophytes, aceto-orcein stain gives good results. For squash preparations of the archesporial tissue, the tissue from the capsule is squeezed out on a slide and immersed in a drop of aceto-orcein. No prior fixation of the fresh material is required. The slide is

slightly heated and the pressure is applied with a needle. The squash preparation of the archesporial tissue is now ready to study various stages of meiosis. The haploid chromosome number of the plant can be determined by counting the meiotic bivalents by this technique. Lewis (1957) studied somatic mitosis in liverworts and mosses by pretreatment of the material "with 8-hydroxyquinoline as a 0.002 molar aqueous solution". Vaarama (1953) used the same technique for meiotic studies of several mosses.

Temporary preparations are sealed by ringing the cover glass with rubber solution. For making permanent preparations, the squash slides are passed through a slowly ascending alcohol series and mounted in Euparol or other suitable mounting medium.

SOME STUDIES ON MITOSIS 29.2

C E Allen (1912) studied cell structures, growth and division in the antheridia of *Polytrichum juniperum*, and later on worked on a chromosome difference correlated with sex differences in *Sphaerocarpos* (Allen, 1917). It was E Heitz (1928) who first reported heterochromosomes in *Pellia epiphylla*, a liverwort. Heitz later on studied mitosis in liverworts and mosses. K Yan (1957), a Japanese bryologist, worked on cytology of several Japanese mosses and equated sex chromosomes with heterochromosomes, but the term "**heterochromosome**" is not a synonym of sex chromosome. A Vaarama made significant contribution in cytology of bryophytes. He observed many heavily stained heteropycnotic bodies of variable sizes within an interkinesis nucleus of *Pleurozium schreberi* (Vaarama, 1954). In the mitotic chromosome of this bryophyte, the chromatids get separated from each other prior to anaphase even at the locus of centromers. The chromatids remain attached together due to sticky matrix.

In some bryophytes, Heitz (1928) reported the presence of chromosomes and their segments "which remained dense and deeply stained at stages (e.g. prophases) in contrast to the other chromosomes which were in large part diffuse and lightly stained". He described such chromosomes and their parts as **heteropycnotic**. These chromosomes are made up of different material, which is known as **heterochromatin**.

SOME STUDIES ON MEIOSIS 29.3

Since it is difficult to get the adequate preparations of the stages of meiotic prophase, the details of the process of meiosis in most of the bryophytes is, therefore, difficult to study. In Grimmitaceae, a family of mosses, meiosis has been studied by Vaarama (1949). The bivalent contains two chiasmata, one in each chromosome arm. The chiasma is situated either in the proximal or in the distal part of the chromosome arm. The frequency of the chiasma and also the number of interstitial chiasmata varies in different species of mosses belonging to Grimmiaceae.

In almost all bryophytes studied so far, "the chromosome compliment contains a heterobivalent which deviates from the autosome bivalent in its (i) larger size, (ii) asymmetry, and (iii) heterochromacity at interkinesis, mitotic and meiotic prophase stages." In several pleurocarpous mosses, the heteropycnotic chromosome pair develops in a very specialised way during meiotic prophase. During pachytene stage, the heteropycnotic chromosome, which lies on the surface of a vesicle-like body, disappears. In this manner, a ring-shaped bivalent develops. This bivalent differs in appearance from the other bivalents. Vaarama (1953) named this bivalent **M-bivalent** or **special bivalent**."

Vaarama (1954) studied the structure and behaviour of meiotic bivalents in *Hedwigia ciliata*, a moss. In diplotene-diakinesis stages of this moss, the chromatids of the special bivalent "are either quite separate from each other or united pairwise or in chains or rings by terminal contacts which are not chiasmata". The chromatids are negatively heteropycnotic at diakinessis and metaphase-I stages. The chromatid pairs are situated opposite each other at both sides of the metaphase plate. It appears that the chromatids of special bivalent are quite independent in their function.

In *Pleurozium schreberi*, meiotic prophase starts with a stage exhibiting optically single strands, according to Vaarama (1954). The chromatids of bivalent halves as well as chromosomes of anaphase-II stage are "clearly double and the half-chromatids have matrices of their own" (Vaarama, 1954). Frequent exchanges in the location of centromeric activity takes place in meiosis.

Meiosis in *Sphagnum* has been studied in detail by Sorsa (1955). He reported an unusual centromere in *Sphagnum*, and also tripolar spindles in mosses. His researches have been published in Vol. I of ***Hereditas***. Sorsa (1955) described "the diploid chromosome number in *Sphagnum* sporophytes has 9 bivalents and 1 univalent while the species with tetraploid sporophytes (e.g. *Sphagnum robustum* and *S. squarrosum*) were found to have 19 bivalents." However, according to Bryan (1955) and Holmen (1955), the "haploid or gametophytic number in *Sphagnum* is 19 plus the m-chromosomes and that the diploid or sporophytic number is 38 (19 homologous pairs) plus the m-chromosomes". Bryan (1955) clearly observed 19 bivalents in addition to the m-chromosomes in the spore mother cell of *Sphagnum erythrocalyx*.

Study of chromosomes with particular emphasis on meiosis in about 40 species of 16 genera of American mosses was done by Steere et al. (1954). This has been published in ***Mem. Torrey Botanical Club*** (Vol. 20). Several of these species show polyploidy. More than ten of these species possess the so-called **accessory chromosomes**. Large-sized heteromorphic bivalent chromosomes were observed in several species, and these were assumed by these workers as sex chromosomes. From these studies, they concluded that "the cytological behaviour of bryophytes parallels that of phanerogams very closely".

Postmeiotic changes in *Physcomitrella patens*, *Desmatodon randii* and *Funaria hygrometrica* have been studied by Ripetsky and Matasov (1975).

Six sub-stages of meiotic prophase in *Ditrichum pallidum* have been described by Brown and Lemmon (1980), and their research has been published in Vol. 83 of ***Bryologist***. Some aspects of these stages are described below:

Stage 1 Just before meiosis, each sporocyte produces a thick layer of sporocyte wall. It consists of fibrillar polysaccharides. This wall, present between archesporial cell wall and protoplast, survives throughout the formation of spore. The archesporial cell wall dissolves and/or disintegrates, and due to this, the sporocytes are released into the spore chamber. A large number of ribosomes are also present in the cytoplasm.

Stage 2 Synaptinemal complexes start developing in this stage, which also show almost all features of Stage 1.

Stage 3 Nuclei containing well-developed synaptinemal complexes start shifting towards sporocyte periphery in this stage. They also "assume the acentric bouquet appearance". Fine, tightly packed unpaired chromosomes are present in the nucleus. Soon they show the typical pachytene structure.

Stage 4 Centrally-located pachytene nuclei are seen.

Stage 5 Diffused stage of nuclei with relaxed chromatin are seen. Cytoplasmic depressions produce lobes in tetrahedral arrangement. Several microtubules also now develop and also proliferate around the plastid in each of the four lobes and finally ensheath the nucleus.

Stage 6 The nuclear membrane dissociates and the chromatin again condenses into chromosomes. Soon, the appearance of kinetochore-microtubule attachment is seen.

Development of diploteine starts with the formation of chiasmata in the bivalents.

In yet another study, Brown and Lemon (1980) studied stages of meiosis in *Ditrichum pallidum* after prophase. According to them, during metaphase-I in this species, "the bivalents are distributed along the equator of an open spindle consisting of continuous microtubules. Microtubules are attached at kinetochores". The distribution of both plastids and mitochondria is associated with the lobing pattern in the cytoplasm of metaphase-I sporocyte. Most notable is the positioning of one of the four plastids into each of the cytoplasmic lobes. Meiosis- II occurs after a short intrameiotic interphase. Young spores are separated within the tetrad. The spores are invariably arranged tetrahedrally.

HETEROCHROMATIN 29.4

Chromatin is the complex of proteins, DNA and small amounts of RNA of which chromosomes are composed.

Heterochromatin is a condensed region of chromatin in the interphase nucleus that stains heavily with basic dyes. Inactive nuclei contain large amounts of heterochromatin.

Euchromatin is an expanded region of chromatin in the interphase nucleus, which stains lightly with basic dyes. Metabolically active nuclei show large amounts of euchromatin.

Chromatin of chromosomes is of definite help in their selective staining. It is specifically possible during cell division when chromosomes are thick and condensed. Heitz (1928) was the first to see and study heterochromatin in a bryophyte, while studying gametophytic cells of *Pellia endivaefolia*. Presence of heterochromatin is of specific interest in sex-associated chromosomes. It distinguished sex-associated chromosomes from otherwise similar chromosomes. According to the studies of Segawa (1965) and Ono (1970), Y-chromosomes contain more heterochromatin than the X-chromosomes. Some other details of heterochromatin are discussed under Article 29.6 (Sex-Associated Chromosomes).

CHROMOSOME NUMBER 29.5

Counting of chromosomes is of primary concern in the cytology of bryophytes. Several workers have worked on this aspect of this fascinating group of plants. To name a few are Wilie (1957), Proskauer (1958), Anderson (1962), Fulford (1965), Khanna (1965), Smith and Newton (1968), Moore (1970, 1977), Fritsch (1972, 1982), Smith (1978) and Newton (1977, 1984). Different groups of bryophytes (Hepaticopsida, Anthoceropsida and Bryopsida) are quite different from each other in their chromosome numbers.

29.5.1 Chromosome Number of Hepaticopsida

Hepaticopsida generally show a uniformity in their chromosome numbers. Smith and Newton (1968) and Smith (1978) reported $n = 8$ or 9 in liverworts. Calobryales and Sphaerocarpales have $n = 9$ or $n = 8$ and $n = 9$, respectively. Marchantiales generally have the chromosome number as $n = 9$ or in its multiple. In *Riccia*, it is $n = 8$, 16, 24 and 48. Jungermanniales have $n = 9$, while in Metzgeriales the predominant number is $n = 9$ with a few deviations (e.g. $n = 10$ in *Aneura* and $n = 20$ in *Riccardi*a).

29.5.2 Chromosome Number in Anthoceropsida

According to Proskauer (1958), the chromosome number in members of Anthocerotopsida is $n = 5$ while Berrie (1960) reported that it is $n = 6$ in species found in Japan. As mentioned earlier also, members of Anthoceropsida, Hepaticopsida and Bryopsida have very different chromosome numbers as reported by Newton (1984) while studying the frequency of chromosome numbers in this group (Fig. 29.1).

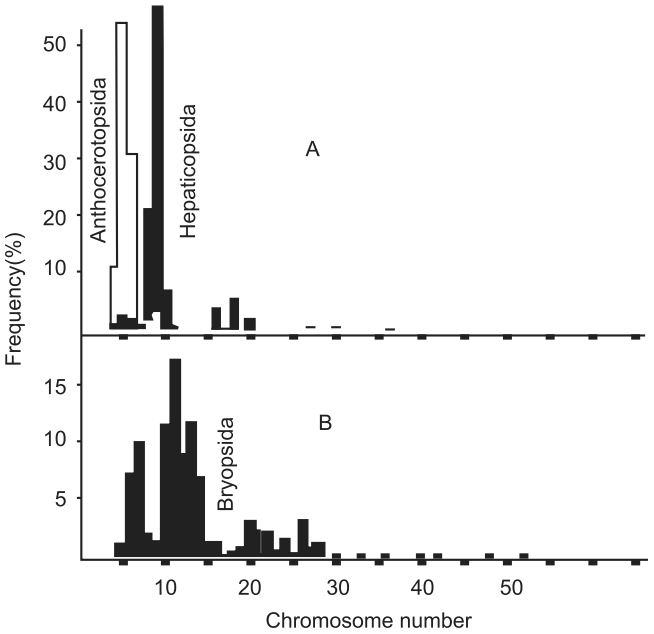


Fig. 29.1 Frequency of chromosome number in all the three groups of bryophyta. A, Anthoceropsida and Hepaticopsida; B, Bryopsida (after Newton, 1984)

29.5.3 Chromosome Number in Bryopsida

Frequency of chromosome number in Bryopsida, shown in Fig. 29.1B, shows that mosses are quite variable in their chromosome number. However, many genera and families are considered haploid with $n = 6$ and $n = 7$. Many of the moss genera with 10–14 chromosomes are considered basically diploid.

In Andreaeales, the chromosome number of $n = 10$ and $n = 11$ have been reported in three species of *Andreaea*. The recent trend is to consider *Takakia* as a moss under the order Andreaeales, and Inoue (1973) reported $n = 4$ and $n = 5$ for two species of *Takakia*, the lowest chromosome number in mosses.

Ulothrix, a green alga, also possesses $n = 4$, the lowest basic chromosome number in green algae, which are thought to be the ancestors of bryophytes by scientists working on the phylogeny of this group.

A polyploid series of $n = 9$, 18, 27 and 54 has been reported in *Physcomitrium pyriforme*, a common green-house moss of temperate regions. In *Sphagnum*, the most worked-out moss, chromosome complement of $n = 19 + 2$ microchromosomes or $38 + 4$ microchromosomes have been reported.

EXTRA CHROMOSOMES AND SEX-ASSOCIATED CHROMOSOMES 29.6

Chromosomes complements of bryophytes differ from that of other groups in several characteristics including (i) size, (ii) degree of hetero-chromaticity, (iii) mode of pairing, and (iv) segregation in the process of meiosis. Some specialised chromosomes are present in liverworts, e.g. **sex chromosomes**, **micro-chromosomes**, and other **heteropycnotic chromosomes**.

29.6.1 Microchromosomes and Heteropycnotic Chromosomes

Microchromosomes are dot-like or short rod-like structures, as in most Hepaticopsida. Extremely small microchromosome is a small accessory chromosome found in members of Anthoceropsida and Bryopsida.

Heteropycnotic chromosomes are very small and also called **h-chromosomes**, as in *Takakia lepidozioides*, *Calobryum rotundifolium* and many mosses. A heteropycnotic chromosome is about 1/3 to ½ of the longest autosomes of the genus. According to Berrie (1968), an h-chromosome is of "partly heteropycnotic nature combined with the fact that it is no longer than any other member of the chromosome complement".

29.6.2 Sex-associated Chromosomes

Allen (1919) was the first to discover sex chromosomes in *Sphaerocarpos donnellii*, a liverwort. Heitz (1932) discovered them in *Ceratodon purpureus*, a moss. Since then, sex chromosomes have been discovered and discussed in several bryophytes by many workers including Lorbeer (1934), Allen (1945), Tatuno (1941), Lewis (1961), Vitt (1968), Khanna (1971), Berrie (1974), Newton (1979), Fritsch (1982) and Kumar (1983).

The female specific X-chromosome in *Sphaerocarpos donnellii* is the largest member of the complement (Fig. 29.2A), while the male specific Y-chromosome is the smallest (Fig. 29.2B). Lorbeer (1934) reported in *Lunularia cruciata* and *Oxymitra paleacea* that Y-chromosome is larger in these genera than X-chromosome, a rarely seen condition. In *Pellia endivaefolia*, Tatuno (1941) reported yet another exception, where sex chromosomes are smallest members of the complement. Berrie (1974) also reported the similar condition in *Plagiochila praemorsa*, a liverwort.

According to Lorbeer (1938, 1941), *Sphaerocarpos* shows strong evidence for X-and Y- as sex-associated chromosomes. In this liverwort, the plants remain female even after the distal portion of X-chromosome is deleted. Opposite to this, plants of *Sphaerocarpos* with "radiation-damaged X-chromosome may be male in absence of Y-chromosome" according to Knapp (1936).

