Bryophytes: Distribution, Habitat and Affinities

1. Meaning of Bryophytes:

Bryophyta (Gr. Bryon = mass; phyton = plant), a division of kingdom Plantae comprises of mosses, Hornworts and Liverworts. They are groups of green plants which occupy a position between the thallophytes (Algae) and the vascular cryptogams (Pteridophytes).Bryophytes produce embryos but lack seeds and vascular tissues. They are the most simple and primitive group of Embryophyta. They are said to be the first land plants or non-vascular land plants (Atracheata). Presence of swimming antherozoids is an evidence of their aquatic ancestory.

2. Origin of Bryophytes:

Nothing definite is known about the origin of Bryophytes because of the very little fossil record. There are two views regarding the origin of Bryophytes.

(i) Algal Hypothesis of Origin:

There is no fossil evidence of origin of Bryophytes from algae but Bryophytes resemble with algae in characters like-amphibious nature, presence of flagellated antherozoids and necessity of water for fertilization.

This hypothesis was supported by Lignier (1903), Bower (1908), Fritsch (1945) and Smith (1955) etc. According to Fritsch (1945) and Smith (1955) Bryophytes have been originated from the heterotrichous green algae belonging to the order Chaetophorales for e.g., Fritschiella, Coleochaete and Draparnaldiopsis.

(ii) Pteridophytean Hypothesis of Origin:

According to this hypothesis Bryophytes are descendent of Pteridophytes. They are evolved from Pteridophytes by progressive simplification or reduction.

This hypothesis is based on certain characters like-presence of type of stomata on the sporogonium of Anthoceros and apophysis of mosses similar to the vascular land plants, similarly in the sporophytes of some Bryophytes (e.g., Anthoceros, Sphagnum, Andreaea) with some members of Psilophytales of Pteridophytes (e.g., Rhynia, Hormophyton etc.)

This hypothesis was supported by Scot (1911), Kashyap (1919), Kidston and Lang (1917-21), Haskell (1914) Christensen (1954), Proskaner (1961), Mehra (1968) etc.

3. Distribution of Bryophytes:

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

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

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

4. Habitat of Bryophytes:

Bryophytes grow densely in moist and shady places and form thick carpets or mats on damp soils, rocks, bark of trees especially during rainy season. Majority of the species are terrestrial but a few species grow in fresh water (aquatic) e.g., Riccia fluitans, Ricciocarpos natans, Riella etc. Bryophytes are not found in sea but some mosses are found growing in the crevices of rocks and are being regularly bathed by sea water e.g., Grimmia maritima.

Some Bryophytes also grow in diverse habitats e.g., Sphagnum-grows in bogs, Dendroceros-epiphytic, Radula protensa. Crossomitrium -epiphyllous, Polytrichum juniperinum-xerophytic, Tortula muralis-on old walls. Tortula desertorum in deserts, Porella platyphylla-on dry rocks, Buxbaumia aphylla (moss), Cryptothallus mirabilis (liverwort) are saprophytic.

5. General Characters of Bryophytes:

1. Plant body is gametophytic, independent, dominant, autotrophic, either thalloid (i.e., thallus like, not differentiated into root, stem and leaves) or folise (Fig 1), containing a rootless leafy shoot.

