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GEN. ACCOUNT: UNIFYING FEATURE OF ARCHAEGONIATES AND ADAPTATIONS TO LAND HABIT

CLASSIFICATION : STROTLER AND CRANDLE, 2009 , UPTO CLASS WITH DIAGONOSTIC CHARACTERS AND EXAMPLES

LIFE HISTORY : GAMETOPHYTE STRUCTURE AND REPRODUCTION, DEVELOPMENT AND STRUCTURE OF SPOROPHYTE, SPORE DISPERSAL. *MARCHANTIA* , *ANTHOCEROS* , *FUNARIA*

PHYLOGENY : UNIFYING FEATURE OF ARCHAEGONIATES AND TRANSITION TO LAND HABIT, ORIGIN OF ALTERNATION OF GENERATION (HOMOLOGUS AND ANTITHETIC THEORY, EVOLUTION OF SPOROPHYTE (PROGRESSIVE AND REGRESSIVE THEORY) , ORIGIN OF BRYOPHYTES

IMPORTANCE OF BRYOPHYTE: PLANT SUCCESSION, POLLUTION MONITORING, ECONOMIC IMPORTANCE WITH SPECIAL REFERENCE TO *SPHAGNUM*

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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.

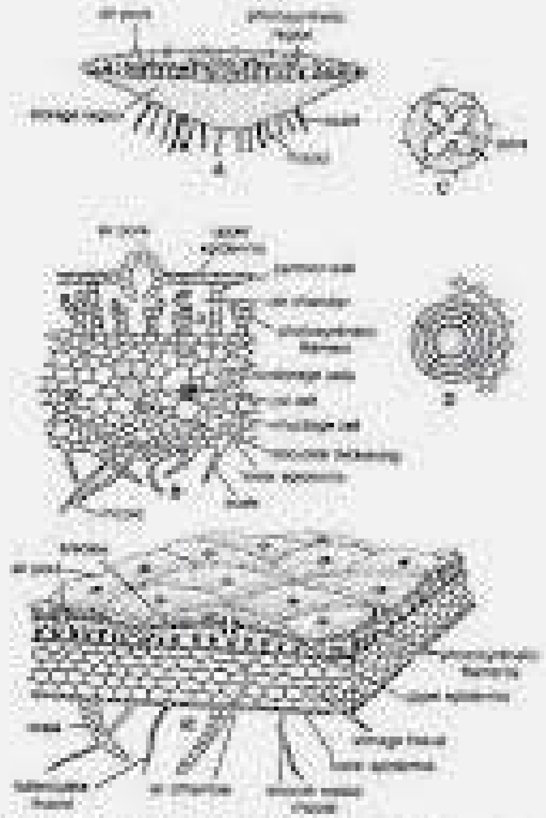
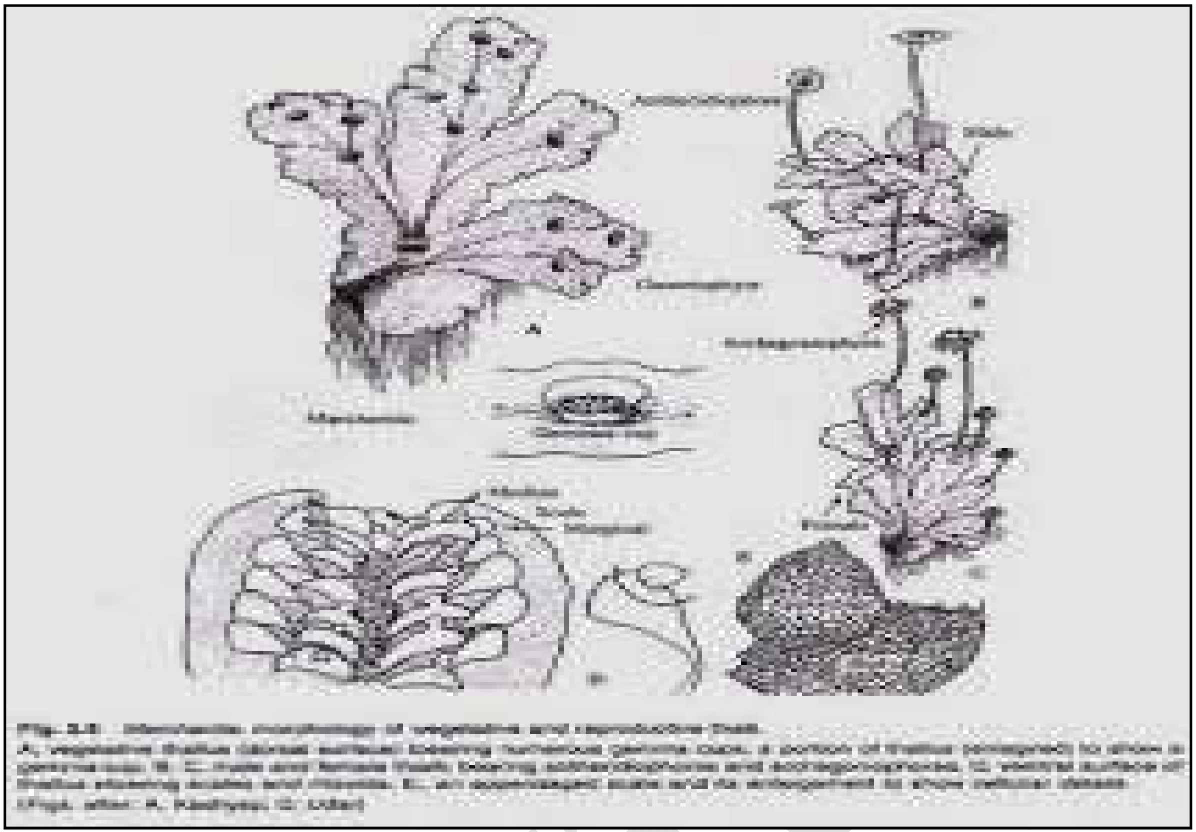


