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UNIFYING FEATURE OF ARCHAEGONIATES AND TRANSITION TO LAND HABIT

AMPHIBIAN NATURE OF BRYOPHYTA

DIAGONISTIC CHARACTERS AND EXAMPLES HEPATICOPSIDA , ANTHOCEROTOPSIDA , BRYOPSIDA (PROSKAUER , 1957) , LIFE HISTORY OF MARCHANTIA AND FUNARIA , ECOLOGICAL AND ECONOMIC IMPORTANCE

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Bryophytes are "Avascular Archegoniate Cryptogams" which constitute a large group of highly diversified plants. In the early twentieth century, it was suggested that the Pteridophytes and Spermatophytes are the vascular plants and they form a distinct group within Embryophyta, which should be named as **Trachaeophyta** (parallel to Bryophyta). While the name **Archegoniatae** was proposed to include Bryophyta, Pteridophyta and Gymnosperms as all these three are having archegonia (female sex organ).

Tippo (1942) divided the plant kingdom into two subkingdoms (i) **Thallophyta** and (ii) **Embryophyta,** which were further divided into Phylum (Phyla). But according to the International Code of Botanical Nomenclature (ICBN), the term ‘phyla’ is not appropriate for the group of plants and it should be changed to the ‘divisions’. However, Tippo divided Embryophyta into **Bryophyta** and **Trachaeophyta.** He also suggested an alternative name **Atracheata** to Bryophyta .

Hofmeister (1851) for the first time investigated alternation of generations in Bryophytes and indicated that the Bryophytes and Pteridophytes share certain common features like Multicellular gametangia, True alternation of generation of dissimilar generations, warranting their consideration as one large group, generally called as‘Archegoniatae’. According to him, the Archegoniatae shows two well-marked and distinct generations (Gametophyte and Sporophyte), which follow one after the other in alternate manner. The gametophyte is sexual phase in the life-cycle which produces gametes in the sex organs while sporophyte is asexual phase in the life-cycle which produces spores in the spore bearing organ – sporogonium/sporangium. Bryophytes show sharply defined heteromorphic alternation of generations in which the gametophytic phase and the sporophytic phase are entirely different in their morphology as well as in function. The main plant body is gametophyte, which produces antherozoids and eggs in antheridia and archegonia respectively. After fertilization (syngamy) the zygote is formed which develops into the sporophyte. The sporophyte is generally differentiated into foot, seta and capsule. Spores are produced in the capsule after meiosis. The spore is the first cell/stage of the haploid/gametophytic generation, which ends at the egg till it is unfertilized. The zygote/fertilized egg is the first cell/stage of the diploid/sporophytic generation and it remains till the reduction division (meiosis) takes place in the sporogenous tissue. The spore mother cell represents the last stage of the sporophytic generation. Bryophytes stand at a higher level than the algae as they (Bryophytes) are more complexed in morphologyHence, in the plant kingdom Bryophytes have been placed in between Algae and Pteridophytes. The similarities with the algae are in the nature of photosynthetic pigment (chlorophyll), cell wall component, photosynthetic product (reserve food-starch) and the flagella. Besides, water is necessary for the sexual reproduction (process of fertilization) in both the groups. However, they (Bryophytes) differ prominently in having multicellular sex organs - (Antheridia and Archegonia) which are protected by the sterile jacket while in the algae, the sex organs (Antheridia and Oogonia) are unicellular which are not jacketed. With Pteridophytes, the Bryophytes share the common life-cycle pattern of heteromorphic alternation of generations and the multicellular, jacketed sex organs – Antheridia and Archegonia. Besides, the zygote and embryo (embryonic sporophyte) is permanently retained within the archegonium in both the groups. However, they differ mainly in the vascular tissue. Bryophytes lack typical vascular tissue while the pteriodophytes have well developed vascular system having xylem and phloem. Apart from this, in Bryophytes the main plant body is the gametophyte (either being leafy or thalloid) and the sporophyte is attached as well as dependent on the gametophyte. The sporophytic phase is never free living and independent. The sporophyte is differentiated into foot, seta and capsule and it has a limited growth.

While in the Pteridophytes, the main plant body is the sporophyte, which is of course attached to the gametophyte initially for a short period in the life - cycle but it is fully independent at maturity. The sporophyte is differentiated into well developed root, stem and leaves. They are perennial and have unlimited growth.

Bryophytes, “Liliputians of Plant Kingdom” are essentially small plants ranging from few millimeters to few centimeters. This is the only plant group, which exhibits a remarkable range of morphological diversity not found in any other group of the plant kingdom. With the exception of few aquatic forms, they are truly first land inhabiting plants. They represent a phase in the evolution when the plants have migrated from water to land but they seem to be incompletely adapted to the land habit, as they still require water for the

process of fertilization in completing their life - cycle. The ciliate antherozoids have to swim in the film of water for the act of fertilization. Their complete dependence on water for successful fertilization imposes serious restriction on their distribution. They are mainly confined to moist and humid places and are also described as "Amphibians of Plant Kingdom" This plant group continuously survived on Earth at least 75 million years before the age of the dinosaurs.

Habitat

Bryophytes are basically shade loving land plants, capable of growing on moist soil. They form small, vivid, green patches on the floor in all possible shades of green. Sometimes they form cushion, extensive mats or a thin or thick blanket cover on the tree trunk, tree branches and even sometimes on the leaf surface also.

Gametophyte

The Bryophytes generally form a natural group where the main plant body is a gametophyte. It is a conspicuous, long-lived, prominent and independent phase in the life cycle as compared to that of sporophyte. Due to presence of chloroplast, it is nutritionally self- sufficient. The gametophyte, although small, yet are highly diversified and well developed. The plant body is either undifferentiated (thalloid forms) or differentiated (leafy forms) into definite axis and leaves. In the leafy form, the stem (axis) and leaves are entirely different from true vascular plants (Trachaeophytes) as they belong to gametophytic phase whereas in the vascular plants they are the parts of the sporophyte. In fact, in Bryophytes, the axis and leaves are caulidia (central axial column) and phillidia (lateral appendages) but for the sake of convinience the terms axis (stem) and leaves are commonly used. The true roots are entirely absent in Bryophytes. The functions of roots, the attachment of the plant to the substratum and the absorption of water and minerals, are mainly performed by simple hair like structures called as rhizoids. The rhizoids are generally unicellular, simple (smooth walled) in hornworts; simple, tuberculate or sinuate in liverworts or multicellular, oblique septate in mosses.

Reproduction

The sex organs are always dorsal in position in the thalloid forms while in the leafy forms they are terminal/apical on the leafy axis. Some times male sex organs may be axillary in position as in most of the leafy liverworts.

Antheridia

The male reproductive organ – antheridia have a short or long stalk and spherical to elongated or clavate to cylindrical antheridial body. The androgonial cells /androcytes/ antherozoid mother cells are protected by a single layer of sterile jacket. Each of the androcyte gives rise to a single ciliated motile antherozoid.

Archegonia

The female reproductive organ is the archegonium, which is more or less flask shaped. The swollen basal portion of archegonium is called as venter and somewhat narrow, slender, elongated upper portion is called as neck. The archegonium consists of an axial row of number of neck canal cells, a ventral canal cell and a single, large egg, which are surrounded by sterile jacket.

Fertilization

The mature antheridium dehisces and releases antherozoids. They swim in the film of water and reach to the neck of the arehegonium. At the time of fertilization the neck canal cells disintegrate. The antherozoid swims upto the archegonial venter passing through the neck and fertilizes the egg.

Embryo

The fertilized egg starts dividing immediately after the fertilization without undergoing any resting period and remains inside the archegonial wall. It develops into a multicellular embryo, which differentiates into the sporophyte. Simultaneously, the cells of the archegonial venter actively divide to form a protective covering around the developing sporophyte and it is called as calyptra.

Sporophyte

The sporophyte consists of foot, seta and capsule. The foot is parenchymatous, conical structure, which remains embedded in the gametophytic tissue and derives nourishment for the developing sporophyte. Seta is the stalk, which holds the capsule. This may be of variable length. The capsule is the main fertile portion of the sporophytic generation. It has 1-many layered capsule wall enclosing archesporium. The archesporial cells get differentiated into spore mother cells only in mosses or both the spore mother cells and the elater mother cells in liverworts and hornworts. The spore mother cells, after meiotic division, form spore tetrads having haploid spores. The elater mother cells form elaters, which are sterile and help in the dispersal of spores. The Bryophytes are homosporous. All the spores are of same size. Under suitable conditions, the spore germinates to form new gametophyte either directly (as in liverworts and hornworts) or a distinct phase intervenes which is called as protonema (as in mosses). The buds develop on the protonema to form new gametophyte.

Marchantia

Habitat and Distribution

Marchantia – the type genus of the order Marchantiales, is a terrestrial form usually grows in moist and shady places. It is widely distributed all over the world.

About 11 species have been validly recorded from India. These are *M. emarginata (M. palmata), M. assamica, M. paleacea (M. nepalensis), M. subintegra, M. polymorpha, M. robusta (M. indica, M. kashyapii), M. linearis, M. pandei, M. papillata subsp. grossibarba, M. hartlessiana and M. gemminata.* The genus is represented in all the four major Bryogeographical regions of India but they show maximum distribution in Himalayas. The genus shows dense growth in hilly areas. However, Marchantia paleacea and M. polymorpha are found in plains also.

