Unit - V

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Salient features of Bryophytes

1. Bryophytes grow in damp and shady places.

2. They follow heterologous haplodiplobiontic type of life cycle.

3. The dominant plant body is gametophyte on which sporophyte is semiparasitic for its nutrition.

4. The thalloid gametophyte differentiated in to rhizoids, axis (stem) and leaves.

5. Vascular tissues (xylem and phloem) absent.

6. The gametophyte bears multi-cellular and jacketed sex organs (antheridia and archegonia).

7. Sexual reproduction is oogamous type.

8. Multi-cellular embryo develops inside archegonium.

9. Sporophyte differentiated into foot, seta and capsule.

10. Capsule produces haploid meiospores of similar types (homosporous).

11. Spore germinates into juvenile gametophyte called protonema.

12. Progressive sterilization of sporogenous tissue noticed from lower to higher bryophytes.

13. Bryophytes are classified under three classes: Hepaticae (Liverworts), Anthocerotae (Hornworts) and Musci (Mosses).

Classification of Bryophytes:

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

1. Hepaticae (Hepaticopsida = Liverworts)

2. Anthocerotae (Anthocertopsida= Hornworts)

3. Musci (Bryopsida= Mosses)

Class 1. Hepaticae or Hepaticopsida:

1. Gametophytic plant body is either thalloid or foliose. If foliose, the lateral appendages (leaves) are without mid-rib. Always dorsiventral.

2. Rhizoids without septa.

3. Each cell in the thallus contains many chloroplasts; the chloroplasts are without pyrenoi.

4. Sex organs are embedded in the dorsal surface.

5. Sporophyte may be simple (e.g., Riccia) having only a capsule, or differentiated into root, seta and capsule (e.g., Marchantia, Pallia and Porella etc.)

6. Capsule lacks columella.

7. It has 4 orders:

(i) Calobryales

(ii) Jungermanniales

(iii) Spherocarpales

(iv) Marchantiales.

Class 2. Anthocerotae or Anthocerotopsida

1. Gametophytic plant body is simple, thalloid; thallus dorsiventra without air cambers, shows no internal differentiation of tissues.

2. Scales are absent in the thallus.

3. Each cell of the thallus possesses a single large chloroplast with a pyrenoid.

4. Sporophyte is cylindrical only partly dependent upon gametophyte for its nourishment. It is differentiated into bulbous foot and cylindrical capsule. Seta is meristematic.

5. Endothecium forms the sterile central column (i.e., columella) in the capsule (i.e. columella is present). 6. It has only one order-Anthocerotales.

Class 3. Musci or Bryopsida:

1. Gametophyte is differentiated into prostrate protonema and an erect gametophores

2. Gametophore is foliose, differentiated into an axis (=stem) and lateral appendages like leaves but without midrib.

3. Rhizoids multi-cellular with oblique septa.

4. Elaters are absent in the capsule of sporangium.

5. The sex organs are produced in separate branches immersed in a group of leaves.

6. It has only three orders:

(i) Bryales,

(ii) Andriales and

(iii) Sphagnales.

Economic importance of Bryophytes

1. Protection from soil erosion:

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

2. Soil formation:

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

3. Water retention:

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

4. Peat:

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

5. As food:

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

6. Medicinal uses:

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

7. Other uses:

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

Origin of Bryophytes

The bryophytes are quite soft and delicate and, therefore, they lack fossil records. There are no known fossil bryophytes more primitive than the forms of to-day. However, there are two schools of thought about their origin.

According to one school of thought they are evolved from the green Thallophyta the algae; and according to the other school they have been descended from the pteridophytes. Majority of the workers support their origin from the algal ancestors.

Origin from algae:

This view of the origin of bryophytes has been supported by most of the bryologists. Though there is no fossil connection between algae and bryophytes yet there are so many points in support of this view, such as-the necessity of water for the act of fertilization; their amphibian nature and the presence of ciliated antherozoids.

These points support the view that they have been originated from aquatic ancestors. Lignier in 1903, pointed out that the algae gave rise to a connecting link known as 'prohepa tics' and thereafter bryophytes originated from this connecting link on one hand and the pteridophytes on the other.

Bower (1908) also supported this view and said that the Archegoniatae have been evolved from the aquatic ancestors, i.e., the algae. The bryophytes resemble in many respects the green algae, i.e., Chlorophyceae, and Fritsch (1916, 1945) has advocated that the Chaetophorales gave rise to the bryophytes.

There seems no apparent relation between the antheridium and the archegonium of the bryophytes and the antheridium and the oogonium of the algae. In none of the algae the egg is surrounded by any cellular jacket as it is always enclosed within a protective layer (jacket layer) in the case of bryophytes.

According to many workers the sex organs of the bryophytes have been evolved from those of the algae as follows: According to this view the antheridium and archegonium of broyphytes originated from gametangia of a type similar to that of Ectocarpus. In Ectocarpus (Phaeophyce- ae) the gametangium consists of a number of cells, each of which gives rise to a gamete. As soon as the migration from the water to land took place, there arose the necessity for the protection of the gametes from desiccation.

With the result the outer layer of the cells of the gametangium became sterile and functioned as a protective layer. This way, the antheridium has been derived from the algal gametangium. For the derivation of the archegonium from such structure, it has been suggested that after the formation of the protective wall, further sterilization took place, and in the centre an axial row of cells developed.

According to this view the neck canal cells were originally female gametes, which later on lost their walls and cytoplasm. The ventral canal cell is the sister cell of the oosphere and very rarely it may be fertilized. However, Ectocarpus is not a member of Chlorophyceae, but it is presumed that bryophytes have been originated from green algae. According to Smith (1938) the reproductive cells of Schizomeris and antheridia of Chaetonema are quite alike to that of the gametangia of Ectocarpus.

According to Church (1919), the bryophytes have been originated from the marine ancestors and not from the fresh water ancestors. This theory could not get general support because of the lack of evidences from paleobotany and geology. According to majority of workers the bryophytes have been originated from Chlorophyceae which are commonly found in fresh waters and rarely in sea waters.

Origin from pteridophytes:

According to other school of thought the bryophytes have been originated (descended) from pteridophytes by means of reduction. Though this view could not get general support yet several workers postulated the evidences in support of this view. According to Lang (1917), Kidston and Lang (1917), Scott (1923), Halle (1936), Haskell (1949) and Christensen (1954) the bryophytes have been descended by the process of reduction from pteridophytes. Kashyap (1919) also supported the view, because of common resemblances of the two groups.

Similarities between sporangia of some members of Psilophytales (Rhynia, Horneophyton and Sporogonites) with capsules of Anthocerotales, Sphagnum and Andreaea led to conclude this hypothesis. The Psilophytales are the oldest pteridophytes in which the sporophytes were rootless, leafless and dichotomously branched with terminal sporangia.

Such sporophytes resemble the bryophytes, especially the members of Anthocerotales and are thought to have evolved by progressive reduction. Proskaeur (1960), thinks that if bryophytes are polyphyletic in origin, at least Anthocerotales originated from Psilophytales like Horneophyton. According to Kashyap (1919), “bryophytes represent a degenerate evolutionary line of pteridophytes or in more correct term, the bryophytes are descendents of pteridophytes.”

Distribution of Bryophytes

Bryophytes are distributed throughout the world, from polar and alpine regions to the tropics. Water must, at some point, be present in the habitat in order for the sperm to swim to the egg (see below Natural history). Bryophytes do not live in extremely arid sites or in seawater, although some are found in perennially damp environments within arid regions and a few are found on seashores above the intertidal zone. A few bryophytes are aquatic. Bryophytes are most abundant in climates that are constantly humid and equable. The greatest diversity is at tropical and subtropical latitudes. Bryophytes (especially the moss Sphagnum) dominate the vegetation of peatland in extensive areas of the cooler parts of the Northern Hemisphere.

The geographic distribution patterns of bryophytes are similar to those of the terrestrial vascular plants, except that there are many genera and families and a few species of bryophytes that are almost cosmopolitan. Indeed, a few species show extremely wide distribution. Some botanists explain these broad distribution patterns on the theory that the bryophytes represent an extremely ancient group of plants, while others suggest that the readily dispersible small gemmae and spores enhance wide distribution.

The distribution of some bryophytes, however, is extremely restricted, yet they possess the same apparent dispersibility and ecological plasticity as do widespread bryophytes. Others show broad interrupted patterns that are represented also in vascular plants.

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

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

In hills they grow during the summer or rainy season. Winter is the rest period. In the plains the rest period is summer, whereas active growth takes place during the winter and the rainy season. Some Bryophytes have also been recorded from different geological eras e.g., Muscites yallourensis (Coenozoic era), Intia vermicularies, Marchantia spp. (Palaeozoic era) etc.

Fossil Bryophytes

1. Fossil Hepatophyta (Marchantiophyta)

The earliest record of vegetative fossil bryophyte remains is the liverwort from the Upper Devonian of New York which has been assigned to the form-genus Pallavicinites, (= Hepaticites) devonicus

The reproductive structures are not found with any of the species of Pallavicinites. The vegetative features suggested that the species of Pallavicinites may be more closely related to the anacrogynous Jungermanniales.

Various species of Pallavicinites have been described from the Carboniferous to the Pleistocene deposits and can easily be compared with living bryophyte genera like Pallavicinia, Metzgeria, Treuba and Fossombronia.

Diettertia, an interesting hepatic, has been identified from Cretaceous era which may be more closely compared with the Jungermanniales.

The best known bryophyte fossil is Naiadita lanceolata that has been described by Harris (1938) from the Rhaetic (Upper Triassic) of England The spores of Naiadita show the closest resemblance to the member of the Marchantiales and Sphaerocarpales.

The type of spores, unicellular rhizoids, the nature of archegonia and capsules suggested that Naiadita represents a liverwort similar to the living genus Riella of Sphaerocarpales. However, Schuster (1966) argued that the vege-tative features of Naiadita showing closer proximity to the Calobryales.

A fossil bryophyte, Marchantiolites, has been described from the Lower Cretaceous rock of central Montana. M. porosus has been identified from the Jurassic deposit of Sweden. Marchan-tiolites has been placed in the Marchantiales due to the similarity in the airpores.

A thalloid bryophyte identified from the Upper Triassic of South America has been placed in the genus Marchantites. Ricciopsis, a rosette- shaped bryophytic thallus has been identified from the Jurassic of Sweden.