Fig. 1 (A-E). Marchantia. Internal structure of the thallus. (A) Vertical Transverse Section (V.T.S.) of thallus (diagrammatic), (B) V.T.S. of thallus (a part cellular), (C) Air pore as seen in the ventral view, (D). Air pore as seen in the dorsal view, (E). V.T.S. of thallus in three dimensional view.



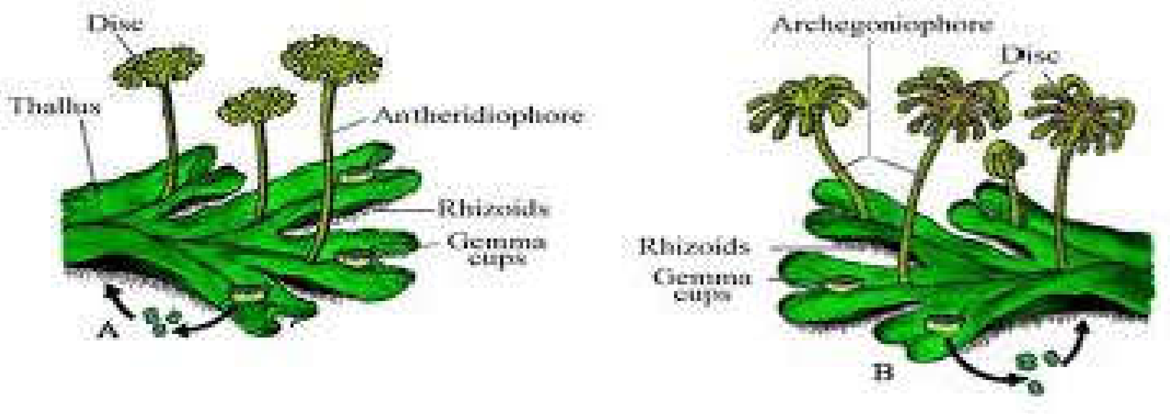


Fig: ***Marchantia spp.*** (A) Male plant, (B) Female plant.

Marchantia sp.