Gametophyte

The plants are large, dorsiventral, dichotomously branched thallus. A mature thallus may attain a length of 2-10 cm. They form very large green patches over the substratum (Fig. 8: 1). The thallus has a distinct midrib, which is marked by a shallow groove on the dorsal surface of the thallus and is projected on the ventral side. Often the mid rib portion forms a distinct blue streak as in case of *M. paleacea*. The apex of the thallus is notched in which the growing point is located. The dorsal surface of the thallus has distinct polygonal areas, which have a distinct central pore. They are smaller in the apical regions while they are larger in basal portion. The ventral surface of the thallus has rhizoids and ventral scales. The rhizoids are of two types: simple and tuberculate. (i) The simple rhizoids are smooth walled and generally present all over the ventral surface in between the ventral scales. They mainly help in the attachment of the thallus to the substratum. (ii) Tuberculate rhizoids are comparatively narrow and have small tubercles or peg like projections in the walls. They generally form dense tuft along the midrib and can absorb sufficient amount of water through capillaries thus mainly help in the absorption. However, the distribution of rhizoids is not so particular and both the types of rhizoids may be intermixed. The ventral scales are multicellular, unistratose membranous structure. They are present in 2-3 rows on both the sides of midrib. They may be termed as marginal, laminar and median starting from the margin. There are two types of ventral scales: marginal unappendaged and median appendaged. The appendaged scales have three main parts: (i) an apical appendage (ii) a short constricted neck and (iii) a prominent basal decurrent body through which it is attached to the thallus from apex towards the base. The margin of the scales has many mucilage papillae. The oil cells are present, scattered in between the cells. The ventral scales are mainly protective in function and help in retaining the moisture. The appendages of the appandaged scales bend over the thallus apex and protect the growing point.

Thallus anatomy

The thallus is internally differentiated into upper, narrow assimilatory (photosynthetic) zone and lower, broad storage zone. The assimilatory zone consists of air chambers, pores and assimilatory filaments. Air chambers are present in a single row. They are well defined and partitioned by unistratose septa. Each chamber opens out side by a central pore, present in the roof of chamber formed by the upper epidermis. These epidermal pores are not simple but very characteristics barrel shaped. The half of barrel is projected outside above the epidermis and other half of the barrel is projected inside the air chamber. The opening (pore) is bounded by number of cells, which are present in concentric rings. These pores on the outerside (observed from dorsal surface) are more or less rounded – oval while on the innerside they may be rounded, angular , stellate or cruciate depending upon the arrangement of the cells, whether they are evenly placed, superimposed or projected. At the base of the air chambers number of assimilatory filaments are present which may be branched or unbranched. The cells of the filament are chlorophyllous densely packed with the chloroplasts . Just beneath the assimilatory zone, the storage zone is present. It consists of all the thin walled parenchymatous cells, which are packed with the starch grains. Besides some of the cells are filled with the oil, while some other, are filled with mucilage, called as oil cells and mucilage cells respectively. In some species, mucilage canals are also present. They are elongated tubes, filled with the mucilage, and are lined by distinctly demarcated cells. They are mostly present in mature thalli and generally traverse in midrib portion. Besides, some thick walled cells – scleroids, are also present, scattered in between the thallus cells. The outermost layer on lower side of the thallus forms lower epidermis. Some of cells get elongated and develop into rhizoids. Ventral scales are also attached to it, which appear as a uniseriate, filament of beaded cells, in the section of thallus.

Growth of the thallus

The growth of a mature thallus takes place by a group of apical cells present in the apical notch. In the young gametophyte developing from sporeling, there is a single, 2-sided apical cell, which divides to form group of marginal meristem.

Vegetative/asexual reproduction

In *Marchantia*, vegetative reproduction may take place by death and decay of the older thallus portion due to which apical thallus lobes get separated and develop into individual thalli. This mode of fragmentation is quite common. Sometimes adventitious branches develop from ventral surface of thallus or any other part like stalk and disc of archegoniophore which get detached from parent thallus and develop into independent thalli. In this genus *Marchantia*, the most specialized method is the formation of characteristic asexual reproductive bodies called as gemmae. They are produced in a cup like structure . These gemma cups develop near the growing point and have number of gemmae attached to the base of the cups associated with numerous small, clavate, mucilage papillae. The margins of the cups may be smooth, dentate or frilled depending upon the different species. A mature gemma has unicellular stalk and multicellular biconvex discoid body . It has two lateral notches in which the growting point is located. Due to these notches it takes a shape of the number '8'. Both the growing points are opposite to each other and have a single marginal row of apical cells. All the cells of gemmae are chlorophyllous having number of chloroplast. Some of the marginal cells are colourless, devoid of chloroplasts called as rhizoidal cells, which form rhizoid at the time of gemma germination. Some of the cells are filled with oil, called as oil – cells.

Development of gemma and gemma cups

At the beginning, the gemma cups appear as a circular area near the apex of the thallus. The epidermal cell of this area protrudes out as an outgrowth in the form of papilla. It acts as gemma initial and divides transversely forming basal cell, stalk cell and primary gemma cell. The stalk cell does not divide further and forms a short, single celled stalk of gemma. The primary gemma cell divides transversely producing a 4-5 celled filament, which further divides in both the vertical and horizontal planes forming multicellular gemmae. Initially, the gemmae are unistratose but later on by periclinal division, they become thick in the center forming typical discoid gemmae . Meantime the thallus tissue grow upward all around forming a hollow cup. Mucilage papillae also develop from the inner wall of the cup.

Gemma dispersal and germination

The mucilage papillae secrets the mucilage, which absorbs moisture and swells up causing the gemmae to break as their stalks are slender. The detached gemmae are dispersed by splashing of rain drops or washed away by rain water. Under suitable conditions, when gemma falls on the soil, it starts germinating. The rhizoidal cells, which are in contact with the soil, develop into the rhizoids and absorb water. Soon the apical cells become active and two young thalli start developing in opposite direction. Gradually the central part of the gemma disintegrates. Two young thalli become separated and develop into new independent thalloid gametophyte.

Sexual reproduction

The genus *Marchantia* is strictly dioecious. Both the sex organs, antheridia and archegonia develop on a specialized stalked receptacle called as antheridiophore and archegoniophore respectively.

Antheridiophore

Antheridiophores are always terminal and present at the apices of the thallus. The apical growing point is utilized in their formation, so that the further growth of the thallus is checked. An antheridiophore has an elongated stalk and a terminal flat, lobed disc. The number of lobes may vary from 2-10. The antheridia are embedded in the disc (lobes) inside the antheridial chambers on the dorsal side. The antheridial chambers are present alternate with the air chambers, which are same as found in thallus, having assimilatory filaments and barrel shaped pores. Each antheridial chamber, normally, has single antheridium with short multicellular stalk and more or less ovate – elongated antheridial body. In some species, mucilaginous filaments may arise from the inner wall of antheridial chamber. These mucilaginous cells help in retaining the moisture in the chambers. The antheridia develop in acropetal manner. The older antheridia are present in the center of the disc while the younger ones are near the apex of the lobes.

Archegoniophore

The archegoniophores are also terminal and always present at the apices of the thallus. In this case also the growth of thallus is checked as the growing point is consumed in the formation of archegoniophore. An archegoniophore has elongated stalk and lobed disc of various forms depending upon the species. In *M. polymorpha* the disc has finger like sterile lobes hanging down giving an umbrella like appearance to archegoniophore . The archegonia are superficial and present on fertile lobes of the discs. They also develop in acropetal manner. The young archegonia are present towards the apex of lobes and older archegonia are present in the center of the discs. At initial stage these archegonia are dorsal in position but with the growth, subsequent to fertilization, the lobes get curved downwardly pushing the archegonia towards the lower side of the disc. The archegonia, which were dorsal in position as well as in origin, now become inverted and ventral in position (only). Each archegonium has a long neck and swollen venter with number of neck canal cells, a ventral canal cell and an egg . The neck portion has 6 vertical rows in the jacket. Each archegonium is enclosed in a protective covering called as perigynium while each archegonial group on the lobe is protected by another pendent covering, called as perichaetium. It is unistratose with free, laciniate, fringed margin having filamentous projections. The upper (dorsal) portion of the disc and sterile lobes have distinct (i) assimilatory zone with air chambers, barrel shaped pores as well as assimilatory filaments and (ii) storage zone with parenchymatous cells having starch grains, and oil cells like the thallus.

Stalk of antheridiophore/Archegoniophore

The stalk of both the male and female receptacle is same in the structure. It is small at young stage but till maturity it attains a considerable height and becomes erect. Internally it is differentiated into assimilatory and storage zones, like the thallus. Towards the morphological dorsal side (the side in continuation with the dorsal surface of the thallus), the stalk has assimilatory zone with reduced air chambers, barrel shaped pores and lesser number of assimilatory filaments. This assimilatory zone may be highly reduced to even absent in some species. Adjacent to the assimilatory zone, storage zone is present having thin walled parenchymatous cells. In the central region the cells are narrow, elongated which help in conduction and appear smaller in cross section. Towards the morphologically ventral side (the side in continuation with the ventral surface of the thallus), there are two cavities or furrows, present on lateral sides. These are called as rhizoidal furrows. The rhizoids and scales are present in these cavities.

Development of Antheridiophore/Archegoniophore

The initial stages in the development of antheridial and archegonial discs are same. The growing point, located in the apical notch, divides and redivides dichotomously resulting into many- lobed structure with its own growing point. In antheridial disc, a number of antheridia are produced embedded in the disc while in archegonial disc a number of archegonia are produced on the surface of the disc. Both the sex organs develop in acropetal manner. With the growth, stalk develops at base of the disc, which later on elongates considerably carrying the disc upward. All these structures – stalk and the discs (male and female) as well as gemma cups are the modified thallus tissue to bear the sex organs and gemmae.

Development of antheridium

The development of antheridium is more or less similar as found in other liverworts. The antheridial initial appears near the growing apex of the lobe of the antheridial disc. It becomes evident somewhat in a conical form and remains embedded in the lobe tissue . It divides transversely forming 2- celled rudiment with lower stalk cell and upper antheridial cell. The stalk cell divides in regular manner both transversely and vertically forming a short multicellular stalk. The upper antheridial cell first divides in transverse plane forming 2-4- celled filament, which further divides both vertically as well as periclinally differentiating into outer primary jacket cells and inner primary androgonial cells. The primary jacket cells divide anticlinally forming single layered jacket of antheridium. The primary androgonial cells divide repeatedly producing large number of androgonial cells which, at last, divide diagonally forming two triangular androcytes from each androgonial cell.