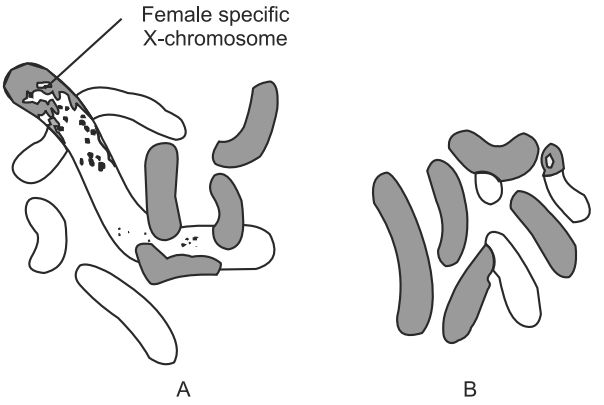


Fig. 29.2 A-B, Sex chromosomes in a complement of *Sphaerocarpos donnellii*; largest one in A is X-chromosome from female plant, while the small one in B is Y-chromosome from a male plant (after Allen, 1919)

Most of the dioecious species of mosses possess sex-associated chromosomes. According to Ramsay (1974), dioecious species of *Macromitrium* show some evidence for dimorphic X- and Y-chromosomes. This characteristic is not, however, seen in monoecious species of *Macromitrium*. It is also seen that monoecious plants are homosporous whereas dioecious plants possess two types of spores, i.e. large and small. Larger spores develop into female plants while smaller spores give rise to male plants. Heterochromatin of interphase nuclei also differs in female and male plants. Sex-related nature of largest heterochromatic chromosome has also been confirmed by Newton (1971) in *Plagiomnium undulatum.*

Mentioned below is a summary of sex-chromosome mechanism in liverworts, as proposed by Berrie (1963):

(i) X/Y consisting of two large chromosomes X and Y;
(ii) x/y consisting of two small chromosomes x and y;
(iii) X/y consisting of a large X chromosome and small y chromosome, as in *Sphaerocarpos*; and
(iv) X_1, X_2, Y mechanism in which the X element is represented by X_1 and X_2 chromosomes, and a Y chromosome, as in some species of *Frullania*.

Clear difference are observed in sex-associated chromosomes in their structure and morphological details in most of the investigated species of bryophytes. According to Segawa (1965) and Ono (1970), Y-chromosomes contain more heterochromatin than X-chromosomes. Newton (1979) has presented a schematic representation of the evolution of sex chromosomes in *Atrium crispum* on the basis of

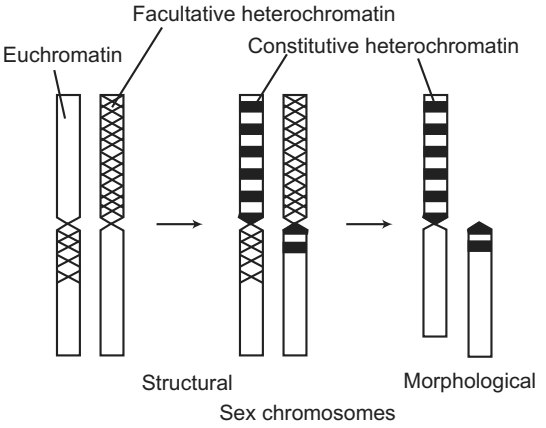


Fig. 29.3 Evolution of sex chromosomes in *Atrium crispum* (after Newton, 1979)

their structure and morphological details. It possesses euchromatin, facultative heterochromatin and constitutive heterochromatin (Fig. 29.3).

29.6.3 Nucleolar Chromosomes

Large heteropycnotic chromosomes, reported along with sex chromosomes or microchromosomes in about half a dozen species of Marchantiales and Acrogynae, have been termed **nucleolar chromosomes** by Berrie (1958, 1968). Nonheteropycnotic nuclear chromosome, attached terminally to the nucleolus, have also been reported by several workers in *Frullania lyellii, Pallavicinia lyellii* and *Riccardia pinguis*. According to Berrie (1963), "in the nucleolar chromosomes, the nucleoli are formed at telophase of cell division on specific chromosomes".

29.6.4 Accessory Chromosomes

Vaarama (1949) observed very small chromosomes in *Grimmia muehlenbeckii*, a moss. Since they resembled the chromosomes of some flowering plants (e.g. *Poa*, *Zea*, etc.), they were named as **accessory chromosomes** by Vaarama. Later on, accessory chromosomes were reported in many other bryophytes, such as *Orthotrichum tenellum*, *Dicranum majus*, etc. Accessory chromosomes in bryophytes are smaller than the normal chromosomes, and are also heterochromatic. Pairing takes place only between two homologous accessory chromosomes. In all the studied species, the accessory chromosomes are not situated in the normal plate either in the first or second metaphase. The accessory chromosomes in most of the species are generally four in number. Rarely, their number may be only two. Anderson and Bryan (1954) reported accessory chromosomes in 16 American species of mosses and interestingly all these species were polyploids.

HYBRIDIZATION 29.7

A natural or artificial process that leads to the formation of a hybrid is known as **hybridization**. A **hybrid** is a plant which results from the cross-fertilization of two different species, subspecies, varieties, strains, etc.

Differing from higher plants, there are only few reports of natural hybridization in bryophytes. It was Wettstein (1923) who made the first artificial cross between two mosses, viz. *Funaria hygrometrica* and *Physcomitrium pyriforme*. In some later studies, Wettstein (1924, 1928) was successful in making several interspecific crosses in species of mosses of Funariaceae and Bryaceae. Although hybrid sporophytes are mostly sterile, in some cases viable spores are also produced by them. Based on his studies, Wettstein (1928, 1932) concluded that the "cytoplasm as well as the chromosomes play an important genetic role. Some characters of the gametophytic progeny are determined by genes, the distribution being Mendelian; some are determined by the cytoplasm, the results being maternal inheritance; some by the combined influence of genes and cytoplasm".

Natural hybrids described in some bryophytic genera include *Bryum, Dicranella, Ditrichum, Funaria, Grimmia, Orthotrichum, Physcomitrella, Physcomitrium, Rhacomitrium, Tetraplodon* and *Weissia*.

Pettet (1964) studied some intergeneric hybrids of Funariaceae.

POLYPLOIDY 29.8

Cells, which have three or more sets of homologous chromosomes in their nuclei, are known as **polyploids**, and the phenomenon of their formation is called **polyploidy**.

Polyploidy is not very common in bryophytes. However, it is seen in most of the members of Marchantiales. According to Schuster (1966), about 15% of the liverworts show polyploidy. Hexaploid forms of *Dumortiera hirsuta* and large-sized polyploid *Targionia lorbeeriana* with $n = 27$ have been reported from Japan. In *Riccia*, polyploidy is seen only in those species which are capable of growing in xeric conditions. Polyploidy is more common in mosses than liverworts. High degree of polyploidy is observed in mosses belonging to Pottiaceae, Funariaceae and Bryaceae.

29.8.1 Autopolyploidy or Intraspecific Polyploidy

A polyploid species with all sets of chromosomes coming from the same species is called **autopolyploid**, and this phenomenon is known as **autopolyploidy** or **intraspecific polyploidy**. Autopolyploidy has been reported in several liverworts, including *Asterella, Calypogea, Cephalozia, Dumortiera, Nardia, Pellia, Riccardia, Riccia* and *Targionia*. Amongst mosses, autopolyploidy has been reported in many genera including *Atrichum, Bryum*, *Distichium, Funaria, Mnium, Pohlia, Sphagnum* and *Weissia.* Several cytologists recognise several polyploid, taxa as independent species (Newton, 1990).

In some mosses, the autopolyploids are morphologically different but in others they are morphologically same. To mention a few examples, "*Sphagnum subsecundum* ($n = 19 + 2m$) and *S. auriculatum* ($n = 38 + 4m$) differ only in the size of their organs" according to Hill (1975). However, according to Smith and Hill (1968), in *Funaria hygrometrica* ($n = 28, 56$), *Atrium undulatum* ($n = 7, 14, 21$) and *Physcomitrium pyriforme* ($n = 26, 52$), "there are no differences between autopolyploids or cytotypes".

29.8.2 Allopolyploidy or Interspecific Polyploidy

A polyploid species with sets of chromosomes from two or more different species is called **allopolyploid**, and this phenomenon is called **allopolyploidy**. This can be the result of hybridization between species.

Allopolyploidy is not well recorded in liverworts. Most of the mosses also do not show allopolyploidy. Wettstein (1932), however, recorded 28 interspecific hybrids in mosses. Out of these 28 hybrids, "24 are between species which are monoecious". In comparison to monoecious species, a low frequency of hybrids is seen between species which are dioecious.

Interspecific hybrids are commonly seen in *Weissia*. Khanna(1960) opined that *Weissia exserta* ($n = 26$) is an allopolyploid derivative of *W. cripta* X *W. controversa*, both having $n = 13$. Pettet (1964) has shown the possibility of interspecific as well as intergeneric hybrids in Funariaceae. Smith (1978) has also shown the possibility of hybridization between *Bryum pendulum* and *B. caespiticium*. Molecular studies of Ripetski (1992) also show that "level of interspecific genetic variability of mosses, is higher than traditionally expected".

CYTOTAXONOMY 29.9

The use of chromosome studies (i.e. number, structure and behaviour) in taxonomic work is known as **cytotaxonomy**. In several mosses, the cytological studies have been used to determine relationships at different levels confirming definite role of cytotaxonomy. A few selected examples of the use of cytotaxonomy in bryophytes are listed below:

1. Anderson and Bryan (1956) separated closely related species of *Fissidense cristatus* ($n = 12 + 1$) and *F. adianthioides* on the basis of their cytology.
2. Yano (1957) discussed chromosome numbers and chromosome morphology of 22 families including 63 genera and 139 species and made karyotypic comparisons of taxa. He opined that members of Fissidentales, Grimmiales, Dicranales, Eubryales and Polytrichales have unique karyotypic characters.
3. Mehra and Khanna (1961) worked on the cytology of mosses. They proposed that their chromosome numbers support their classification based on the structure of peristome. The mosses, possessing a single peristome, differ in range of chromosome number than those possessing double peristome.
4. Kumar (1966), and Smith and Newton (1966) studied the chromosome morphology and chromosome number of *Amphidium lapponicum* and *Ptychomitrium polyphyllum* and sorted out their taxonomic misplacement by placing them in Grammiaceae instead of Isobryaceae.
5. Smith and Newton (1968) studied Polytrichales and observed that all counts in this order of mosses are referable to $n = 7$, 14 and 21. They also opined that Tetrapidales have "evolved by way of simplification from Polytrichales".
6. Steere (1972), Newton (1972) and Ramsay (1974) worked on the cytotaxonomy of several mosses. Chromosome number in Dicranales, Eucalyptales, Rottiales and Grimmiales are $n = 12$, 13 and 14. Low chromosome number ($n = 5$ or 6) has been reported in members of Fissidentales. In *Tortula papillosa,* the chromosome number is $n = 7$ (Newton, 1972) or $n = 6 + 1m$ (Ramsay, 1974).
7. Smith (1978) proposed a phyletic scheme of Bryopsida on the basis of the chromosome numbers. He suggested that members of Polytrichales, Dicranales, Fissidentales, Funariales and Orthotrichales show definite trends while those of Grimmiales, Pottiales, Isobryales, Thuidiales, Hookeriales and Hypnobryales do not show any definite trend in the chromosome numbers.

TEST YOUR UNDERSTANDING

1. Give a precise account of cytogenetics of bryophytes in about 1000 words.
2. Feulgen staining technique is used for studying
   (a) morphology, (b) cytology, (c) genetics, (d) embryology.
3. Aceto-orcein stain gives good results for studying _____ materials of bryophytes.
4. Give a brief account of any one of the following in about 200 words:
   (a) Some studies on mitosis in bryophytes,
   (b) Some studies on meiosis in bryophytes

5. With the help of only one sentence, differentiate between the terms (a) heteropycnotic, and (b) heterochromatin.
6. What do you mean by 'M-bivalent' or 'special bivalent'?
7. Write a detailed botanical note on heterochromatin in bryophytes in about 200 words.
8. Differentiate between (a) chromatin, and (b) heterochromatin in about 100 words.
9. What is euchromatin?
10. Give a detailed account of chromosome number in all the three classes of Bryophyta.
11. What are sex-associated chromosomes? Describe them briefly with special reference to bryophytes.
12. The term 'h-chromosomes' refers to _____ chromosomes.
13. Sex-associated chromosomes are found in most of the _____ species of mosses.
14. What are nucleolar chromosomes and accessory chromosomes? Describe them in brief with particular reference to bryophytes.
15. Write an essay on polyploidy in bryophytes in about 500 words.
16. Describe hybridization in bryophytes in about 100 words.
17. A polyploid species with sets of chromosomes from two or more different species is called _____, and this phenomenon is called _____.
18. Write a note on cytotaxonomy in bryophytes in about 200 words.

30

Ecology of Bryophytes

VIEWS OF JOHANNES ET AL. (2007) ON ECOLOGY OF BRYOPHYTES 30.1

Johannes et al. (2007) published an article in ***Annals of Botany*** (Vol. 99) on cryptogam ecology with particular emphasis on bryophytes, and opined that ecology of bryophytes "has the potential to meet some of the important challenges of understanding and predicting the biogeochemical and climate consequences of large-scale environmental changes". Relevant data for certain biogeochemistry-related characters are available for bryophyte "species in the literature, including those involved in bryophytic nutrition and nutrient recycling, their anti-herbivore defences, and their potentials for carbon gain and losses". However, it may be said that still "very little is known about the role and applicability of functional traits" of bryophytes with respect to biogeochemical cycling. Yet, bryophytes are "paramount determinants of biogeochemistry in several biomes, particularly cold biomes and tropical rainforests, where they (i) contribute substantially to above-ground biomass; (ii) host nitrogen-fixing bacteria providing major soil N input; (iii) control soil chemistry and nutrition through accumulation of recalcitrant polyphenols and through their control over soil and vegetation hydrology and temperature; (iv) promote erosion and also prevent it (biological crusts in deserts); (v) provide staple food to arthropods, with important feedbacks to soil and biota; and (vi) facilitate and compete with vascular plants" (Johannes et al, 2007).

LIMITS OF ECOLOGY OF BRYOPHYTES 30.2

Ecology is the study of organisms in relation to their environment. Ecology of bryophytes may be studied in a number of directions, but here, only a few selected aspects are briefly discussed.

1. Autecology
2. Synecology
3. Succession
4. Factors of the habitat

AUTECOLOGY 30.3

The ecology of a single species in a habitat is known as **autecology**. Tamm (1953) made a significant contribution on the autecology of *Hylocomium splendens*, a moss. He studied the habitat, growth, yield and mineral economy of this species of moss. *H. splendens* forms an almost pure ground cover in coniferous forests of Scandinavia. Its growth depends on the canopy of the coniferous trees. Annual yield of this moss decreases regularly with the distance from the canopy of the tree. Distance from the tree canopy also shows its effect on the nutrient concentration in this species of moss.