The similar rosette-shaped thallus has been identified from Deccan Intertrappean beds of India and has been placed in the modern genus Riccia.

2. Fossil Anthocerotophyta (Hornworts)

There are no reports of fossil Anthocero-tophyta thalli, although some reliable reports of hornwort spores are available from the Cretaceous (Maastrichtian) rocks of North America. The spores are trilete, circu-lar and possess a distinct cingulum with variable ornamentations which are comparable with the modern hornwort genus Phaeoceros.

3. Fossil Bryophyta (Mosses)

The fossil record of the mosses is much less complete as compared to the fossil hepatics, though they are recorded as early as the Permian. An impression of a leafy shoot of Muscites plumatus has been described from the rocks of Lower Carboniferous age.

This plant shows an axis, covered with helically arranged leaves. Sex organs, sporophyte capsules or rhizoids were not associated with the gameto-phytic plant. Several species of Muscites have been reported from the Upper Carboniferous of France and the Triassic of Africa.

An extensive moss flora has been identified by Neuberg (1960) from the Permian rocks of Siberia, of which six identified genera (Intia, Salairia, Uskatia, Polyssaiuria, Bajdaieira and Buchtia) were placed under the Bryales and three (Protosphagnum, Vorentannularia and Jungajia) to a new order, the Protosphagnales.

The genus Protosphagnum has leaves comparable to the modern genus Sphagnum, except for the pres-ence of a midrib.

Ignatov (1990) described a diverse flora of well-preserved gametophytes of mosses from the Upper Permian of the Russian platform which are comparable to the modern forms like Dicranales, Pottiales, Funariales, Leucodontales and Hypnales.

The permineralised well-preserved moss, Mercerea augustica, has been described by Smoot and Taylor (1986) from the Permian of Antarctica. The plant has a delicate axis to which are attached helically arranged leaves containing a midrib and rhizoids. Reproductive organs or sporophytes are not found associated with the plants. The external morphology and anatomy of the axes suggest its affinity with the Bryidae.

Several compression fossils of true mosses have been described from the Mesozoic, of which Tricostium and Yorekiella from the Jurassic of the Bureja Basin, Russia and Aulacomnium heterostichoides from deep water varved clays (Eocene) of a fresh water lake in British Columbia.

The well-preserved Aulacomnium heterosti-choides has been extensively studied which is very closely related to the present day living species, Aulacomnium heterostichum found in eastern North America and eastern Asia.

4. Problematic Fossil Bryophytes

The Lower Devonian compression fossil Sporogonites is one of the oldest plants that resembles a bryophyte. The plant consists of many parallel-oriented sporangial stalks that ter-minate in elongate capsules, developed from a common thallus.

The sporangium is multilayered and possibly contains a central columella. Numerous trilete spores are present in the spo-rangium. Sporogonites has been considered to be an early hornwort or gametophyte-bearing sporophyte of a moss.

A Precambrian bryophytic fossil, Longfengshania, has been described from China which shows striking similarity with Sporogonites. This unusual fossil of Precambrian age makes it doubtful about the validity of its systematic position. Tortilicaulis is an early Devonian fossil described from South Wales that shares a few morphological features common with the modern liver-worth Pellia.

Evolution of Sporophyte

According to the complexity of structure, the sporophye of bryophytes may be arranged in a series between the simple and the most elaborate. The series start with the simple sporophyte of riccia, runs through that of sphaerocarpos , anthoceros, marchantia and finally ends in a highly complex sporophye of funaria and pogonatum. However, the evolution of sporophytes has been explained with the help of two theories put forward by botanist- a) Theory of sterilization b) Reduction Theory

1.Theory of Sterilization

This theory was put forward by BOWER and supported by Cavers, Campbell and Smith. This theory illustrates that a natural advance in the progressive elaboration and complexity of the sporophyte. The fundamental of principle upon which he formulated his argument is " the progressive sterilization of the potentially fertile cells (sporogenous tissue)" .

Instead of forming spores and serving a propogating function they remain sterile. These sterile cells are put to the other uses such as nutrition , support , dehiscence , dispersal etc. This hypothesis of Bower is called "Theory of Sterilization".

The detail process of Sterilization of some of the important genera discussed as follow-

(a) Riccia Sporophyte- In riccia, zygote divide and redivides to farm a spherical mass of 20-30 undifferentiated cell. Periclinal segmentation forms an inner mass of cell called endothecium and outer single layer amohithecium. The amohithecium forms the single layered capsule wall. The endothecium forms the central mass of sporogenous tissue. Practically , all the sporogenous cells are fertile and develop into spores. However, few of them undergo degeneration to form the nurse cells.

The sporophye of riccia is simplest among all of the bryophytes and has least amount of sterile cells. The entire embryo froms the spore producing capsule. There is not foot and Seta. It is just a spore producing organ without any distributing function.

(b) Marchantia Sporophyte- Sterilization of fertile cells is more advanced in the genus. Half of the embryo divided from the hypobasal regions remians sterile. It forms the foot and Seta. The upper epibasal half is fertile and forms the spore producing capsule. The sterile cell elongate, develop spirally thickened walls and become the elators. A few of the cells of sporogenous cells at the top may be differentiated into sterile, apical cell.

The capsule of Marchantia has both spore producing and spore distributing body. It illustrates a step further in the progressive sterilization of the sporogenous tissue.

(c) Anthoceros Sporophyte- It illustrates a step further than riccia and Marchantia in the progressive sterilization ot the potentially of fertile tissue. The endothecium cells become completely sterile and forms a group of cells known as columella. The sporogenous cells arise from the innermost layer of the amohithecium.

It surrounds the columella. The sporogenous cells become differentiated into spore mother cell and pseudo-elaters. The archegonium of anthoceros is extremely reduced. The outer amohithecium develops into several cells layer thick capsule wall. The capsule wall develops a well ventilated photosynthetic tissue protected by the Epidermis.

(d) Funaria Sporophyte- In funaria major portion of the Sporophyte remain sterile to form the foot and Seta. The capsule is differentiated into central column of andothecium surrounded by many layered amphithecium. The inner layer of the endothecium forms the sterile columella and the superficial cell form the sporogenous tissue. Thus the archesporium arise from the outermost layer of cells of the endothecium.

It is thus extremely reduced and consists of single layer of fertile tissues. The amohithecium become differentiated into the Epidermis , photosynthetic tissue of the capsule wall and the outer spore sac.

The Bower theory of sterilization gives a clear explanation of the evolution of sporophye into upward direction. This theory is more conveincing and reliable.

2. REDUCTION THEORY

This theory was put forward by kashyap, church, Goebal and Evans. They hold that the evolution of sporophye has been in downward direction. They hold the fact that evolution of Sporophyte is retrogressive evolution. They mainly based their theory on the reduction of different organs which result in the simplification of Structure of Sporophyte.

On the basis of this view the simplest type of Sporophyte of riccia is considered as the most advance one. The significant steps in the reduction series are- Simplification of dehiscence appratus.

Reduction of the green photosynthetic tissue in the capsule wall.

Disappearence of stomata and intercellular spaces.

Increase in the thickness of capsule wall.

The gradual elimination of foot and Seta.

All these changes accompanied by the progressive increase in the fertility of sporogenous cells. The changes eliminates the presence of sterile cells and elater in the capsule.

Evidence from comparative morphology and experimental genetics support the view that the simple Sporophyte of riccia is an advanced but a reduced structure.

Evolution of Sporophytes and Gametophytes in Bryophytes

Evolution of Sporophyte in Bryophytes

The sporophyte of bryophytes is called sporogonium which generally consists of a sin-gle, terminal sporangium (monosporangiate) with a bulbous foot and with or without an unbranched stalk or seta. The sporogonium is very delicate, short-lived and nutritionally dependent on its gametophyte.

The sporophytic phase begins with the formation of a diploid zygote within the venter of the archegonium. In the simplest form of sporophyte (e.g., Riccia) the entire zygote is taking part in the formation of stelile capsule wall and the central sporogenous cells. In complex forms, zygote differentiates and sporogenous cells form more sterile tissues.

There are two opposing theories regarding the evolution of sporophyte in bryophytes:

(i) Theory of Progressive evolution i.e., Evo-lution of sporophytes by the progressive sterilisation of potentially sporogenous tissue:

This theory was advocated by Bower (1908- 35) and supported by Cavers (1910) and Campbell (1940). According to this theory, the primitive sporophyte of bryophytes was simple and most of the sporogenous tissue was fertile (e.g., Riccia) and from such a sporophyte, the more complex sporophytes (e.g., mosses) have been evolved by the progressive sterilisation of potential sporogenous tissue. This theory is also known as “theory of sterilisation”.

The increasing sterilisation of sporogenous tissue from simple sporophyte of Riccia to the most complex type of Funaria can be arranged through the following stages:

First stage

The simple sporophyte of Riccia consists of a single-layered sterile jacket enclo-sing sporogenous cells with a very few absorp-tive nutritive cells (nurse cells). The zygote divides by a transverse wall, followed* by a vertical wall to form a four-celled embryo. Subsequently 20-30 celled embryo is formed by further divisions, in which periclinal divisions differentiate a single layered outer amphithecium and the inner multicellular mass, the endothe-cium.

Here the zygote has no polarity. The amphithecium forms the sterile jacket while the whole sporogenous cells (endothecium) differen-tiates into spores with a very few sterile nurse cells, possibly the forerunners of elaters.

Second stage

In this stage, the zygote divides transversely to form a hypobasal and an epibasal cells. A small foot is formed from the hypobasal cell. The epibasal cells differentiates into an outer amphithecium and inner endothe-cium.

The amphithecium forms a single-layered sterile jacket of the capsule, while the endothe-cium differentiates into fertile sporocytes and long sterile elater-like nurse cells without the thickening bands. Thus, the zygote has polarity showing more sterilisation of sporogenous cells like nurse cells and sterile foot. This stage has been noted in Corsinia.

Third stage

The development of sporo-phyte is like that of Corsinia, but there is more sterilisation of sporogenous tissue. This condition is noted in Sphaerocarpus sporophyte which consists of a sterile bulbous foot, a narrow sterile seta developed from hypobasal cell and a fertile capsule developed from endothecium containing sporocytes and sterile nurse cells.