Later on, androcytes differentiate into coiled, biflagellate spermatozoids. Simultaneously, the adjacent cells of lobe divide and encircle the developing antheridia. Thus mature antheridium remains embedded in antheridial chamber.

Development of archegonium

The archegonial development is also similar to other liverworts. However, it differs in the number of cells in the vertical rows of archegonial neck region. The archegonial initial makes it appearance as a projection (papillate outgrowth) on the lobe of archegonial disc. It divides into upper and lower cell. The upper cell divides thrice vertically by oblique walls, which intersect each other resulting into an axial and three peripheral cells. Now, each of the three peripheral cells divides vertically resulting into six rows of cells forming the jacket of neck, which is a characteristic feature of the order Marchantiales. Now axial cell divides to form four cover cells, 4-6 neck canal cells, a ventral canal cell and an egg. After fertilization, these archegonia become shifted on the lower side of the disc. New archegonia may develop at this stage but on the ventral side and remain inverted.

Fertilization

After the maturity of antheridium, if water falls on the disc, it finds its way to antheridial chamber. The jacket cells of the antheridium ruptures when they come in contact with water releasing androcytes in a long smoke like column. The androcytes spread on the water surface and antherozoids get liberated vary soon. According to Strassburger (1869) when the water drops fall over the surface, they spread the antherozoids to longer distance upto 2 feet by splashing of water drops. The water drops containing antherozoids, fall over the archegonial disc, which may flow over the edges reaching to the archegonial neck and fertilization takes place.

Sporophyte

The mature sporophyte has distinct foot, seta and capsule. The foot is broad somewhat conical in shape and anchors the sporophyte in the tissue of archegonial disc and derive nourishment for developing sporophyte. The seta is short massive, which elongates at maturity. The capsule is more or less spherical to oval in shaped with single layered capsule wall, spores and elaters. The cells of the capsule wall have thickening bands in the form of stripes. The spores are very small and numerous. They may be polar or cryptopolar. The polar spores are globose, without triradiate mark and with two spore coats (exine and intine) while the cryptopolar spores are somewhat tetrahedral in shape (not globose) with indistinct triradiate mark and three spore coats – exine, intine and perinium or perisporium. The elaters are long narrow, pointed at both the ends having 2-3 spiral thickning bands.

Development of sporophyte

The zygote first divides by transverse or somewhat oblique wall forming upper and lower cell. The next division may be at right angle to the first division resulting into a quadrant embryo (e.g. *M. polymorpha* - Durand, 1908, and *M. domingensis,* - Anderson 1929, or the next division may be parallel to the first division resulting into filamentous (3- celled)) embryo (e.g. *M. chenopoda* - Mc Naught, 1929. In case of *M. polymorpha* the upper cells (facing downward as archegonia are inverted in position) develop into capsule and lower cells develop into seta and foot. In case of *M. domingensis* the upper cells form the capsule and part of seta while the lower cells form the part of seta and foot. In 3- celled filamentous embryo of *M. chenopoda*, the upper cell forms capsule, middle cell forms seta and lower cell forms foot. With these developments, the cells of the archegonial venter start dividing periclinally forming multilayered calyptra around the developing sporophyte. The cells adjacent to venter also divide to form single layered membranous perigynium around the venter. Now the cells of the embryo divide in various planes forming more or less a globular multicellular structure. The terminal portion becomes somewhat broader than the inner portion and becomes distinct to form capsule. Now periclinal divisions takes place and it gets differentiated into outer amphithecium and inner endothecium. The amphithecium forms the single layered capsule wall in which thickening bands develop at maturity. The cells of the endothecium repeatedly divide forming numerous sporogenous cells. These cells elongate, separate from each other and get differentiated into (i) broader fertile cells and (ii) narrow elongated sterile cells. The fertile cells have dense cytoplasm and prominent nuclei. They divide repeatedly by transverse divisions producing number of daughter cells, which are arranged usually in one row sometimes in two rows within the parent cell wall. These are spore mother cells. During the process, after nuclear division clevage starts in the protoplast from peripheral region, which gradually deepens and the parent cell divides into two cells, each having its own wall. The cell wall of each generation is clearly visible in the fertile cell. In *M. palmata* (now *M. emarginata*) and *M. domingensis* eight spore mother cells are produced while in *M. polymorpha* 32 spore mother cells are produced. Subsequently parent cell wall disintegrates and spore mother cells become free, which divide meiotically to form spore tetrads. The sterile cells are elater mother cells, which do not divide further, simply elongate to form long tapering elaters. The cytoplasm gradually disappears and 2-3 spiral thickening bands develop in their inner wall. The elaters are hygroscopic in nature and help in spore dispersal. In *Marchantia*, the spore mother cells and elaters mother cells do not belong to same generation and the difference is of many generations. As a result very large number of spores are produced in comparison to lesser number of elaters. For e.g. in *M. polymorpha* the ratio between the spore mother cell to elater mother cell in 32:1, hence ratio between spores and elaters is 128:1.

Dehiscence of the capsule

At maturity, the seta elongates pushing the capsule out through the calyptra, perigynium and perichaetium. Now the capsule gets exposed to drier environment. Due to loss of moisture in the cells of the capsule wall, the capsule splits irregularly into 6-8 valves. The spores fall down as capsule (archegonia/sporophyte) is inverted. Coiling and uncoiling of elaters further fascilitates the spore dispersal by loosing the spore mass. The falling spores are carried away by wind current.

Spore germination

Under suitable condition, the spores germinate. The spore first divides into two cells . One of the cells elongates to form germ rhizoid, while the other cell, which has dense chloroplasts, divides to form 2-3- celled filament. Now the cells of filament divide in other planes forming a group of cells. The cellular structure (sporeling) thus produced may be branched or unbranched. Gradually the cells are added to the developing gametophyte and a row of marginal meristematic cells appear towards the apex. By the activity of these cells, thallus grows further. In some cases, at early stage a 2-sided apical cell is formed which cuts off number of cells. Finally it divides into group of apical initial cells, which lie in the apical notch produced at the apex of the thallus.

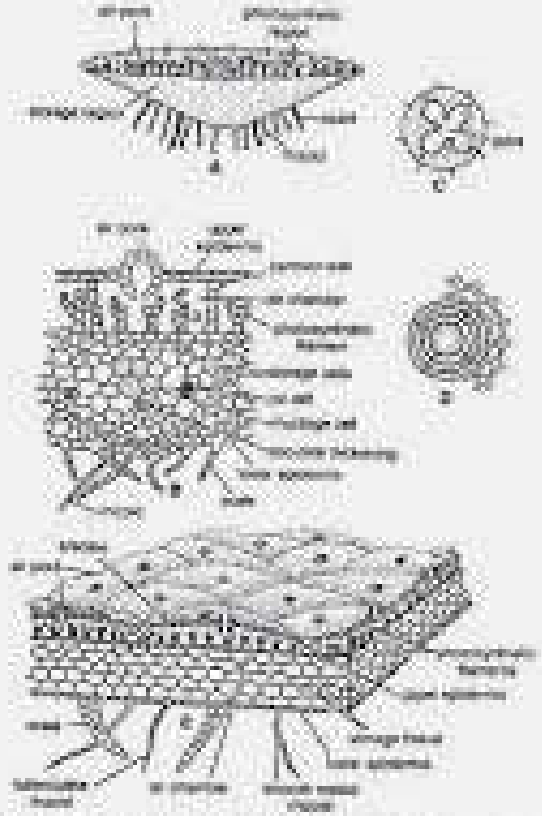
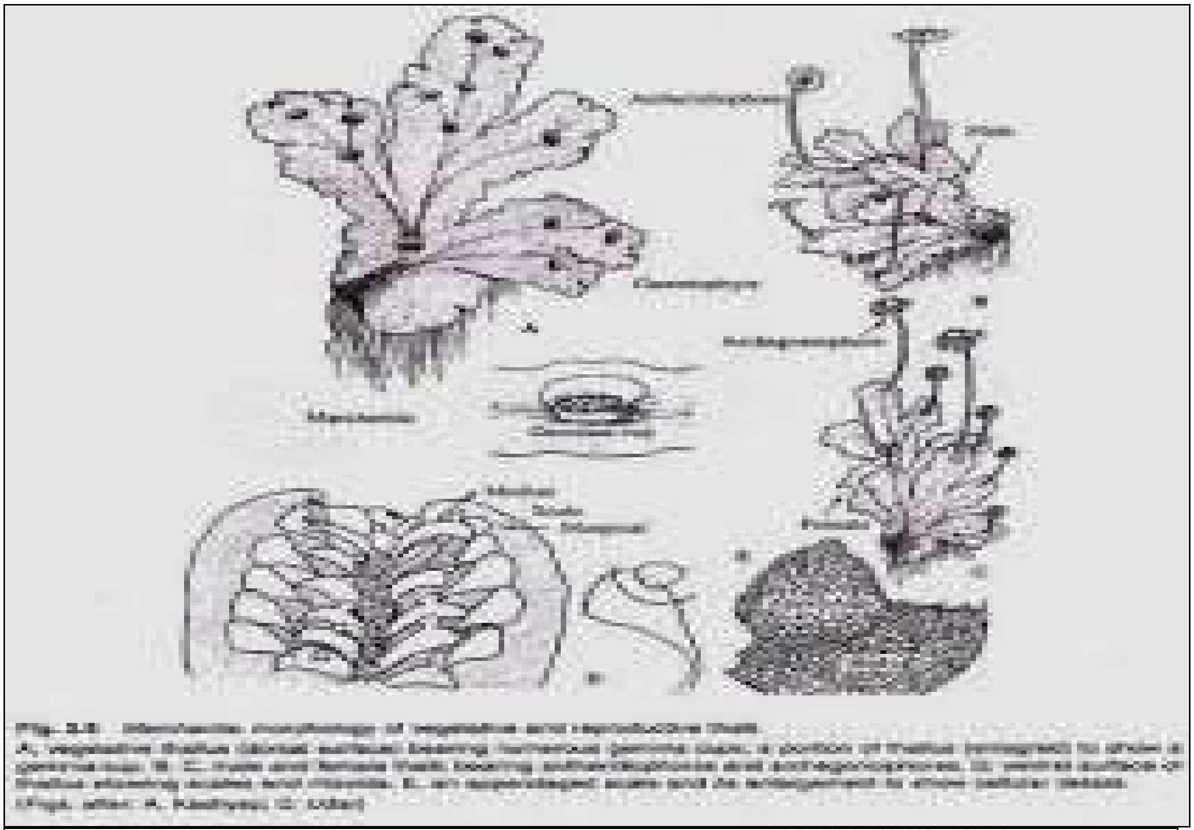


Fig. 3. (A-E). Marchantia. Internal structure of the thallus. (A) Vertical Transverse Section (V.T.S.) of thallus (diagrammatic), (B) V.T.S. of thallus (a part cellular), (C) Air pore as seen in the ventral view, (D) Air pore as seen in the dorsal view, (E) V.T.S. of thallus in three dimensional view.