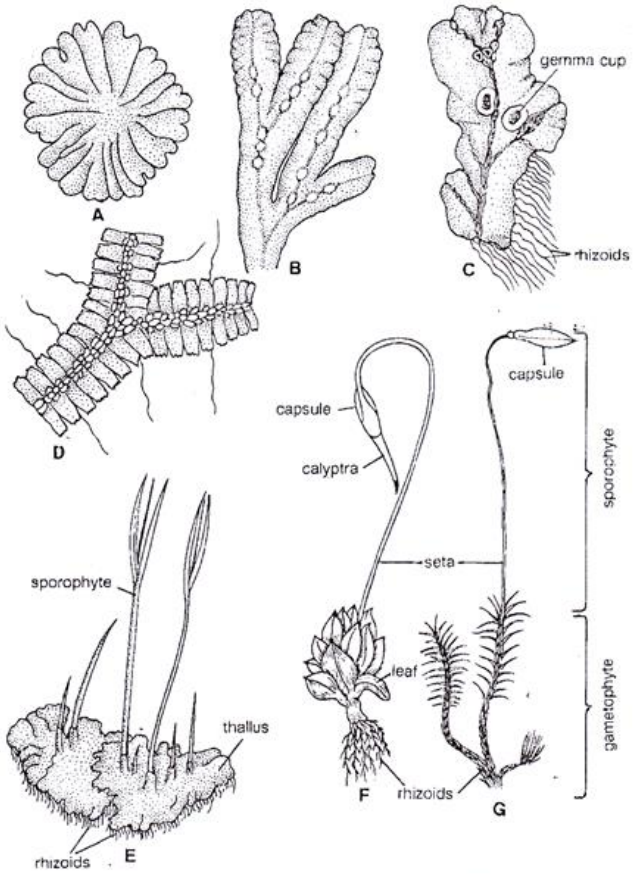

Fig. 1. (A–G). Bryophytes. External features. (A) *Riccia* (Rosette habit), (B) *Riccia* (thallus), (C) *Marchantia*. (D) *Porella*, (E) *Anthoceros*, (F) *Funaria*, (G) *Polytrichum*.

2. Plant body is very small and ranges from a few mm. to many cm. Zoopsis is the smallest bryophyte (5 mm.) while the tallest bryophyte is Dawsonia (50-70 cms.).

3. Leaves and stems found in vascular plants are absent, Koch (1956) termed these **'leaf'** and **'stem'** like structures as **'axis'** and **'phylloid'** respectively.

4. Roots are absent. Functions of the roots are performed by rhizoids. Cells are also capable to absorb moisture directly from the ground or atmosphere. Therefore, Bryophytes can also survive on the moist soils.

5. Rhizoids may be unicellular, un-branched (e.g., Riccia, Marchantia, Anthoceros) or multicellular and branched (e.g., Sphagnum, Funaria).

6. In members of order Marchantiales (e.g., Riccia, Marchantia) scales are present. These are violet coloured, multicellular and single cell thick. They protect the growing point and help to retain the moisture.

7. Vascular tissue (xylem and phloem) is completely absent. Water and food material is transferred from cell to cell. However, in some Bryophytes (e.g., mosses) a few cells in groups of 2-3 are present for

conduction of water and food (photo assimilate). These cells are known as hydroid (collectively hydrom) and leptoids respectively. Cuticle and stomata are absent.

6. Classification of Bryophytes:

The term Bryophyta was first introduced by Braun (1864), however, he included algae, fungi, lichens and mosses in this group. Later, algae, fungi and lichens were placed in a separate division Thallophyta and liverworts, mosses in division Bryophyta. The rank of division Bryophyta to this well-defined group of plants was first given by Schimper (1879).

Eichler (1883) was the first to divide Bryophyta into two groups:

Group I. Hepaticae

Group II. Musci.

Engler (1892) recognised Hepaticae and Musci as two classes and divided each class into the following three orders:

Division. Bryophyta:

Class I. Hepaticae divided into three orders:

Order 1. Marchantiales

Order 2. Jungermanniales

Order 3. Anthocerotales

Class II. Musci divided into three orders:

Order 1. Sphagnales

Order 2. Andreaeales

Order 3. Bryales.

Due to isolated characters of Anthoceros and related genera, Howe (1899) raised the order Anthocerotales to the rank of a class and divided division Bryophyta into three classes:

Class I. Hepaticae

Class II. Anthocerotes

Class III. Musci.

This system of classification was followed by Smith (1938, 1955), Takhtajan (1953), Wardlaw (1955) and Schutser (1958) but preferred to call class Anthocerotes as Anthocerotae. International code of Botanical Nomenclature (ICBN) suggested in 1956-that the suffix-opsida should be used for the classes and such usage had already been proposed by Rothmaler (1951) for the classes of Bryophytes.