Fourth stage

This stage is represented by Targionia, where the sporophyte consists of a sterile bulbous foot, a sterile narrow seta and a fertile capsule. Here about half of the endothe-cial cells produce fertile sporogenous tissue, while the remaining half gives rise to sterile elaters with 2-3 spiral thickening. Hence, in Targionia, more sterilisation of sporogenous tissue has been observed.

Fifth stage

This stage is illustrated by Marchantia, where further sterilisation of sporogenous tissue has been noted in compari-son with Targionia. In Marchantia, the sterile tissue consists of a broad foot, a massive seta, a single-layered jacket of capsule, sterile apical cap at the apex of capsule and a large number of long elaters with spiral thickening.

Sixth stage

This stage is represented by some members of Jungermanniales like Pellia, Riccarclia, etc. Here more sterilisation of sporogenous tissue has been observed. Sporophyte is differentiated into foot, seta and capsule having multilayered jacket. The sporoge-nous tissues produce mass of sterile elatophores and diffuse elaters.

Seventh stage

This stage is illustrated by members of Anthocerotophyta like Anthoceros. Here marked reduction in the sporogenous tissue has been noted. The multilayered capsule diffe-rentiates into epidermis with stomata and chloro-phyllous cells.

The central columella derived from endothecium is composed of 16 vertical rows of sterile cells. The further sterilisation of sporogenous tissue has been observed in the for-mation of pseudoelaters which are elongated 3-4 celled, simple or branched structure without thickening band

Eighth stage (Final stage)

The members of Bryopsida like Funaria, Polytrichum, Pogonatum etc., show the highest degree of sterilisation. The sporophyte is differentiated into a foot, a long seta and a capsule. The sterile tissue of capsule consists of the apophysis, operculum, many- layered jacket, the columella, trabeculae, the wall of spore sac and the peristome. The sporogenous tissue is restricted to the spore sacs only, hence it forms a negligible portion in the sporophyte.

(ii) Theory of Regressive evolution i.e., evolu-tion of sporophytes due to the progressive reduction or simplification

This theory is known as regressive or retro-gressive theory, and supported by several scien-tists like Church (1919), Kashyap (1919), Goebel (1930) and Evans- (19391 According to this theo-ry, the most simple sporophyte of Riccia (com-prised of a simple capsule) is the most advanced type which has been evolved by the simplifica-tion or progressive reduction of the complex sporophytes (foliose with complex assimilatory tissue and functional stomata) of mosses (e.g. Funaria, Pogonatum, Polytrichum etc.)

The stages of progressive reduction of the foliose sporophyte (primitive type) to the simpler sporophyte (advanced type) have been enu-merated:

(a) The semiparasitic foliose sporophyte gradually lost its leaves and became embedded within the gametophyte.

(b) There is a gradual reduction of the assimilatory (photosynthetic) tissue in the sporo-phytes and subsequently this tissue is confined only to the jacket of capsule (e.g., Funaria, Anthoceros).

(c) Stomata are restricted in the apophysis region (e.g. Funaria, Polytrichum) that communi-cate with the intercellular spaces. In Sphagnum, the stomata of apophysis are non-functional and become rudimentary. In all liverwort members stomata are completely absent in sporophytes.

(d) The capsules of most mosses (Funaria, Polytrichum, Sphagnum, etc.), hornwort (Antho-ceros) and some jungermanniales (Pellla, Porella) are multilayered which subsequently became single-layered (Marchantia, Plagiochas- ma, Riccia) by reduction.

(e) The foot and seta are well-developed in mosses (Pogonatum, Funaria, etc.) and some liverworts (Pellia, Marchantia, etc.). The seta became much reduced and form a narrow sterile part of the sporophyte (Corsinia, Targionia).

In hornworts, the sporophyte is made up of a foot and an elongated capsule only, seta is absent. Finally, in Riccia foot and seta are absent and the sporophyte is represented by a single capsule only, which is supposed to be the most simple as well as advanced sporophyte among bryophytes.

(f) The sporophytes of mosses show the highest degree of sterilisation with a negligible amount of sporogenous tissue. There has been gradual reduction in the sterile tissue of the cap-sule, with simultaneous increase in the amount of sporogenous tissue.

In hornworts, a good amount of sporogenous tissue is formed from the inner layer of amphithecium. In liverworts (Riccia, Marchantia) the entire endothecium gives rise to sporogenous cells.

Evolution of Gametophytes in Bryophytes:

The evolution of thalli in bryophytes is a much disputed problem. There is no substantial fossil evidences of bryophytes that support to the sequential evolution theory of gametophytes among bryophytes.

There are two opposing theo-ries regarding the nature of the vegetative struc-ture of the primitive bryophytic gametophyte and its subsequent evolution:

1. The upgrade or the progressive evolution theory, and

2. The down-grade or the regressive evolution theory.

1. The upgrade or the progressive evolution theory

According to this theory, the primitive game-tophyte was a simple, dorsiventral, prostrate thal-lus, both in external as well as in internal forms. Cavers (1910) and Campbell (1891-1940) were the main proponents of this theory. The evolution of gametophytes took place from liverworts to mosses in an ascending series of gradually increasing complexity with regard to the organi-sation of internal tissue and sex organs.

According to Cavers the ancestor gametophyte resembles the present day Sphaerocarpus and Marchantiales has been considered as a blind line of evolution from the hypothetical Sphaero-Riccia. While Campbell suggested that thalli of the present day Riccardia and Metzgeria resem-ble the simplest ancestral gametophyte. From the simple thallus, the evolution of complex gameto-phytes took place in two different lines.

In the first line, the gametophyte retained its external simple, thallose form as found in Marchantiales. Simultaneously there was a gra-dual increase in complexity in cellular organisa-tions. This has been evidenced by the nature of pores, air chambers and the aggregation of sex organs in a definite receptacle (e.g. Marchantia).

The sexual receptacles show a wide range of organisation. In Riccia, the individual sex organs are scattered over the median portion of the thal-lus. In Marchantia, the sex organs are borne on a complex stalked receptacle called gametophore.

An intermediate condition in between the Riccia and Marchantia has also been observed where sex organs are aggregated into a cushion-like or ridge-like receptacle. These receptacles are borne on the thallus — dorsally or terminally.

In the second line, the gametophytes retained their simple internal structure (lack of airpores and air chambers). But there was a gradual elaboration of the external part of the gametophyte leading to the formation of the appendicular organs.

Further, the thalloid forms were replaced by the leafy forms. This has been observed in the members of jungermanniales and Calobryales. These leafy forms finally led to the establishment of the higher degree of internal differentiation of the tissue in Bryopsida.

2. The downgrade or the regressive evolution theory

According to the downgrade theory, the primitive gametophyte was an erect leafy shoot having radial symmetry (members of Calobryales and true mosses). From such ancestral forms the dorsiventral thalli of liverworts and hornworts got evolved in reverse direction i.e., regression of increasing simplicity.

Among the proponents of the downgrade theory, Wettstein (1903-1908), Church (1919), Evans (1939), Goebel (1930) and Kashyap (1919) are the most prominent scientists.

Kashyap (1919) advocated the regressive evolution from the results of his extensive studies of Indian Marchantiales.

The principal points in the reduction series from Marchantia as the basic type along the various phyletic lines have been summarised below

(a) Reduction in the number of involucre

In Marchantia, sex organs are well-protected by many involucres. A gradual reduction in the number of the involucres has been observed in Conocephallum, Aitchinsoniella and Exormo- theca, which has been finally culminating in Tarefionia with a single involucre

(b) The loss of assimilatory filaments in the air chamber

A gradual reduction series has been noted in many members . In Marchantia and Preissia, the thallia show complexity in having air pores and air chambers full of assimilatory filaments. There is a gradual reduction in the assimilatory filaments in Conocephallum conicum (the filaments are short in the air chambers), Wiesnerella decundata (the filaments rudimented into papillate cells). The assimilatory filaments ultimately disappear in the aquatic Dumortiera hirsuta .

(c) Simplification of Pores

In complex forms like Marchantia and Preissia, the pores are complex, barrel-shaped and present both on the thallus and the discs of the gametophores. In Conocephallum and Reboulia, discs bear only barrel-shaped pores, while thalli bear only sim-ple pores.

In Exormotheca and Stephansoniella, the pores are simple both on the thallus and in the discs. The well-defined pores are totally absent in Riccia .

(d) The gradual shifting of the stalks of antheridiophores and archegoniophores from the terminal to dorsal position

Mehra (1969) pro-posed the above hypothesis. In Marchantia, the antheridia and archegonia are borne terminally on the stalked gametophores. In Preissia qua- drata and Plagiochasma articulatum, the stalk is initially terminal, but becomes dorsal by the further growth of the thallus.

A further downward shifting of the stalk is observed in Corsinia and Boschia, where the female receptacle almost becomes sessile by the elimination of the stalk

Sphagnum

Plant body is gametophytic and consists of two stages

Juvenile stage and leafy gametophore Juvenile stage: It is also called protonema and is formed by the germination of the spores. It is irregularly lobed thallus like structure and one cell in thickness. It is attached to the substratum by multicellular rhizoids with oblique septa. From the protonema arises the erect leafy gametophyte called the gametophore

(a) Leafy Gametophore:

It represents the adult form. The adult gametophyte (gametophore) is perennial and can be differentiated into axis or 'stem' and 'leaves'.

Stem:

It is erect and may be a foot or more in length with a diameter up to 1.2 mm. The stem is well branched, the branching being usually lateral. Near the apex of the stem the branches are short and of limited growth and are clustered together closely to form a compact head called Comal tuft or coma The coma formation occurs due to the presence of very short internodes at the apex of the stem.

Lower down on the stem are borne additional elongated branches. They occur usually in tufts of 3-8 (commonly five) in the axil of every fourth leaf on the main stem. These branches are of two types

Part of the Stem Showing Two Types of Branching

(a) Divergent branches

These branches grow out laterally from the stem and extend outward in a horizontal position.

(b) Drooping or Flaogelliforms branches

These branches grow out laterally from the stem; droop or hang or run very close to the stem. These pendent or de-current branches act as water conductors.