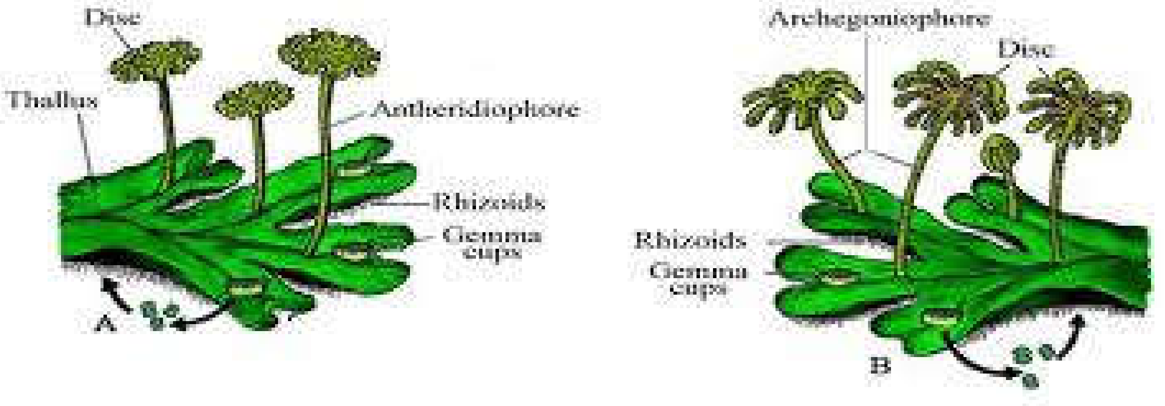


Fig: ***Marchantia spp***. (A) Male plant. (B) Female plant.

Marchantia sp.

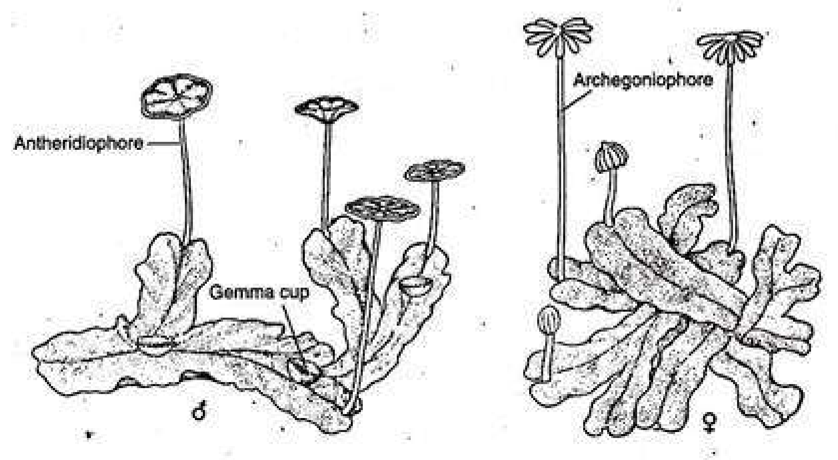


Fig. 6.8 : Male and female plants of *Marchantia polymorpha*

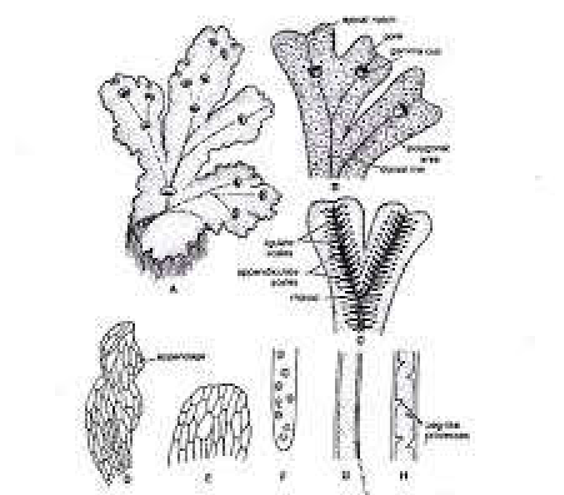


Fig. 1. (A-H). Marchantia. Thallus structure (A) Vegetative thallus, (B) Dorsal surface, (C) Ventral surface, (D) Appendiculate scale, (E) Ligulate scale, (F) Tuberculated rhizoid (surface view), (G) Smooth-walled rhizoid, (H) Tuberculated rhizoid showing internal view.

Vegetative structure of Marchantia

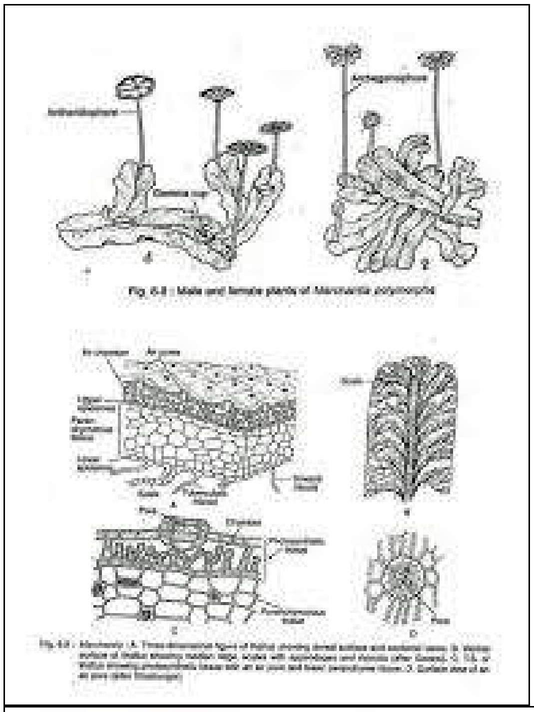
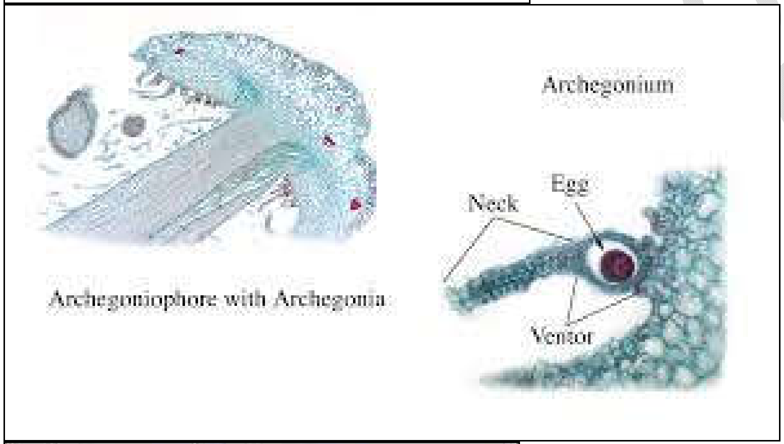
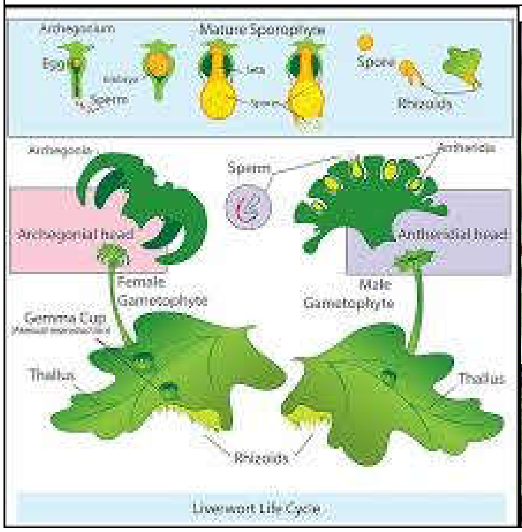
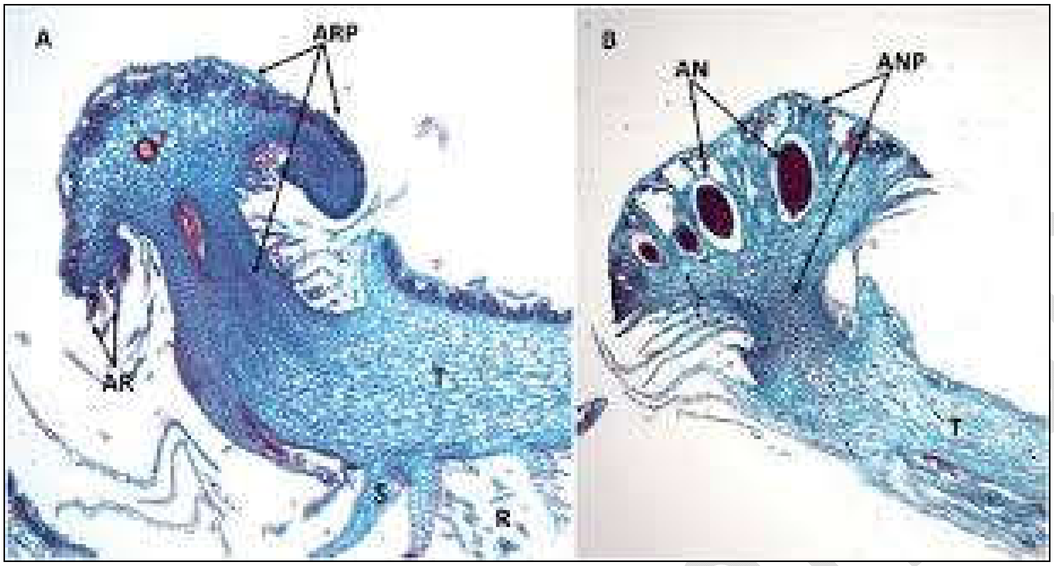