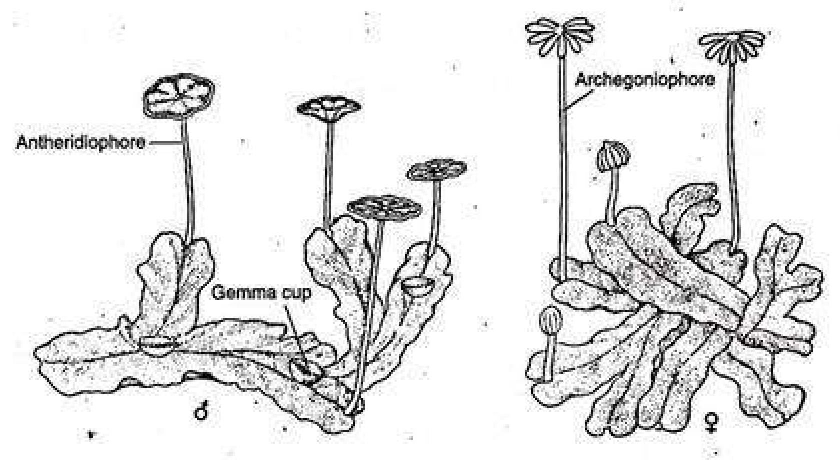


Fig. 6.8 : Male and female plants of *Marchantia polymorpha*

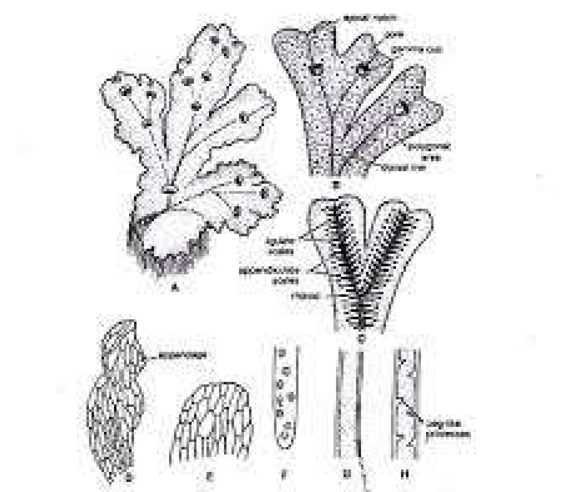


Fig. 1. (A-H). Marchantia. Thallus structure (A) Vegetative thallus. (B) Dorsal surface. (C) Ventral surface. (D) Appendiculate scale. (E) Ligulate scale. (F) Tuberculated rhizoid (surface view). (G) Smooth-walled rhizoid. (H) Tuberculated rhizoid showing internal view.