(b) 'Leaf'

Leaves are borne on the main stem as well as on the branches. On the stem they are little apart while on the branches they are overlapping. Leaves are arranged in a spiral manner with a phyllotaxy of 2/5 i.e., sixth leaf will come above the first leaf. They are thin, small, fleshy, oblong with a broad base. The margin is entire with acute apex.

Mid rib is lacking. If seen in surface view the leaf consists of meshes composed of two different types of cells: small living photosynthetic cells containing chlorophyll and large, hyaline rhomboidal cells. (Fig. 4A). These cells are provided with small pores. These pores are rounded in shape and mainly concerned with intake of water.

Spiral thickenings are also present in the cells . These thickenings compensates the absence of mechanical' issue. The leaves on the branches are smaller in size than stem. These leave are compactly arranged in the imbricate fashion

(ii) Internal Structure of Sphagnum

(a) Axis or 'Stem'

The transverse section of axis can be differentiated into 3 distinct zones

(i) Cortex or hyaloderm

(ii) Prosenchymatous region or hadrome

(iii) Central cylinder or Medulla.

(i) Cortex:

It is the outermost region of the axis. Its cells are small and form compact tissue. In young axis, the cortex is only one cell thick. In S. subsecundum it is single layered throughout its life but in majority of species it is composed of many layers. In S. recurvum, S. obtusum, it is composed of two to three layers of hyaline cells.

In S. acutifolium, S. squarrosum it is composed of two to five layers of cells . In S. palustre, these cortical cells develop spiral thickenings and large oval perforations on their walls. In branches the cortical cells remain one cell thick. Cortical cells store water. These cells absorb water by capillary action and thus compensates for the absence of rhizoids in the adult gametophytic plant.

T.S. 0f Axis

In some species of Sphagnum for e.g., S. molluscum, S. tenellum, some cortical cells elongate to form a long curved structure with a curved neck and an opening. These modified cells resemble a retort hence; these cells are called 'retort cells' . There cells are inhabited by small microscopic animals. These cells are absent in those species in which the thickenings and pores are present in the cortical cells.

(ii) Prosenchymatous region

Cortex is followed by a cylinder of narrow, thick-walled elongated cells. It is 4-6 layered and surrounds the medulla. It gives the mechanical support to the axis' tissue.

(iii) Medulla or Axial Cylinder

It is composed of thin walled, colourless, parenchymatous cells . It is like the pith of the higher plants and functions as storage region.

(b) 'Leaf'

Transverse section (T.S.) of leaf shows that it is one cell thick. In young leaves the cells are rectangular, and are of same size.

However, in mature leaves the T.S. appears as beaded or moniliform due to the presence of two types of cells large, hyaline or capillary cells and the small, green assimilatory or Photosynthetic cells., The two kind of cells regularly alternate with each other. S. acutifolium the hyaline cells bulge towards the underside of the leaf and the green cells arc triangular. The base of the triangle is directed upwards

In S. tenellum both types of cells are just reverse to this . In S. squarrosum the green cells are hemmed in, above and below, by the hyaline cells, and may appear spindle-shaped in transverse-section. Their ends reach neither the upper nor the lower surface of the leaf . Hyaline cells are dead and filled with water while assimilatory cells are alive and photosynthetic in function.

Reproduction in Sphagnum

Sphagnum reproduces by vegetative and sexual methods.

(i) Vegetative Reproduction

It takes place by the following methods

(a) Innovation:

It is the common method of reproduction. It takes place by the formation of special vegetative branches known as innovations. Occasionally one of the branches in the axillary cluster become robust and grows upwards. This branch shows all the characteristics of main axis and known as innovation. Each innovation develop into a new plant when detatch from the parent plant.

(b) Multiplication of Protonemal Branches

Any marginal cell of the primary protonema may become meristematic and forms a green cellular filament. In apical portion grows into flat, thallus-like green secondary protonema. Marginal cells of secondary protonema form the leafy gametophore.

(c) Regeneration

The growth of new tissues or organs to replace those lost or damaged in injury is known as regeneration. Sphagnum has great power of regeneration.

During dessication, the growth of the Sphagnum is checked because the physiological activities like respiration and photosynthesis are suspended, but the cytoplasm shows a high degree of resistance to dessication. When water is available these activities are resumed and normal growth of the plant takes place. Such plants are known as pallacuophytes.

(ii) Sexual Reproduction in Sphagnum

Sexual reproduction is oogamous. It takes place by the formation of male and female reproductive organs which develop on special branches. Sphagnum may be monoecious or dioecious. Monoecious species are protandrous.

(a) The Antheridium

The antheridia or the male sex organs develop on the catkin like short lateral branches known as the antheridial or male branches . These branches develop near the apex of the main shoot of the plant. These branches bear the leaves which are just like the foliage leaves but in comparison they are shorter .

These leaves are brightly coloured (commonly yellow, purple, brown, bright red or dark green). In the axil of each leaf solitary antheridium develops (antheridsia occur alternately arranged with the leaves) . A mature antheridium consists a long stalk and a globular body.

The stalk may be as long as the body of the antheridium. It consists of the two to four rows of cells which are 8-10 cells in length. The antheridial body is covered by a single layered sterile jacket which encloses many androcytes. Each androcyte metamorphosis into a spirally coiled biflagellate antherozoid.

When the antheridium is mature, the apical cells of the jacket absorb water, swell and undergo irregular separations which turn backwards. The antherozoids are liberated and swim in water

(b) The Archegonium

One to five archegonia develop at the tip of the short archegonial branches . The leaves of the archegonial branches are green and much larger than the vegetative branches. These leaves are called perichaetium . These leaves protect the archegonia, young sporophytes and provide food to the developing sporophytes.

The archegonia which develop directly from the apical cell of the archegonial branch are known as the primary archegonia while the remaining one are known as secondary archegonia. A nature archegonium is long and stalked structure possessing venter and a long neck enclosing 8 or 9 neck canal cells, a venter canal cell and an egg cell

Fertilization in Sphagnum

The process of fertilization is identical with other bryophytes. Water is essential for fertilization.

At the time of fertilization the neck canal cells along with the venter canal cell disintegrate to form a clear passage for the antherozoids. They enter through the cover cells and reach up to the egg, but only one fuses with the egg to form the zygote. In S. subsecundum the venter canal cell is persistent and fuses with the egg cell to form zygote.

The Sporophyte

The sporogonium develops from only one archegonium. The other archegonium, however, may also persist for some time. The mature sporogonium is differentiated into foot and capsule. Both are connected by a short, narrow neck like constriction which represents the suppressed seta, sporogonium is elevated on a short cylindrical, leafless stalk, the pseudopodium .

The pseudopodium is gametophytic and it is formed by the post fertilization intercalary growth of the axis of the archegonial branch. The pseudopodium together with the basal portion of the calyptra forms a sac-like structure, the vaginula which encloses the foot. The main functions of the pseudopodium are to elevate the capsule for above the perichaetial leaves, to compensate the suppression of seta and to help in the dispersal of spores.

Foot

It is bulbous and made up of parenchymatous cells. The main function is to absorb the food material for the developing sporophyte.

Capsule

It is spherical and dark brown in colour. It contains central columella which is over arched by a done shaped spore sac containing haploid spores . The wall of the capsule is 4-6 layers thick. The outer layer of the capsule wall is called epidermis. The cells of the epidermis are compactly arranged and contain chloroplasts.

It has many non-functional and rudimentary stomata. In young sporogonium, a circular, convex disc is present at the top of the capsule. It is called operculum. It is separated from the rest of the capsule region by a circular (ring like) groove of thin walled cells called annulus.

Dispersal of spores or Dehiscence of capsule

On sunny days the columella of mature capsule dries up, breaks down and forms a large air cavity below the air sac. Air enters in this cavity through the rudimentary stomata.

The wall of the capsule dries up under the influence of the sun and spherical form of the capsule gradually becomes cylindrical . The imprisoned air in the capsule is compressed and held under considerable pressure due to change in the shape of the capsule.

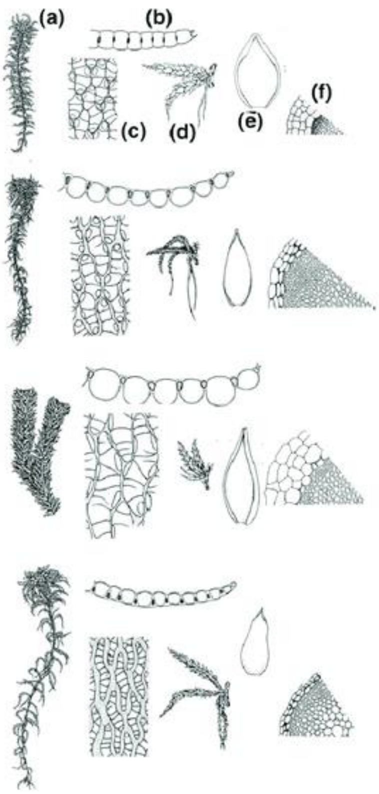
The operculum also dries and shrinks. Due to this a little difference in the tension is thus set up. It puts a strain on the thin celled annulus cells which finally rupture under the mounting pressure of imprisoned air. The operculum is blown off with explosive force.

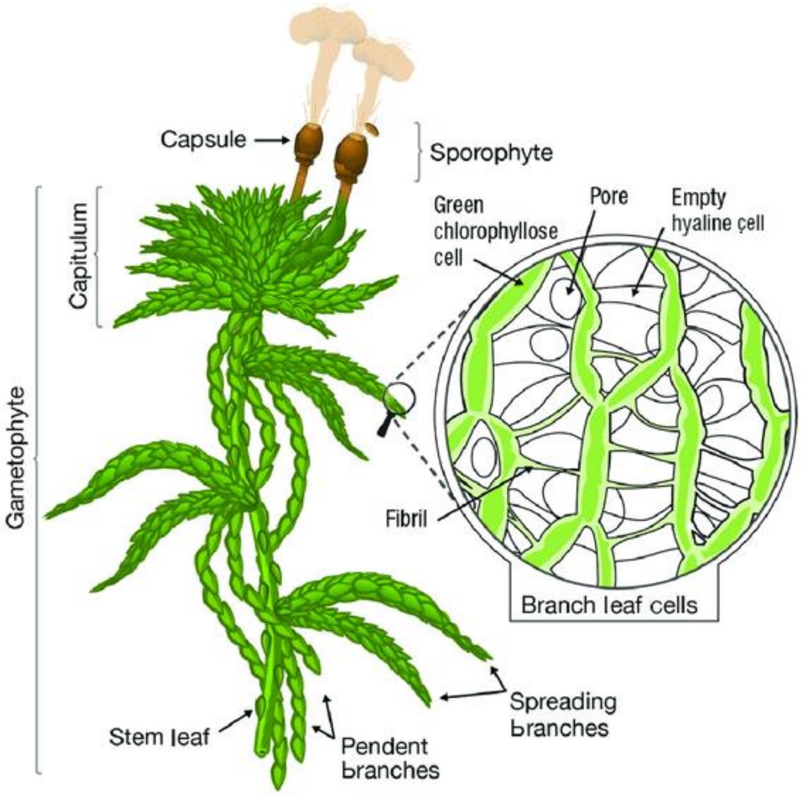
The pressure of imprisoned air also ruptures the spore sac and the cloud of yellow or orange coloured spores is blown to a height of several centimeters in the atmosphere . The method of spore discharge is, therefore, known as the air gun or explosive mechanism.