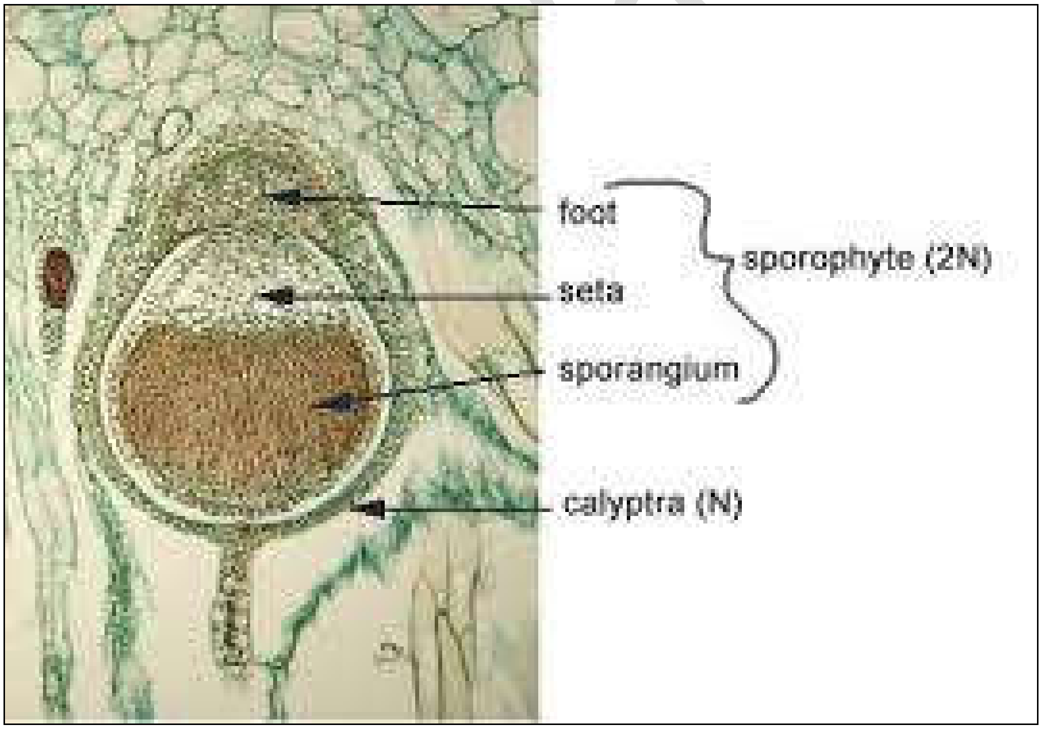
Fig. 6.8 : Male and female plants of Marchantia polymorpha







Marchantia archaegoniophore and antheridiophore : Section



Marchantia sporophyte

Anthocerotopsida

The class Anthocerotopsida is a small group of plants in which the gametophyte is rather simple, however, sporophyte is comparatively complex and horn like or needle like. Hence members of this group are commonly called as 'Hornworts'. The plants are dorsiventral, lobed thallus without any internal tissue differentiation. The thallus may be compact or spongy. Air chambers and pores are absent. Rhizoids are smooth walled. The ventral scales are totally lacking. The epidermal cells usually have single, large, plate like chloroplast with conspicuous pyrenoid bodies. Distinct *Nostoc* chambers and mucilage chambers are also present inside the thallus. The sex organs are embedded in the gametophytic tissue. Antheridia are present in groups or singly within the androecial chamber. They are endogenous in origin formed by the hypodermal cell on the dorsal side of the thallus . The archegonia are exogenous in origin formed by outer cell but they remain embedded in thallus tissue with six rows of cells in the neck portion. The sporophyte is differentiated into capsule and foot only. Seta is absent. The capsule is cylindrical 'horn' like and is not determinate in growth. The basal portion of the capsule is meristematic. It continues to grow and adds to the upper portion of the capsule. Capsule wall is multistratose 4-6 layered, chlorophyllous with or without stomata. The sporogenous tissue is amphithecial in origin. The entire endothecium forms the central sterile portion-columella. Sometimes the columella may be absent as in some species of *Notothylas*.

The class Anthocerotopsida (=Anthocerotae) distinctly differs from class Hepaticopsida in many features like

(1) the presence of only thallose gametophytes (2) the presence of large chloroplasts with pyrenoid bodies, (3) embedded sex organs (4) endogenous origin of antheridium (5) indeterminate growth of the sporophyte (6) presence of meristematic zone at the base of capsule, (7) absence of seta (8) presence of 1-4 celled elaters (pseudoelaters) along with the spores which are amphithecial in origin (9) presence of stomata on the capsule wall.

Besides above features, the sporophyte in this group is partially independent due to presence of stomata, chlorophyll (chloroplasts) and columella. Further it shows symbiotic relationship with blue green alga. Due to these distinctive features this group, which was earlier placed in Hepaticae as Anthocerotales at order level, has been raised to the class level. Earlier only single family Anthocerotaceae and single order Anthocerotales was recognized in the class Anthocerotae (Muller, 1940) but later on two families Anthocerotaceae and Nothylaceae have been recognized (Reimer, 1954; Proskaur, 1960, Schuster 1984b). Bharadwaj (1981), however, recognized three families: Anthocerotaceae, Phaeocerotaceae and Notothylaceae. Hassel de Menendez (1986) introduced fourth family

Leiosporocerotaceae to place the new genus *Leiosporoceros* (see also Hassel de Menendez, 1988). Recently, Stotler and Stotler (2005) proposed revised classification of Anthocerotophyta, recognizing the group as phylum and divided it into two classes, three orders and four families. Class (i) - Leiosporocerotopsida with order – Leiosporocerotales (one family – Leiosporocerotaceae), and Class (ii) - Anthocerotopsida with orders (a) Anthocerotales (one family - Anthocerotaceae) and (b) Notothyladales (two families - Notothyladaceae and Dendrocerotaceae).

The type genus *Anthoceros* was established by Micheli (1729), which was adopted by Linnaeus (1753). Then in subsequent years more taxa were introduced. Chronologically these are: (2) *Notothylas* (Sullivant, 1845), (3) *Dendroceros* (Nees, 1946), (4) *Megaceros* (Campbell, 1907), (5) *Aspiromitus* (Stephani, 1916), (6) *Phaeoceros* (Proskauer, 1951), (7) *Folioceros* (Bhardwaj, 1971), (8) *Leiosporoceros* (Hassel de Menendez, 1986), (9) *Sphaerosporoceros* (Hassel de Menendez, 1986), (10) *Mesoceros* (Pippo, 1993), (11) *Hattorioceros* (Hasegawa, 1994) and (12) *Nothoceros* (Hasegawa, 1994). At present the group includes eleven genera. The family (I) Leiosporocerotaceae with (1) *Leiosporoceros* (II) Anthocerotaceae with (2) *Anthoceros*, (3) *Folioceros*, (4) *Sphaerosporoceros* (III) Notothyladaceae with (5) *Notothylas,* (6) *Hattorioceros*, (7) *Mesoceros*, (8) *Phaeoceros*, and (IV) Dendrocerotaceae with (9) *Dendroceros*, (10) *Megaceros*, (11) *Nothoceros.* **In India the group is representated by 5 genera: *Anthoceros,***

Folioceros, Phaeoceros, Megaceros, Notothylas **along with 38 taxa (Asthana and Srivastava, 1991; Asthana and Nath, 1993; Singh, 2003)**

Bryopsida

The class **Bryopsida (Musci)** has acquired a separate, independent status, parallel to the class Hepaticopsida (Hepaticae) since very beginning. This group is mainly characterized by exclusively leafy gametophytes. Generally they are erect growing (acrocarpous) while some others are prostrate growing (pleurocarpous). Some epiphytic forms may be hanging or pendulous (see Schofield and Hebant 1984). They are differentiated into axis and spirally arranged leaves. The leaves are usually with distinct midrib being multistratose in midrib portion and unistratose in wing portion. The rhizoids are multicellular and obliquely septate. The sex organs are always terminal, present in groups. They are exogenous and develop by means of an apical cell. They are associated with multicelullar uniseriate paraphysis and are protected by perigonial (male bracts) or perichaetial (female bracts) leaves. Antheridia are stalked with clavate to elongated cylindrical antheridial body. Archegonia are also stalked with long neck. Peristome is an important feature of the moss capsule and helps in spore dispersal. Besides, protonema – a short intervening phase is present in between the spore and adult gametophyte). The sporophyte is of determinate growth and partially independent due to presence of chloroplasts and stomata in the capsule wall. It (sporophyte) consists of foot, seta and capsule. Foot is embedded in the apical gametophytic axis. Seta is much elongated, stout, rigid and elongates before the maturation of the capsule. The capsule is generally cylindrical – elongated with outermost multilayered capsule wall, the central sterile column – columella, and in between the spore sac, which has spores only. Elaters are totally absent. The sporogenous tissue is endothecial in origin. The capsule has a distinct operculum, which gets removed at maturity. At the mouth of the capsule there is **a fringe of peristome teeth (Arthrodontous or Nematodontous type)**, which help in the dispersal of spores. The moss spores, after germination form a short distinct phase – protonema first. On the protonema, buds are produced which develop into adult gametophytes. Thus a single spore gives rise to number of gametophytes. This is one of the main reasons why mosses are more dominant than the liverworts and hornworts where a single spore gives rise to a single, adult gametophyte in both the liverworts and hornworts. Bryopsida includes a large number of mosses, which are variously classified by giving importance to one or the other characters.

