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E-Content

CORE COURSE 4

ARCHAEGONIATE (BOT-A-CC-2-4-TH)

THEORITICAL (Credits 4, Lectures 60)

BRYOPHYTES

1. General Account :

1.1. General characteristics and adaptations to land habit,

1.2. Classification (Strotler and Crandle Strotler, 2009) up to class with diagnostic characters and examples.

2. Life History: Gametophyte structure and Reproduction, Development and Structure of sporophyte, Spore dispersal in:

2.1. *Marchantia*, 2.2. *Anthoceros*, 2.3. *Funaria*.

3. Phylogeny:

3.1. Unifying features of archaegoniates; transition to land habit,

3.2. Origin of Alternation of Generations (Homologous and Antithetic theory),

3.3. Evolution of Sporophytes (Progressive and Regressive concept),

3.4. Origin of Bryophytes.

4. Importance :

Role of bryophytes in: 4.1. Plant succession, 4.2. Pollution Monitoring, 4.3. Economic importance of bryophytes with special reference to *Sphagnum*.

1. GENERAL ACCOUNT

General characteristics

- The term 'Bryophyte' comes from Greek word 'Bryon' means tree-moss and 'phyton' means plant.
- The term is collectively used for Liverworts, Hornworts and Mosses.
- The Plants occur mostly in damp and shaded habitat.
- They are terrestrial but requires water to complete their life cycle which is why they are called '*Amphibians of plant kingdom*'.
- The plant body is thallus like, i.e. prostrates or erect and not differentiated into true roots, stem and leaves.
- The plant is attached to the substratum by rhizoids that are unicellular or multicellular.
- Plants lack true vascular system and hence called non-vascular plants.
- Main plant body is gametophyte which is haploid and bears multicellular and jacketed sex organs (antheridia and archegonia).
- Sexual reproduction is always oogamous type.
- Distinct alternation of generation between independent gametophyte which produces sperm and eggs and dependent sporophyte which contains spores.
- They follow heterologous haplodiplobiontic type of life cycle.
- The antheridium produces antherozoids, which are biflagellated and the flask shaped archegonium produces an egg.
- The antherozoids fuse with egg to form a zygote that develops into a multicellular sporophyte.

- The sporophyte is differentiated into foot seta and capsule and is dependent on the gametophyte for its nutrition.
- Cells of sporophyte undergo meiosis to form haploid gametes that develops into juvenile gametophytes known as protonema.

Adaptation to land habit

Bryophytes are mostly terrestrial but they require sufficient amount of water for their growth. They are incompletely adapted to land habitat and they require water for the maturation of sex organs after fertilization to complete their life cycle.

The Bryophytes develop certain characters for Adaptation to land habit that includes-

- The plant body is compact and covered with epidermis.
- Presence of waxy cuticle that protect the plants tissue from drying out.
- Presence of gametangia that protects the gametes against drying.
- Development of rhizoids organ for attachment and absorption of water.
- Presence of airpores for atmospheric absorption of carbon dioxide for photosynthesis.
- Development of jacketed sex organs for protection against drying and mechanical injury.
- Production of large number of thick walled spores.
- Dispersal of spores by wind.

Classification of Bryophytes (Crandall & Stotler, 2009)

PHYLUM: MARCHANTIOPHYTA

Characters:

- Gametophytic plant body which is dorsi ventral and is either thalloid or foliose.
- Rhizoids without septa.
- Each cell in the thallus contains many chloroplasts; the chloroplasts are without pyrenoid
- Sex organs are embedded in the dorsal surface.
- Sporophyte may be simple (e.g., *Riccia*) having only a capsule, or differentiated into foot, seta and capsule (e.g. *Marchantia*, *Pellia* and *Porella*)
- Capsule lacks columella.

CLASS: HAPLOMITRIOPSIDA

Characters:

- ✓ Plants with leaf-like appendages at nodes.
- ✓ Stems secreting copious mucilage from epidermal cells.
- ✓ Apical cells tetrahedral.
- ✓ Androecia and gynoecia are loosely organized.
- ✓ One primary androgonial initial in early ontogeny.
- ✓ Spermatids with a massive spline.
- ✓ Sporophytes large, enclosed by a fleshy shoot calyptra.
- ✓ Example: *Haplomitrium*, *Treubia*



Haplomitrium sp. (source: iNaturalist.org)

CLASS: MARCHANTIOPSIDA

Characters:

- ✓ Plants thalloid, rarely leafy, thallus typically differentiated into assimilatory and storage tissues.
- ✓ Presence of persistent ventral scales.
- ✓ Rhizoids usually dimorphic (occasionally only smooth).
- ✓ Oil bodies large, single in idioblastic cells (rarely absent).
- ✓ Gametangia on specialised branches or dorsal on the thallus.
- ✓ Antheridia enclosed singly in perigonial chambers, with 4 primary androgonial initials.
- ✓ Sporophytes usually enclosed by an involucre seta.
- ✓ Capsule wall usually unistratose.
- ✓ Spores usually polar and highly ornamented.
- ✓ Gemmae, when present, multicellular, typically contained in specialised receptacles (gemma cups).
- ✓ Example: *Marchantia*, *Sphaerocarpos*.



Marchantia sp. (source: Gupta et al 2015)

CLASS: JUNGERMANNIOPSIDA

Characters:

- ✓ Plants thalloid or leafy.
- ✓ Oil bodies usually present in all cells.
- ✓ Rhizoids monomorphic, smooth-walled.
- ✓ Antheridia with 2 primary androgonial initials in early ontogeny.
- ✓ Embryos filamentous, seta elongation pronounced.
- ✓ Capsule 2-walled or more.
- ✓ Sporocytes lobed, spores cryptopolar to apolar, rarely polar.
- ✓ Example: *Pellia*, *Porella*



Porella sp. (source: plantlet.org)

2. LIFE HISTORY

GAMETOPHYTE STRUCTURE IN BRYOPHYTES:

- In bryophytes the long-lived and conspicuous generation is the gametophyte.
- The gametophyte is the dominant and most familiar form.
- The gametophyte form shows several developmental stages: the *spore*, the *protonema*, and the *gametophore*, which produces the sex organs.