He changed the class names as:

Class I. Hapaticae as Hepaticopsida.

Class II. Anthocerotae as Anthoceropsida

Class III. Musci as Bryopsida.

Proskauer (1957) suggested that the class name Antheoceropsida should be ch; _ Anthocerotopsida. Parihar (1965) and Holmes (1986) followed Proskauer's sysuaa classification and divided Bryophyta into three classes : Clase I. Hepaticopsida Class II. Anthocerotopsida Class III. Bryopsida.

Class I. Hepaticopsida (Liverworts):

General Characters:

1. This class includes about 280 genera and 9500 species.

2. The name of this class is derived from a latin word Hepatica which means liver. Hence members of this class are commonly known as liverworts.

3. Plant body is gametophytic and the gametophyte is either thalloid or foliose.

4. Thalloid forms are prostrate, lobed, dorsiventral and dichotomously branched.

5. In foliose forms, **'leaves'** are entire, lobed or divided and without **'midrib'**. 'Leaves arranged in two to three rows on the axis.

6. Rhizoids are unicellular and branched.

7. Photosynthetic cells contain many chloroplasts.

8. Pyrenoids are absent.

9. Sex organs are borne dorsally or apically, superficial or embedded in gametophytic tissue

10. Members may be monoecious or dioecious.

11. Sporophyte is either simple or represented by capsule only (e.g., Riccia) or may differentiated into foot, seta and capsule (e.g., Marchantia).

12. Archesporiuin is endothecial in origin.

13. Sporogenous tissue either forms only spores (e.g., Riccia) or is differentiated into sterile elater mother cells and fertile spore mother cells.

14. Columella is absent in the capsule.

15. Elaters are unicellular, hygroscopic with spiral thickenings.

16. Capsule wall is one to several layers thick and without stomata.

17. Dehiscence of the capsule is irregular or in definite number of valves.

18. Spores on germination form the gametophytic plant body.

19. Plants show heteroinorphic alternation of generation.

Campbell (1936) divided the class Hepaticopsida into four orders:

Order 1. Marchantiales (e.g., Riccia, Marchantia).

Order 2. Sphaerocarpales (e.g., Sphaerocarpos).

Order 3. Jungermanniales (e.g., Pellia).

Order 4. Calobryales (e.g., Calobryum).

Schuster (1953, 1958) divided the class Hepaticae into two sub-classes:

Sub-class 1. Jungerinanniae. It includes four orders:

Order I. Calobryales (e.g., Calobryum)

Order 2. Takakiales (e.g., Takakia)

Order 3. Jungermanniales (e.g., Pellia)

Order 4. Metzgeriales (e.g., Metzgeria)

Sub-class 2. Marchantiae.

It includes three orders:

Order 5. Sphaerocarpales (e.g., Sphaerocarpos)

Order 6. Monocleales (e.g., Monoclea)

Order 7. Marchantiales (e.g., Marchantia).

Class II. Anthocerotopsida (Hornworts):

General Characters:

1. This class is represented by about 6 genera and 300 species.

2. Plant body is flat, dorsiventral, thalloid, gametophytic and variously lobed.

3. Smooth walled rhizoids are present.

4. Tuberculated rhizoids and scales are absent.

5. Internally the thallus is not differentiated into zones.

6. All cells are alike.

7. Air chambers or air pores are absent.

8. Each cell has a single chloroplast and each chloroplast contains a single pyrenoid.

9. Mucilage cavities open on the ventral surface by slime pores.

10. Sex organs are embedded in the thallus.

11. Antheridia develop either singly or in groups in closed cavities called antheridial chambers.

12. The sporophyte is differentiated into foot, an intermediate zone or meristematic zone and capsule.

13. Due to the presence of the meristematic zone, the sporophyte shows indeterminate growth i.e., it continues to grow indefinitely.

14. Archesporium is amphithecial in origin.

15. Sporogenous tissue forms the fertile spores and sterile elaters. Elaters do not have spiral thickenings and are known as pseudo elaters.