Funaria

Habitat and Distribution

Funaria is a cosmopolitan genus, widely distributed in temperate and tropical regions of the world. It is commonly found growing on moist rocks, soils or on the walls. *Funaria hygrometrica* is a very common species growing extensively in the hills of various parts of the country. It is also called as bonfire/postfire species as it is a pioneer, agent, which first appears in colonization at the burnt sites rich in ash and nutrient contents.

Gametophyte

The plants are small, erect growing and differentiated into axis and spirally arranged leaves. The leaves are small, sparsely arranged at the base while large, crowded at the apex, forming rosette. They are simple, ovate - elongated, broad at base and pointed at apex, with smooth margins and distinct mid rib. The rhizoids are present at base of the axis. They are multicellular, oblique septate, brown and form a tangled mass.

Axial & leaf anatomy

The axis shows very simple internal organization. It has an outer single layered epidermis, followed by 3-5 layered cortex with thick walled cells in mature plants enclosing central conducting region with narrow elongated cells. In the apical portion of axis, the leaf traces are present which end blindly in the cortex. The leaf has well defined narrow, multistratose mid rib with thin walled narrow cells surrounded by a sheath of thick walled cells. The lateral wings are broad, unistratose with thin walled, elongated, rectangular to rhomboidal cells with numerous discoid chloroplasts. The marginal cells are somewhat projected near the apex giving an appearance of dentate margin.

Apical growth

The apical growth of the axis takes place by a definite apical cell with three cutting faces giving the radial symmetry to the axis with the three rows of leaves corresponding to three cutting faces.

Vegetative reproduction

Usually plants propogate vegetatively by the separation of branches from parent axis. Besides, multicellular, brown, bud like structure called as gemmae may develop on rhizoidal branches of protonema, which are the means of vegetative propogation.

Sexual reproduction

The plants are monoecious (autoecious) and protandrous. Both the sex organs develop on separate branches of same plant. The antheridia develop first on the main axis. Later on side branches develops which are more vigourous, and bear archegonia. These female shoot are higher and dominant than the male shoot.

Antheridia

The antheridia are present in groups at the apex of shoot. They are surrounded by conspicuous perigonial leaves and are associated with chlorophyllous, multicellular uniseriate, filamentous paraphysis with terminal swollen cell. A mature antheridium has multicellular stalk and elongated cylindrical antheridial body with single layered jacket and numerous androcytes.

Archegonia

The archegonia are also present in groups at the apex on archegonial shoot associated with uniseriate paraphysis. A mature archegonium is stalked and flask shaped with narrow elongated neck and swollen archegonial venter. The jacket in neck portion is unistratose with six vertical rows of cells while it is bistratose in archegonial venter. The axial row has 6-many neck canal cell, a ventral canal cell and an egg. The development is typical moss like through an apical cell as in case of *Pogonatum*.

Fertilization

Fertilization takes place in usual manner. The mature antheridium dehisces when it comes in contact with water, releasing antherozoids. The cover cell, neck canal cells and ventral canal cell of archegonium disintegrate creating the passage. The spermatozoids swim chemotactically and fertilize the egg.

Sporophyte

The sporophyte has a small foot (embedded into gametophytic axis), an elongated, rigid, brown seta and a pear shaped, dark brown coloured, somewhat asymmetrical, curved capsule . **The capsule has three distinct parts: (i) basal apophysis (ii) middle theca and (iii) apical opercular region. (i) The apophysis is distinct with outer most epidermal layer along with stomata followed by spongy chlorophyllous tissue with air spaces. In the center thin walled elongated cells are present which are devoid of chloroplasts. (ii) The theca portion has 2-3 layered capsule wall without stomata** followed by large air spaces traversed by elongated trabeculae and then there is spore sac, which has 3 layered wall on outerside and single layered wall on innerside. In the center columella is present which has thin walled parenchymatous cells. (iii) The opercular region is separated from the theca by a distinct constriction where 2-3 layers of radially elongated cells are present forming the rim. Annulus is present just above the rim having 5-6 layers of cells with elongated uppermost cells, which help in the separation of operculum At the capsule mouth, (edge of the rim) peristome is present, which is arthodontous type having two rings of sixteen peristome teeth. The outer ring (exostome) has 16 large, brown coloured teeth with transverse thickening band. The inner ring also has 16 thin, delicate, pale or colourless teeth.

Dehiscence of capsule

Due to loss of moisture in dry weather, the delicate thin walled annulus acts as weak point and the operculum get removed exposing hygroscopic peristome, which help in spore dispersal.

Spore germination

Under suitable conditions, the exospore (spore coat) rupture at one or two points producing the germ tubes which elongate and develop into branched filamentous protonema. Some erect branches become green due to chloroplasts and called chloronomea while other growing on substratum and develop rhizoids. Buds develop on protonemal filaments, which further develop into new gametophyte by the activity of apical cell.

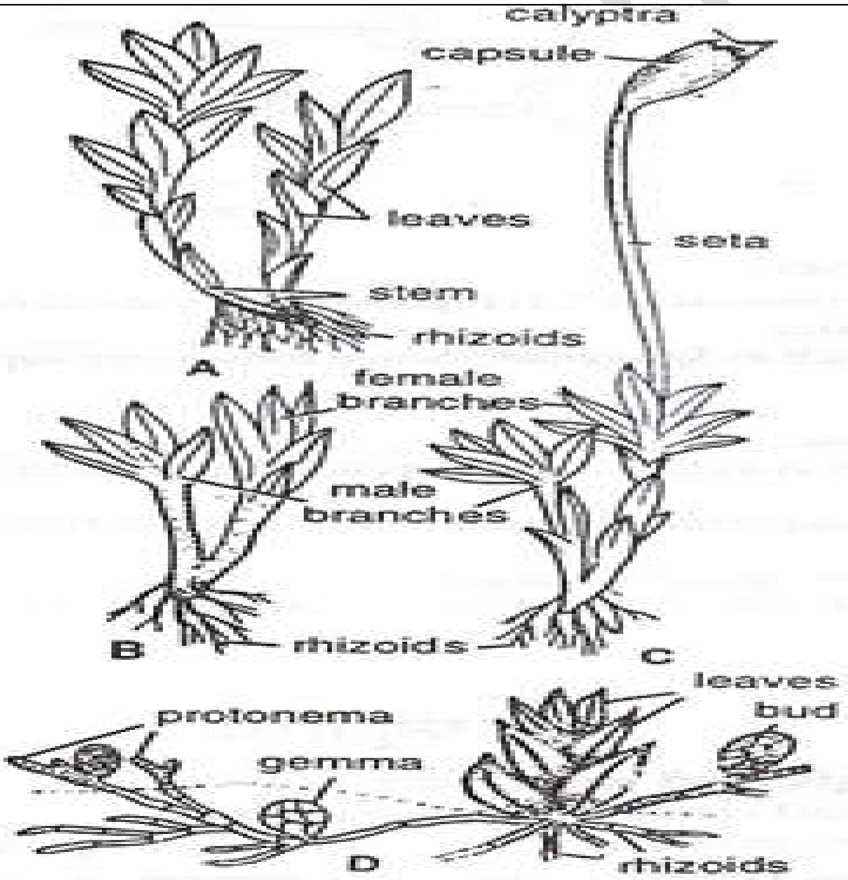


Fig. 194. *Funaria. A, Vegetative plants; B, Plants with male and female branches; C, A mature plant bearing a sporophyte; D, Protonema and young gametophyte.*

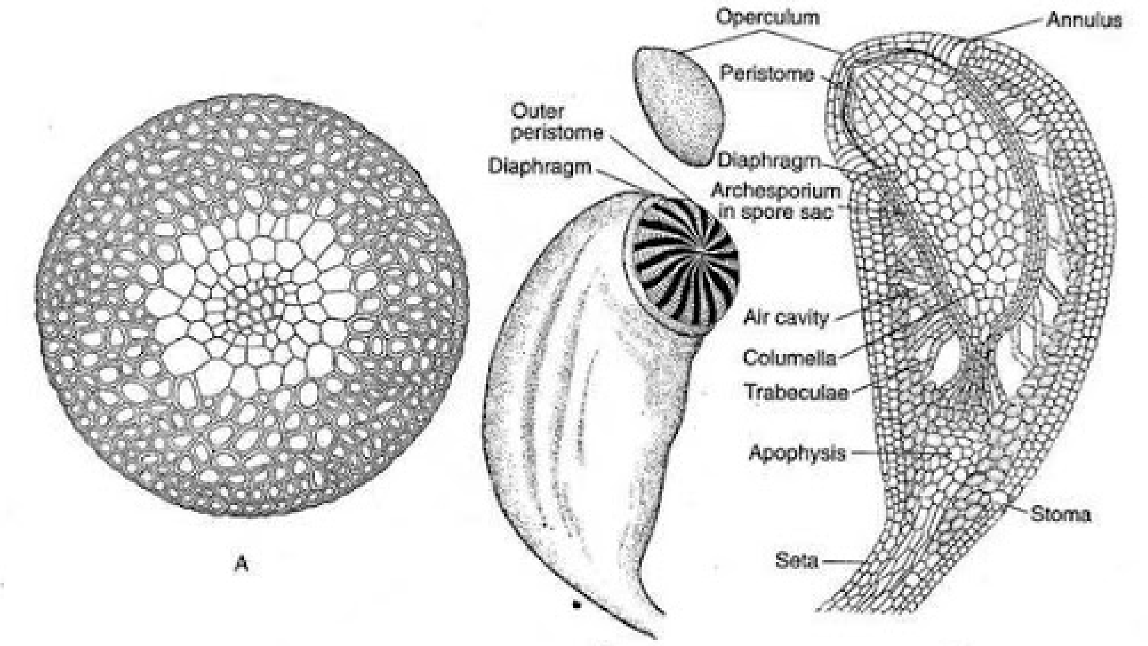


Fig. 6.50 : *Funaria hygrometrica* : A. T.S. of seta, B. Mature capsule with operculum removed (shown on side), C. L.S. of capsule

FUNARIA SPOROPHYTE

Special notes on bryopsida

The peristomate or true mosses (Superclass V) have traditionally been divided into two broad morphological groups, namely, acrocarps and pleurocarps, based on the position of the perichaetia and subsequent sporophytes (Fig. 1). Acrocarps are characterized by erect or ascending shoot systems that are either unbranched or only sparingly branched. Branching is typically sympodial with the branches morphologically comparable to the determinant main shoot from which they arise.