Spores of bryophytes are generally small, 5–20 micrometres on the average, and usually unicellular, although some spores are multicellular and considerably larger. Spores have chlorophyll when released from the sporangium. They are generally hemispheric, and the surface is often elaborately ornamented.

Protonema, which grows directly from the germinating spore, is in most mosses an extensive, branched system of multicellular filaments that are rich in chlorophyll. This stage initiates the

accumulation of hormones that influence the further growth of newly formed cells. When specific concentrations of the hormones are reached, the branches of the protonema generate small buds, which in turn produce the leafy gametophore.

Gametophore:

In moss gametophores the leaf-like phyllids of the shoots are spirally arranged on the stem in more than three rows. Phyllids often have elaborate ornamentation on the cell surfaces. This ornamentation is often important in rapid water uptake. Although the phyllid begins its growth from an apical cell, cells are soon cut off between the apical cell and the base, and further division of these cells results in the elongation of the structure and also in the production of one or more midribs. The gametophore is often attached to the substratum by root-like rhizoids. The rhizoids are structurally similar to cells of the protonema, but they lack chlorophyll. In some mosses, rhizoids closely invest the stem among the leaf bases and perform a significant function in external water conduction and retention before its absorption by stem and leaves.



The internal structure of the stems of moss gametophores is usually simple. The outer cells are often thick-walled and supportive, while the inner cells are generally larger and have thinner walls. Some mosses, however, have considerable tissue differentiation in the stem. In the moss subclass Polytrichidae, for example, a complex conducting strand is often formed in the centre of the stem. It consists of an internal cylinder of water-conducting cells (the hydroids) surrounded by layers of living cells (leptoids) that conduct the sugars and other

organic substances manufactured by the gametophore. This conducting system is analogous to that of the vascular plants, except that it lacks lignin (a carbohydrate polymer), and it closely resembles that found in the fossils of the earliest land plants.



(Source: britannica.com)

In gametophores of leafy liverworts, the leaf-like structures are arranged in two or, usually, three rows. The plants are often flattened horizontal to the substratum. Rhizoids are generally confined to the undersurface of the stem and are important in that they form attachments and influence water retention and uptake by the plant.



In gametophores of thallose liverworts and hornworts, an internal conducting strand is rarely developed. In a few genera of the liverwort order Metzgeriales, the water-conducting cells have a form similar to water-conducting cells of vascular plants, but the cells of the liverworts and hornworts, like those of mosses, lack the lignin that characterizes the cell walls of water-conducting cells of vascular plants.

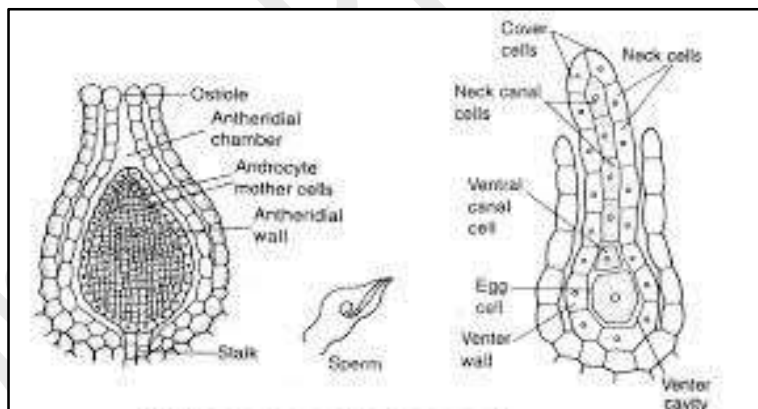
(Source: britannica.com)

REPRODUCTION IN BRYOPHYTES:

Bryophytes may reproduce both sexually and vegetatively. Sexual reproduction involves the mixing of the genes of two parents, with the potential to produce new plants that differ, genetically, from each parent. In vegetative reproduction, there is no such mixing and each new plant is derived from just one parent plant.

Sexual Reproduction

1. Sexual reproduction is highly oogamous.
2. Male and female sex organs are known as antheridia and archegonia, respectively.
3. Sex organs are jacketed and multilayered.
4. Antheridium is stalked, pear shaped or oblong and has an outer one cell thick jacket which encloses a mass of fertile cells called androcytes. Each androcyte metamorphoses into biflagellate antherozoid.
5. Archegonium is stalked, flask shaped structure. It has a basal swollen portion called venter and an elongated neck. The neck is filled with many neck canal cells whereas venter has a large egg cell and a small venter canal cell.
6. Antherozoids are attracted towards the neck of the archegonium chemotactically by certain substances (like sugars, malic acid, proteins, inorganic salts of potassium etc.) present in the mucilaginous substance formed by the degeneration of neck canal cells and venter canal cell.
7. Water is essential for fertilization.
8. The fertilized egg or zygote is the beginning of the sporophytic phase. It is retained within the venter of the archegonium.



(Source: premabotany.blogspot.com)

Vegetative Reproduction

Bryophytes possess a characteristic feature and that is their tendency towards extensive vegetative reproduction. The vegetative reproduction takes place in favourable season for vegetative growth. Majority of the Bryophytes propagate vegetatively and it is brought about in many ways.

Some important methods of vegetative reproduction are as follows:

1. By death and decay of the older portion of the thallus or fragmentation.
2. By persistent apices.
3. By tubers.

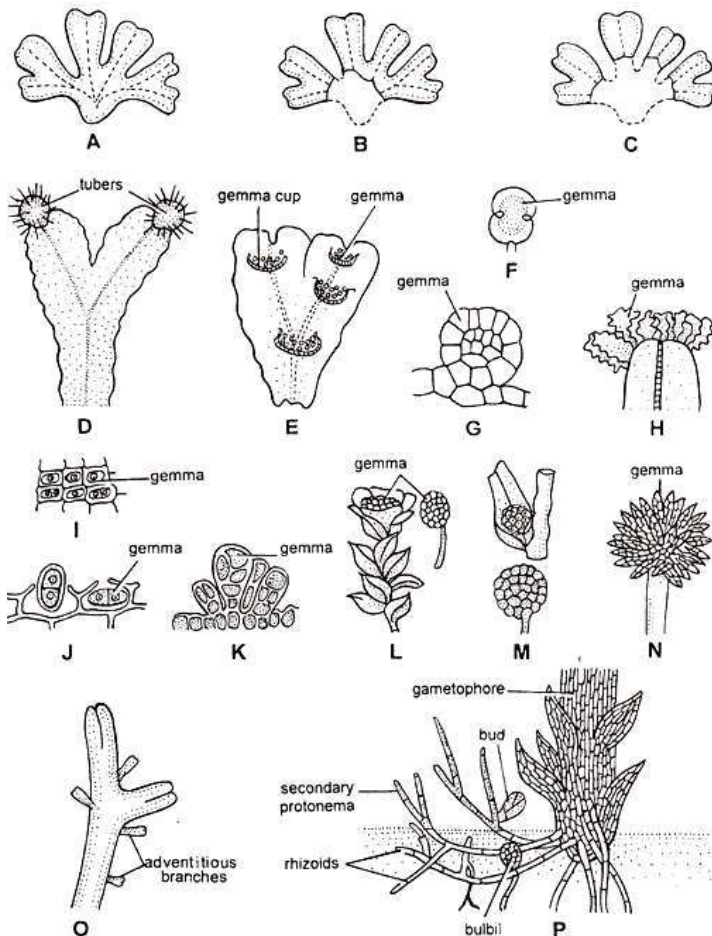
4. By gemmae.
5. By adventitious branches.
6. By Regeneration.
7. By innovation.
8. By primary protonema.
9. By secondary protonema.
10. By bulbils.
11. By apospory.
12. By cladia.
13. By separation of whole shoots.
14. By separation of shoot tips.
15. By rhizoidal tips.

1. By Death and Decay of the Older Portion of Thallus or by Fragmentation:

In Bryophytes the growing point is situated at the tip of the thallus. The basal, posterior or older portion of the thallus starts rotting or disintegrating due to ageing or drought. When this

process of disintegration or decay reaches up to the place of dichotomy, the lobes of the thallus get separated.

These detached lobes or fragments develop into independent plants by apical growth. This is the most common method of vegetative reproduction in *Riccia*, *Marchantia*, *Anthoceros* and some mosses like *Sphagnum* (Fig. 1 A-C).



(Source: biologvdiscussion.com)

2. By Persistent Apices:

Due to prolonged dry or summer or towards the end of growing season the whole thallus in some Bryophytes (e.g., *Riccia*, *Anthoceros*, *Cyathodium*) dries and get destroyed except the growing point. Later, it grows deep into the soil and becomes thick. Under favourable conditions it develops into a new thallus.

3. By Tubers:

Tubers are formed in those species which are exposed to dessication (drying effect of the air). Towards the end of the growing season, the subterranean branches get swollen at their tips to form the underground tubers. On the periphery of a tuber are two to three layers of water proof corky, hyaline cells develop.

These layers surround the inner cells which contain starch, oil globules and albuminous layers. During the unfavorable conditions the thallus dies out but the dormant tubers remain unaffected. On the return of the favourable conditions each tuber germinates to form a new plant e.g., *Riccia*, *Anthoceros*, *Conocephalum*, *Conicum*, *Fossombronia* etc. Thus, tubers also serve as organ of perennation(Fig).

4. By Gemmae:

Gemmae are green, multicellular reproductive bodies of various shapes. These are produced in gemma cups, on the surface of the leaves, on stem apex or even inside the cells. They get detached from the parent plant and after falling on a suitable substratum gemmae give rise to a new individual directly (e.g., *Marchantia*) or indirectly (e.g., Mosses).

Some common forms of gemmae produced in different Bryophytes are:

Class I. Hepaticopsida:

(A) Multicellular, discoid, gemmae:

- (i) Produced in gemma cup on dorsal surface e.g., *Marchantia*, *Lunularia* (Fig. 1 E, F).
- (ii) Produced on leaves e.g., *Radula* (Fig. 1 G).
- (iii) Produced on erect gemmiferous branches e.g., *Metzgeria uncigera* (Fig. 1 H).

(B) One to four celled gemmae:

- (i) One to three celled gemmae on stem apex e.g., *Lophozia heterocolpa*.
- (ii) One to three celled gemmae on leaves e.g., *Marsupellae marginata*, *Lophoziabarbata*.
- (iii) Two celled gemmae produced within any external cell of the thallus e.g., *Riccardia multifida*(Fig. 1 I, J).
- (iv) Three to four celled gemmae produced in the axils of the leaves e.g., *Treubia*.

(C) Sub spherical gemmae: Produced in abundance in flask shaped gemma receptacle e.g., *Blasia*.

(D) Star shaped gemmae: Produced on the dorsal surface of the thallus e.g., *Blasia*.



(Source: anbg.gov.au)

Class II. Anthocerotopsida:

Multicellular gemmae produced along the margins of the dorsal surface of the thallus e.g., *Anthoceros*.

Class III. Bryopsida:

- (A) Articulated gemmae: Produced on the leaves e.g., *Ulota phyllantha*, *Orthotrichum lyelli* etc. (Fig. 1 K).
- (B) Multicellular gemmae:
- (i) Stalked, green, lenticular gemmae produced at the tip of shoot e.g., *Tetraphis pellucida* (Fig. 1 L).
 - (ii) Globular, produced at the base of the stem e.g., *Bryum rubens*, *B. erythrocarpum* (Fig. 1M).
 - (iii) Fusiform, produced at the ends of distinct leafless terminal stalk e.g., *Aulacomnium androgynum* (Fig. 1N).
 - (iv) Produced on the rhizoids of leafy shoots e.g., *Tortula stanfordensis*, *Ditrichum cylindric*, *Bryum erythrocarpum* etc.

5. By Adventitious Branches:

The adventitious branches develop from the ventral surface the thallus e.g., *Ricciafluitans*, *Anthoceros*. On being detached from the parent plant these branches develop into new thalli. In *Marchantia*, *Dumortiera* these branches develop from archegoniophore while in *Pellia* these branches arise from the dorsal surface or margins of the thallus (Fig. 1 O).

6. By Regeneration:

The liverworts possess an amazing power of regeneration. Part of the plant or any living cell of the thallus (e.g., rhizoid, scales) are capable of regenerating the entire plant e.g., *Riccia*, *Marchantia* etc.