16. Capsule wall is four to six layered thick and epidermis has the stomata.

17. Capsule matures from apex to base and usually dehisce by two valves.

The class Anthocerotopsida has only a single order Anthocerotales. Muller (1940), Proskauer and Reimers (1954) divided the order Anthocerotales in two families:

Family 1. Anthocerotaceae (e.g., Anthoceros)

Family 2. Notothylaceae (e.g., Notothylas).

Class III. Bryopsida (Mosses):

General Characters:

1. It is the largest class in Bryophyta and includes about 700 genera and 14,000 species.

2. The main plant body is gametophytic and can be differentiated into two stages-juvenile stage and leafy stage or gametophore.

3. Juvenile stage is represented by green, filamentous branched structures called protonema. It develops from the germination of the spore.

4. Gametophores are erect leafy branches which develop on the protonema.

5. Gametophores can be branched or un-branched and can be differentiated into three parts-rhizoids, **'stem'** and **'leaves'**.

6. Branches arise below the **'leaves'**.

7. **'Leaves'** are with midrib, un-lobed and arranged spirally in three to eight rows on the axis or

8. Rhizoids are multicellular, filamentous, branched with oblique septa.

9. The axis is differentiated into central conducting strand enclosed by cortex.

10. Sex organs borne apically in the groups on main **'stem'** or a branch.

11. The sporophyte is green in early stages and can be differentiated into foot, seta and capsule.

12. The seta is usually elongated and rigid.

13. Columella is usually present and endothecial in origin.

14. Archesporiurn (spore forming tissue) is differentiated only in spores.

15. Elaters are absent.

16. Dehiscence of capsule takes place by separation of lid or operculum.

17. Peristome helps in the dispersal of spores.

18. Spores on germination produce the protonema.

Bower (1935), Wettstein (1933-1935), Campbell (1940) divided the class Bryopsida into that orders:

Order 1. Sphagnales

Order 2. Andreaeales

Order 3. Bryales.

Dixon (1932) gave the above orders the rank of sub-class and divided the Bryopsida into three sub-classes:

Class. Bryopsida (Musci)

Sub-class I. Sphagnales

Sub-class II. Andreaeales

Sub-class III. Bryales.

Smith (1938, 1955) divided the class Bryopsida into three sub-classes:

Sub-class 1. Sphagnobrya

Sub-class 2. Andreaeobrya

Sub-class 3. Eubrya.

Reimers (1954) divided the class Bryopsida into 5 sub-classes and he used suffix-idae for the sub-class:

Sub-class 1. Sphagnidae-1 order. Sphagnales-1 family.

Sub-class 2. Andreaeidae-1 order. Andreaeales-1 family.

Sub-class 3. Bryidae-12 orders

Sub-class 4. Buxbaumiidae-1 order. Buxbaumilaes-2 families.

Sub-class 5. Polytrichidae-2 orders. Polytrichales and Dawsoniales-2 families.

Parihar (1955) divided the class Bryopsida into 3 sub-classes:

Sub-class 1. Sphagnidae

Sub-class 2. Andreaeidae

Sub-class 3. Bryidae.

Various characters are used for the classification of Bryophytes.

Some important characters are:

(i) External and internal structure of the thallus.

(ii) Types of rhizoids.

(iii) Types of scales.

(iv) Position of sex organs.

(v) Structure and nature of sporophyte.

(vi) Degree of sterilization in the sporophyte.

7. Adaptations of Bryophytes to Land Habit:

Bryophytes are first land plants. Evidences support that Bryophytes are evolved from Algae. During the process of origin they developed to certain adaptations to land habit.