Perichaetia are differentiated at the tip of the main or primary shoot and terminate its growth, so further plant growth occurs only if a branch is produced below the perichaetium; such branches are called subfloral innovations. Pleurocarps are generally characterized by creeping shoot systems, with extensive lateral branching. In such systems, the indeterminant main stem may be morphologically distinct from the secondary and tertiary level branches that arise from it (C. La Farge 1996). Perichaetia in pleurocarps are produced at the tips of very short, basally swollen lateral branches that are morphologically distinct from the vegetative branches. Because of the extremely reduced size of the perichaetial branches, the sporophytes appear to arise from scattered positions all along the primary stem. Cladocarpic mosses produce perichaetia at the tips of unspecialized lateral branches that display the same heteroblastic leaf series as the vegetative branches. Such branches are themselves capable of branching, and these mosses are neither acrocarpic nor pleurocarpic (La Farge). Although acrocarps, pleurocarps, and cladocarps tend to have different branching architectures, it is the morphology of the perichaetium-bearing module that defines the groups, not branching habit (La Farge). Pleurocarps form a natural, monophyletic lineage of true mosses (B. Goffinet and W. R. Buck 2004), but cladocarpy has evolved in several different lineages. Acrocarpy, which appears to be the plesiomorphic condition, also characterizes the Takakiopsida, Andreaeopsida, and

Andreaeobryopsida. The main stems of *Sphagnum* (Superclass II) display a furcate or dichotomous branch architecture (H. A. Crum 1984). Along the main stems, fascicles of branches are produced in every fourth leaf (H. Leitgeb 1869), with three or more branches per fascicle. At least two branches in each fascicle hang downwards and are appressed to the stem,

while one to three are divergent. Despite their distinctive fascicled arrangements, all branch development in *Sphagnum* is like that of other mosses, with each branch arising from a single axillary bud initial (Leitgeb). At the apex of the main shoot, the abundant developing fascicles are tightly clustered into a dense tuft called the capitulum. Archegonia terminate special, short branches in the capitulum.

The Peristome

In the majority of stegocarpous mosses, spore dispersal is mediated by the peristome, a circular system of teeth that is inserted on the mouth of the urn, to the inside of the operculum. The developmental history and architecture of the peristome provide a suite of important systematic characters . Peristomes are of two fundamentally different types, nematodontous, which are found only in Polytrichopsida and Tetraphidopsida, and arthrodontous. In a nematodontous peristome, the teeth are constructed of bundles of whole, dead cells. Commonly in the Polytrichopsida, 32 or 64 (rarely 16) short lingulate teeth, comprised of up to four layers of vertically elongate, very thick-walled cells, are attached by their inner surface to a membranous expansion of the columella called the epiphragm. The release of the operculum exposes small slits between the teeth through which the spores are slowly released. In the Tetraphidopsida, there are four erect, wedge-shaped peristome teeth, each of which represents a quadrant of the peristomial cell layers. In contrast to the cellular peristomes of these taxa, arthrodontous peristomes, found in the rest of stegocarpous mosses, consist at maturity only of remnants of paired, periclinal cell walls. As reviewed by several authors (e.g., S. R. Edwards 1984; A. J. Shaw and H. Robinson 1984; W. R. Buck and B. Goffinet 2000), arthrodontous peristomes differentiate from the three innermost layers of the amphithecium formed by fundamental square divisions (K. Goebel 1900–1905, vol. 2) in the apex of the embryonic capsule. Following H. L. Blomquist and L. L. Robertson (1941), these are termed the outer peristomial (OPL), primary peristomial (PPL), and inner peristomial layers (IPL). The number of cells in the peristomial layers in a 1/8 slice of a transverse section is expressed as the peristomial formula (Edwards 1979); thus, a peristomial formula of 4:2:3 describes a capsule with 32 OPL, 16 PPL, and 24 IPL cells. The number and arrangement of cells in the peristomial layers cannot always be determined with certainty in mature capsules, so peristomial formulae are generally not included in taxonomic descriptions.

Arthrodontous peristomes are of two major types, namely, **haplolepidous and diplolepidous** . The haplolepidous peristome consists of a single ring of 16 teeth that are formed by cell wall deposition on the paired walls of the PPL and IPL. The peristomial formula is always 0(4):2:3, with a single column of PPL cells forming the outer (dorsal) surface of each tooth, and unequal parts of two IPL cells forming the inner (ventral) surface. Consequently, the outer surface of the tooth, which may be variously ornamented with horizontal striae, trabeculae, or papillae, lacks median or divisural lines (= vertical cell walls). The teeth can be forked at their apices, as in the Dicranaceae, or be fused at the base into an elongate tube, or basal membrane, or be divided into 32 long narrow, filaments, e.g., the Pottiaceae. Development from the OPL is highly reduced or absent, forming at best prostomial bumps at the base of the peristome (S. R. Edwards 1984). Diplolepidous peristomes have the same number of cells in the OPL and PPL as haplolepidous peristomes, but display substantial variation in the IPL numbers, with peristomial formulae ranging from 4:2:4 to 4:2:14. Two sets of teeth are differentiated, the exostome, or outer peristome, formed by deposition on the paired walls of the OPL and PPL, and the endostome, formed at the PPL–IPL wall junctures. The exostome typically consists of 16 teeth, equal to the number of cells in the PPL, while the outer surface of each tooth bears a divisural line that marks the two columns of cells of the OPL. The teeth may be joined together in pairs, or secondarily divided, and are often highly ornamented, especially on the outer surface (A. J. Shaw 1985). The architecture of the endostome is likewise variable, with different patterns of surface ornamentation on outer and inner surfaces (Shaw and J. R. Rohrer 1984). In a diplolepidousalternate peristome (D. H. Vitt 1984) of the bryoid or hypnoid type, the endostome comprises a basal, often keeled membrane, topped by 16 broad, perforate segments that alternate with the exostome teeth. One to four uniseriate cilia occur between the segments, opposite the exostome teeth. In some taxa, the endostome segments are highly reduced or absent, and the inner peristome consists only of cilia (Fig. 5). In contrast, in the diplolepidous-opposite peristome of the Funariales, there is no basal membrane, the endostome segments occur opposite the exostome teeth, and there are no cilia . In some taxa, e.g., *Orthotrichum,* a short, rudimentary system of processes, called a prostome or preperistome, is formed just to the outside of the outer teeth. Movements of the exostome teeth of diplolepidous taxa as well as the single ring of teeth of haplolepidous taxa are due to the differential composition of the wall deposits on the outer versus the inner surfaces of the teeth. Specifically, one surface readily absorbs water and elongates, while the other does not. This differential response to water absorption causes the teeth to bend when moistened. In many taxa the teeth close over the mouth of the capsule when moistened, so spores are released only when the air is dry, but in others they bend outward when wet, allowing spore release in moist conditions (D. M. J. Mueller and A. J. Neumann 1988). With drying, the teeth return to their original stance. This process can be repeated several times, resulting in the gradual release of the spores from the capsule. Arrest of peristome development can result in the loss of segments, cilia, teeth, the entire endostome or exostome, or the whole peristome. Stegocarpous mosses that lack a peristome, e.g., *Physcomitrium*, are termed gymnostomous. Although they lack a peristome at capsule maturity, such mosses, nonetheless, display characteristic peristomial layers in their developing capsules, and can be aligned with peristomate taxa using their peristomial formulae.

Ecological and economical importance of Bryophyta

1. Ecological importance:

The liverworts, mosses and lichens are supposed to be the pioneers in establishing vegetation where other vegetation seems to be practically impossible.

They colonize the barren rocks and exposed areas of hills, and make them suitable for growing angiospermic and other plants by depositing humus soil and plant debris. In the beginning the forms and grasses grow, and ultimately shrubs and trees also establish, and the whole area converts into dense wood.

However the Sphagnum plants are of great ecological importance. When these plants establish themselves in some lake or other areas full of water, sooner or later they cover the whole surface of the water. Due to deposition of plant debris the surface may be raised.

The Sphagnum plants along with other hydrophytes form a dense surface covering over the water below. This covering gives the appearance of the soil from the surface. These areas are known as quacking bogs. Later on these bogs are converted into swamps. Ultimately these swamps are replaced by the forest growth of mesophytic type

A few bryophyotes play an important role in checking the soil erosion. They are capable of holding the soil by their extensive carpets, and prevent the soil erosion to some extent. (Also see ‘ecology of bryophytes’).

2. Packing material:

Most of the mosses are used as packing material after being dried. They make a fairly good packing material in the case of glass ware and other fragile goods.

Especially the dried peat mosses (Sphagnum spp.) are used to pack bulbs, cuttings and seedlings for shipment.

3. Used in seed beds:

Since the peat mosses have remarkable power to absorb and hold water like a sponge, they are extensively used in seed beds and green houses to root cutting. The peat mosses (Sphagna) are also used to maintain high soil acidity required by certain plants.

4. As a source of fuel:

The peat is also a potential source of coal. Dried peat may be used as fuel. In Ireland, Scotland and other European countries the peat is used for fuel. In colder parts of the world where peat reaches its greatest development, the lower layers of peat become carbonized, and after the ages have passed, becomes available to human kind in the form of coal.