7. By Innovation:

In *Sphagnum* one of the branches in the apical cluster instead of forming drooping branches or divergent branches, develop more vigorously than the others and continues the growth upwards.

This long upright branch has all the characteristics of main axis. It is called innovation. Due to progressive death and decay of the parent plant these innovation become separated from the parent plant and establish themselves as parent plants.

8. By Primary Protonema:

Primary protonema is the filament like stage produced by the developing spores of the mosses. It produces the leafy gametophores. It breaks into short filament of cells by the death of cells at intervals. Each detached fragment grows into a new protonema which bears a crown of leafy gametophores e.g., *Funaria*.

9. By Secondary Protonema:

The protonema formed by other methods than from the germination of spores is called secondary protonema. It may develop from any living cells of the leafy gametophore i.e., from leaf, stem, rhizome, injured portion of the leafy gametophore, antheridium, paraphysis or archegonium. From this arise the leafy gametophores or lateral buds in the same manner as in primary protonema e.g., *Funaria*, *Sphagnum* (Fig. 1 P).

10. By Bulbils:

These are small resting buds develop on rhizoids. Bulbils are devoid of chlorophyll but full of starch. On germination bulbils produce a protonema which bears leafy gametophores (Fig. 1 P).

11. By Apospory:

The production of diploid gametophyte from the unspecialized sporophyte without meiosis is known as apospory e.g., *Anthoceros*. In *Funaria* green protonemal filaments may arise from the unspecialized cells of the various parts of sporogonium. These protonemal filaments bear lateral buds which develop into leafy gametophores.

12. By Cladia:

These are the small or broad detachable branches which help in vegetative reproduction. These are of two types:

- (i) Leaf cladia: Arising from the individual cell of the leaf e.g., *Plagiochila*, *Bazzania*, *Frullania fragilifolia* etc.
- (ii) Stem cladia: These cladia arise from the stem and occupy the same position as sexual branches e.g., *Bryopteris*.

13. By Separation of Whole Shoots:

A number of catkins like deciduous branches develop over the entire surface of the gametophytic plant. On separation these branches develop into new plant e.g., *Pohlia nutans*.

14. By Separation of Shoot Tips:

It occurs in *Campylopus piriformis*. The separated shoot tips develop into new plant.

15. By Rhizoidal Tips:

The apical part of the young rhizoids divide and re-divide to form a gemma like mass of cells e.g., *Riccia glauca*. These cells contain chloroplast and are capable to develop into new thallus.

DEVELOPMENT AND STRUCTURE OF SPOROPHYTE:

1. Without resting period, the zygote undergoes repeated divisions to form a multicellular structure called the embryo.
2. The first division of the zygote is always transverse and the outer cell develops into embryo. Such an embryogeny is called exoscopic.
3. Embryo develops into a sporophyte or sporogonium.
4. The sporophyte is usually differentiated into foot, seta and capsule. In certain cases it is represented only by capsule (e.g., *Riccia*) or by foot and capsule (e.g., *Corsinia*).
5. Sporophyte is attached to parent gametophytic plant body throughout its life. It partially or completely depends on it for nutrition.
6. Foot is basal, bulbous structure. It is embedded in the tissue of parent gametophyte. Its main function is to absorb the food material from the parent gametophyte.
7. Seta is present between the foot and capsule. It elongates and pushes the capsule through protective layers. It also conducts the food to the capsule absorbed by foot.
8. Capsule is the terminal part of the sporogonium and its function is to produce spores.
9. All Bryophytes are homosporous i.e., all spores are similar in shape, size and structure.
10. Capsule produces sporogenous tissue which develops entirely into spore mother cells it e.g., *Riccia*) or differentiated into spore mother cells and elater mother cells (e.g., *Marchantia*, *Anthoceros*).

11. Spore mother cells divide diagonally to produce asexually four haploid spores which are arranged in tetrahedral tetrads.
12. Elater mother cells develop into elaters (e.g., *Marchantia*) or pseudo elaters (e.g., *Anthoceros* which are hygroscopic in nature. Elaters are present in liverworts and absent in mosses.
13. Venter wall enlarges with the developing sporogonium and forms a protective multicellular layer called calyptra (gametophytic tissue enclosing the sporophyte).

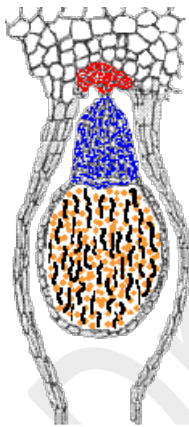
Life cycle – Sporophyte development

1. Liverworts

In liverworts with a seta, the seta elongates only when the spore capsule has matured, quite the opposite to what happens in mosses. Liverwort setae elongate by cell expansion and so are fairly flimsy.

Apart from calyptrae you can find a variety of other protective coverings over the young sporophytes. Perianths are found in the leafy liverworts and result from the fusion of two or three leaves around the archegonium. The perianths are the pleated dome-like structures.

Hidden within the perianth is the embryonic sporophyte within its calyptra. Perianths vary in size, shape and pleating and help to identify species. An expanding sporophyte would push through a perianth and leave a tubular remnant around the base of the seta. The bulbous green cylinder around the base of the pale seta is a perianth.



(Source: anbg.gov.au)

The spore capsules of the thallose liverwort *Targionia hypophylla* are produced at thallus apices and are contained within protective, blackish involucre. The involucre is bi-valved, with the margins firmly pressed together until the spores have matured. Then the involucre opens to expose capsule and spores. In this photo click for photo you can see several open involucre.

A number of thallose liverworts produce their sporophytes in umbrella-like structures. An example is the genus *Marchantia*. Each such "umbrella", or archegoniophore, is not itself a sporophyte but is in fact gametophyte tissue. The part of the "umbrella" at the top of the stem is called the female receptacle or carpocephalum. The receptacle is initially on the thallus surface and the stalk grows to raise it. The archegonia are found on the female receptacle and initially they are in the upper surface and face upward. They are fertilized when the stem is still fairly short. The stem continues to grow and the receptacle continues to grow by centrally added tissue. This moves the fertilized archegonia outward and the receptacle eventually folds over to orient the developing sporophytes so that they face down. The following stylized diagram shows three stages in that process with the coloured dots indicating the positions of six archegonia.