These are:

1. Development of compact plant body covered with epidermis.

2. Development of organs for attachment and absorption of water e.g., rhizoids.

3. Absorption of carbon dioxide from atmosphere for photosynthesis e.g., airpores.

4. Protection of reproductive cells from drying and mechanical injury i.e., jacketed sex organs.

5. Retention of zygote within the archegonium.

6. Production of large number of thick walled spores.

7. Dissemination of spores by wind.

8. Bryophytes: Amphibians of Plant Kingdom:

Bryophytes are also known as amphibians of plant kingdom because water is needed to complete the life cycle. In animal kingdom class Amphibia (Gr. Amphi = two or both; bios = life) includes those vertebrates which are amphibians in nature i.e., they can live on land as well as in water. Similarly, majority of the bryophytes are terrestrial but they are incompletely adapted to the land conditions.

They are unable to grow during dry season and require sufficient amount of water; for their vegetative growth. Water is absolutely essential for the maturity of sex organs ar. fertilization. Without water they are unable to complete their life cycle. On account of their complex dependence on external water for completing their life cycle, Bryophytes along with Pteridophyte are regarded as amphibians of plant kingdom.

9. Alternation of Generation in Bryophytes:

Bryophytes show a distinct and sharply defined heteromorphic alternation of generation. In the life cycle of these plants, there exist two distinct phases. One is haploid (X) or gametophytic phase (produces gametes). It is the dominant and independent phase of the life cycle. It produces the male and female sex organs i.e., antheridia and archegonia respectively.

Haploid gametes i.e. antherozoids and eggs are produced inside the sex organs. Antherozoids are produced in antheridia and eggs are produced in archegonia. The gametes fuse to form a diploid (2x) zygote. The zygote is the starting point of the next phase of the life cycle.

On germination the zygote forms the second diploid adult of the life cycle called sporophyte or sporogonium. Sporogonium produces spore mother cells in the capsule region, which undergo meiosis and form the haploid spores called meiospores. The zygote, embryo, sporogonium and spore mother cells together constitute the sporophytic generation.

This generation is dependent completely or partially on the gametophytic generation for its nutrition. Each meiospore germinates and produces a gametophytic plant which again bears the sex organs. In this way the life cycle goes on. Because the two generations (gametophytic and sporophytic) appear alternately in the life cycles, Bryophytes show alternation of generation.

Since the generations differ completely in their morphology i.e., gametophyte is either thalloid or foliose, and the sporophyte usually consists of foot, seta and capsule, it is called heteromorphic alternation of generation.

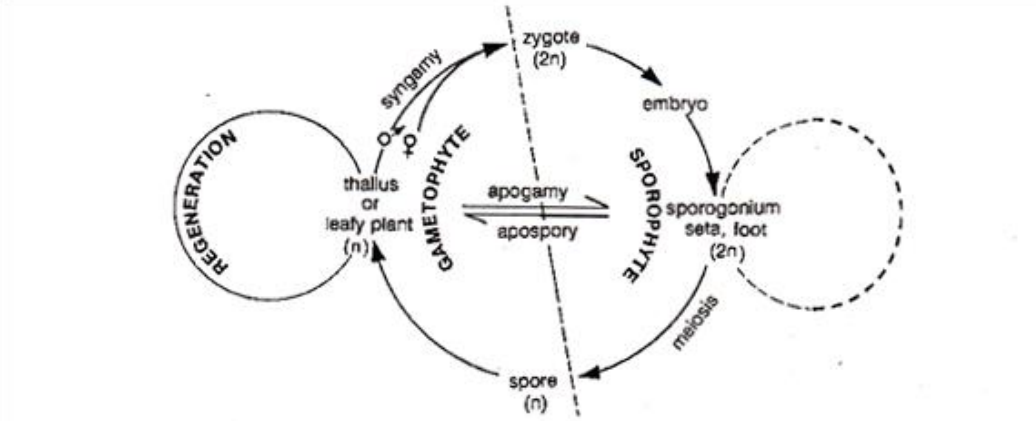

Fig. 2. Life cycle or heteromorphic alternation of generation in Bryophytes (diagrammatic representation)

Apogamy and Apospory in Bryophytes:

Bryophytes are endowed with a remarkable regeneration capacity. Parts of the plant or any living cell of the thallus are capable of regenerating the entire plant. The sporophytic cells regenerate to form a protonema on which appear gametophytes. This regeneration of diploid gametophyte from a sporophyte without the formation of spores is called apospory.