Tallis (1958) studied the autecology of widely distributed species of a moss (*Rhacomitrium lanuginosum*). This study shows a particular combination of quite large-scale environmental factors. In the tropical regions, this moss is "restricted to rocks on the higher mountains but its lower altitudinal limit drops progressively northwards until in Northern Oceanic regions, and in the Arctic, it may be abundant at sea level". Its typical growth form is a group of lateral branches arranged in definite zones along the main axis, and according to Tallis (1959), "only one zone is formed each year". Annual growth rate varies from 5 to 15 mm and never exceeds 20 mm per annum in British conditions. Due to its very slow growth in calcareous grasslands, it is usually absent in such habitats. It is so because it (*R. lanuginosum*) is unable to compete with much faster-growing higher plants. Rainfall, air humidity and temperature are the major factors which govern the geographical distribution of *R. lanuginosum.*

Autecological studies of bryophytes are of definite use from various points of view. Presence of some larger bryophytes serve as guides to forest authorities regarding the conditions and characters of land. Copper mosses are of particular interest in establishing the prospects of particular ores in the region. Many bryophytic species act as indicators. *Polytrichum* and *Rhacomitrium* are invariably acid indicators, whereas *Detrichium flexicaule* and *Encalypta streptocarpa* are indicators of base-rich conditions.

With reference to bog ecology, *Sphagnum* is of outstanding importance. About a dozen species of this moss play essential roles in bog ecology as elucidated by Ratcliff and Walker (1958).

SYNECOLOGY 30.4

The ecology of all the organisms found in a habitat or an ecosystem is known as **synecology**. Synecology of bryophytes may be studied by (i) recognition of communities of bryophytes; (ii) recognition of different growth forms among bryophytes; (iii) applying quantitative methods in describing vegetation of bryophytes; (iv) studying succession process and the time required for its completion; and (v) studying habitat conditions.

30.4.1 Recognition of Communities of Bryophytes

The group of species of plants, animals, or both, living in the same habitat and interacting with each other is known as **community**. A bryophytic community includes several species of bryophytes. For example, a mossy covering containing several species (e.g. *Brachythecium ratabulum, Bryum capillare, Ceratodon purpureus*, *Cryphaea heteromalla, Frullania dilatata* and *Hypnum cupressiforme*) represents a **bryophytic community**. All these species in a community (i) compete with each other, (ii) react upon one another, (iii) possess different morphology and growth rate, and (iv) survive with each other as

efficiently as possible. The change that is observed or seen in a particular bryophytic community is a very slow process. It may take decades for a particular bryophytic community in its various stages of succession prior of attaining a climax.

For more details, the readers may consult ***Phytosociology and Ecology of Cryptogamic Bryophytes*** by Barkman(1958).

30.4.2 Recognition of Different Growth-Forms among Bryophytes

Bryophytic vegetation can also be analysed by studying growth-form representatives of a community. Five categories of growth-forms among bryophytic community, recognised by Gimingham and Robertson (1950) and Gimingham and Birse (1957), are cushions, turfs, canopy-formers, mats and wefts.

1. **Cushions** include two types of cushions, namely **large cushions** (e.g. *Leucobryum*) and **small cushions** (e.g. *Grimmia*).
2. **Turfs** include **tall turfs** (e.g. *Polytrichum commune*), **short turfs** (e.g. *Bryum argenteum*) and **open turfs** (e.g. *Polytrichum aloides*).
3. **Canopy-formers** (e.g. *Mnium undulatum*).
4. **Mats** include four types, namely **rough mats** (e.g. *Eurhynchium striatum*), **smooth mats** (e.g. *Frullania tamarisci*), **thread-like mats** (e.g. *Eurhynchium praelongum*) and **thalloid mats** (e.g. members of Marchantiales and Metzgeriales).
5. **Wefts** including **rhizoid-free weft** (e.g. *Hylocomium splendens*) and wefts with **frequent tufts of rhizoids** (e.g. *Thuidium tamariscinum*).

A sixth category of **pendulous forms** has been erected by Iwatsuki (1960), a Japanese bryologist. It is represented by genera such as *Barbella, Pseudobarbella* and *Floribundaria*. A community in different types of habitats, however, exhibits different growth forms. In a community occurring near water, four successive zones may be seen as the distance from the water increases. These are **smooth-mat forms** (e.g. *Eurhynchium riparioides*), replaced successively by **rough-mat forms** (e.g. *Cratoneura filicinum*), **thalloid-mat forms** (e.g. *Conocephalum conicum*) and **dendroid forms** (e.g. *Thamnium alopecurum*). Impact of soil type and groundwater level on the composition of bryophytic communities has been studied by Gimingham and Brynard (1960).

30.4.3 Applying Quantitative Methods in Describing Vegetation of Bryophytes

Several recent studies of applying quantitative methods in describing bryophytic vegetation are now available in the literature, but a few pioneer ones are those of Hope-Simpson (1941), Jenny (1941), Cornish (1954) and Perring (1959, 1960)

Hope-Simpson (1941) studied the vegetation of English chalk grassland with particular emphasis on bryophytes and lichens and also compared their occurrence in other calcareous grasslands. His studies published in the ***Journal of Ecology*** are focused on the bryophytic flora in an exact quantitative form. These studies, however, give no indication of the size of the area surveyed and also show least emphasis on the account of the habitat and height of the turf. Eight species considered as of outstanding importance in chalk grassland are *Acrocladium cuspidatum*, *Camptothecium lutescens, Dicranum scoparium, Fissidens taxifolius, Hylocomium splendens, Pseudoscleropodium purum, Rhytidiadelphus squarrosus* and *R. triquetrus*.

Cornish (1954) studied the origin and structure of the grassland types of Central North Downs. Her studies on bryophytic communities has been published in ***Journal of Ecology*** and are based on physiography and past history of the bud.

Jenny (1941) proposed the concept of **independent variable** to study the chalk grassland of Britain, and his studies have been supported and extended by Perring (1959, 1960). Jenny's method of study include "changes in soil and vegetation values in relation to changes in one independent variable whilst keeping all the others constants". For studying bryophytic vegetation, Perring gave due emphasis to topography, i.e. sensitivity of particular species to different slopes. Perring (1960) also gave due consideration to factors such as humidity, pH, carbonates, and exchangeable calcium, potassium and phosphates.

30.4.4 Studying Succession Process and Time Required for its Completion

The process of development of vegetation, involving changes of species and communities with time is known as **succession**. It occurs because the growth of plants alters the biotic and edaphic factors of a habitat, making possible the colonisation of other species, Doignon (1949) of France studied succession of bryophytes on rotting logs, and concluded that so gradual and slow are the various stages of succession that it may well be over 30 years before the same type of bryophytic flora is restored.

A clear picture of succession of bryophytes on a living tree was given by Barkman (1958). The pioneer colonisers were lichens, and after about 25 years appeared the liverwort *Frullania dilatata*. Within a few years now developed the species of *Ulota*, *Orthotrichum* and some more genera. Then after about 10 years developed mosses like *Neckera* and *Anomodon* and liverworts like *Porella platyphylla*. The mature tree was finally inhabited by bryophytes such as species of *Leucodon* and *Zygodon* after about 40 years. In several cases, it takes 100 to 120 years for the completion of succession process of bryophytic communities.

30.4.5 Studying Habitat Conditions

The place or kind of place, in which an organism, community or association is found, is known as **habitat**. Mosses and liverworts are important components of the flora on the trunks and branches of trees, which thus function as their habitat. A detailed account of habitat of bryophytes may be gathered from ***Phytosociology and Ecology of Cryptogamic Bryophytes*** of Barkman (1958). Bryophytic vegetation on the branch or trunk of trees is affected by (i) daily movements of the sun and availability of sunlight, (ii) direction of the prevailing wind in the region, and (iii) availability of the water supply or moisture. Nutrient supply and acidity are also important for the bryophytic flora in a particular habitat. A rich epiphytic flora is available on the trees having high nutrient status and neutral pH. A habitat with salty water is generally avoided by mosses, and almost none of them lives in sea water. *Funaria hygrometrica*, however, can grow where the concentration of salts is permanently very high. A halophytic community of bryophytes consisting of mosses (e.g. *Grimmia maritima, Hypnum cupressiforme, Pottia heimii* and *Totella flavovirens*) has been found to be salt-tolerant by Shacklette (1961). Shacklette's findings have been published in Vol. 64 of ***Bryologist***.

SUCCESSION 30.5

As mentioned earlier under Article 30.4.4, **succession** is the process of vegetation development, involving changes of species and communities with time. Succession proceeds towards the natural climatic **climax** where some kind of stability is reached. Ecologists have confirmed that *Funaria*

hygrometrica is a pioneer cononiser, and it is followed in sequential stages of succession by *Ceratodon purpureus* and then *Polytrichum juniperinum* and *P. piliferum* along with *Cladonia*, a lichen. The entire process of succession takes several years to complete.

Secondary succession of terrestrial bryophytes in New Jersey, USA, has been studied and described by Bard (1965). The species present in relative abundance in the initial stages were *Physcomitrium turbinatum, Pleuridium subulatum* and *Weissia controversa*. A leafy liverwort hydrosere has been described on the Yakobi Island, Alaska, by Shacklette (1965), and his study has been published in Vol. 46 of ***Ecology***. Two liverworts of hydrophytic nature of the initial stages of the succession process were *Nardia compressa* and *Scapania paludosa*, and the physiographic climax community was achieved by *Cladothamnus pyroliflorus*. Quarterman (1949) observed that a "*Frullania-Orthotrichum* stage initiates succession of bryophytes on the bark of cedar trees."

FACTORS OF THE HABITAT 30.6

Only major climatic factors (light, temperature and water), and edaphic factors with reference to bryophytes are briefly discussed.

30.6.1 Climatic Factors

1. Light Rocks and the moss communities growing on them are exposed to high light intensities. Mosses growing in caves show tolerance to low light intensities. It is, however, very difficult to separate the effects of light from those of temperature and humidity factors. Generally, it has been observed that bryophytes are less shade-tolerant than many algae and more so than many higher plants. *Marchantia polymorpha* has a tendency to tolerate a very deep shade. An example of shade-tolerant moss is *Thamnium lemani*. Few bryophytes are highly shade-tolerant and restrict themselves only in caves, e.g. *Cyathodium cavernarum* and *Schistostega osmundacea*. Extreme light intensities have lethal effects on such bryophytes. Many species of *Sphagnum* are intolerant of shade.

2. Temperature Much researches have not been done on the maximum temperature limit on which bryophytes can survive, but a few mosses (e.g. *Barbula revoluta* and *Tortula muralis*), have been seen to sustain a temperature as high as 52°C. Clausen (1964) studied the tolerance of liverworts to temperature and desiccation. Many Hepatics can survive for weeks together in a temperature as low as –10°C. Some bryophytes have been seen to survive also in freezing environments as low as –40°C for more than a day (e.g. *Frullania tamarisci, Gymnomitrion corallioides* and *Ptilidium pulcherrinum*).

3. Water Bryophytes are mostly terrestrial, found in moist surroundings, and only a few members are found in the water (e.g. *Riccia fluitans*). Corticolous mosses absorb moisture mainly from the atmosphere. Terrestrial members fulfill their water requirements from both soil and atmosphere. There exist reports which suggest that *Sphagnum* can absorb moisture 16–25 times of its own dry weight when its surrounding atmosphere is supersaturated. Bryophytes also adapt drought-resistant features, if water is relatively scarce or evaporation is excessive. Some examples of drought-resistant bryophytes include *Lunularia cruciata, Torula ruraliformis* and *Anoectangium compactum*. It is actually the humidity which has a profound effect on the distribution of liverworts. Several species of bryophytes occur on Indian hills because of abundant moisture.

30.6.2 Edaphic Factors

Edaphic factors include the effects of the soil in an ecosystem. Bryophytes grow commonly on a variety of substrates including moist soil, humus, rocks, etc.

Along with moist soil, humus is a factor of primary importance. Technically, **humus** is the layer of organic matter at the top of a soil profile. It is the habitat of most decomposers. Many mosses growing on rocks grow actually on humus. Some bryophytes prefer to grow on a particular kind of humus, e.g. *Dicranella cerviculata* shows preference to acid peat, and *Tetraphis pellucida* to decayed woods. Humus-loving mosses are generally saprophytic, and it is believed that microorganisms found in humus are an important factor for these bryophytes.

Bryophytes, which are able to grow on calcareous or other mineral-rich substrata, belong to particular families such as Tortulaceae and Amblystegiaceae. They also serve as indicators for the presence of particular elements, e.g. copper. Nitrogen substances in the soil are essential for growth of bryophytes. Certain mosses (e.g. members of Splachnaceae) are obligately nitrophilous. Some other nitrophilous mosses are *Lunularia cruciata* and *Bryum argenteum.*

For the growth of many bryophytes, the hydrogen-ion concentration of the substratum is also an important factors. Lime has been determined as the commonest cause of hydrogen-ion concentration for bryophytes in the soil. Different species of *Sphagnum* were grown in water-culture solutions maintained at different hydrogen-ion concentrations by Olsen (1923).

Mosses generally avoid salty water. But a few mosses are also halophytes and grow easily in salt-tolerant places, e.g. *Grimmia maritima* and *Tortella nitida*. Epiphytic mosses generally obtain their nitrogen from the humus of the bark on which they are developing.

30.6.3 Biotic Factors

The effects of living organisms on an ecosystem and on each other are studied under biotic factors. Much studies have not been done on this aspect of ecology of bryophytes. Since moss carpets have the power to retain water, they play an important role for seed beds of flowering plants on rocks. Mosses also function as pioneers on sand dunes where they are replaced soon by lichens. Bryophytes are always at a great disadvantage in competition with vascular plants mainly because of the small size and restricted growth of the former. Bryophytes get suppressed easily by the dead remains of higher vegetation.

TEST YOUR UNDERSTANDING

1. Write an essay on ecology of bryophytes in about 1000 words.
2. Ecology of single species in a habitat is known as _____.
3. What is synecology? Describe briefly the synecology of bryophytes in about 500 words.
4. Define the term 'community' with reference to ecology of bryophytes.
5. What do you mean by succession? Describe succession process with reference to ecology of bryophytes.
6. The place, in which an organism, community or association is found, is known as _____.
7. Give an account of climatic and edaphic factors with reference to the ecology of bryophytes.

31 Origin of Bryophytes and Their Fossil History

ORIGIN OF BRYOPHYTES 31.1

Bryophytes are nonvascular plants, mainly terrestrial in habitat, generally susceptible to desiccation, and show heteromorphic alternation of generations, with dominant haploid gametophytic generation and ephemeral sporophytic generation. Our knowledge of the geological history of this group of plants is fragmentary because much is still not known about their fossil records. However, Walton (1928) has shown the presence of bryophytes in the Upper Carboniferous, i.e. about 285,000,000 years ago. Theories regarding the origin of bryophytes are, therefore, mainly based on our studies on ontogeny, comparative morphology, and also analogies of bryophytes with other groups of living land plants.

Two main theories about the origin of bryophytes exist. Of these, one suggests that they are descendents of pteridophytes while the other suggests that bryophytes have their origin from algae. Before discussing some details of both these theories, let us first examine a few details about the monophyletic or polyphyletic nature of this group.

A NOTE ON THE MONOPHYLETIC OR POLYPHYLETIC NATURE OF BRYOPHYTES 31.2

Based on morphological characteristics, workers like Campbell (1895) and cavers (1911) suggested bryophytes to be a monophyletic group. Even phylogenetic trees were constructed on the basis of these characteristics. Satisfactory details of cytology were, however, not available to bryologists in those days, as are available today, and hence the picture was not clear. The theory suggesting bryophytes to be a monophyletic group is, therefore, now nothing more than history. It has been rejected by later workers including Schuster (1966), Chopra (1967) and Crum (1976). A majority of the later workers now believe in polyphyletic origin of bryophytes. But, Fulford (1964) remarked that since detailed information is still not available on a majority of bryophytic genera, all these suggestions about monophyletic or polyphyletic nature of bryophytes are uncertain and tentative, and much more is still to be done in this regard by bryologists.