The accompanying diagram shows a cross-section through an advanced, but not yet open, *Marchantia* sporophyte, attached to the underside of a receptacle. The large cells, left uncoloured, at the top of the diagram constitute part of the receptacle. The red area indicates the foot that anchors the sporophyte to the gametophytic tissue of the receptacle. Blue indicates the seta and below that is the spore capsule filled with spores (orange-brown) and ELATERS (black). The long, grey "fingers" that hang down around the sporophyte indicate the perigynium, a fleshy sleeve that initially surrounds and protects the young sporophyte.

Life cycle – Sporophyte development

2. Hornworts

Hornwort sporophytes lack setae. Each tapering "horn-like" sporophyte, that grows out from a bulbous foot embedded in the thallus is entirely spore capsule. To see the foot you need to dissect the hornwort. The immature sporophyte is green and so, like the immature moss sporophyte, photosynthesizes.



(Source: anbg.gov.au)

A liverwort or moss capsule comes to a definite stop in its development, with the spores having all matured together. The capsule then opens in some way to release the spores. In the hornwort genus *Notothylas* the sporophyte also has a determinate period of growth. By contrast in the other hornwort genera the sporophyte is continually growing from near the base. In theory such a sporophyte could grow indefinitely, though the death of the aging thallus or changes in environmental conditions eventually put a stop to sporophyte growth. Technically the near-basal area in which there is continual cell addition is an example of a meristem. Meristems are found in all plants for all plant growth is via meristematic tissue of some sort.

The meristematic tissue near the base of a hornwort sporophyte is composed of a number of cells. By the production of new cells the meristem is constantly causing the sporophyte to extend upward. This means that the oldest part of the sporophyte is at the apex with regions progressively younger as you go down the sporophyte. When the sporophyte is still very short it is enclosed within a protective sheath (an involucre) but the sporophyte grows through it, leaving a cylindrical remnant around the sporophyte's base. A species of *Megaceros* shows some involucre remnants quite well.

As the spores mature the sporophyte walls change from green to brown, though mature spores may be green to brown, the colour depends on genus. When spores near the apex are mature the sporophyte develops slits there. Generally there are two slits but in some species there is only one and there are also species in which four slits develop. As the sporophyte dries the slits open and the spores can be released. As lower areas of the sporophyte mature the slits extend downward. This photo click for photo shows a number of sporophytes with dried and open upper regions. In many hornworts the slits stop a little before the sporophyte apex so that the sporophyte segments are united at their apices. In a mature sporophyte you will also find pseudo-elaters. These are tiny, filamentous structures that superficially resemble the spiralled elaters that are a feature of the capsules in many liverwort species. However, elaters and pseudo-elaters have different origins and there's more about the differences between elaters and pseudo-elaters. The pseudo-elaters are not spiralled in the genera *Anthoceros*, *Folioceros*, *Phaeoceros*, always spiralled in *Megaceros* and *Dendroceros* and have rudimentary spiral thickenings in *Notothylas*.

Life cycle – Sporophyte development

3. Mosses

Where a seta is present it elongates early, while the spore capsule is still undeveloped, and the elongation is by production of additional cells. In a species with a long seta the growing sporophyte breaks through the enveloping calyptra. The lower part of the calyptra is left

around the base of the seta and the calyptra's upper part is carried aloft, still covering the undeveloped spore capsule. The seta has expanded and there is both a basal calyptral remnant as well as one over the apex of the sporophyte. In this species the calyptra is clearly rather hairy. By contrast, the calyptra of *Encalypta vulgaris* is smooth. The upper part of the calyptra will eventually become loose and will fall off the capsule as it gets close to maturity. The seta of an immature sporophyte is not fairly straight in all species. The seta can be twisted, *Funaria hygrometrica* and even more so by *Campylopus introflexus*. In the latter the immature setae are so contorted that the young spore capsules are held down amongst the leaves of the cushion composed of massed gametophyte plants. It is only near sporophyte maturity that the seta uncoils and raises the spore capsule above the moss cushion.



The early stage of sporophyte development, where there is a seta, is often referred to as the spear stage because the undeveloped spore capsule typically shows, at most, as a slight thickening at the top of the seta and so resembles a spearhead on a spear shaft. The spore capsule will mature and enlarge atop the seta. The seta and immature capsule in the young sporophyte are both green and contain photosynthesizing cells but the sporophyte is still



(Source: anbg.gov.au)

heavily reliant on nutrients passing to it from the gametophyte. A study into photosynthetic activity of the spore capsules of three moss species showed that the photosynthesizing capsule of *Funaria hygrometrica* contributes about 50% of its nutrition needs during the later stage of capsule expansion. For the species *Mnium hornum* is about 20% and for *Pleuridium acuminatum* it is about 10%.

The sporophyte eventually stops photosynthesis and the capsule turns brown late in sporophyte development, as does the seta if present. Here click for photo is a colony of a species in the genus *Bryum* in which all the spore capsules are still immature. Amongst the setae some are green and some are already brown. It is common to see sporophytes in various stages of development.

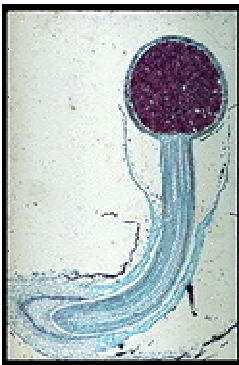
In a species with no seta, or just a very short seta, it is the enlarging capsule that ruptures the calyptra. The sporophyte of *Goniomitrium acuminatum* has a very short seta. The photo shows some enlarged but still green spore capsules, each within the distinctive 8-pleated calyptra of this species.

In the majority of mosses the spore capsule develops a mouth through which the spores will eventually be released. In a small number of moss genera the capsules simply disintegrate or open by means of slits. Where there is a mouth it is at the opposite side of the capsule to the

point where the capsule is joined to the seta. Initially the mouth is covered by a small cap called an operculum. As the spore capsule matures and expands the upper calyptra remnant falls off. When the spores within the capsule are mature the operculum is shed. Once the operculum has been shed the mouth is exposed. In a number of moss species the mouth is surrounded by a bare rim click for photo but a greater number of species have capsules with teeth or hairs around the mouth. The teeth are called peristome teeth and, when present, there may be one ring or two rings of teeth around the margin of the mouth.