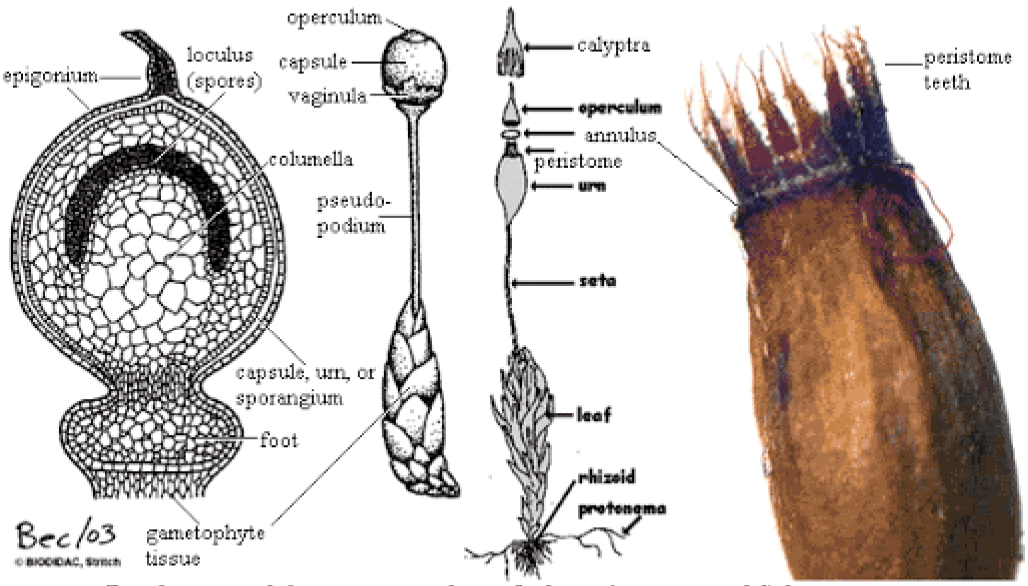
Stages in the Dispersal of Spores

Structure and Germination of Spore :Each spore is uninucteare, triangular to spherical and has two layered wall with a triradiate mark . The outer wall is omanemted and known as exine while the inner wall is smooth and known as intine. The spores remain viable for few months and germinate under favourable conditions. Spores absorb water and swell up.

Exine ruptures and intine comes out in the form of a germ tube. The germ tube divides transversely to form 2-4 celled green filaments . The terminal cell of the filament develops two cutting faces. It cuts segments alternately on the right and left anal forms green, single cell thick plate like structure.It is called primary protonema . The apical cell loses in activity and some marginal cells of the plate like protonema become active and form secondary protonema with rhizoids and leaf buds. These buds gradually develop into leafy gametophores .







Development of the moss sporophyte. Left two images are of *Sphagnum*.
Right two images reflect development of the sporophyte in Polytrichales

Funaria

Plant body is gametophytic and consists of two different stages namely

(i) Juvenile stage represented by primary protonema and

(ii) The leafy gametophore which represents the adult form.

The adult gametophyte (gametophore) is differentiated into rhizoids, axis or ‘stem’ and ‘leaves’ . Rhizoids arise from the base of the axis. They are slender, branched, and multicellular and have oblique septa.

Axis is 1—3 cm. high, upright, slender and branched. Each branch is extra axillary i.e., arise below a leaf. Leaves are sessile, oblong-ovate with entire margin, pointed apex and are arranged spirally on the branches and ‘stem’. Each ‘leaf’ is traversed by a single mid rib . ‘Leaves’ are borne in 1/3 phyllotaxy which becomes 3/8 at maturity.

(ii) Internal Structure

1. Axis or ‘stem’

The transverse section (T. S.) of axis can be differentiated into three distinct regions

(i) Epidermis

(ii) Cortex

(iii) Central conducting strand or central cylinder.

(i) Epidermis

It is the outer most single layered protective covering consisting of small tangentially elongated chlorophyll bearing cells. Cuticle and stomata are absent

Transverse Section of Axis

(ii) Cortex

It is present between the epidermis and conducting tissue. It is made up to parenchymatous cells. Younger part of the cortex contains chloroplasts but in the older part they are lacking. At maturity few outer layers of cortex become thick walled and are reddish brown in colour but those of the inner layers become thin walled.

(iii) Central Conducting Strand

It is made up of long, narrow thin walled dead cells which lack protoplasm. These cells are now commonly called as hydroids. Conducting strand besides providing a certain amount of mechanical support, functions in the upward conduction of water and solutes.

2. Leaf

Transverse section (T. S.) of ‘leaf’ shows a well-defined midrib with two lateral wings. Except the midrib region, the ‘leaf’ is composed of single layer of parenchymatous polygonal cells. The cells contain many large and prominent chloroplasts . The central part of the mid rib has narrow conducting strand of thick walled cells which help in conduction.

Reproduction in Funaria

Funaria reproduces by vegetative and sexual methods.

(i) Vegetative Reproduction

It takes place by the following methods

1. By multiplication of primary protonema

In Funaria, spores on germination form a branched, filamentous, multicellular structure. It's called primary protonema. In it certain colourless separation cells are formed by intercalary divisions. These cells die out and break up the protonema into single cell or many celled fragments. These fragments grow into new protonemata which bear buds. Each bud develops into a leafy gametophore.

2. By secondary protonema

When protonema is developed by other than the germination of spore, it is called secondary protonema. It may be developed from any detached living part of the gametophyte such as 'stem', 'leaves', antheridium, archegonium paraphysis, sterile cells of capsule, seta or when the rhizoids are exposed to sun light in moist atmosphere . It is similar to primary protonema and develops into leafy gametophore.

3. By Gemmae

During unfavorable conditions, the terminal cells of the protonemal branches divide by transverse, longitudinal divisions and form green multicellular bodies of 10-30 cells . These are called gemmae. At maturity gemmae become slightly reddish brown in colour. On the return of favourable conditions gemmae germinate and form new plants.

4. By Bulbils

When such gemmae like structures are produced on rhizoids inside the substratum, these are called bulbils. These are devoid of chloroplasts but capable of developing into leafy individuals under favourable conditions.

5. Apospory

Development of gametophyte from sporophyte without the formation of spores is known as apospory. Any vegetative cell of the sporophyte may form green protonemal filaments which bear lateral buds. These buds later develop into leafy gametophores.

The gametophores thus formed are diploid. Sexual reproduction in such gametophores results in the formation of tetraploid (4n) zygote. The sporophytes from tetraploid are sterile because they are not capable of bearing spores.

(ii) Sexual Reproduction in Funaria

Sexual reproduction is oogamous. Male reproductive structure is known as antheridium and female as archegonium. Funaria is monoecious (having male and female sex organs on the same thallus) and autoicous (antheridia and archegonia develop on separate branches of the same thallus). Sex organs are borne on leafy gametophores in terminal clusters.

The main shoot of the leafy gametophore bears antheridia and act as male branch. Female branch develops as a lateral outgrowth from the base of the male branch and bears archegonia. It grows higher than the male branch. Funaria is protandrous (antheridia mature before the archegonia). It ensures the cross fertilization.

Longitudinal section (L. S.) of male branch shows that its apex is expanded and convex shaped. It bears large number of reddish brown or orange antheridia in different stages of development. Projected antheridia are surrounded by a rosette of spreading leaves called perigonial leaves.

The antheridial cluster with surrounding perigonial leaves is called perigonium. The antheridia are intermingled with large number of sterile hair like club shaped structures called paraphyses (Sing, paraphysis) . Paraphyses store water, protect developing antheridia, help in photosynthesis and dehiscence of antheridium.

Structure of an Antheridium

The antheridium is club shaped. It can be differentiated into two parts

(a) Short multicellular stalk

(b) Body of antheridium

Body of antheridium has sterile, single layered jacket of polyhedral flattened cells. When young the cells of the jacket contain chloroplasts which turn orange or reddish brown at maturity. Jacket encloses a large number of androcytes (antherozoid mother cells).

At maturity the distal end of the antheridium bears one or two thick walled, colourless cells called operculum. The opercular cells become mucilaginous, absorb water and swell, break connections with the neighbouring cells and form a narrow pore. Androcytes ooze out in the form of a viscous fluid through this pore.

Development of Antheridium

Antheridium develops from a single superficial slightly projected cell. It is called antheridial initial. It develops at the apex of the male branch. It divides by a transverse division to form a basal cell and an outer cell . The basal cell form the embedded portion of the stalk. The outer cell forms the entire antheridium and is known as antheridial mother cell. It divides by transverse divisions to form a short filament of 2-3 cells

The lower cells form the lower part of the stalk of the antheridium. The terminal cell of the filament divides by two vertical intersecting walls, thus an apical cell with two cutting faces is differentiated

The apical cell cuts segments in two rows in regular alternate sequence. In this way 5-7 segments cut off . Simultaneously when the apical cell is dividing, the third or fourth segments below the apical cell, starts dividing from base, upwards by diagonal vertical walls.

The first wall divides the segment into two cells of unequal size. Small cell is called jacket initial . Larger cell further divides periclinally into an inner large primary androgonial cell and outer jacket initial. In a transverse section (T. S.) primary androgonial cell appears as a triangular cell . Such type of divisions takes place in all the upper segments except the apical cell which develops into operculum.