Vegetative structure of Marchantia

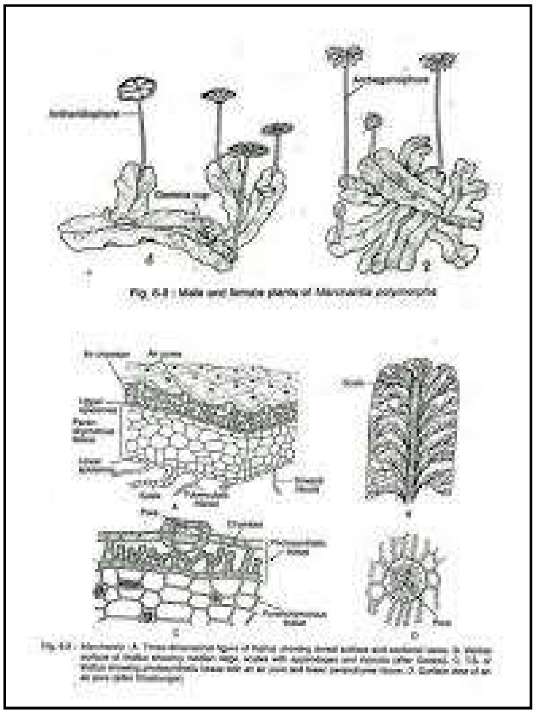
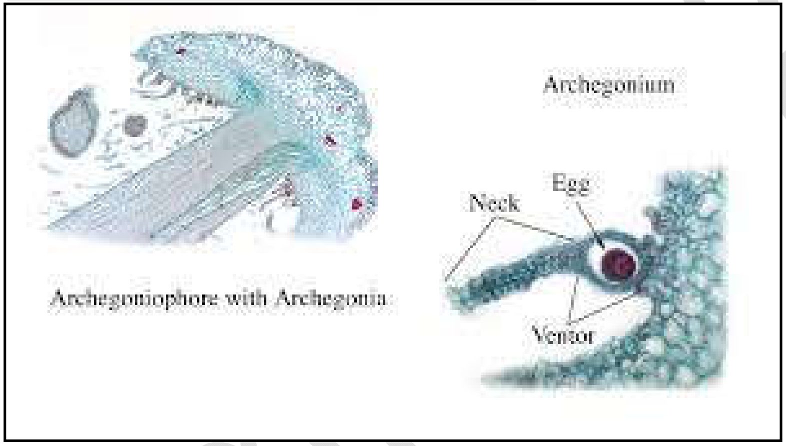
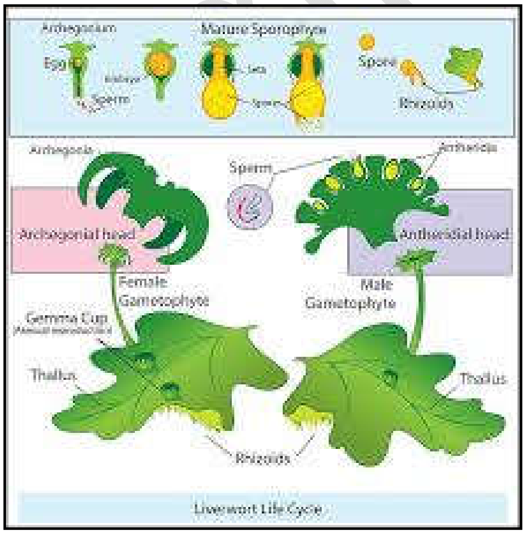


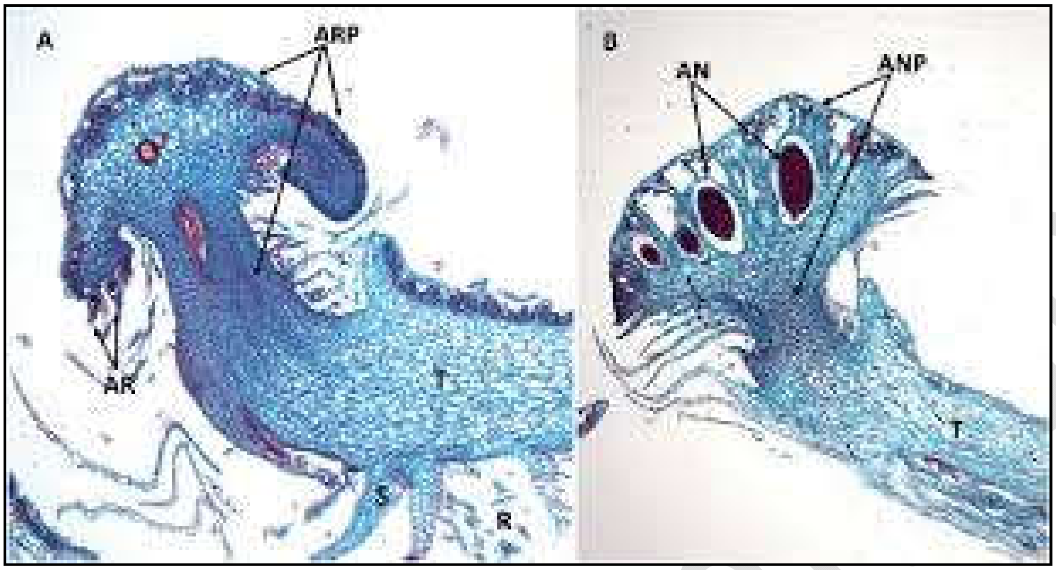
Fig. 6.8 : Male and female plants of *Marchantia polymorpha*