SPORE DISPERSAL IN *Marchantia*

The spores once released are dispersed by air currents and, once they settle somewhere moist, germinate. This recommences the gametophyte generation. The spore first produces a filamentous stage called a *protonema*. These cells are full of chloroplasts. In *Marchantia*, the spore dispersal takes place by the help of hygroscopic movement of elaters. In this case the sporophyte is differentiated into foot, seta and capsule. In the capsule are present numerous spores and elater.



L.S. of Liverwort capsule & stalk (Source: biologie.uni)

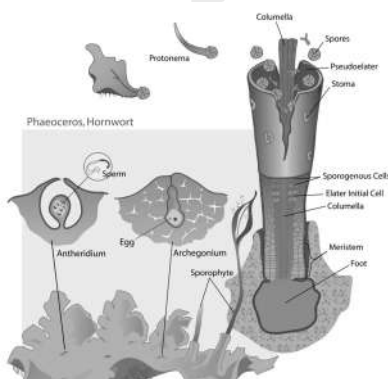
Elaters are dead water-filled cells. Two forces are key here - cohesion between water molecules and adhesion between water molecules and the elater wall.

Under dry conditions water is lost and the elater walls are pulled inwards.

The elater walls have spiral bands of thickening so that as more water is lost the elaters assume a twisted form. The water is in a state of tension. The water "wants" to remain as one cohesive mass. It also "wants" to adhere to the elater wall.

More water is lost. This shifts the balance. The attractive forces between the water and elater are overcome. The elater snaps violently back to its original shape. The water remains as a cohesive mass.

SPORE DISPERSAL IN *Anthoceros*



(Source: internet)

In *Anthoceros*, the spores dispersal takes place by the help of pseudoelaters.

The sporophyte, in this case is highly advanced and is differentiated into foot, rudimentary seta and capsule.

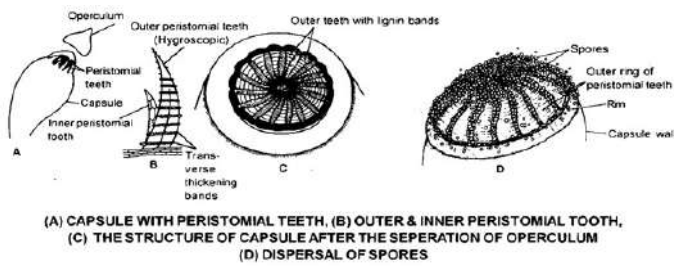
The capsule has a columella, overarching spores and pseudoelaters and the wall of capsule. The wall of capsule in this case splits into 1-4 valves, which remain united of the apex. Pseudoelater is hygroscopic.

In nature, they help in the dispersal of spores. Dehiscence is dependent on the loss of water.

SPORE DISPERSAL IN *Funaria*

In *Funaria* (moss) the spores dispersed by air and gradual activity of peristomial teeth.

In this case the sporophyte is differentiated into foot, seta and capsule, and show a great advance in the mechanism of spore dispersal.



As the capsule matures, a number of changes takes place.

The columella other internal tissue break down leaving the spore sac filled with loose mass of spores. The thin walled cells holding the operculum also breaks down and it becomes

detached and thus expose the double series of teeth of peristome. Tips of the curved peristome teeth fuse in a central disc. Wet teeth elongate and slits between teeth disappear. Dry teeth shrink and gaps develop between teeth, allowing spores to sift out.

3. PHYLOGENY:

UNIFYING FEATURES OF ARCHEGONIATES:

1. Archegoniates are the group of primitive plants, which bears the female reproductive organ is an archegonium (a multicellular, often flask- shaped, egg-producing organ) occurring in mosses, liverworts, ferns, and most gymnosperms.
2. The archegoniates seem to have originated from a monophyletic group of ancient stock of aquatic green algae.
3. Present of sexual organs the female called archegonium and the male called the antheridium.
4. The presence of Chloroplasts containing chlorophyll a, b and carotene.
5. Heteromorphic alternation of generation.
6. The morphological reduction of the sexual or the gametophytic phase was evident in the life cycle of archegoniates.
7. Male gametes are flagellated and motile in bryophytes, pteridophytes, (Cycadales, Ginkgoales) while the female gamete (egg) is non-motile.
8. The alternation of generation is slight different in Bryophytes, Pteridophytes and Gymnosperms.
9. The life cycle of bryophytes shows regular alternation of gametophytic and sporophytic generations.
10. The haploid phase (n) is the gametophyte or sexual generation.
11. It bears the sexual reproductive organs, which forms gametes, i.e. antherozoids and eggs
12. gametic union a zygote is formed which develops into a sporophyte (2n) diploid phase.
13. Since, these embryos derive their nutrition, from the maternal parent (archegonium-bearing gametophyte) this mode of nourishment, that is common to all the archegoniates, is known as *matrotrophy*.
14. Since, each spore develops into a gametophyte, a zygote in an archegoniate can produce large number of gametophytes.
15. The male gametes produced within antheridium are always carried to the archegonium via aqueous medium.

16. In contrast, the egg-cell, in all archegoniates is stationary, static and nonmotile.
17. Interesting events in the life of an archegoniate could occur just because of a specialized female sex-organ, archegonium. The development, of an archegonium is thus regarded as a milestone is the transition to land habit.
18. The transition of plants from aquatic environment to land is probably the most important and significant event, and it happened because the environment had to change so as to suit the plants or plants have to change so as to adapt to changed environment.