Geiger (1990) and others recognised four distinct lines within bryophyta, namely Hepaticopsida, Anthocerotopsida, Bryopsida and Sphagnopsida. All these are individual natural groups with clear differences in their morphology, anatomy, ontogeny of their sex organs, cytology and chemical structure, e.g. biflavonoids are of frequent occurrence in the cell walls of Bryopsida and Sphagnopsida while they have not been isolated from Hepaticopsida and Anthocerotopsida. Michler et al. (1992) employed molecular data to suggest polyphyletic origin of bryophytes. They analysed chloroplast-coded 16S and 23S-rRNA genes of several algae and bryophytes including liverworts, hornworts and mosses, and on these basis, they supported the polyplyletic origin of bryophytes.

Further details of phylogeny are discussed in a separate chapter.

ORIGIN OF BRYOPHYTES FROM PTERIDOPHYTES 31.3

Discovery of Psilophytales by Kidston and Lang (1917–1921) suggested that bryophytes are descendants of pteridophytes. Psilophytales are some of the simplest and probably the oldest pteridophytes, not existing today. The sporophyte of Psilophytales (e.g. *Rhynia, Horneophyton*) was a rootless, leafless, dichotomously branched shoot bearing terminal sporangia. These pteridophytes could be compared on one hand with bryophytes (e.g. Anthocerotales) and, on the other hand, with vascular plants. However, there existed several differences between bryophytes and Psilophytales, such as (i) the sporophyte was physiologically independent in Psilophytales and not in bryophytes, (ii) continued apical growth was shown by Psilophytales and not by bryophytes, and (iii) vascular tissue (xylem and phloem) was present in Psilophytales and absent in bryophytes. There also exist several similarities between Psilophytales and bryophytes. The sporangia of some Psilophytales (e.g. *Rhynia, Horneophyton*) resemble the capsules on several bryophytes (e.g. *Sphagnum, Andreaea*, and some Anthocerotales).

Proskauer (1960) has shown several similarities between capsules of Anthocerotales and Rhyniaceae of Psilophytales. He observed remarkable similarity between the sporangia of *Horneophyton* (of Psilophytales of Pteridophyta) and thickened columnar surface layer and jacket lining layer of *Dendroceros crispus* (of Anthocerotales of Bryophyta). Presence of tracheid-like elements with spiral thickenings in columella of *Anthoceros* also support the pteridophytic origin. Due to such close similarities, botanists opined that bryophytes (especially Anthocerotopsida) may have originated from simplest known vascular plants, such as Psilophytales of pteridophytes.

Two main advocates of pteridophyte ancestry of bryophytes are Haskell (1949) and Christensen (1954). Haskell (1949) opined that bryophytes "represent a group originating from Psilophytalean ancestry, following reduction due to their habitat". Haskell's researches have been published in Vol. 12 of the journal ***Bryologist***. Christensen (1954) published his detailed observations in Vol. 51 of ***Bot. Tidsskr*** where he commented that "bryophytes have descended from pteridophytes". Proskauer (1960), in his series of publications in ***Phytomorphology***, suggested that "Anthocerotopsida originated from forms such as *Horneophyton"* of pteridophytes. The Indian bryologist Shiv Ram Kashyap (1919) also believed that due to several common features, "Hepaticopsida may have arisen from pteridophytes." Pteridophytic ancestry of bryophytes was also postulated by Kashyap and Dutt (1925). Jennings (1928) and Schwarz (1955) have also favoured the idea of bryophyte-origin by way of simplification from Psilophytales.

Lignin is the chemical constituent of tracheids. It is absent in bryophytes. However, its occurrence in the gametophytes and peristome of some mosses (e.g. *Dawsonia*) suggests their origin from

pteridophytes (Siegel, 1962, 1969). Niklas and Pratt (1980), however, have questioned the presence of lignin in bryophytes.

ORIGIN OF BRYOPHYTES FROM ALGAE 31.4

31.4.1 View of Lignier (1903)

Living bryophytes show amphibious nature and due to this, it was suggested by earlier bryologists that bryophytes have originated from aquatic ancestors, like algae. Lignier (1903) was the first to suggest that algal ancestors of bryophytes gave rise to a primitive terrestrial type, the **Prehepatics**, which gave rise to bryophyta, on one hand, and vascular cryptogams, on the other.

31.4.2 View of Bower (1908)

Archegoniatae are plants having archegonia, e.g. bryophytes, pteridophytes and gymnosperms. In his theory of **origin of land flora**, Bower (1908) proposed that Archegoniatae originated from aquatic ancestors (e.g. algae) "inhabiting shallow freshwater or higher levels between marine tide-marks". Amongst the inhabitants of aquatic habitat, bryophytes show resemblances with Chlorophyceae (green algae) due to several features, including (i) the presence of photosynthetic pigments in the assimilatory tissue, (ii) the presence of starch as the metabolic product, and (iii) the presence of cell wall made up of cellulose. Thus, it was concluded that Chlorophyceae were probably the nearest algal relative of Bryophyta.

31.4.3 View of Fritsch (1935, 1945)

F E Fritsch (1935, 1945), a well-known algologist, believed that members of the order Chaetophorales of the class Chlorophyceae contain all characters for the development of more complex types, and "evolution of the archegoniate plants from algae may have followed" the undermentioned course of actions:

1. Development of heterotrichous habit showing formation of different types of filaments or trichomes "in the plane of substratum, i.e. prostrate and in the upright vertical direction, perpendicular to the prostrate system" as in Chaetophorales of Chlorophyceae.
2. Development and formation of parenchymatous structures in the upright filaments as in algal members of Fucales and Laminariales.
3. Initiation and ultimate establishment of apical growing point in the upright filaments, as in Chaetophorales, Fucales, Laminariales, etc.
4. Disappearance of prostrate system and establishment of dichotomous branching in the algal members.
5. Establishment of vascular system in the upright aerial parts, e.g. scalariform thickenings of medullary cells of *Sargassum* and sieve-tube-like elements in *Macrocystis*.
6. Development of cuticle outside the epidermal layer.

Development of protonema in the mosses (Bryopsida) was seen to be equivalent to the prostrate system and of leafy gametophores to the erect filaments of Chaetophorales (algae) by Fritsch (1945). Fully developed heterotrichous habit has been later observed in the developed protonema of mosses.

31.4.4 Some Other Views on the Algal Origin of Bryophytes

The origin of bryophytes from algae, particularly green algae, has also been suggested and supported by workers like Schuster (1966), Chopra (1967), Fott (1974) and Karunen ((1990). It is mainly due to the resemblances in their (i) photosynthetic pigments, (ii) cell-wall components, (iii) flagella, and (iv) food reserves. According to Watson (1971), *recapitulation* of ancestral algal habit can be seen in the filamentous protonema of mosses. Many biological, physiological, reproductive and developmental features also suggest the green-algal ancestry of not only of bryophytes but also of other land plants. It is also evidenced by fossil records that some present-day green algae (e.g. *Coleochaete*, *Chara*, etc.) are quite ancient, extending back to Silurian, i.e. approximately 400 million years ago.

Amongst green algae, Charales (e.g. *Chara*) are generally linked with ancestry of land plants. This is due to the presence of several specific features that are common to both. Only advanced Charales among algae possess **phragmoplast**, which are also characteristic of vascular plants and bryophytes. (**Phragmoplast** is a complex of interdigitating microtubules aligned more or less parallel to the earlier spindle microtubules, developing at the end of mitosis). A majority of other green algae lack phragmoplast. Brown and Lemmon (1990) have also advocated the algal origin of bryophytes. Graham (1980) also opined that Charales also show similarity with other land plants (including bryophytes, pteridophytes and gymnosperms) in microtubular cytoskeleton of their flagellum. Photorespiration in Charales is also similar to the photorespiration in land plants.

Phytochrome is a pigment which controls many of the physiological responses of plants to light. It absorbs the red and far-red wavelengths of light. Scientists have proved the similarity of phytochrome between Charales and land plants.

Hori et al. (1985), on the basis of their molecular studies, opined that "*Nitella*-like green plants may be the direct ancestors of first land plants", in general, and bryophytes in particular.

FOSSIL HISTORY OF BRYOPHYTES 31.5

Due to the fragile and delicate nature of the plant body of bryophytes, we have a very limited knowledge of their fossils. These plants also do not possess a cutinised epidermis and lignified vascular tissues like xylem and phloem. In spite of this, there are some authentic records of fossil liverworts in Upper Devonian and mosses in Carboniferous. Hepatic characters have also been noted in earliest land plant fossils from Ordovician and Silurian, i.e. much before the advent of the vascular plants, by Taylor (1995) and Edwards et al. (1995). Parihar (1987) mentioned that "the fossil Bryophyta do not throw any light on the origin and evolution of the group". A preliminary account of some known fossil Hepaticopsida and Bryopsida is given here.

31.5.1 Fossil Hepaticopsida

1. Hepaticites Walton (1925) was the first to provide authentic details of the relationship of some fossil plants of Upper Carboniferous with some living Hepaticopsida, and these have all been assigned to the form-genus *Hepaticites*, a leafy liverwort (Fig. 31.1A). No reproductive structure of *Hepaticites* was reported by Walton (1925), who compared the species of this form-genus with anacrogynous Jungermanniales of Hepaticopsida. Of the five species of *Hepaticites* described by Walton (1925,

1928), *H. kidstoni* (Fig. 31.1A) had a "broad axial region and two definitely arranged series of leaves or lobes with two accompanying series of smaller scale-like appendages". Due to these characters, *H. kidstoni* resembled the living genus *Treubia*. The other two species (*H. langi* and *H. willsii*) resembled with the living genus *Riccardia* due to their parenchymatous thalli with no midrib. The remaining two species described by Walton are *H. lobatus* and *H. metzgerioides*. The former had an axial region and the lobed wing, while the latter resembled closely the living genus *Metzgeria*, hence named *Hepatites metzgerioides*. Heuber (1961) described *H. devonicus* from Upper Devonian. It had a rhizome-like portion bearing unicellular rhizoids and a dichotomously branched thalloid portion bearing wings and thick midrib. Schuster (1966) shown resemblances of *Hepaticites devonicus* with the present-day *Pallavicinia* and renamed it as *Pallavicinites devonicus*.

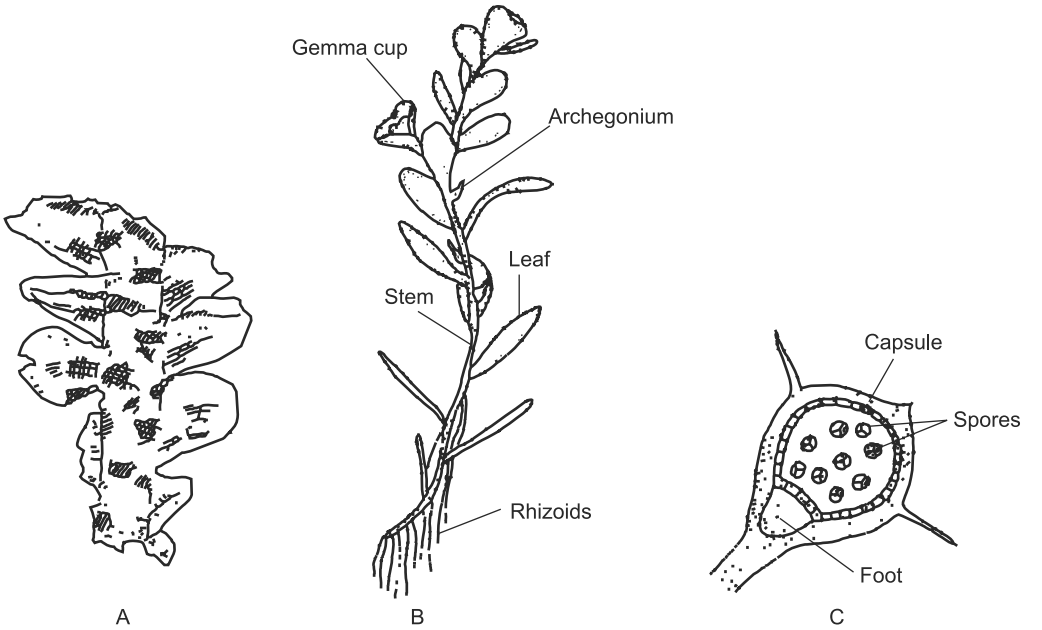


Fig. 31.1 Some fossil bryophytes: A, *Hepaticites kidstoni*; B, Leafy shoot of *Naiadita*; C, Section of sporogonium of *N. lanceolata* showing foot, capsule and spores (A, after Walton; B-C, after Harris)

Harris (1931) described three species of *Hepaticites* (viz. *H. glebas, H. laevis* and *H. rosenkrantzi*) from Jurassic of Greenland, and later on four species (*H. arcuatus*, *H. haiburensis*, *H. hymenoptera* and *H. wonnacotti*) from Jurassic of Yorkshire (Harris, 1961). Two more species described by Harris are *H. amauros* and *H. solenotus* from Triassic of Greenland.

2. Naiadita *Naiadita* (Fig. 31.1B) is the most completely known fossil representative of bryophytes reported from Upper Triassic of England by Harris (1938), who opined that it is quite close to Riellaceae of Sphaerocarpales. Harris described almost all parts (rhizoids, stem, leaf, gemma cups, archegonia, embryo, sporophyte and spore) of this fossil bryophyte, except antheridia. Sparsely branched stem of *N. lanceolata* was 1–3 cm in height. Basal part of the stem had several unicellular rhizoids. A major

part of the stem had parenchymatous cells, and there was no differentiation of tissues. The leaves on the stem were linear in the lower portion while lanceolate to almost round towards the apical portion. Gemma cups having multicellular gemmae were also present. Mature archegonia were surrounded by leaflike lobes of perianth. The sporophyte (Fig. 31.1C) had a spherical capsule and small hemispherical foot with no seta. Columella and elaters were absent while there were present many lenticular spores in the capsule. *Naiadita* is unique in combining features of both liverworts and mosses. It also shows some characteristics resembling that of Marchantiales and Calobryales.

3. Some Other Fossil Hepaticopsida Lundblad (1954) described *Marchantites hallei* from South America and *Marchantiolites porosus*, *Ricciopsis florinii* and *R. scanica* from the coal mines of Skromberga (Sweden). Species of *Ricciopsis* are the forms like *Riccia.* Berry (1919) has earlier described from Upper Cretaceous the forms having affinities with Jungermanniales acrogynae and assigned them to belong to *Jungermannites cretaceous*. Townrow (1959) described *Hepaticites cyathodoides* from the Middle Triassic of Natal. It had several resemblances with *Cyathodium.*

31.5.2 Fossil Bryopsida

Some of the well-preserved fossil mosses belong to the species of *Muscites, Intia* and *Protosphagnum.*

Muscites bertrandi and *M. polytrichaceous* have been described from the Upper Carboniferous, in the form of either compression of leafy shoots or small petrified shoots possessing rhizoids with oblique septa. *M. polytrichaceous* had stems with small univeined leaves, which can be compared with the present-day *Polytrichum* and *Rhizogonium* (Dixon, 1927).