ECOLOGICAL IMPORTANCE OF BRYOPHYTES

1. Ecophysiology of the Group

Bryophytes are widely distributed globally where they contribute to nutrient cycling, water retention, water availability, higher plant biomass, and community maintenance (Jiang et al., 2015). Therefore, other members of the ecological community benefit from the ecosystem services, functions, and processes of bryophytes. For instance, other plants ecologically benefit from the water collected by bryophytes by using it to conduct internal processes (Lakna, 2017). This kind of services may be broadly referred to as ‘buffer system’. Bryophytes perform the environmental quality indicative function because of their sensitivity to levels of moisture in the atmosphere as well as the diversity of chemical groups. The responses of bryophytes to environmental variabilities is a reflection of their ecological and reproductive strategies to ensure their establishment, persistence, and dispersal (Batista et al., 2018). An earlier hypothesis suggesting that bryophyte fertility decreases with increasing latitude and therefore climatic severity have been discredited by the results of Smith & Convey (2002). More so, their sex expression is continuous over long periods regardless of seasons, sites and minimal environmental variations but there may be a seasonal effect on the maturation of gametangia and sporophytes (Maciel-Silva & Válio, 2011). Carbon fixation in mosses saturates at moderate irradiances. Protection against excess excitation energy in mosses involves a high capacity for photosynthetic electron transport to oxygen and high non-photochemical quenching, activated at high irradiance, alongside high reactive oxygen species tolerance (Proctor and Smirnoff, 2011). Even with their vascular limitations, bryophytes, and mosses, in particular can occupy large surface areas including even those polluted with heavy metals due to their unique biochemically driven life cycle strategies and physiological behaviors (Glime, 2017a). As poikilohydric organisms bryophytes equilibrate more or less rapidly with external moisture conditions (Wagner et al., 2014). More so, due to their Poikilohydric strategy for water and nutrients, bryophytes survival and growth are highly dependent on their external environment (Marschall, 2017). The author further posited that they are able to lose most of their cell water without dying up, only to resume normal metabolism after rehydration, gaining positive carbon balance over wet-dry cycles and can maintain efficient photosynthesis under low light conditions, have low chlorophyll *a/b* ratios, and their optimum growth is possible within a limited temperature range. Although bryophytes are abundant everywhere, the tropical forests tend to hold a huge diversity of bryophytes, particularly liverworts and mosses but their abundance and ecological importance contrast strongly with the availability of information on the ecophysiology of this plant group in the tropics (Wagner et al., 2014). Small size and lack of lignified vascular tissue have enhanced the selection for physiological means of drought survival, including metabolic shutdown and the ability to revive with a minimum or at least sustainable level of destruction (Glime, 2017a). Factors that influence bryophyte ecophysiology include vertical gradients of light,

humidity, wind speed and temporal variability inside a forest (Wagner et al., 2014). More so, leaching and decomposition of bryophyte organic material result in a pulsed release of nutrients after rehydration of dry mosses while many bryophytes spend most of their lives in a dry and inactive state. Carbon gain and growth are restricted to periods of sufficient hydration and capturing and storing moisture are crucial abilities for bryophytes (Wagner et al., 2014). Although air humidity correlates with moss cover within the tropical lowlands, there is no correlation

between bryomass and precipitation. Due to the ability of bryophytes to provide moisture, appropriate temperature, and also organic matter and minerals after their death, they play an important role in the maintenance and replenishment of forest cover (Saxena & Harinder, 2004). Tropical montane forests and temperate rainforests, appears to be particularly favorable for bryophyte growth. This tropical environment sets particular limits and requirements for bryophyte functioning and growth. They have a relatively low optimal temperature for growth and a low acclimatization potential for high temperatures (Marschall, 2017). Considering that temperature acclimatization is importance for the physiological basis of altitudinal distribution, bryophytes with their small and resistant spores are able to disperse

over long distances by wind. Increase in epiphytic bryomass with increasing water content often result from interactions related to water storage and transport processes at different scales and are determined by various morphological traits including the density, size, and disposition of phylloid, as well as by whole-clump architecture (Romero et al., 2005). In relatively wet habitats, bryophytes are likely to display a low intensity of the photochemistry of photosynthesis (Liepiņa & Ievinsh, 2013).

ECONOMIC IMPORTANCE OF BRYOPHYTES

There is limited information on the diverse economic relevance of bryophyte. For instance, Chandra et al. (2017) reported that in spite of their implication in popular herbal and food remedy among the tribal people of Africa, America, Europe, Poland, Argentina, Australia, New Zealand, Turkey, Japan, Taiwan, Pakistan, China, Nepal and India; very limited knowledge is available about the medicinal properties of bryophytes. The most commonly used bryophytes are *Marchantia*, *Sphagnum*, *Polytrichum*, *Conoceph alum*, *Climacium*, *Hylocomium*, *Hypnum*, *Rhytidiadelphus*, *Thuidium*, *Antitrichia*, *Bryum*, *Dicranum*, *Fontinalis*, *Funaria*, *Philonotis*, *Pleurozium* and *Rhizomnium* (Harris, 2008; Glime, 2017b). From the ancient times, bryophytes were used in packing, plugging as well as in decoration (Chandra et al., 2017). Bryophytes are considered to be nutritionally useless to humans because no references concerning use as foods for humans have been found unlike their use as medicines (Asakawa et al., 2013). Some bryophytes are attractive to herbivores. Mosses are used for decorative purposes in homes (Saxena & Harinder, 2004). *Marchantia polymorpha* is used in the winery to soaks up the wine and makes a tasty treat (Glime, 2017b). Their durability and elasticity may be the reason why they are used to stuff and fill in chinks in wooden buildings, industrial and domestic upholstery, hassocks, between the panes of glass in double glazed windows, balls, and dolls (Thomas & Jackson 1985; Pant & Tewari 1990; Glime, 2017b). *Neckera complanata*, a species that has been used in bedding in Europe while Sphagnum is used in America as an absorbent to serves as an insulator to keep warm, dry or cool (Glime, 2017b). Sphagnum has been implicated in making clothes, soap, and ointment for dressing wounds. A number of mosses make ideal lamp wicks including *Dicranum elongatum*, *Racomitrium lanuginosum,* and *Sphagnum* (Glime, 2017b). Tribal people use these plants to cure various ailments in their daily lives including to cure hepatic dis orders, skin diseases, cardiovascular diseases, antitumor properties, used as antipyretic, antimicrobial, wound healing, etc. (Chandra et al., 2017). More so, active constituents of bryophytes are widely used as antibacterial, antifungal, cytotoxic, antitumor and insecticidal (Asakawa, 2007; Ucuncu et al., 2010).

The phytochemistry of bryophytes is not a hot topic because of their very small size and the difficulty associated with their collection and identification (Asakawa et al., 2013). Liverworts contain a number of mono-, sesqui- and di-terpenoids, aromatic compounds like bibenzyl, bis-bibenzyls, acetogenins, sesquiterpenes, diterpenes and lipophilic aromatics, which are enantiomers of those found in higher plants that are produced from its cellular oil body (Huang et al., 2009; Asakawa et al., 2013). These authors upon investigation verified that these chemical compounds derived from liverworts display a characteristic odor, and can have interesting biological activities including allergenic contact dermatitis, antimicrobial, anticancer, antifungal and antiviral, cytotoxic, insecticidal, insect anti- feedant, superoxide anion radical release, 5-lipoxygenase, calmodulin, hyaluronidase, cyclooxygenase, DNA polymerase β, and α-glucosidase. Phytochemical evaluation of bryophytes became popular since the last decades with the use of new methods in gas chromatography, mass spectrometry, nuclear magnetic resonance, high-performance liquid chromatography and thin layer chromatography and x-ray to isolate and structurally elucidate bioactive molecules present in bryophytes (Banerjee, 2001; Dey & Mukher jee, 2015). Phytochemical investigations implicate the presence of biologically active metabolites from carbohydrates, lipid, protein, steroids, polyphenols, terpenoids, organic acids, sugar alcohols, fatty acids, aliphatic compounds, acetogenins, phenylquinones, and aromatic and phenolic (Pant, 1998; Saxena & Harinder, 2004). They have also found application in phytotherapy (Drobnik & Strebel, 2014). Hepaticology, the scientific study of liver shaped plant bodies evolved from liverworts through the "Doctrine of Signature" concepts. It is essentially post-Linnaean although 'Hepatics' started a long time ago in the pre-Linnaean period (Asthana, 2006). According to this concept, God would sign each plant in some ways to indicate its medicinal value, hence the resemblance of a plant or its parts to indicates the cure of any ailment or disease of that particular organ in that particular plant (Asthana, 2006). The economic cost of their roles in erosion control, environmental bioindicators, as material for seedbeds, fuel, medicines and food sources, pesticides, nitrogen fixation, moss gardening, treatment of waste, construction, clothing, furnishing, packing, genetic engineering and for soil conditioning and culturing remain invaluable in sustainable terms (Saxena & Harinder, 2004; Glime, 2007). Due to their high-water holding capacity, bryophytes are used in horticulture as a soil conditioner and additives for cultivation (Saxena & Harinder, 2004). Hornworts form symbiotic relationships with nitrogen=fixing bacteria and produce pores that may be homologous to stomata. Peat result when plant matter such as ***Sphagnum*** accumulates under waterlogged conditions without completely undergoing decomposition due to lack of sufficient oxygen, appropriate temperatures, nutrients, and pH. This matter can be used as peat fuel and may be harvested/dugged out in blocks, dried, and burned for heat in Ireland, Russia, Ireland, Finland, Sweden, Germany, United States and Poland. They have also been implicated in agriculture to increase the water-holding capacity of and lightens the soil. Physiologists and even medical scientists are realizing the potential of the bryophytes in understanding gene function and in producing needed proteins (Glime, 2017a). Bryophytes are good environmental indicators. For instance, mosses are also good indicators of acid rain, because they lack a protective epidermis and cuticle and, hence, are more susceptible than the vascular plants (Saxena & Harinder, 2004).