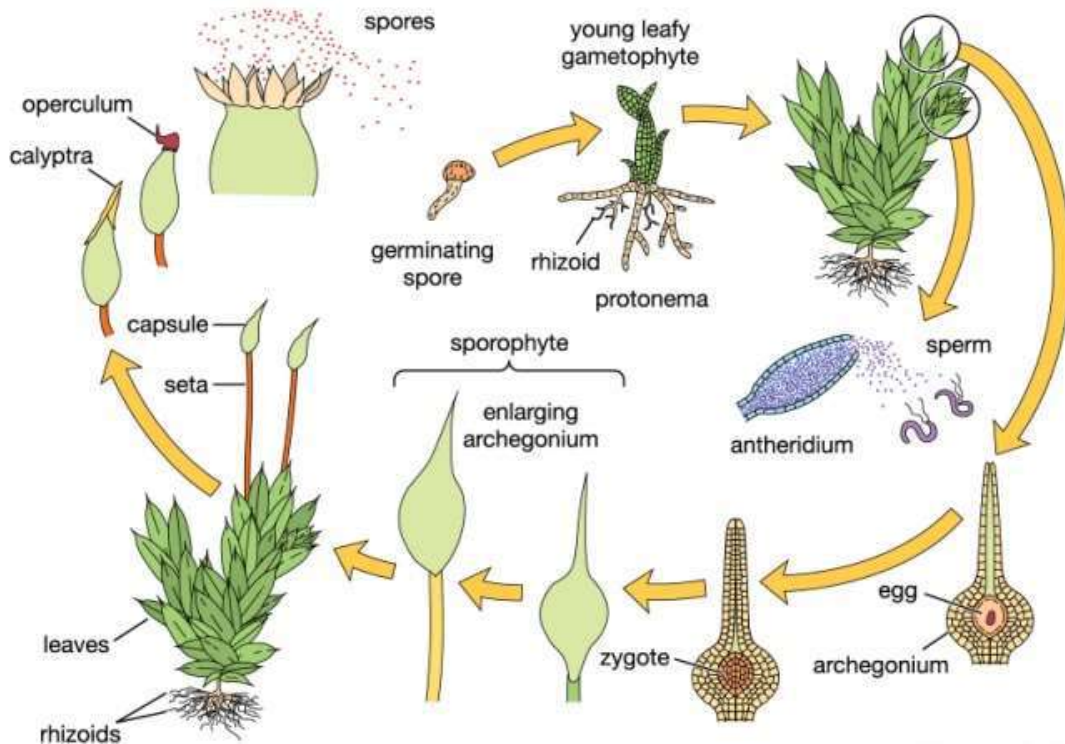
ORIGIN OF ALTERNATION OF GENERATIONS

Alternation of generations, also called *metagenesis* or *heterogenesis*, is the alternation of a sexual phase and an asexual phase in the life cycle of an organism. The two phases, or generations, are often morphologically, and sometimes chromosomally distinct.

In Bryophytes

The alternation of generations is very distinct.

It appears in the haplodiplontic type of life cycle



The life cycle shows regular alternation of gametophytic and sporophytic generations. The haploid phase (n) is the gametophyte or sexual generation. It bears the sexual reproductive organs, which form gametes, i.e. antherozoids and eggs. Gametic union of a zygote is formed, which develops into a sporophyte ($2n$) diploid phase. The sporophyte forms spores, which always germinate to form gametophytes. In bryophytes, the gametophyte is quite independent, whereas the sporophyte is dependent somehow or other on the gametophyte for its nutrition. The gametophyte produces the sporophyte and the sporophyte returns to the gametophyte, and thus there is regular alternation of generations. During the formation of spores, the spore mother cells divide meiotically and haploid spores are formed. The production of the spores is the beginning of the gametophytic or haploid phase.

The spores germinate and produce gametophytes, which bear sex organs. Ultimately, the gametic union takes place and zygote is resulted. It is diploid (2n). This is the beginning of the sporophytic or diploid phase.

- **Homologous theory**

The homologous theory simply stated that a mass of cells forming mitotically from the zygote adopted the same developmental plan of the gametophyte, but giving origin to a diploid sporophyte. Their organism is haploid for most of their life cycle, and diploid only in the zygote phase (haplontic cycle).

- **Antithetic theory**

The sporophyte and gametophyte are basically distinct with the gametophyte representing the primitive ancestral phase and the sporophyte being a new structure resulting from increasingly retarded zygotic reduction.

The antithetic theory maintains that the sporophyte and gametophyte generations are fundamentally dissimilar and that the sporophyte originated in an ancestor organism with haplontic cycle by the zygote dividing mitotically rather than meiotically, and with a developmental pattern not copying the developmental events of the gametophyte. The sporophyte generation was an innovation of critical significance for the land-plant evolution.

EVOLUTION OF SPOROPHYTE IN BRYOPHYTES:

The sporophyte of bryophytes is called sporogonium which generally consists of a single, 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.

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

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

This theory was advocated by Bower (1908-35) and 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 enclosing sporogenous cells with a very few absorptive 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 endothecium.

Here the zygote has no polarity. The amphithecium forms the sterile jacket while the whole sporogenous cells (endothecium) differentiate 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 differentiate into an outer amphithecium and inner endothecium.

The amphithecium forms a single-layered sterile jacket of the capsule, while the endothecium 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 sporophyte 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 endothelial 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 comparison 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*, *Riccardia*, etc. Here more sterilisation of sporogenous tissue has been observed. Sporophyte is differentiated into foot, seta and capsule having multilayered jacket. The sporogenous 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 differentiates into epidermis with stomata and chlorophyllous 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 formation 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., evolution of sporophytes due to the progressive reduction or simplification:

This theory is known as regressive or retro-gressive theory, and supported by several scientists like Church (1919), Kashyap (1919), Goebel (1930) and Evans (1939). According to this theory, the most simple sporophyte of *Riccia* (comprised of a simple capsule) is the most advanced type which has been evolved by the simplification 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 enumerated:

- (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 sporophytes 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 communicate 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 (*Anthoceros*) and some jungermanniales (*Pellia*, *Porella*) are multilayered which subsequently became single-layered (*Marchantia*, *Riccia*) by reduction.
- (e) The foot and seta are well-developed in mosses (*Pogonatum*, *Funaria*, etc.) and some liverworts (*Pellia*, *Marchantia*, etc.). The seta becomes 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 capsule, 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.

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 today. 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.

(i) Algal origin of Bryophytes

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 'prohepaties' 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 bryophytes originated from gametangia of a type similar to that of *Ectocarpus*. In *Ectocarpus* (Phaeophyceae) 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.

(ii) Pteridophytic origin of Bryophytes

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. Proskauer (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."