Neuberg (1956, 1958, 1960) described well-preserved fossil mosses from Lower and Upper Permian rocks of Angaraland of former USSR. *Intia vermicularis* (Fig. 31.2A) and *I. variabilis* (Fig. 31.2B) are two such mosses, remarkably similar to present-day *Bryum* and *Mnium*. Other species of fossil mosses described by Neuberg are *Intia falciformis*, *I. angustifolia, Salairia longifolia, Uskatia conferta, Polyssaievia spinulifolia, Buchtia ovata* and *Bajdaievia linearis*.

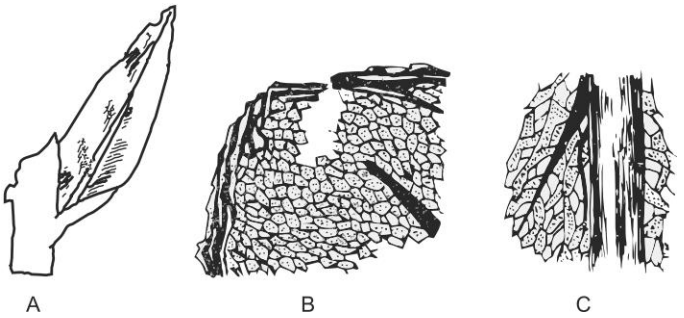


Fig. 31.2 Some fossil mosses A, *Intia vermicularis* showing a leaf and part of stem; B, *I. variabilis* showing part of the leaf enlarged; C, Part of leaf of *Protosphagnum nervatum* near nerve and leaf cells (A-C, after Neuberg)

Fossils of the leaf genus *Protosphagnum* (Fig. 31.2C) are similar to present-day *Sphagnum*. They possessed a network of two types of cells arranged in a specific manner, in which dividing colourless cells are clearly visible. A new order Protosphagnales has been created by Neuberg (1960). Three

genera included in this order are *Jungagia, Protosphagnum* and *Vorcutannularia*. These genera possess two kinds of cells in their leaves, thus resembling closely the present-day *Sphagnum*. Gam (1962) criticised the inclusion of these three genera under an independent order Protosphagnales and has tried to establish their affinity with orders like Polytrichales and Dicranales.

Fossil mosses were of rare occurrence in the Mesozoic. Berry (1928), however, reported *Muscites lesquereuxi* from the Late Cretaceous of North America, and Townrow (1959) described *M. guescelini* from Triassic of Natal.

Many members of Bryopsida, reported from Cenozoic include the form-genera *Polytrichites, Plagiopodopsis* and *Palaeohypnum.*

TEST YOUR UNDERSTANDING

1. Write a detailed note on the monophyletic or polyphyletic nature of bryophytes in about 200 words.
2. Give an account of the origin of bryophytes.
3. Bryophytes are descendants of pteridophytes. Elaborate this statement in about 250 words.
4. Explain various views about the origin of bryophytes from pteridophytes.
5. Discovery of which fossil order suggested that bryophytes are descendants of pteridophytes?
6. Write an essay on the origin of bryophytes from algae.
7. Define the term 'archegoniatae'.
8. Archegoniatae includes which of the following?
   (a) Bryophytes, (b) Pteridophytes, (c) Gymnosperms.
9. Explain the view of F E Fritsch regarding the origin of bryophytes from algae.
10. Explain the following terms: (a) Phytochrome, (b) Phragmoplast
11. Give an account of fossil history of bryophytes in about 500 words.
12. Write short notes on:
    (a) *Hepaticites,* (b) *Naiadita.*
13. Give a brief description of some fossil Hepaticopsida.
14. What do you know about fossil mosses? Explain them in some detail.
15. What is common amongst the following?
    (a) *Intia,* (b) *Muscites,* (c) *Protosphagnum*
    These are _____ _____.

32 Economic Importance of Bryophytes

UTILITY OF BRYOPHYTES: A GENERAL OVERVIEW 32.1

The economic importance of bryophytes (liverworts, hornworts and mosses) is relatively unknown to most people. But in different parts of the world, bryophytes are now widely used because they (i) modify their microclimate, (ii) serve to conserve moisture, (iii) check soil erosion on hilly slopes, (iv) serve as a seed bed for forest cover, (v) help in pollution monitoring, and also (vi) are now considered as new sources of pharmaceutical products. Viewed from a broad perspective, bryophytes are used (i) in horticulture, (ii) for household purposes, (iii) for their ecological importance, (iv) in preparing several pharmaceutical products, and also (v) in the biomapping of atmospheric precipitation.

Some of the specific uses of these nonvascular plants are briefly discussed here in this chapter.

ECOLOGICAL USES OF BRYOPHYTES 32.2

Bryophytes have been found to be good indicators of environmental conditions, and this aspect of these plants has been discussed in detail in Chapter 23.

MEDICINAL USES OF BRYOPHYTES 32.3

32.3.1 Some General Examples of Medical Uses

1. In the ancient times, various mosses (e.g. *Bryum, Mnium, Philonotis*) were crushed into a kind of paste and applied as a poultice.
2. Burned ash of mosses, mixed with honey and fat, is used as an ointment for cuts and wounds in several parts of our country.
3. *Marchantia polymorpha* and *M. palmata* are used as medicines for boils and abscesses by Himalayan Indians.
4. A paste made from various species of *Riccia* is applied externally to cure ringworm.

5. Traditional medicines are made in China from over three dozen bryophytes to treat various illnesses like bronchitis, tonsilitis, tympanitis, cardiovascular diseases and skin diseases.
6. Extracts made from *Rhodobryum giganteum* and *R. roseum* can enhance flow of blood in the aorta by as much as 25% to 30% in some animals. These species are used to treat cardiovascular diseases and nervous prostration.
7. A blood-clotting factor IX is produced from transgenic *Physcomitrella* and used in the treatment of haemophilia-B.
8. *Sphagnum* has been used for various medicinal purposes. Calcified peat is very effective as a germicide. Peat water has antiseptic and astringent properties. Sphagnol is a distillate of peat tar and highly valuable in treating eczema, psoriasis, hemorrhoids, scabies, insect bites, acne and other skin diseases. Dried *Sphagnum* is sold in China to treat hemorrhages (Bland, 1971).
9. Due to the presence of several biologically active compounds, bryophytes survive in nature, in spite of the absence of thick cuticle and bark. These compounds protect bryophytes from fungi and other microorganisms, and due to this, they are of medicinal value to humankind. For details of biologically active compounds in bryophytes, refer Chapter 24.
10. Extracts of liverworts, such as *Pallavicinia* and *Reboulia*, are well-known for their antifungal and antimicrobial activities. It is due to the presence of lunularic acid in these genera.
11. Antibiotically active substances have also been extracted from some mosses, such as *Polytrichum*, *Sphagnum* and *Atrichum*.
12. Petroleum-ether extracts of *Barbula* and *Timmiella* are highly effective against Gram-negative and Gram-positive bacteria.
13. Skin infections caused by bacteria such as *Bacillus subtilis*, and fungi such as *Candida albicans* and *Trichophyton mentagrophyte* can be checked by the extract of *Plagiochila stevensoniana*.
14. Extracts of some liverworts act as stomach poison in some animal pests (e.g. *Arion lusitanicus*).
15. Certain compounds effective against leukaemia have been isolated from *Plagiochila fasciculata*. Diplophyllin, a compound isolated from some species of the liverwort *Diplophyllum*, is significantly effective against human epidermoid carcinoma.
16. *Sphagnum* is extensively used for dressing wounds. Its pads are preferred in place of cotton, because they easily absorb liquids as much as four times than cotton, and are cooler, softer and less irritating to skin than cotton.
17. *Marchantia polymorpha* was widely used in earlier times in China and India to treat liver ailments. According to Bland (1971), it "cools and cleanses the liver, removes yellow jaundice, and also removes inflammation". It is also used to treat pulmonary tuberculosis in some parts of Europe, according to Bland (1987). According to Hu(1987), it is still used in China "to treat jaundice of hepatitis and as an external salve to reduce inflammation."
18. *Polytrichum commune* is used to reduce inflammation and fever, as a detergent diuretic, laxative and hemostatic agent according to Hu (1987). Plants of this species are boiled to make a "tea" to treat common cold. It also dissolves stones of the kidney and gall bladder (Gulabani, 1974).
19. *Haplocladium microphyllum* is used to treat bronchitis, cystitis, tonsilitis and tympanitis.

32.3.2 Antibiotics from Bryophytes

Liverworts and mosses rarely show signs of infection in nature and it is mainly due to their characteristic of "inhibition of microorganisms in products of bryophytes", e.g. *Sphagnum portoricense, S. strictum, Conocephalum conicum* and *Dumortiera hirsuta* (Madsen and Pates, 1952). McCleary et al. (1960) opined that mosses are a definite source of antibiotics. Antimicrobial activity of the extracts of *Porella, Pallavicinia* and *Reboulia* has also been confirmed by workers like Belcik and Wiegner (1980) and Isoe (1983). Antibiotic properties in over a dozen mosses (e.g. *Atrichum*, *Polytrichum* and *Sphagnum*) has also been investigatd by McCleary and Walkington (1966).They suggested that these mosses "strongly inhibited either or both Gram-positive and Gram-negative bacteria". *Dicranum scoparium* strongly inhibited all bacteria except *Escherichia coli*. Species of *Barbula* and *Timmiella* also show high occurrence of antibacterial activity according to researches of K G Gupta and B Singh (1971). Ichikawa et al. (1983) tested nearly 80 species of mosses and "found antimicrobial activity in nearly all of them".

"Peat humic acids possess **antiviral activity** against herpes simplex virus types 1 and 2" (Klocking et al., 1976). Extracts of *Sphagnum* and *Camptothecium* possess antiviral active humic acids that can inhibit the growth of polio virus, according to Witthauer et al. (1976).

32.3.3 Anti-cancerous Properties of Bryophytes

1. Extract of *Polytrichum juniperinum* has anti-cancer activity against Sarcoma 37 in mice (Belkin et al., 1952).
2. A compound diplophylline, obtained from *Diplophyllum albicans* and *D. taxifolium* shows anti-cancerous activity against human epidermoid carcinoma (Ohta et al., 1977).
3. Compounds, such as sesquiterpenoids, costunolide and tulipinolide, effective against carcinoma of vasopharynx, have been isolated from *Conocephalum supradecompositum, Frullania monocera, Lepidozia vitrea, Marchantia polymorpha, Plagiochila semidecurrens* and *Porella japonica* by Asakawa (1982) and Matsuo et al. (1981, 1984).
4. Spjut et al. (1986) of the US National Cancer Institute tested over 200 species of bryophytes (184 species of mosses and 23 species of liverworts) and found that extracts of 43 species possess anti-cancerous properties. Most active of these bryophytes belong to Brachytheciaceae, Dicranaceae, Grimmiaceae, Hypnaceae, Mniaceae, Neckeraceae, Polytrichaceae and Thuidiaceae.
5. Anti-leukemic activity of Marchantin-A from *Marchantia polymorpha* and riccardin from *Riccardia multifida* has also been reported by Asakawa et al. (1982).

BRYOPHYTES AS FOOD SOURCE 32.4

Bryophytes as food source for animals are not very important. However, "Alaskan reindeer occasionally graze on *Aulacomnium turgidum, Hylocomium splendens* and *Polytrichum"* (Band, 1971). During scarcity of fresh food, bryophytes may be the source of specific needs of some animals, e.g. *Barbella pendula* has a high content of Vitamin B_{12}, which is not easily available in many vegetarian diets. For giving good vitamin and iron diet, piglets and some other animals are given a diet of milled peat moss (*Sphagnum*). According to JH Bland (1971), the "Chinese consider mosses to be a famine food". In

some European countries, *Sphagnum* contributes to the flavour of Scotch Whisky, according to N G Miller (1981). According to G B Pant and S D Tewari (1989), Kumauni Indians use some bryophytes (e.g. *Anomodon, Entodon, Hypnum*, etc.), wrapped in a cone of *Rhododendron companulatum* leaves, to serve as a filter for smoking tobacco. Some aphids depend on mosses as food for their larvae. Since mosses have very low calorific values, some scientists are now exploring this aspect of bryophytes.

HORTICULTURAL USES OF BRYOPHYTES 32.5

Since long, bryophytes have been used in horticulture as "soil additives, ground cover, dwarf plants, greenhouse crops, potted ornamental plants and for seedling beds" (Sjors, 1980). Besides its common use in making poles to support climbing plants, *Sphagnum* is also used for other decorative horticultural purposes including "making baskets and covering flower pots and containers for floral arrangements" (Thomason, 1994). Wet plants of *Sphagnum* are used in nurseries for shipping living plants. Gardeners use *Sphagnum* in air layering, a method of propagating plants. In Japan, preparation of landscape types is an alternative horticultural art, in which several mosses (e.g. *Bartramia pomiformis, Leucobryum neilgherrense* and *Polytrichum commune*) are used. Mosses are also used as an important element for bonsai, where they help to stabilise the soil and retain moisture.

HOUSEHOLD USES OF BRYOPHYTES 32.6

Bryophytes, especially mosses, are used for decorative purposes in many countries including Finland, England, France, Japan and USA. Because of the absorbent and insulating properties, *Sphagnum* is the most useful household moss. Dried plants of *Climacium japonicum* are used in Japan for making ornamental white flowers. Mats are prepared and sold in the market in many parts of India. Beddings, mattresses, cushions and pillows are prepared by stuffing mosses in many parts of India. In some parts of Himalayas, mosses are used as insecticides and insect repellents while storing grains. A cheap kind of cloth is prepared by mixing *Sphagnum* with wool in Germany. Head cushions for carrying vessels of water and other heavy articles are prepared by several mosses including *Hylocomium, Hypnum* and *Trachypodopsis*. Several bryophytes (e.g. *Hypnum, Macrothamnium, Neckera*, *Sphagnum*, etc.) are used for packing of apples, plums and other fruits in India.

Climacium americanum is used or making wreaths and crosses. Moss roses are prepared from *Hylocomium splendens. Bryum* is collected and used for floral arrangements in USA. *Rhytidiadelphus* is used in craft display in hotels. Green carpets for floral exhibitions are prepared from species of *Hylocomium* and *Rhytidiadelphus*. Several bryophytes are graceful looking than many aquatic higher plants, and are, therefore, used in aquaria, e.g. *Bryum pseudotriquetrum, Riccia fluitans, Ricciocarpus natans, Fontinalis antipyretica* and *Rhacopilum aristatum* (Takaki et al, 1982).

HOUSE CONSTRUCTION 32.7

Bryophytes are used in the construction of houses, furnishing, boats, and other items in the parts of the world where woody plants are scarce and bryophytes are common. Moss mats are used with grasses,

shrubs and bamboo to make doors at the openings of huts in several parts of Himalayas. ***Peatcrete*****,** and ***peatwood***, the products made from *Sphagnum* peat, are used as construction materials. Peat-based pasteboard and wrapping paper is manufactured in the USA. In Phillippines, bryophytes are used as fillers between wooden posts of walls and shingles of roofs (Tan, 2003). *Fontinalis antipyretica* has been used as fire insulation between the chimney and walls in countries like Norway, Denmark and Finland (Thieret, 1956). According to Pant and Tewari (1989), shepherds in Himalayan highlands use several bryophytes as chinking in temporary summer homes. Some such bryophytes are species of *Actinothuidium, Anomodon, Entodon, Herbertus, Floribundaria, Philonotis, Plagiochila* and *Trachypodopsis.* In some countries of Europe, *Sphagnum* is stuffed between timbers of houses to deaden sound. In Russia, pressed and heated slabs of *Sphagnum* are used to insulate houses and refrigerators (Rue et al. 1977). Mosses are now being widely used throughout Germany as a roofing material. *Polytrichum commune* is used to make nautical ropes in Belgium. According to Rue et al. (1977), "**peatcork** is made from the coarse fraction of peat, while **peatfoam** is an ultra-light construction material based on peatmoss and foamed resin".