All the jacket initials divide only by anticlinal divisions to form a single layered wall of antheridium . Primary androgonial cells divide and re-divide to form the androcyte mother cells. The cells of the last cell generation are called androcyte mother cells. Each androcyte mother cell divides further and form two androcytes. Each androcyte produces a single biflagellate sperm or antherozoid or spermatozoid. Each antherozoid is elongated, spirally coiled, bi-flagellated structure

Female Branch or Archegoniphore

The female branch arises from the base of the male branch. Longitudinal section (L. S.) of female branch shows that many archegonia intermingled with paraphyses occurs at its apex (Fig. 7A). The terminal cell of paraphyses is not swollen. The cluster of archegonia is enclosed by a group of green foliage ‘leaves’ called perichaetial leaves. The archegonial cluster with the surrounding perichaetial leaves is called perichaetium.

Structure of an Archegonium

A mature archegonium is flask shaped structure. It remains attached to the female branch by a massive stalk. It consists upper elongated slender neck and basal globular portion called venter.The neck is slightly tubular, twisted, single layered and consists of six vertical rows of neck cells, which enclose an axial row of ten or more neck canal cells. The venter wall is two layered and encloses venter canal cell and egg cell. Venter canal cell is situated just below the neck canal cells.

Development of Archegonium

Archegonium develops from a single superficial cell called the archegonial initial . It differentiates at the apex of the female branch. Archegonial initial divides by transverse division to form the basal cell or stalk cell and a terminal cell.

The basal cell divides and re-divides to form the stalk of the archegonium. The terminal cell functions as archegonial mother cell . It divides by three intersecting walls forming three peripheral cells enclosing a tetrahedral axial cell . The peripheral cells divide anticlinally to form a single layered wall of venter which later becomes two layered.

The axial cell divides, transversely to form an outer primary cover cell and inner central cell . The outer primary cover cell functions as aplical cell with four cutting faces (three lateral and one basal). It cuts off three lateral segments and one basal segment. Each lateral segment divides by a vertical wall so that the six rows of cells form the neck of the archegonium . Each basal cell adds to neck canal cell.

The inner central cell divides by transverse division into an outer primary neck canal cell and an inner primary venter cell . Primary neck canal cell undergoes transverse divisions to form a row of neck canal cells.

Thus in Funaria the neck canal cells have double origin (lower and middle neck canal cells in the neck canal are derived from the primary neck canal cell while those in the upper portion of neck are derived from the primary cover cell). The primary venter cell divides by transverse division to form the venter canal cell and egg cell

Fertilization in Funaria

Water is essential for fertilization. The opercular cells of the antheridium rupture and releases mass of antherozoids. When archegonium reaches at maturity, the neck canal cells and venter canal cell disintegrate to form a mucilaginous mass. It absorbs water, swells up and comes out of the archegonial mouth by pushing the cover cells apart. This mucilaginous mass consists chemical substances (mainly sugars). The cover cells of the neck separate widely from each other and form a passage leading to the egg. Rosette like perigonial leaves serve as splash cup from which rain drops disperse antheroziods to some distance (rain drops falling on the archegonial cluster situated at lower level). Many antherozoids enter the archegonial neck because of chemical response but only one of them fuses with the egg to form the zygote. Union of male and female nuclei is complete within 10 hours. Fertilization ends the gametophytic phase.

Sporophytic Phase

Zygote is the first cell of the sporophytic phase. Development of sporophyte takes place within the venter of the archegonium.

Structure of Sporophyte

The sporophyte is semi-parasitic in nature, the mature sporophyte can be differentiated into three distinct parts—foot, seta and capsule.

(i) Foot

It is the basal portion of the sporogonium. It is small dagger like conical structure embedded in the apex of female branch. It functions as anchoring and absorbing organ.

(ii) Seta

It is long, slender, stalk like hygroscopic structure. It bears the capsule at its tip. It raises the capsule above the apex of leafy gametophore. Its internal structure is more or less similar to axis. The epidermis is followed by thick walled cortex which surrounds the axial cylinder. It is mechanical in function and also conducts the water and nutrients to the developing capsule .

(iii) Capsule

It is the terminal part of the sporophyte and is developed at the apex of the seta. It is green in colour when young but on maturity it becomes bright orange coloured. It is covered by a cap like structure called calyptra. (gametophytic tissue develops from the upper part of the archegonium).

Internal Structure of the Capsule

Longitudinal Section (L.S.) of the capsule shows that it can be differentiated into three distinct regions-apophasis, theca and operculum

(a) Apophysis

It is the basal sterile part of the capsule. It is bounded by the single layered epidermis which is interrupted by stomata. The sotmata have single ring like guard cells (Fig. 11 C, D). Below the epidermis is spongy parenchyma. The central part of the apophysis is made up of elongated thin walled cells forming a conducting strand. It is called neck of the capsule. It is the photosynthetic region and connects seta with capsule.

(b) Theca

It is the middle, slightly bent spore bearing region of the capsule. It lies between the apophysis and operculum.

(i) Epidermis

It is the outer most layer. It is single layered with or without stomata.

(ii) Hypodermis

It is present below the epidermis. It consists two to three layers of compactly arranged colourless cells.

(iii) Spongy parenchyma

It consists two to three layers of loosely arranged chlorophyllous cells. It is present inner to hypodermis. These cells are capable to manufacture their own food but dependent on gametophyte for water and mineral nutrients. Therefore, the sporophyte of Funaria is partially dependent on gametophyte.

(iv) Air spaces

These are present just below the spongy parenchyma and outside the spore sacs. Air spaces are traversed by green cells (chlorenchymatous cells) called trabecular (elongated parenchymatous cells).

(v) Spore sac

These are present below the air spaces on either side of the columella. It is 'U' shaped and broken at the base. (It separates its both arms).

It has an outer wall (3-4 cells thick) and an inner wall (single cell in thickness). Between the outer wall and inner wall is the cavity of the spore sac. When young, the cavity of the spore sac is filled with many spore mother cells. At maturity the spore mother cells divide by meiotic divisions and form many haploid spores.

(vi) Columella

It is the central part of the theca region. It is made up of compactly arranged colourless parenchymatous cells. It is wide above and narrow below, connecting the central strand of apophysis. It helps in conduction of water and mineral nutrients.

(c) Operculum

It is the upper region of the capsule. It is dome shaped and consists four to five layers of cells. The outermost layer is thick walled and called epidermis. Operculum is differentiated from theca by a well-marked constriction. Just below the constriction there is a diaphragm (rim). It is composed of two to three layers of radially elongated pitted cells.

Immediately above the rim is annulus which consists of 5-6 superimposed layers of cells. Its upper cells are thick but two lowermost layers of cells are thin. Annulus separates the theca from the operculum. Below the operculum lies the peristome . It is attached below to the edge of the diaphragm. The peristome consists of two rings of radially arranged peristomial teeth. In each ring there are sixteen teeth.

The teeth are not cellular but they are simply the strips of the cuticle. The teeth of the outer ring are conspicuous, red with thick transverse bands while the teeth of the inner ring are small, delicate, colourless and without transverse bands. Inner to peristome teeth lies a mass of thin walled parenchymatous cells.

Development of Sporophyte

Soon after fertilization, the zygote secretes a wall around it and enlarges in size. It divides by a transverse wall forming an upper epibasal cell and lower hypo basal cell . Epibasal cell divides by two intersecting oblique walls. It differentiates an apical cell with two cutting faces in the epibasal cell . Similarly, the hypo basal cell differentiates an apical cell .

The entire sporophyte is differentiated by the activity of these two apical cells. So, the development of embryo sporophyte is bi-apical. Epibasal apical cell develops into capsule and upper portion of the seta while the hypo basal apical cell develops into foot and remaining part of the seta. Both apical cells cut out alternate segments and form the elongated filamentous structure of young sporogonium .

Development of Capsule

A cross section through the upper portion of the young sporogonium shows a two identical segments which divide by a vertical division at right angle to the previous one to form a quadrant (4 celled stage) . Each cell of the quadrant divides by anticlinal wall in such a way that a smaller almost triangular cell and a larger more or less rectangular cell is formed. Each rectangular cell now divides by a periclinal division. It results in formation of a group of four central cells surrounded by 8 peripheral cells. The central tissue is known as endothecium and the peripheral cells from the amphithecium . From these two group of cells the further development takes place. There is formation of different rings by anticlinal and periclinal divisions.

The amphithecium divides by periclinal division to form two concentric layers. The inner layer of 8 cells is called first ring The cells of the outer layer divide by anticlinal divisions to form 16 cells . This is followed by the periclinal division in this layer. The inner part of this layers is called the second ring . Again the outer layer of these two layers divides anticlinally to form 32 cells. This layer divides periclinally to form two layers of 32 cells. The inner layer is called third ring. Similarly by periclinal divisions fourth and fifth ring of 32 cells are formed.

The four cells of the endothecium also divides similarly to amphithecium. The first division is curved and anticlinal . The second division is periclinal . It results in the formation of a central group of 4 endothecial cells, surrounded by 8 peripheral endothecial cells. Further development of the tissues in the capsule region takes place by these amphithecial rings and endothecial cells.

It can be studied under the following three headings . Development of fertile (theca) region (middle portion of young capsule)

The fertile region in capsule comprises archesporium lined by outer and inner spore sac. Archesporium is endothecial in origin. Its cells may undergo sub-divisions to form two cell layers thick spore mother cells which by meiosis form tetrad of spores. Elaters are absent.

Dehiscence of the Capsule

Funaria is a stegocarpous moss (dehisce along a pre-determined line) Dehiscence of the capsule is achieved by ‘breaking off’ of annulus. As the capsule matures it becomes inverted due to epinasty. The thin walled cells of the annulus break away, the operculum is thrown off and the peristome teeth are exposed.

The outer peristomial teeth (exostome) are hygroscopic. The inner peristomial teeth (endostome) do not show any hygroscopic movements but act as a sieve allowing only a few spores to disperse at a time. The lengthening and shortening of the outer peristomial teeth help in the dispersal of spores.

In high humidity the exostome absorb water, increase in length and curve inwards. In dry weather, the exostome teeth lose water, bend outwards with jerky movements. It allows the dispersal of spores from the capsule in instalments. At maturity the seta also shows jerky movements. Twisting and swinging of seta in dry weather further aids in the dispersal of spores.