4. IMPORTANCE

ROLE OF BRYOPHYTES IN PLANT SUCCESSION AND POLLUTION MONITORING

- **Bryophytes and plant succession**

Among the bryophytes, the mosses are considered to be the most potent forms in successional process. They colonise over the nutrient-poor sites where no other plant can survive. After death and decay, they form humus which increases the fertility of a soil. Thus, the accumulated organic matter containing soil becomes favourable for the microorganisms. The microorganism increase the nutrient availability and makes the site suitable for growth of higher plants. The important species under this category are *Cephalozia media*, *Isopterygiumelegans*, *Lepidoziaseptans*, *Pelliaepiphylla* and *Tetrapispellucida*.

- **Bryophytes and pollution monitoring**

Bio-indicators refers to all organisms that depict the quality of the environment on the basis of changes in morphology; physiology etc. but bio-monitors provide both qualitative and quantitative information. The use of organisms as monitors of the environment is known as biomonitoring and the organisms are known as bio-monitors. The preferred organisms are those that are able to accumulate the pollutants, be available throughout the year, easy to capture and identify, be relative sedentary and are cosmopolitan in distribution. The accumulated pollutants are easily measured by the analysis of organisms that provide the information about the level of pollutant deposition.

- ***Bryophytes as bio-indicators of water pollution***

The life form of bryophytes is very simple so they are comparatively more affected by polluted waters than other groups. The polluted water also affects the benthic and marginal soils thus it directly affects the aquatic bryoflora and directly or indirectly affects those bryophytes which grow in its banks.

The bryophytes absorb the water either by rhizoids or by entire surface of plant or by both ways. The movement of water within plant body of a bryophyte takes place either by central strand or by free space of cell or cell to cell or external capillary space. Therefore, if water is polluted, it certainly affects the life forms of bryophytes including external morphology,

anatomy, fertilization, spore formation and physiology. Hence, the bryophytes have been reported by Kumar and Sinha(1989) to be more sensitive to water pollution than air pollution. Saxena and Glime (1991) have proposed several arguments for the use of aquatic bryophytes to monitor pollution. Empain (1967) and Trollope and Evans (1976) believed that bryophytes can provide integrated information of pollution within a system. Some aquatic bryophytes which are pollution tolerant species have been recommended to monitor the levels of pollution in water. These species are:

Amblystegium riparium: It is a moss which is cosmopolitan in distribution and found in running and stagnant water or sewage rich in nutrition.

Eurhynchium riparioides: It is a moss which is found only in northern region of world and have reported pollutant contents and heavy metals on these waters.

Fontinalis antipyretica: A moss which is also restricted in northern part and grows in both stagnant and running water. Welsh and Dinny (1980) have analysed Cu and Pb and the moss.

Fontinalis squamosa: It is also restricted in distribution. McLean and Jones (1975) have reported the details of pollutants and heavy metals.

Pandey *et al.* (1986), Sinha (1988) and Kumar and Sinha (1989), during a comprehensive study of River Ganga, have reported some specific bryophytes which appear on its banks and are affected by river water quality. These bryophytes are

Riccia gangetica: A pollution tolerant species. The tuberculate rhizoids and marginal scales are more developed in highly polluted sites. It is a monoecious species.

Riccia frostii: A pollution sensitive species which grows in lesser polluted sites. The sensitivity towards polluted water is due to presence of only smooth-walled rhizoids, absence of scales and separate male and female plants.

Funaria hygrometrica: Found only on those sites where cremation takes place and benthic and marginal soil is rich in P & Ca.

Physcomitrium indicum: It is a moss which absorbs the heavy metals.

Pandey *et al.* (2001) have reported that bryophytes growing on the river banks of Ganga absorb very high levels of heavy metals like Cr, Zn and Ni.



A moss bag in monitor metal content in water (Source: Govindaparyari *et al.* 2019)

- ***Bryophytes as bio-indicators of air pollution***

The bryophytes have been reported to be good indicators of air pollution. The bryophytes are very sensitive to air pollution. Air pollution can also create “moss deserts” and force many

sensitive species to retreat. They are very widely used to measure heavy metal air pollution, especially in large cities and in areas surrounding power stations and metallurgical works. Heavy metals, such as lead, chromium, copper, cadmium, nickel, and vanadium, accumulate in the cell walls.

It has been reported that air pollutants affect the habitat and growth form of bryophytes. The sensitivity of bryophytes towards air pollution increases from terricolous to saxicolous and corticolous species. The moss protonema is more sensitive than its mature gametophores (Gilbert, 1969).

Daly (1970) reported some bryophytes which are able to tolerate levels of pollution on stone walls than on tree trunks. Some species are *Tortula princeps*, *Bryum rubrum*, *Ceratodon purpureus* and *Pohila cruda*.

Bryophyte species sensitive to air pollution are *Ulota crispa*, *Platydictya subtile*, *Paraleucobryum longifolium*, *Frullania muscicola*.



A moss bag to monitor the air metal contents of the site (Source: Govindaparyi *et al.* 2019)

- **Economic importance of bryophytes with special reference to Sphagnum**

There is limited information on the diverse economic relevance of bryophyte. It was 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*, *Conocephalum*, *Climacium*, *Hylocomium*, *Hypnum*.

1. *Sphagnum*, a large genus of peat mosses, is by far the most economically important bryophyte.
2. *Sphagnum* is used in seed beds and green houses as a rooting medium because of its water absorbing and water holding capacity.
3. *Sphagnum* and other mosses accumulate a thick, compacted, semi-decomposed layer atop the mineral soil. This deposit, called peat, can be cut out in blocks, dried, and burned as fuel for cooking and heating.
4. It is also used to pack bulbs, cuttings and seedlings for shipment; and to maintain high soil acidity required by some plants.
5. Tons of *Sphagnum* are harvested throughout the world and then sold in the nursery industry in many countries.

6. During World War I, *Sphagnum* was used on a large scale as a wound dressing because its acidic sterile tissue acts as both an antiseptic and an absorbent.
7. Some important by products of *Sphagnum* peat are paraffin, acetic acid, ammonia. It is used as stable litter and bedding.
8. *Sphagnum* is of great ecological importance, used in the biological reclamation of watery wastes. It plays a role as pioneer settling in hollows which, without it, would only be sterile sheet of water.
9. Moss spread far and wide over the surrounding vegetation and creating a water-logged condition, creating death of adult trees and prevents growth of young seedlings, destroying vast areas of forests.
10. The economic cost of bryophytes roles in erosion control, environmental bioindicators, as material for seed beds, 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.

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