MOSS INDUSTRY 32.8

Being highly absorbent and permeable, *Sphagnum* can absorb metals. Due to these characteristics, it is used as an effective filtering and adsorption agent for treating wastewater and effluents of factories containing toxic discharge of heavy metals, e.g. silver, copper, cadmium, mercury, iron, lead, etc. It is also used in filtering oils, dyes, detergents and even microorganisms. Active carbon, used in many chemical industries, can also be produced from *Sphagnum*. Peatmoss (*Sphagnum*) is also used in producing several high-quality products in the industries related to pollution control and bioremediation. Several mosses have oil-absorbing qualities, and are therefore useful for oil spills on waterways. Some bryophyte-derived products are used to absorb fluids containing acetone, benzene, chloroform, corn oil, diesel fuels, gasoline, jet fuels, kerosin, oil-based ink, paraffin oils, xylenes, etc. *Sphagnum* is highly useful because it has the ability to hold up to 30 times its weight in water. It is, therefore, an excellent material for shipment of plants, flowers and fresh vegetables. It is used on a large scale for storage of roots and bulbs, and also for hydroponics gardening. Insulator sheets for houses are also manufactured from *Sphagnum* and other mosses. In France, moss carpets of various sizes are also prepared. These can be easily fixed along lawns, roads, playgrounds, etc.

FUEL FROM BRYOPHYTES 32.9

In several European countries, including Finland, Sweden, Poland and West Germany, liverworts and mosses are used as a fuel. Products like low and intermediate BTU gas, ethylene, hydrogen, methanol and natural gas are produced from peat. Methane is produced on a large scale from peat mosses (e.g. *Sphagnum*). The heating value of peat is said to be superior than that of wood. According to the reports of United Nations (1981), "nearly half the world's annual peat production is used for fuel, with peat resources worldwide estimated to be equivalent to 100–200 million tons of oil, or about half the known gas reserves". Peat is said to be a clean-burning fuel. In the past few decades, peat has received unprecedented attention as an alternative fuel source.

According to Boffey (1975), the "former Soviet Union burned an estimated 70 million tons, and Ireland 3.5 million tons of mosses in one year to produce electricity". Richardson (1981) opined that about "25% of the fuel in Ireland is moss-based". However, improved methods are needed for harvesting, drying and conversion of peat mosses to a burning fuel, according to Lindstrom (1980).

Besides the above-mentioned uses of peat, "Finland is exporting pulverised peat to northern Sweden, where use in industry and municipal heating, power generation, and oil burners of pulp and paper companies is increasing" (Summerton, 1981).

PESTICIDES FROM BRYOPHYTES 32.10

According to Yepsen (1984), bryophytes contain natural pesticides in their body. Sesquiterpene hemiacetyl plagiochiline, a poison extremely potent in mice, is present in the liverwort *Plagiochila* according to Matsuo (1983). This pesticide also inhibits the feeding of an African army worm, according to Asakawa et al. (1980). Pesticides, like ferulic acid and coumaric acid, have also been isolated from *Brachythecium rutabulum* and *Mnium hornum* (Davidson et al, 1984). Asakawa (1990, 2001) also isolated many terpenes and other phenolic compounds having pesticidal properties from species of *Porella.*

CLOTHING FROM BRYOPHYTES 32.11

According to Hedenas (1991), *Sphagnum* is used in Germany "to line hiking boots, where it absorbs moisture and odour." *Sphagnum*, along with *Dicranum*, are also used for lining diapers, in which it keeps babies clean and warm. According to Gottesfeld and Vitt (1996), the famous "Johnson & Johnson Company uses *Sphagnum* in diapers and sanitary napkins". Most commonly utilised species for these purposes is *Sphagnum magellanicum*. In Phillipines and New Guinea, women use mosses to decorate ceremonial masks and also to decorate headwear and clothing (Tan, 2003). In some parts of Germany, "wool was woven with *Sphagnum* to make good, cheap cloth". Pant and Tiwari (1989) mentioned that "women in villages of Kumaun, India, stuff mosses (*Hylocomium, Hypnum, Trachypodopsis*) into cloth sacks to make head cushions". Such cushions also absorb leaking water as they carry vessels.

BRYOPHYTES USED FOR CULTURING 32.12

Bryophytes, specially mosses, are particularly useful for special purposes, such as culturing or growing of ferns (e.g. the moss *Octoblepharum albidum*) and orchids (e.g. species of *Hypnum, Leucobryum, Rhytidiopsis*). Tan (2003) has mentioned that in Manila, "*Leucobryum* is substituted for peat moss and induces good root sprouts on orchid cuttings". *Sphagnum* has now proved to be an essential requirement in the technique of air-layering. According to Pant (1989) *Begonia* and *Fuchsia* produce "buds and flowers more profusely if their pot has a layer of moss to separate the humus-rich top and the bottom soil".

BRYOPHYTES AS SEED BEDS 32.13

Some bryophytes, specially mosses, are used as **seed beds**. According to Cox and Westing (1963), "*Sphagnum* extracts induce germination of jackpine (*Pinus banksiana*) seeds, and aqueous extracts of *Polytrichum commune* and *Sphagnum* spp. stimulate growth of *Larix* seedlings". Mosses actually provide the necessary humidity for germination. It has been proved by Equihua and Usher (1993) "that *Calluna vulgaris* grew better and produced more flowers when it occurred in moss beds".

MOSS GARDENS 32.14

In Japan, Great Britain, United States and some other developed countries, mosses are used to create feelings of calmness, quietness or peace in gardens. These gardens are called **moss gardens**. Moss gardens provide an uncluttered look of shades of green. In Japan, moss gardens are often associated with Buddhist temples. One such temple, namely Kyoto's Kokedera in Japan, is commonly called the **moss temple**. Two most commonly used taxa for moss gardens belong to species of *Pogonatum* and *Polytrichum*. Some other species grown in moss gardens are *Dicranum scoparium, Leucobryum bowringii, Rhizogonium dozyanum* and *Trachycystis microphylla*. When fully grown, these mosses provide looks of mounds or cushions, and look like miniature hills bearing rolling landscape. A well-developed moss garden is at Chatsworth, Great Britain, where as many as 33 mosses and 4 liverwort species have been grown to provide a calm, beautiful and peaceful atmosphere. Some beautiful mosses grown in this garden are *Dicranum scoparium, Hylocomium splendens, Neckera crispa, Polytrichum commune* and *Rhizomnium punctatum*. Ando (1972) has mentioned that a moss garden in the home of famous poet William Wordsworth has cushions of *Polytrichum commune*. In spite of beautiful looks, a moss garden is still an effort of wealthy people to increase the charm of their properties.

BRYOPHYTES AND GENETIC ENGINEERING 32.15

Much work has not been done so far on genetic engineering of bryophytes. Through the application of the techniques of genetic engineering, however, bryophytes in the modern era are likely to be a substantial source of human medicines, and provide a gene bank for making proteins, sugars, enzymes or fatty acids. These techniques may also be soon helpful in permitting crop plants to survive cold, drought, or infestations. With the genetic engineering techniques used for mosses, it is now at least theoretically possible to manipulate the genomes of plants to endow them with the desirable traits for human use. According to Hoffman (1992), some specific characteristics of bryophytes (e.g. their ability to survive drought, and their ability to become functional within 24 hours) have aroused the imagination of agriculturists from the point of view of genetic engineering.

Scott and Oliver (1994) have "isolated several genes specific for the recovery of desiccated gametophytes of mosses". Hohe et al. (2002) have used "the tiny moss (*Physcomitrella patens*) to produce human proteins". *P. patens* and some other mosses "have a high frequency of homologous recombination". It is the only bryophytic plant being used to produce the blood-clotting factor IX for pharmaceutical purposes. Most mosses require no antibiotics during culture, and therefore, the

contamination of the final product can be avoided. The small size of *Physcomitrella patens* allows lab culturing, thus reducing the possibility of escape of transgenetic plants.

TEST YOUR UNDERSTANDING

1. Write a detailed essay on economic uses of bryophytes.
2. Bryophytes are now proving to be of definite medicinal uses for mankind. Comment in about 500 words.
3. Make a list of ten bryophytes of medicinal value for us.
4. *Sphagnum* is of great importance for us. Comment in about 300 words.
5. Write a note on antibiotics from bryophytes.
6. Bryophytes have some proven anti-cancerous properties. Comment.
7. Write short scientific notes on:
   (a) Bryophytes as source of food,
   (b) Horticultural uses of bryophytes.
8. Which moss is a proven bryophyte of the moss industry?
9. Bryophytes are now widely used as source of fuel and pesticides. Elaborate this statement.
10. What are moss gardens?
11. Two most commonly used bryophytic taxa for moss gardens belong to *Pogonatum* and _____.
12. Write a note on bryophytes and genetic engineering.

Appendix I

Answers to TEST YOUR UNDERSTANDING

Chapter 1

1. Braun (1864) 2. mosses 3. bryophytes 5. Bryophyta
6. No 10. Yes 12. flask

Chapter 2

2. Rothmaler (1951)

Chapter 3

1. Liverworts 3. Marchantiopsida 8. Only one (*Takakia*) 16. *Haplomitrium*

Chapter 4

1. Jungermanniales 3. only smooth-walled 4. Absent
5. Jungermanniales Anacrogynae 6. Jungermannineae 7. Metzgerineae
9. Jungermannineae 10. Madothecaceae 19. *Jubula* 27. endothecial
29. *Cryptothallus*

Chapter 5

1. *Geothallus* 2. Bottle hepatics 7. Aquatic 8. endothecial
9. very small

Chapter 6

2. Marchantiales 3. Schuster (1963) 4. Only one genus, namely *Monoclea*
6. Giant thallose-liverworts 8. Absent

Chapter 7

2. Chambered hepatics 3. *Riccia* 6. scales 7. tuberculate
8. not 9. dorsal 10. one 11. absent
13. *Oxymitra* 15. *Riccia fluitans* 16. terrestrial 23. Two
25. flask 29. *Marchantia polymorpha* 35. barrel
41. seta

Chapter 8

2. Proskauer (1957) 3. Horned liverworts 5. No 6. Absent
7. pyrenoid 8. intercalary meristem 9. amphithecial 10. Notothylaceae
11. *Megaceros* 16. *Anthoceros* 18. (c) 22. Embedded

Chapter 9

2. mosses 4. No 5. protonema 6. pleurocarpous
8. columella 9. absent 11. bog mosses 12. Andreaeales
15. No

Chapter 10

2. Sphagnales 3. *Sphagnum* 5. Only one, i.e. *Sphagnum*
6. perennial 17. amphithecial 22. Members of Andreaeales
25. *Andreaea* 26. Absent 27. Pseudopodium
29. Bryales 31. *Funaria hygrometrica* 32. No
39. microscopic 40. Four 41. Four-toothed moss 43. *Archidium*

Chapter 11

3. haploid 4. gametophyte 5. sporophyte, spores 6. *Zoopsis argentea*
7. foliose

Chapter 12

4. diploid 5. spores 6. foot 8. *Riccia*
10. capsule

Chapter 13

2. spermatophytes, sporophyte 3. meiosis 4. gametophytic
5. haploid 6. spore 8. homosporous 10. (a)

Chapter 14

5. day-neutral bryophytes 6. True 8. neutral

Chapter 15

4. heteromorphic 5. archegonia, bryophytes 7. W Hofmeister (1851)
10. Farlow (1874) 11. Pringsheim (1876) 13. Celakovsky (1874) 15. W H Lang (1909)

Chapter 16

2. phylogeny 3. genome 4. bryophytes 5. two
7. Anthocerotopsida 8. cladistics 10. (b) 11. Marchantiophyta

Chapter 17

6. Yes 7. phytochrome 8. metabolism 9. senescence
10. napthaline acetic acid, Trichlorophenoxy-acetic acid

Chapter 18

3. tuber 4. plural

Chapter 19

1. archesporium 6. *Pellia* 7. *Riccardia*
8. amphithecium, endothecium 10. endothecial 11. amphithecial

Chapter 20

2. apogamy, apospory 4. Yes 10. Pringsheim (1876)

Chapter 21

3. ectohydric 4. *Funaria hygrometrica* 6. *Ephemeropsis* 8. *Frullania*

Chapter 22

4. *Marchantia polymorpha* 5. *Marchantia polymorpha* and *Sphagnum*

Chapter 23

3. Yes 7. bryometer

Chapter 24

3. Over 400 7. *Marchantia polymorpha* (Compound: marchantin-A)
8. *Reboulia hemisphaerica*

Chapter 25

9. Ribulose 1, 5-biphosphate carboxylase oxygenase

Chapter 26

3. S R Kashyap and P N Mehra

Chapter 27

2. Zygote 3. independent 4. gametophyte 5. spores
8. *Riccia* 9. *Funaria* 12. Reduction theory

Chapter 28

4. *Leucobryum glaucum* 5. external conduction
8. (d) 10. (d) 11. Polytrichales 13. food

Chapter 29

2. (b) 3. fresh 12. heteropycnotic 13. dioecious
17. allopolyploid, allopolyploidy

Chapter 30

2. autecology 6. habitat

Chapter 31

5. Psilophytales 8. All of these 15. fossil mosses

Chapter 32

8. *Sphagnum* 11. *Polytrichum*

Appendix II

Comparative Tables Related to Bryophyta

Tables Already Discussed in the Text

1. Differences between algae and bryophytes (See Table 1.1; Chapter 1; Article 1.16.1, a)
2. Differences between bryophytes and pteridophytes (See Table 1.2; Chapter 1.; Article 1.16.2, b)
3. Differences between Hepaticopsida, Anthoceropsida and Bryopsida (See Table 2.1; Chapter 2; Article 2.2)
4. Comparison of sporogonium of *Riccia* and *Marchantia* (see Table 7.1; Chapter 7; Article 7.8)
5. Differences between Anthocerotopsida and Hepaticopsida (See Table 8.1; Chapter 8; Article 8.11)
6. Differences between Hepaticopsida and Bryopsida (See Table 12.1; Chapter 12; Article 12.4.2)
7. Approximate number of spores per plant in some bryophytes (See Table 12.2; Chapter 12; Article 12.5.4)
8. Origin, position and fate of archesporium in some common genera of bryophytes (See Table 19.1; Chapter 19; Article 19.4)
9. Growth-forms classification for tropical forest bryophytes as proposed by Richards (1983) (See Table 21.1; Chapter 21; Article 21.2)
10. Biological activity and effects of some liverworts and mosses of medicinal importance (See Table 24.1; Chapter 24; Article 24.2).