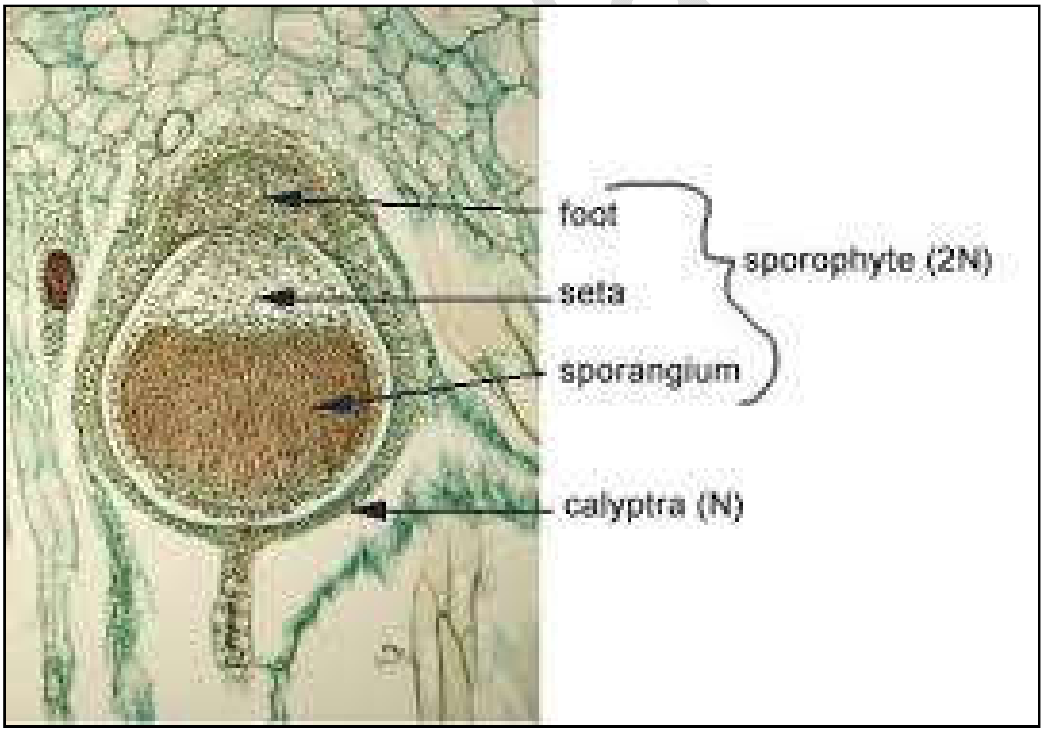
Archegoniophore with Archegonia



Liverwort Life Cycle



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.