Conversely a gametophyte may form a mass of cells which may regenerate a sporophyte. This regeneration of a diploid sporophyte from a gametophyte, without the formation of gametes is called apogamy. Aposory and apogamy are rarely found in life cycle of Bryophytes.

10. Rhizoids and Scales in Bryophytes:

Rhizoids:

In Bryophytes roots are absent and the functions of the root i.e., anchorage and absorption is performed by the filamentous structures known as rhizoids.

Rhizoids may be unicellular, un-branched (Fig. 3B-D) in thallose forms of Hepaticopsida and Anthocerotopsida (e.g., Riccia, Marchantia, Anthoceros) or multicellular and branched in foliose forms of Bryopsida (Fig. 3 E) (e.g., Funaria, Polytrichum) Multicellular rhizoids possess oblique cross walls.

Unicellular rhizoids are of two types smooth-walled and tuberculated (Fig. 3 B-D). The members of order Marchantiales (e.g., Riccia, Marchantia) possess both types of rhizoids while Anthocerotales (e.g., Anthoceros) possess only smooth walled rhizoids.

In thalloid forms rhizoids are borne on the ventral surface (Fig. 3 A) along the mid rib, however, in foliose forms rhizoids arise from the base of the **'stem'**. In aquatic Bryophytes (e.g., Riccia fluitans, Ricciocarpus natans) rhizoids are absent.

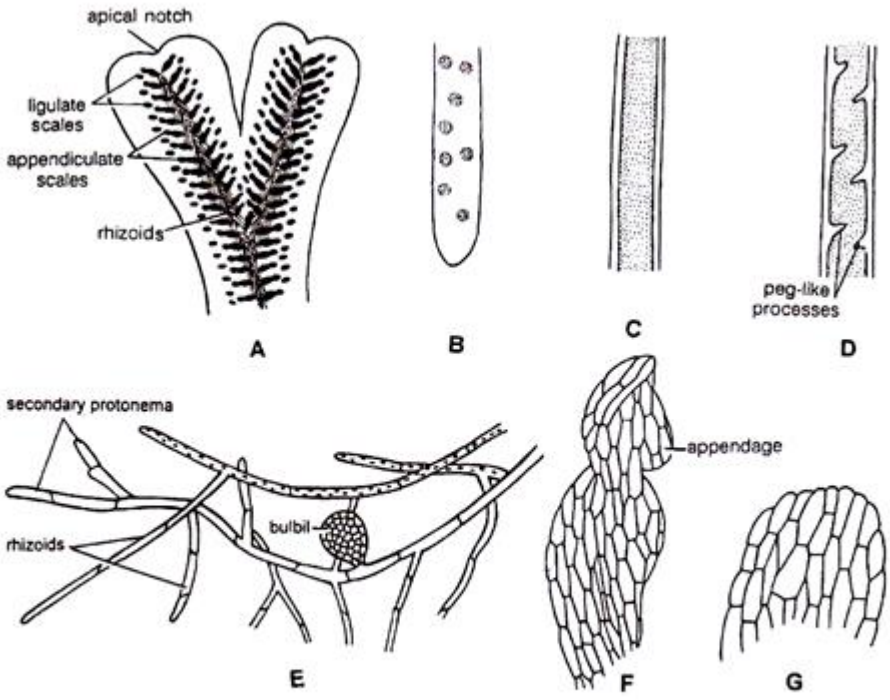

Fig. 3. (A–G) *Marchantia*. Scales and rhizoids. (A) *Marchantia* thallus : Ventral surface showing rhizoids and scales, (B) Tuberculated rhizoid (surface view), (C) Smooth walled rhizoid (surface view), (D) Tuberculate rhizoid (internal view), (E) Multicellular rhizoids, (F) Appendiculate scale, (G) Ligulate scale.

Scales:

Scales are present only in the members of order Marchantiales and absent in all Bryophytes. The scales are multicellular, violet coloured and single cell thick. They are violet in colour due to the presence of the pigment anthocyanin. Scales develop on the ventral surface of the thallus (Fig 3A).