Table A.1 *Comparison of external features of gametophyte of* ***Riccia, Marchantia, Pellia, Porella, Anthoceros, Sphagnum, Polytrichum and Funaria***

S. No.	Character	Riccia	Marchantia	Pellia	Porella	Anthoceros	Sphagnum	Polytrichum	Funaria
1.	Plant form	Thalloid, prostrate, dorsiventrally flattened, with a distinct midrib; each lobe of thallus has an apical notch at the distal end, which contains growing point of the thallus.	Thalloid, prostrate, flat, dorsiventral, with a distinct midrib; thalli larger than *Riccia*; an apical notch is also present as in *Riccia*.	Thalloid, prostrate, flat and dorsiventral; thalli with sinuous overlapping margins; larger than *Riccia* but smaller than *Marchantia*; thinner than *Riccia* and *Marchantia*; with a distinct midrib.	Plant body is prostrate, flat, dorsiventral; contains a central branched axis with two dorsal and one ventral rows of leaves.	Thalloid, prostrate, dorsiventrally flat and irregularly lobed; midrib is not distinct.	Plant body has an erect and radially symmetrical gametophore which contains many green and sessile leaves.	Gametophores are differentiated into underground rhizome and many radially symmetrical aerial, erect branches containing leaves.	Plant body is foliose; gametophore is differentiated into well-branched rhizoids, erect axis or stem and many leaves
2.	Branching	Dichotomously branched.	Same as in *Riccia*.	Same as in *Riccia*.	Monopodial.	Dichotomously branched, but thallus becomes irregular due to unequal growth.	Branches develop from the axil of every fourth leaf; all branches are alike in aquatic species, but in semi-aquatic species the branches are of two types i.e. pendent branches and divergent branches.	Branching is lateral; branches are not axillary.	Same as in *Polytrichum*.
3.	Rhizoids	• Unicellular and unbranched • Present on ventral surface in the midrib region. • Two types, i.e. smoothwalled and tuberculate.	• Same as in *Riccia* • Same as in *Riccia* • Same as in *Riccia*	• Same as in *Riccia* • Same as in *Riccia* • Only of one type, i.e. smoothwalled; tuberculate rhizoids are absent	• Same as in *Riccia* • Same as in *Riccia* • Same as in *Pellia*	• Same as in *Riccia* • Same as in *Riccia* • Same as in *Pellia*	• Multicellular with oblique septa • Present only on young gametophores • All are of only one type.	• Long, branched multicellular, usually coiled to form rope-like structure • Present on underground rhizome • All are of the same type.	• Long, well-branched, multicellular with oblique septa • Present only at the base of the gametophore • All are of the same type.
4.	Scales	Multicellular, present in a single row along the margins of the thallus; all are of only one type.	Multicellular, present in 2-3 rows on either side of midrib on the ventral surface; of two types, i.e. ligulate and appendiculate	Absent	Absent	Absent	Absent	Absent	Absent

Contd...

S. No.	Character	Riccia	Marchantia	Pellia	Porella	Anthoceros	Sphagnum	Polytrichum	Funaria
5.	Leaves	Absent	Absent	Absent	Arranged in 3 rows, i.e. 2 dorsal or lateral rows and one ventral row; leaves lack midrib; they are unequally lobed.	Absent	Thin, sessile, small-sized leaves present in 3 vertical rows on the axis in 2/5 type of phyllotaxy; midrib absent in mature leaves.	Leaves develop on underground rhizome and also on aerial parts; on rhizome they show 1/3 type of phyllotaxy but on aerial branches leaves are larger and show 3/8 type of phyllotaxy; midrib present.	Leaves are sessile, simple, spirally arranged on the axis and exhibit 3/8 type of phyllotaxy; each leaf possesses a clear midrib.

Table A.2 *Comparison of the internal structure (anatomy) of the gametophyte of* ***Riccia, Marchantia, Pellia*** *and* ***Anthoceros***

S.No.	Character	Riccia	Marchantia	Pellia	Anthoceros
1.	Differentiation	Thallus is differentiated internally into • upper photosynthetic region, and • lower storage region	Same as in *Riccia*	Thallus is undifferentiated, i.e. homogeneous	Same as in *Pellia*
2.	Upper epidermis	Not well-defined, but the terminal or outermost cells of the upper photosynthetic region function as epidermis.	Well-defined; wall of the upper epidermal cells appear comparatively thick.	Not well-defined	Same as in *Pellia*
3.	Air pores	Not well-defined, but continuity of epidermis is broken by some porelike structures, which are the outer openings of the air spaces present between photosynthetic filaments.	Well-developed, barrel-shaped air pores, made up of 4-8 superimposed tiers of cells; each tier has 4-5 cells; air pores remain projected partly above the thallus surface.	Absent	Absent
4.	Photosynthetic region	Made up of vertical columns of chlorophyll-containing green cells; chloroplasts in these cells are discoid.	Made up of many chambers; each chamber contains some unbranched or branched photosynthetic filaments.	Some dorsal cells of the middle region, and also some cells of wings are green and represent photosynthetic region.	All cells of the gametophyte contain chloroplasts and are, therefore, photosynthetic.
5.	Pyrenoids	Absent	Absent	Absent	Each cell has a large chloroplast with a single pyrenoid.
6.	Air chamber	Present in between the photosynthetic filaments.	Many air chambers, arranged in a single row, just below the upper epidermis; a single-layered partition wall separates them from each other.	Absent	Absent
7.	Storage region	Ventral part of thallus is the storage region; made up of parenchymatous cells.	Same as in *Riccia*; some mucilage cells are also present.	All cells of thallus form storage region.	Same as in *Pellia*; some mucilaginous cavities are present in the ventral region.
8.	Lower epidermis	Possess smooth-walled and tuberculate rhizoids.	Same as in *Riccia*; also possess scales.	Possess smooth-walled rhizoids.	Same as in *Pellia*.

Table A.3 *Comparison of male sex organs/antheridia of* ***Riccia, Marchantia, Pellia, Porella, Anthoceros, Sphagnum, Polytrichum*** *and* ***Funaria***

S. No.	*Character*	*Riccia*	*Marchantia*	*Pellia*	*Porella*	*Anthoceros*	*Sphagnum*	*Polytrichum*	*Funaria*
1.	Differentiation of sex in species	Mostly monoecious; only a few dioecious.	Mostly dioecious; only a few monoecious.	Both monoecious as well as dioecious.	Mostly dioecious.	Both monoecious as well as dioecious.	Same as in *Anthoceros*.	Dioecious.	Monoecious but autoecious.
2.	Position of antheridium	Situated in the antheridial chamber, which remains embedded in the dorsal surface of thallus.	Present on the lobes of peltate disc of the antheridiophore.	Present on the dorsal surface of the thallus on either side of midrib, embedded in the antheridial chamber.	Develop on some specialised antheridial branches in the axil of leaf.	Present in the antheridial chambers covered by roof on the dorsal surface of thallus.	Present singly in the axil of each leaf of specialised male or antheridial branches.	Present in groups at the base of each perichaetial leaf at the apices of male gametophore.	Situated in clusters at the apices of antheridial branches, enclosed by a group of leaves.
3.	Number of antheridia in each antheridial chamber	One antheridium in each antheridial chamber.	Same as in *Riccia*.	Same is in *Riccia*.	Only one antheridum in the axil of each leaf of antheridial branche.	One to four or even more antheridia in each antheridial cavity.	One in the axil of each leaf of the antheridial branch.	Many antheridia develop in groups at the tip of the male gametophore.	Develop in groups at the terminal part of gametophore.
4.	Structure	Shortly-stalked, globose or club-shaped body, covered by a single-layered jacket.	Stalked, oval or conical in shape; jacket single-layered.	Same as in *Riccia*; shape somewhat spherical.	Stalk very long; body spherical; antheridial jacket 2-3 layered in the basal part.	Stalk multicellular, body club-shaped; jacked single-layered throughout.	Stalk very long; present in the axil of leaf; jacket single-layered.	Stalked, club-shaped; jacket of cells surround mass of androgonial cells.	Massive stalk, club-shaped body; single-layered jacket; an operculum is present at the apex of jacket.
5.	Antherozoids	Unicellular, uninucleate, curved and biflagellate.	Same as in *Riccia*.	Spirally coiled, biflagellate.	Rod-shaped, biflagellate.	Same as in *Riccia*.	Spirally coiled with a terminal flagellophore, bearing two flagella.	Spirally coiled, uninucleate, and biflagellate.	Same as in *Polytrichum*.

Table A.4 *Comparison of female sex organs/archegonia of* ***Riccia, Marchantia, Pellia, Porella, Anthoceros, Sphagnum, Polytrichum*** *and* ***Funaria***

S. No.	*Character*	*Riccia*	*Marchantia*	*Pellia*	*Porella*	*Anthoceros*	*Sphagnum*	*Polytrichum*	*Funaria*
1.	Position of archegonium	Develop in archegonial chambers, embedded on the dorsal surface of thallus.	Develop on the dorsal surface of the disc present on the top of archegoniophore.	Develop in groups of 4-10 on the dorsal surface of thallus on either side of midrib.	Develop at the apex of archegonial branch in large number between the leaves.	Archegonia are embedded on the dorsal surface of the thallus with only their cover cells projecting beyond the surface.	Develop at the apex of the archegonial branches in between perichaetial leaves, usually in groups of 2-5; position is acrogynous.	Develop at the apex of archegonial head on a female plant; surrounded by coloured perichaetial leaves; appear like a small flower.	Situated at the apices of female branches inside the cluster of leaves; intermingled with paraphyses.
2.	Structure	Flask-shaped structure; shortly stalked; with a broad venter and long neck, venter wall is one-celled; neck consists of 6 vertical rows of cells, 6-9 cells in height and possesses 4 neck canal cells and 4 cover cells; venter contains a ventral canal cell and an egg.	Same as of *Riccia*; neck has 4-8 neck canal cells surrounded by 6 vertical rows of jacket cells; cover cells are indistinct.	Flask-shaped as in *Riccia*; jacket of neck consists of 5 vertical rows of cells and encloses 6-8 neck canal cells; venter is two-layer thick; cover cells are 4 but indistinct.	Same as of *Pellia*; neck is broad and consists of 5 vertical rows of cells and encloses 6-8 neck canal cells.	Embedded in the thallus and are in direct contact with the vegetative cells; neck canal cells are 4 in number; cover cells are also 4.	Flask-shaped, stalked structure with a broad venter and long twisted neck; venter as well as lower portion of neck are 2-4 cells in thickness; neck canal cells are 8-9 in number; cover cells indistinct.	Flask-shaped, stalked and greatly elongated; venter is many-celled thick; neck consists of 6 vertical rows of cells; large number of neck canal cells are present; a single cover cell is present at the top.	Flask-shaped with a multicellular massive stalk, a broad venter and narrow twisted neck; wall of venter is double-layered; 6 or more neck canal cells.

Table A.5 *Comparison of the sporophyte of* ***Riccia, Marchantia, Pellia, Porella, Anthoceros, Sphagnum, Polytrichum*** *and* ***Funaria***

S. No.	Character	Riccia	Marchantia	Pellia	Porella	Anthoceros	Sphagnum	Polytrichum	Funaria
1.	Parts of the sporophyte and its position	Only capsule embedded in the thallus; foot and seta absent.	Foot, seta and capsule; capsules are seen in a disc of mature archegoniophore, on the lower side.	Foot, seta and capsule; horizontally placed on the thallus.	Foot, seta and capsule; present on the specialised archegonial branches of female plants.	Foot, meristematic zone and capsule; develop on the dorsal surface of thallus; a distinct seta is absent.	Foot and capsule; seta is very small neck like suppressed tissue; present at the apices of short, bud-like female branches.	Foot, seta and capsule; present at the apex of female gametophore; seta is very long.	Foot, seta and capsule; develop at the apex of archegonial branches.
2.	Protective coverings	A double-layered calyptra around the young sporophyte.	Calyptra, perigynium and perichaetium.	Double-layered calyptra;	Calyptra, perianth and involucre (formed by bracts of female branches).	Calyptra, also known as involucre.	Calyptra and perichaetium; pseudopodium develops in mature sporophytes; calyptra and distal end of pseudopodium form a saclike veginula.	Calyptra surrounds the young capsule completely; at maturity the calyptra covers only apical part of capsule.	Calyptra, which is shed at maturity.
3.	Foot	Absent	Basal, bulbous part which anchors the sporophyte to the disc of archegoniophore.	Conical, parenchymatous, extends like a collar around the base of seta.	Indistinct foot; globose in young sporophyte	Bulbous, well-developed, parenchymatous,	Well-developed, massive and bulbous; haustorial in function.	Dagger-shaped, parenchymatous.	Small, conical, dagger-shaped structure.
4.	Seta	Absent.	Present; short, stout, and connects foot to the capsule; parenchymatous but its cells become highly vacuolated when mature.	Present; contains abundant starch when young.	Same as in *Pellia.*	Absent; the meristematic tissue, present in between foot and capsule, functions as seta.	Absent; a narrow, non-meristematic, necklike part, however, is present in between foot and capsule.	Very long, slender reaching up to 5 cm or more in length; differentiated internally into an epidermis, sclerenchymatous hypodermis, parenchymatous cortex and a central cylinder composed of hydroid cells.	Long, slender, twisted, and differentiated into epidermis, cortex and central conducting strand.
5.	**Capsule** (i) Shape	Globose, embedded in the thallus.	Oval.	Same as in *Marchantia.*	Oval	Horn-like	Globose.	Polygonal.	Obique or asymmetrical; pear-shaped; curved.

Contd...

S. No.	Character	Riccia	Marchantia	Pellia	Porella	Anthoceros	Sphagnum	Polytrichum	Funaria
	(ii) *Wall*	Single-layered, which also disorganises soon.	Single-layered capsule wall; persistent.	Capsule wall composed of 2 to 3 layers; persistent.	Capsule wall consists of 2 to 6 cells in thickness.	Capsule wall is 4-6 layered, of which the outermost layer forms epidermis, ventilated with stomata; cells of inner wall layers contain chloroplasts.	Capsule jacket consists of 4-6 layers, of which the outermost layer is an epidermis containing rudimentary stomata.	Capsule wall is several-layered; all cells of wall layers contain chloroplasts.	Wall many-layered; 2-3 inner wall layers are green and contain intercellular spaces; 2-3 outer layers beneath the epidermis are parenchymatous.
	(iii) *Archesporium*	Originates from endothecium; elaters absent.	Same as in *Riccia*; elaters present.	Same as in *Marchantia*.	Same as in *Marchantia.*	Develops from the inner layer of amphithecium; pseudoelaters present.	Develops from inner layer of amphithecium.	Develops from the outer layer of endothecium.	Same as in *Polytrichum.*
	(iv) *Elaterophore*	Absent	Absent	Present	Absent	Absent	Absent	Absent	Absent
	(v) *Columella*	Absent	Absent	Absent	Absent	Present	Present	Present	Present
	(iv) *Operculum*	Absent	Absent	Absent	Absent	Absent	Present	Present	Present
	(vii) *Annulus*	Absent	Absent	Absent	Absent	Absent	Present	Present	Present
	(viii) *Peristome*	Absent	Absent	Absent	Absent	Absent	Absent	Present	Present
6.	*Dehiscence of capsule*	Spores liberate after death and decay of thallus without any special mechanism.	Wall of the capsule splits longitudinally into several valves; spore dispersal is facilitated also by the hygroscopic nature of elaters.	Wall of the capsule splits longitudinally into 4 valves; elaters also help in spore dispersal.	Same as in *Pellia.*	Capsule dehisces by longitudinal splitting of its walls into 1-4 valves; dispersal is facilitated also by elaters, columella and valves of the capsule.	Operculum separates and spores are dispersed by special explosive mechanism.	Capsule dehisces and spores are dispersed by Censor mechanism with the help of epiphragm and peristomial teeth.	Operculum separates and capsule dehisces due to the hygroscopic movement of peristomial teeth.