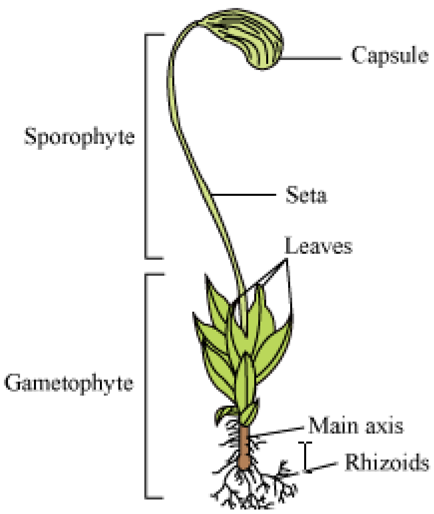
Structure and Germination of Spore

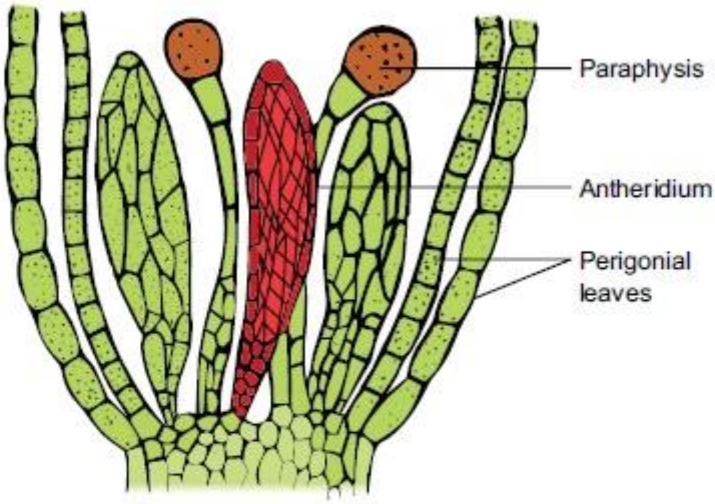
Spore is the first cell of the gametophytic phase. Each spore is spherical , 12-20 µ in diameter and surrounded by two wall layers . The outer wall is thick, smooth, brown and known as exosporium, while the inner wall is thin, hyaline and called endosporium. Spore wall encloses single nucleus, chloroplasts and many oil globules.

Under favourable conditions (sufficient moisture) spores germinate. Exosporium ruptures and endosporium comes out in the form of one or two germ tubes . Each germ tube is multicellular, green with oblique septa. The germ tube grows in length, divides by septa to form green algal filament like structure called primary protonema

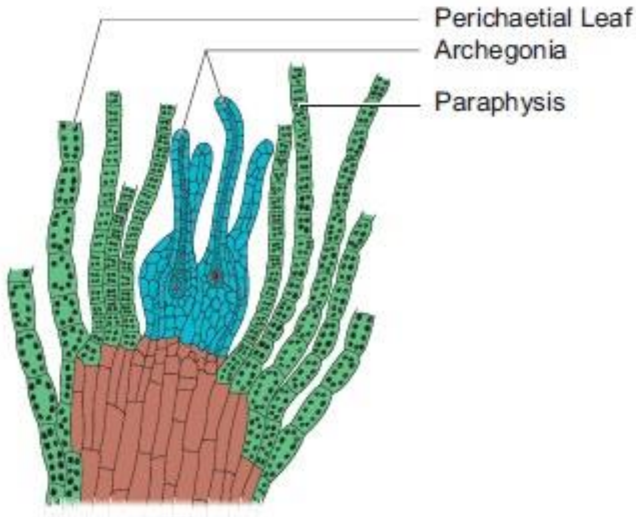
Primary Protonema

It is the juvenile (young) stage of the gametophyte formed by the germination of spore. It forms two different types of branches. Most of the branches grow horizontally on the moist surface of the soil and are known as chloronemal branches (positive phototrophic, thick and rich in chloroplast) while some branches grow down in the soil and are called rhizoidal branches (non-green, thin and possess oblique septa) . These branches can develop chlorophyll if expose to light. Rhizoidal branches function as anchoring and absorbing organs while chloronemal branches develop minute green buds behind the cross walls which develop into leafy gametophores. From one primary protonema many moss plants develop, so the moss is gregarious in habit. Primary protonema is short lived.



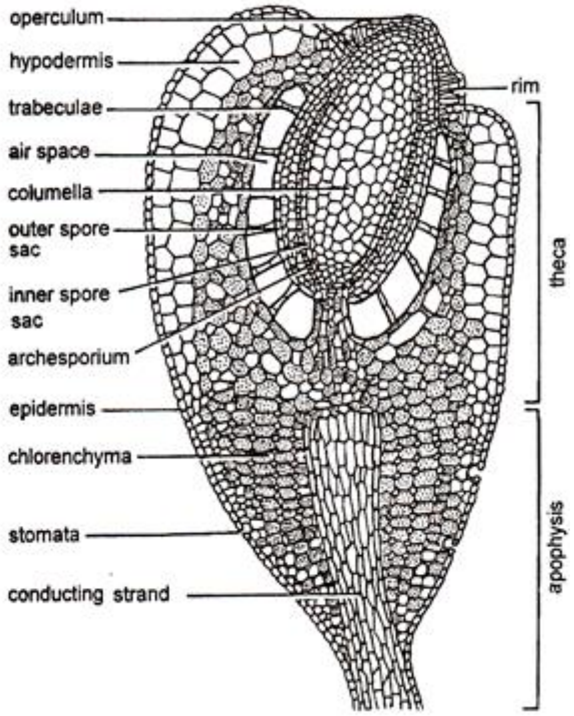


a) Antheridial head



b) Archegonial head

Figure 2.21: *Funaria* - Sexual reproduction



operculum
hypodermis
trabeculae
air space
columella
outer spore sac
inner spore sac
archesporium
epidermis
chlorenchyma
stomata
conducting strand
rim
theca
apophysis

Polytrichum

Polytrichum, often known as ‘squirrel tail moss’ or ‘air moss’, is one of the common mosses of Indian Archipelago and Aus-tralia, which grows in the rainy season on damp ground, near the base of tree trunks and side walls of cities forming dense tufts and patches. There are about 92 species of Polytrichum, of which 4 are commonly found in India, viz., P. commune, P. juniperinum, P. densifolium., and P. xanthopilum.

The Gametophyte of Polytrichum

The gametophyte is differentiated into two portions – a prostrate and much-branched alga-like filamentous portion, the protonema, and an upright per-sistent leafy shoot, the gametophore.

The filamen-tous protonema is transi-tory arid shows two kinds of branches

i. The ordinary green ones with straight transverse septa, and

ii. The brown-walled ones with strongly oblique septa, the rhizoids.

If abundant moisture is present, this proto-nema grows to a consider-able extent and sooner or later there arise, from its distal end of the cells, lateral pear-shaped mul-ticellular cell-masses (buds), from each of which a leafy gametophore is produced.

The gametophore, which is independent at matu-rity, often reaches a height of 20-40 cm. and is always differentiated into an angular stem and closely-set, thick, rigid, spirally arranged leaves (with angular divergence 5/13, 14/34, etc.). The leaves are small, very numerous, lanceolate to linear in A, outline, and with a very broad and strong midrib, projecting beyond the apex of the lamina.

The lamina which develops only at the extreme margin of the midrib is usually more or less incurved. A leaf, when viewed with a pocket lens, shows that, as if, there are several narrow mid-ribs. But when sectioned and examined under microscope, these are found to be thin vertical plates of chloroplast-containing cells, the lamella, along the middle region of the leaf and are the incurved margins of the lamina, which protect them in dry weather. At the base of the shoot nu-merous rhizoids develop and these often become closely twisted together to form cable-like strands.

A cross-section of a mature aerial stem shows three distinct regions

i. A firm epidermis,

ii. A comparatively thick cortex and

iii. A central cylinder.

A few outer layers of cells of the cortex are thick- walled and dark-coloured like the epidermis, but more compact than the inner colourless parenchymatous ground tissue.

The central cylinder is composed of two tissue elements; thick-walled, dark-coloured cells with living protoplasts (sterieds) especially abundant towards the centre, and larger, thin-walled, empty cells (hydroids), almost destitute of protoplasm and resembling vessels of true vas-cular plants.

Starch has been noted in the outer cells of the cortical region. This central cylinder is separated from the cortex by an incomplete pericycle-like sheath of thin-walled living cells. ‘Leaf traces’ are also present in the cortex and these are structurally similar to the central cylinder.

Reproduction in Polytrichum

Polytrichum reproduces both by vegetative and sexual methods. The protonema multiplies by the separation of its branches, which may grow into few protonemata. Often colourless separation cells appear and break the protonema into several filaments. Gemmae are often developed from the terminal cells of the protonemal branches. These gemmae may directly give rise to new protonemata. Vegetative reproduction may also be carried on by the development of secondary protonemata, which are formed from any part of the plant, e.g., rhizoids, leaves or stem. Some times protonemata are produced from the sporongonium without the formation of spores. This is a case of apospory.

Polytrichum is usually dioecious and the sex organs, antheridia and archegonia, are borne separately at the apices of male and female gametophores respectively, forming the so-called 'inflorescences'. Each inflorescence consists of a group of sex organs which are surrounded by specialized leaves, perichaetial leaves, quite different in form and colour from those on the stem.

The conspicuous male inflorescence consists of a group of antheridia intermingled with peculiar sterile green hairs (paraphyses) and is surrounded by broad, reddish and membranous perichaetial leaves. The growth of the apical region of the stem is, however, not stopped by the formation of antheridia and is further growth may be resumed when the formation of antheridia as totally stopped.

This inflorescence is regarded as a compound structure, since groups of antheridia develop at the base of each leaf of the inflorescence and it is quite probable that each group represents a condensed branch.

Each antheridum is a shortly stalked, club-shaped body containing within it many mother cells of the spermatozoids (androcyte cells) and within each of which a biflagellate spermatozoid is developed. When ripe, the antheridium has a yellowish or orange colour and opens at the top (multicellular opercular cap), the whole mass of spermatozoids mother cells escape and finally from these mother cells the spermatozoids are discharged in the sur-rounding film of water, which wets the surface of the moss bed.