They may be arranged in one row (e.g., young thallus of Riccia) or in two rows on each side of the mid rib (e.g., Targionia) or in two to four rows on each side of the mid rib (e.g., Marchantia) or irregularly distributed over the entire ventral surface (e.g., Corsinia).

In Riccia the scales are ligulate (Fig. 3G) while in Marchantia the scales are of two types-ligulate and appendiculate (divided by a narrow constriction into two parts—body and appendage, Fig. 3F). Scales protect the growing point by covering their delicate cells and secreting slime to keep them moist. The scales are absent in some aquatic members of order Marchantiales e.g., Riccia fluitans.

11. Archesporium in Bryophytes:

The archesporium is the first cell generation of the sporogenous tissue. It divides and re-divides to form a mass of cells. It is a solid tissue and also called sporogenous tissue. The cells of the last cell generation of solid tissue separate from each other and are known as spore mother cells. The origin, position and fate of archesporium varies in different members of Bryophytes.

It is as follows:

Classes and orders	Origin	Position	Fate
Class I. Hepaticopsida			
Order. Marchantiales			
Riccia	Endothecium	Fills the cavity of the capsule.	Spore mother cells and in some species few nurse cells.
Marchantia	Endothecium	Fills the cavity of the capsule.	Spore mother cells, elater mother cells and in few species apical cap (*e.g., M. chenopoda*).
Order. Mertzgeriales			
Pellia	Endothecium	Fills the cavity of the capsule.	Spore mother cells, elaters and basal elaterophore.
Order. Jungermanniales			
Porella	Endothecium	Fills the cavity of the capsule.	Spore mother cells and elaters.
Class II. Anthocerotopsida			
Order. Anthocerotales			
Anthoceros	Inner layer of amphithecium	Arches over the columella.	Spore mother cells and pseudoelaters.
Class III. Bryopsida			
Order. Sphagnales			
Sphagnum	Inner layer of amphithecium	Dome shaped, lies in the upper parts of the capsule and archs over the columella.	Spore mother cells.
Order. Funariales			
Funaria	Outer layer of the endothecium	Barrel shaped and surrounds the columella.	Spore mother cells.
Order. Polytrichales			
Polytrichum	Outer layer of the endothecium	Surrounds the columella.	Spore mother cells.

12. Affinities of Bryophytes:

From evolutionary point of view Bryophytes occupy an intermediate position between the Algae and the Pteridophytes. They show affinities with both Algae and Pteridophytes.

Resemblance of Bryophytes with Algae:

1. Plant body simple, thalloid and gametophytic.

2. Autotrophic.

3. Gametophytic phase is dominant.

4. Roots are absent.

5. Cell wall is made up of cellulose.

6. Pigments (chlorophyll a, chlorophyll b, α and β carotene, Lutin, Violaxanthes and Xeoxanthin) are similar in chloroplast.

7. Vascular tissue is absent.

8. Antherozoids are motile (bi-flagellated).

9. Flagella are whiplash type.

10. Water is essential for fertilization.

11. A filamentous protonema is produced by Bryophytes (juvenile stage in mosses) which resembles with the filamentous green algae.

12. In order Anthocerotales of Bryophytes, plastids are with pyrenoids which is a characteristic of Chlorophyceae (Green algae).

Resemblance of Bryophytes with Pteridophytes:

1. Plants are terrestrial.

2. Primitive simple leafless and rootless sporophytes of Pteridophytes (members of order Psilophytales) can be compared with the sporophytes of Bryophytes.

3. Sexual reproduction is oogamous.

4. Androcytes are enclosed by sterile jacket layer.

5. Antherozoids are flagellated.

6. Water is essential for fertilization.

7. Permanent retention of zygote within the archegonium.

8. Zygote forms the embryo.

9. Moss capsule is similar to terminal sporangium and columella of Psilophytales.

10. Both Bryophytes and Pteridophytes are characterised by heteromorphic alternation, of generation.