Appendix III

Glossary of Bryophytic Terms

Abaxial	On the underside of a leaf, that is, pointing away from the stem
Acrocarpous	Mosses, which have an upright stem, with the sex organs at the apex
Acrogynous	Possessing the stem terminated by archegonia
Acropetal	Development of organs successively towards the apex, i.e. the oldest at the base and youngest nearest to the apex
Acuminate	Possessing a gradually diminishing point
Adaxial	On the top side of the leaf, that is, pointing towards the stem
Adnate	United with another organ
Adventitious	Produced abnormally
Alternation of generations	The life cycle of bryophytes, pteridophytes, and spermatophytes, which consists of a haploid gametophyte producing gametes followed by a diploid sporophyte, producing spores
Alveolate	Possessing cavities on the surface, generally of the spores
Amphithecium	Outer layer of a developing sporophyte of a bryophyte
Anacrogynous	Stem not being terminated by archegonia and continuing to grow
Androcyte	Antherozoid mother cell; actually the cell which later develops into antherozoid
Androgonial cell	Any cell within an antheridium other than androcyte mother cell or androcyte
Annular	Like a ring
Antheridium	The male sex organs of the cryptogams
Antherozoid (spermatozoid)	Unicellular, small, motile male gamete bearing flagella
Antical	Upper surface, usually of stem or leaf
Anticlinal	A division perpendicular to the surface

Apogamy	Asexual reproduction in which embryos and propagules are produced without the occurrence of meiosis
Apophysis	The sterile tissue at the basal part of the capsule of some mosses, present immediately at the tip of seta and below the spore sac
Apospory	Formation of a diploid gametophyte from the vegetative cells of the sporophyte, that is, without the production of spores
Appressed	Lying flat for the whole length of the organ
Archegoniatae	Plants having archegonia
Archegonium	The flask-shaped, female organ of bryophytes, pteridophytes and gymnosperms; usually consists of a hollow neck, and a swollen base containing the egg
Archesporium	The first cell generation of sporogenous tissue, from which the spores of sporogonium are ultimately derived
Areolate	Small spaces marked on the surface, usually of spores
Autoecious	Possessing male and female organs on the same plant but on separate branches
Autotrophic	Able to synthesize food from simple chemical compounds, using energy from light or chemical reactions
Basipetal	Such a development of organs in which the youngest structures are at the base and oldest at the apex
Biseriate	In two rows
Bisexual	Organisms with male and female reproductive organs on the same individual
Blepharoplast	A cylindrical structure found at the base of cilia composed of nine sets of triplet microtubules
Caducous	Falling off early
Calyptra	A protective covering around the young capsule derived from the archegonium
Capillary	Hairlike
Capsule	Part of the sporogonium that contains spores
Carpocephalum	Female receptacle
Chlorophyll	Green colouring matter of plants
Chlorophyllous	Containing chlorophyll
Chloroplasts	Granules containing chlorophyll
Ciliate	Fringed with hairs
Clavate	Club-shaped
Columella	Central column of sterile cells in a capsule

Compressed	Flattened out
Cryptogams	A general name for all plants except gymnosperms and angiosperms; cryptogams reproduce by spores
Costa	Midrib of the thallus
Deciduous	Falling off
Dehisce	To split open
Dichotomous	Dividing equally into two, especially of branches
Dimorphic	An organism with two different forms
Dioecious	With antheridia and archegonia on different plants
Diploid	Of cells with two sets of chromosomes in their nuclei; the sets are set to be homologous
Diploid generation	The sporophyte
Distichous	Disposed in two rows
Divergent	Spreading apart
Dorsal	The surface of the leaf, away from the stem; the upper surface of a thallus
Dorsiventral	With dorsal and ventral surfaces
Egg	A female gamete
Elaters	Bunch of long, thin cells in the capsule of the sporophyte of a liverwort; have spiral thickening of the cell wall; alter their position with changes in humidity, and help in dispersal of spores
Embryo	The young plant developed within the archegonium; the product of the repeated mitotic divisions of the zygote
Embryophyta	A group that includes bryophytes, pteridophytes and spermatophytes
Endemic	Of taxa that are found only in one particular place or area
Endogenous	Arising from deep-seated tissue
Endothecium	The inner tissues in the young sporophyte of bryophytes, giving rise to the sporogenous tissue and/or the columella
Epibasal	Forming the upper part of the embryo
Epiphragm	A membrane which closes the opening of theca in the sporophyte of some mosses, e.g. *Polytrichum*
Epiphyllous	Developing on leaves
Exogenous	Arising from the superficial tissue
Exotic	Non-native
Extant	Species which exist at present
Extinct	Species which no longer exist
Fertilization	Fusion of a male gamete with a female gamete to form a zygote

Filiform	Threadlike
Fimbriate	Fringed
Flagellum	A fine thread-like branchlet; a long motile thread, consisting of a membrane enclosing a series of parallel microtubules
Foliar	Belonging to a leaf
Foliose	With leaves
Foot	An organ of attachment and nutrition; the lowest part of the sporophyte
Fossil	The remains or marks left by dead organisms, converted to stone over geological time
Frond	The leaf of a fern or palm
Fusiform	Tapering at both ends like a spindle
Gametangium	Any organ which produces gametes
Gamete	A haploid sex cell whose function is to join with a gamete of the opposite sex, to form a diploid zygote
Gametophyte	The haploid generation in an alternation of generations; in bryophytes, the gametophyte is the main vegetative stage; the gametophyte is the generation producing gametes
Gemmae	Small groups of green cells produced in the cup-shaped structures on the surface of thalloid liverworts
Gemmiferous	Bearing gemmae
Generation	A set of individuals of roughly equal age or stage of development; the parents are one generation, and the progeny represents the next generation
Granulose	Composed of grains
Habit	The appearance of a plant, e.g. herb, shrub or tree
Habitat	The place or kind of place in which an organism, community or association is found
Haploid	The cells with one set of chromosomes in their nuclei
Haploid generation	The gametophytic generation
Hepatic	A liverwort
Heteromorphic	A condition in which two phases of the life-cycle are morphologically dissimilar
Heterosporous	Producing two kinds of spores, usually of different sizes
Homologous	Of two similar chromosomes which pair with each other during meiosis
Hyaline	Transparent, or without colour
Hygrophyllous	Plants which require a large supply of moisture for their growth and development
Hypobasal	Forming the lower part of the embryo

Hypogynous	Inserted below the archegonium
IAA	Indole acetic acid, the most common auxin
Incised	Cut sharply
Incubous	Of a kind of growth in leafy liverworts, in which the front of each leaf lies on top of the leaf in front of it
Innovation	A newly-formed shoot which continues growth at the death of the older stem
Intine	The inner coat of the wall of a spore
Involucre	A tubular structure serving to protect the archegonia and calyptra
Involute	Having the edges rolled inwards
Juvenile	Very early forms
Karyogamy	Fusion of two nuclei after plasmogamy
Keel	A ridge-like the keel of a boat
Lacerate	Irregularly torn or cleft
Lacuna	A space, particularly in between the tissues
Lamella	A plate of tissue
Lamina	The parts of the leaf on either side of the midrib
Leafy liverwort	A liverwort in which the gametophyte has a simple stem, growing from the apex and bearing small leaves in rows along it
Lenticular	Like a double convex lens
Lignified	Woody
Liverwort	A group of bryophytes, which differ from mosses in having less differentiated cells in the gametophyte, and in usually having elaters in the capsule
Lumen	The cavity inside a cell
Lysigenous	A cavity developed by the disintegration and dissolution of cells
Marsupium	The fruiting receptacle of certain liverworts
Medulla	The parenchyma or sclerenchyma inside the vascular strands
Meiosis	The cell division that produces haploid sex cells from diploid cells; also called reduction division
Meristem	Any tissue of actively dividing cells, which produce the cells of the other plant tissues
Micron	A measure of length equal to one millionth of a metre (or 1/1000 millimetre); symbol μ
Midrib	The costa (thallus); vein of the leaf
Mitosis	Vegetative or somatic cell division in which chromosomes in the nucleus are duplicated into two chromatids

Monoecious	A condition when antheridia and archegonia develop on the same plant
Morphogenesis	The development of shape and structure of organs and tissues
Moss	One of the three main groups of bryophytes; mosses differ from liverworts in having more differentiated cells in the gametophyte; the gametophyte of a moss usually possesses stem with leaves
Multifid	Divided into many lobes
Neck	The upper part of the archegonium
Neck canal cells	The cells present in the neck canal of an archegonium
Nodulose	Knotted, or thickened
Obcordate	Inversely heart-shaped
Ontogeny	The process of development of an individual from zygote to adult
Oogamous	Possessing a small motile male gamete and a large nonmotile female gamete, as in bryophytes and pteridophytes
Oogonium	A reproductive organ, which produces female gametes
Oosphere	The female gamete, produced in an oogonium
Oospore	A dormant, thick-walled zygote, formed after the fertilization of an oosphere
Operculum	A lid, which covers the pore at the apex of a moss capsule; the operculum opens to allow spores to escape
Ostiole	The tubular neck of the cavity containing antheridia
Palea	The chaff scales or ramenta of many ferns
Papillose	Covered with papillae
Paraphyllia	Very fine, minute leaflike appendages on the stem of mosses and some liverworts
Paraphyses	Small, one-cell-thick hairs, often with a large round cell at the top; grow among the antheridia in mosses
Paroicous	A condition in mosses when antheridia are present below the archegonia on the same branch or stem
Parthenogenesis	A condition in which an embryo develops from an unfertilized egg
Peat	A kind of litter layer found in some very wet or waterlogged habitats, such as bogs, which decomposes very slowly, often under very acidic conditions; peat layers may be as thick as several layers
Pedicel	A short stalk
Perianth	Inflated envelope surrounding the fertilized archegonium
Perichaetial	Leaves surrounding the archegonia
Perennation	The survival of an organism over successive years, or of a dormant organ during unfavourable seasons

Periclinal	A cell division, in which wall runs parallel to the surface of a plant organ
Perigonium	Some specialised bracts around the male flower or antheridia
Perigynium	An involucre of female inflorescence in some bryophytes
Peristome	A set of tooth-like plates under the operculum of the capsule of a moss; the plates are called *peristomial teeth*
Phloem	One of the conducting tissues in the vascular system; phloem, unlike xylem, is mainly a living tissue made up of sieve elements and companion cells
Phylogeny	The evolutionary history of an organism or taxonomic group of organisms
Pleurocarpous	Of mosses, which have a stem with many branches, spreading across the ground; sex organs are borne on short side branches
Postical	Belonging to lower surface of thallus, stem or leaf
Procumbent	Lying along the ground
Propagule	Any reproductive unit which gives rise to a new individual
Protandrous	When male sex organs are produced prior to the formation of female sex organs
Protonema	The young, often filamentous, gametophyte of a moss in the early stages after the germination of the spore
Pseudoelaters	Sterile cells mixed with spores in the capsule of *Anthoceros*
Pseudoperianth	A soft gametophytic sheath, which usually develops late and surrounds the young sporogonium in some bryophytes
Pyrenoid	A small grain of protein in the chloroplast of some plants, around which starch is deposited
Radial	Spreading from a common axis or centre
Receptacle	The top of the stalk bearing reproductive organs (antheridia or archegonia)
Regeneration	The growth of new tissue on a part of a plant that has been damaged; or, the growth of new plants from perennating organs, e.g. rhizome
Reniform	Kidney-shaped
Reproduction	The process in which an organism produces offspring like itself
Reticulate	Like a network
Retort cells	Specialised enlarged cortical cells of the young branches of some bryophytes, e.g. *Sphagnum*
Rhizoid	A thread-like cell which grows from the lower surface or base of a bryophyte, and functioning like a root
Rhizome	A stem which grows along under the ground, bearing buds which produce shoots; a root-like underground stem
Rosette	Structure in which leaves or young parts are arranged in a light spiral; or a pattern of organs like a rose

Saccate	Like a bag
Scale	A flat, thin, semitransparent plate of cells
Schizogenous	Internal spaces which are produced by separation of cells
Sclereid	Kind of cell found in the sclerenchyma of some plants, with heavily lignified walls
Serrate	Toothed like a saw
Sessile	Without a stalk
Seta	Stalk of the sporophyte of a bryophyte
Sinuate	Wavy
Somatic	Of any process or part of an organism that is not connected with sexual reproduction, e.g. mitosis is a somatic cell division
Sperm	Motile, flagellated, male sex cell
Spore	Small round cell with a thick wall from which a whole new plant is produced in bryophytes, pteridophytes and spermatophytes; spores are haploid and are produced by the sporophyte
Spore mother cell	A cell which divides by meiosis to produce spores
Sporogenous	A tissue in which spores are produced
Sporogonium	The spore-bearing generation developing from the fertilized egg; the sporophyte of bryophytes
Sporophyte	The non-sexual generation, or the part bearing spores; the diploid generation in an alternation of generations
Stellate	Star-shaped
Stylus	A small, awl-like lobule
Synoicous	A condition in mosses, when the archegonia and antheridia are mixed together in the same involucre
Taxon	Any taxonomic group, e.g. a species, a genus, a family
Terete	Cylindrical, not angular
Tetrad (Tetrahedral)	Spores remaining united in groups of four until mature
Thalloid (Thallose)	Possessing the form of a thallus
Thallus	More or less undifferentiated plant body, flat and broad like a frond, and without distinct roots, stems and leaves
Theca	Major part of capsule of mosses
Trigonous	Having three obtuse angles
Trilete	Bearing a triradiate tetrad scar
Tristichous	Arranged in three rows
Truncate	Cut abruptly

Tuber	An organ of perennation and vegetative reproduction, a tuber is a thick underground stem in which food remains stored; buds on the tuber grow into new plants
Turgor	The tension on a cell wall due to the pressure of water inside the cell
Vacuole	A liquid-filled space in a cell, surrounded by a membrane
Vascular cylinder	A tube of vascular tissue consisting of xylem and phloem
Variety	A taxonomic group within a species or a subspecies
Vegetative	Any part of a plant which is not involved in sexual reproduction
Vegetative reproduction	A type of asexual reproduction in which a whole new plant is produced from an organ, which is not involved in sexual reproduction
Vein	One of the many lines which can be seen on the surface of a leaf, marking the position of a vascular bundle
Venter	The lower part of the archegonium
Ventral	Pertaining to that surface of a flattened thalloid plant which faces the substrate
Ventral canal cell	A cell in the upper part of the venter of an archegonium and situated above the oosphere
Vermiform	Worm-shaped
Verrucose	Covered with wart-like protuberances
Vesicle	Any small body in a cell or organelle which is surrounded by a membrane and contains products of metabolism
Vestigial	A small or reduced structure
Wavelength	The length of a wave of light; different wavelengths have different colours and different levels of energy
Weed	A plant growing where it is not wanted by humans
Whiplash flagellum	A flagellum without hairs on its surface
Whorl	A group of three or more plant structures arising at the same level on a stem and forming a ring around it
Xeromorphic	Plants with characteristics suited to very dry habitats, such as deserts
Xerophyte	A plant that lives in a desert or other dry habitats
Xylem	A tissue in the vascular system of a plant, consisting of tracheids, vessels, parenchyma and sclerenchyma
Zoospore	A motile flagellated spore
Zygote	A diploid cell which is produced by the fusion of two haploid gametes
Zygotene	A stage in the first meiotic prophase, when the homologous chromosomes come together to form bivalents

Appendix IV
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