The archegonia, borne on a separate plant, are also in a cluster at the apex of the gametophore and the perichaetial leaves usually remain folded over them.

Each archegonium is a flask-shaped body with a very short stalk and consists of two parts

i. A basal swollen portion, the venter, and

ii. A comparatively long upper portion, the neck.

The venter contains a ventral canal cell and a female cell, theoosphere, or ovum, or egg. In this case there are a variable number of neck cells.

When an archegonium matures, a passage is established due to the disorganization of the canal cells. This passage becomes filled with a mucilagenous substance containing canesugar. Fertilization takes place in water. Biflagellate spermatozoids, swimming by means of flagella, come in the neighbourhood of archegonium; these being attracted by the canesugar penetrate the neck, but only one of them fuses with the ovum.

The fertilized ovum then sur-rounds itself with a cell wall and becomes an oospore. The ova of several archegonia may be fertilized forming oospores, but the one which is formed first begins to grow on getting food, while the rest dry up, so that only one, sporophytic develops over a leafy gametophore. With fertilization and formation of oospore, the sporophytic or diploid generation begins.

The Sporophyte of Polytrichum

The oospore gradually passes into an embryo, which ultimately gives rise to the sporogonium, the sporophytic generation of the moss plant. Due to the rapid growth of the sporogonium, the upper portion of the archegonium-neck becomes torn off, so that it is carried off in the form of a cap, ultimately forming a very large hood-shaped calyptra covered with a dense growth of hairs.

The sporogonium consists of three parts

(a) A sac-like upper part, the capsule,

(b) A slender stalk called seta, and

(c) A small foot by means of which it is attached to the gametophyte.

The capsule is at first green in colour owing to the possession of chloroplasts and in its lower portion it bears a few stomata. Within the capsule the sporogenous tissue develops, from which ultimately spores are formed (four spores from each spore mother cell due to reduction division).

A large part of the central tissue of the capsule remains sterile forming the so-called columella and the conical upper part, the operculum, which becomes detached from the lower part as lid in order to allow these spores to escape; the operculum is prolonged into a beak-like rostrum.

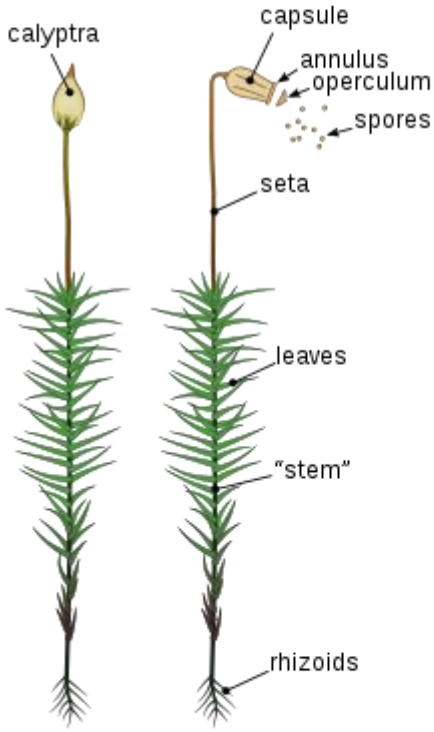
Just beneath the operculum there is a complicated structure known as peristome consisting of 32 or 64 'teeth' in a circle around the mouth of the spore-cavity of the capsule. These are nothing but bundles of thickened fibrous cells, regularly arranged in crescent form resem-bling the spokes in a wheel and have got a profound taxonomic importance. These teeth help to scatter the spores.

The tip of the columella is expanded into the epiphragm, filling the space inside the peristome ring. There are two large intercellular spaces sur-rounding the sporogenous tissue, one on its outer side and the other between it and the columella, and are traversed by narrow filamentous strands of cells containing chloroplasts. At maturity the capsule finally becomes horizontal and dorsiventral.

With reduction division and formation of spores, the gametophytic or haploid generation begins.

The New Gametophyte of Polytrichum

When the spores mature they are shed by means of peristome. These may rest for some time but when they germinate under favourable conditions, they directly give rise to protonemata. Lateral buds arise from the protonema and each produces a new moss plant.


calyptra
capsule
annulus
operculum
spores
seta
leaves
“stem”
rhizoids

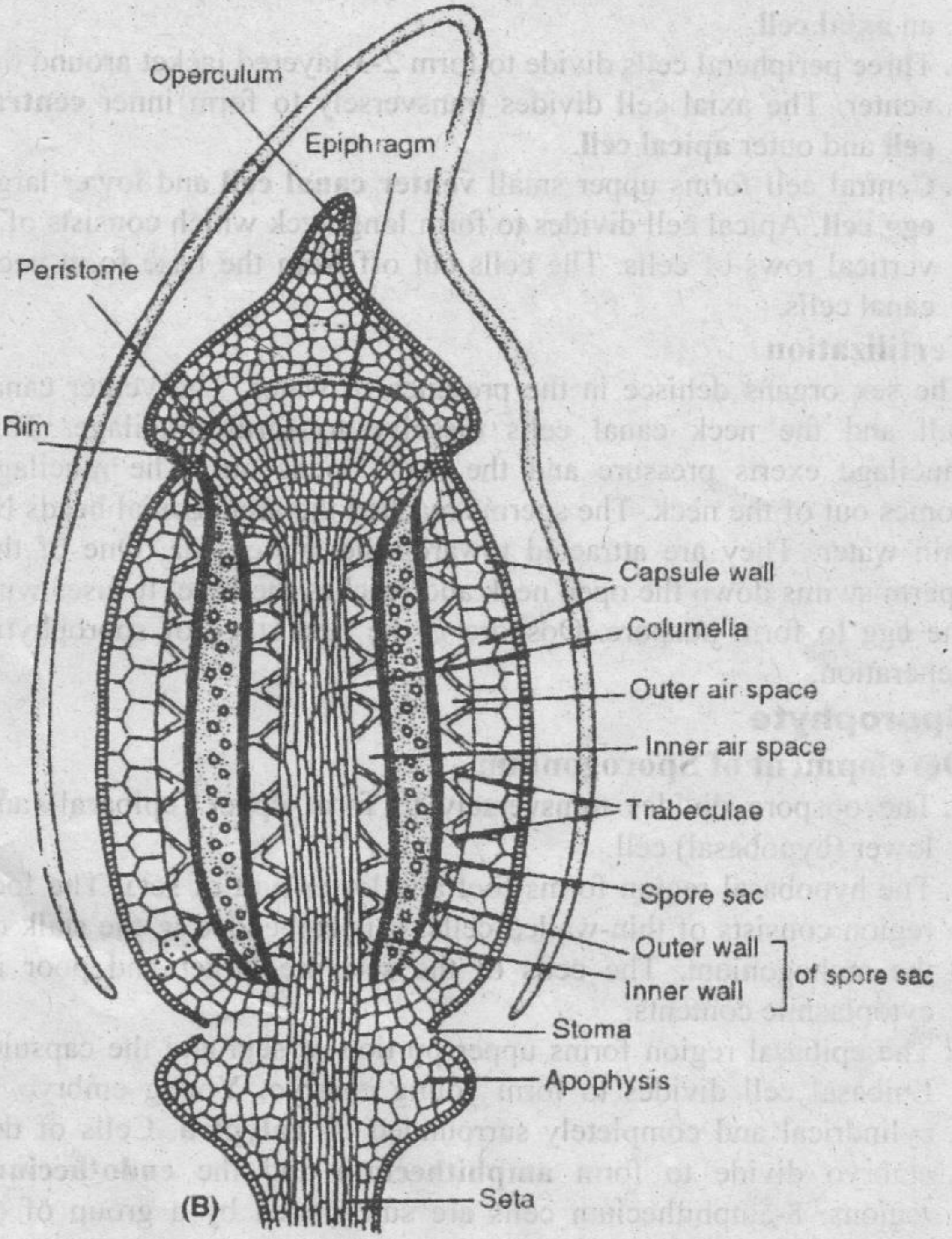


Fig: V.S of capsule

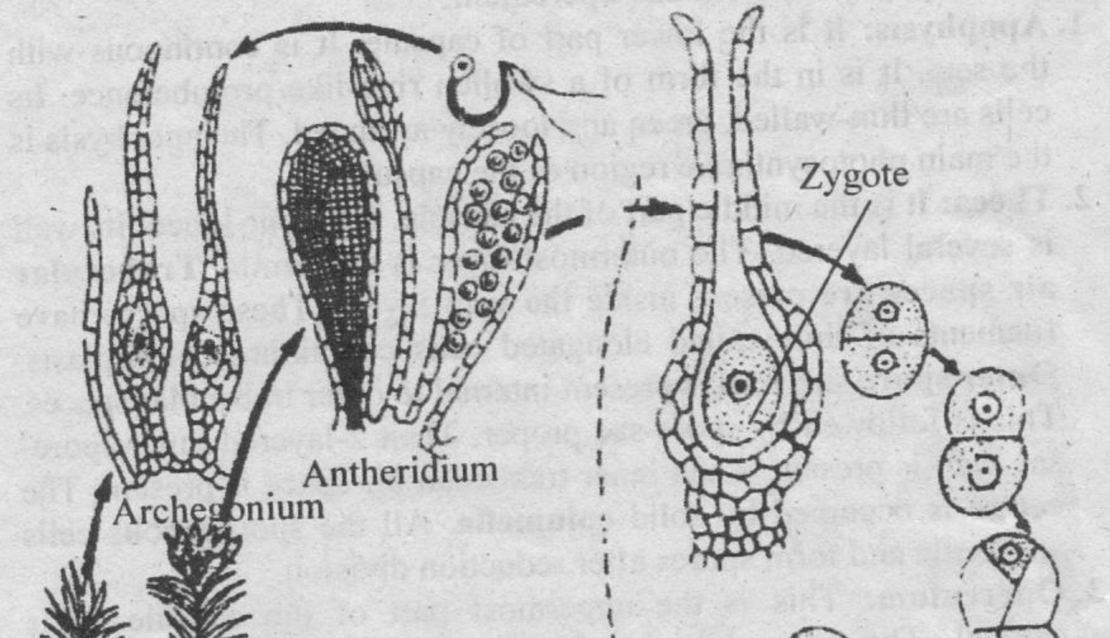


Fig: Life cycle of Polytrichum