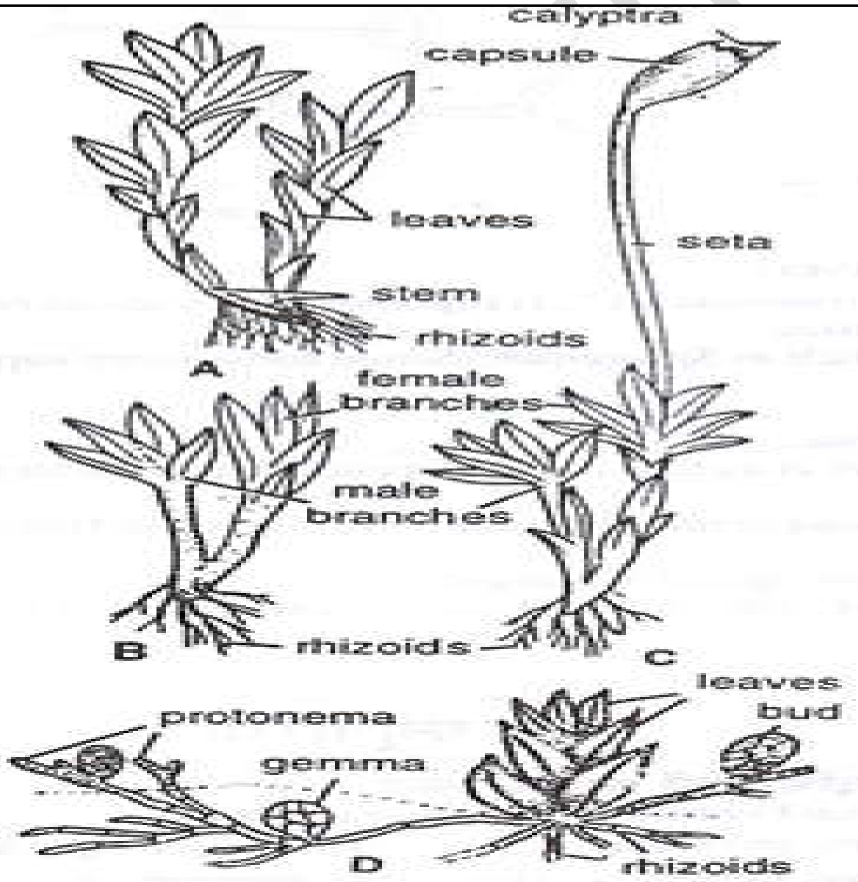


Fig. 194. *Funaria*. A, Vegetative plants; B, Plants with male and female branches; C, A mature plant bearing a sporophyte; D, Protonema and young gametophyte.

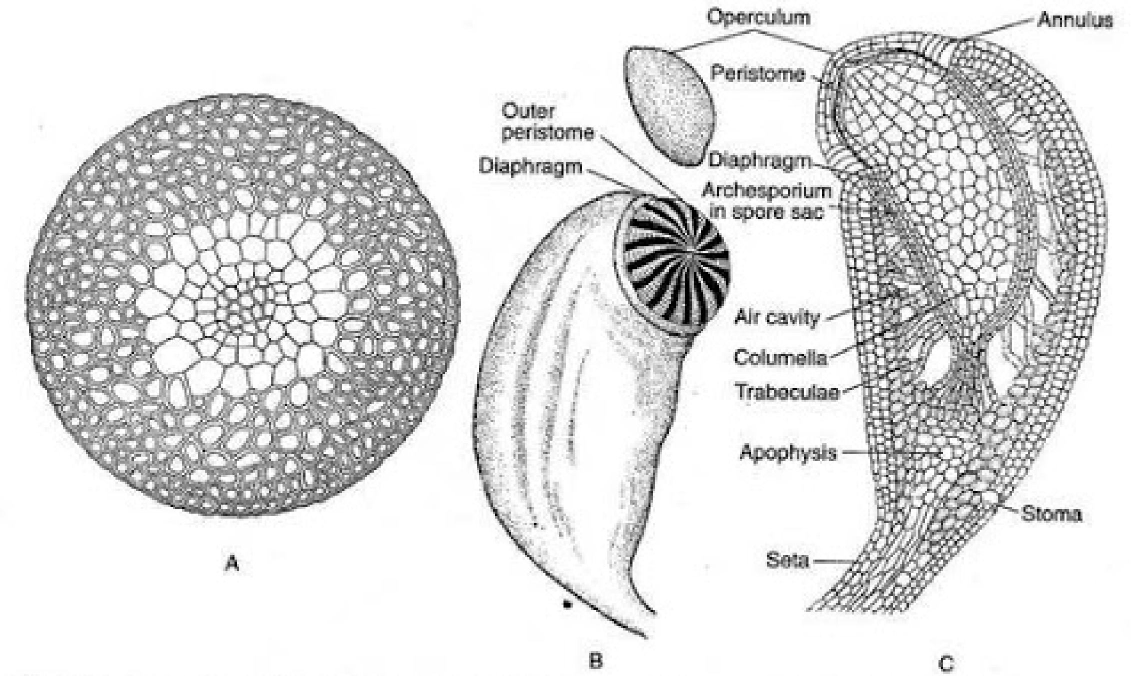


Fig. 6.50 : *Funaria hygrometrica* : A. T.S. of seta, B. Mature capsule with operculum removed (shown on side), C. L.S. of capsule

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*, *Conocephalum*, *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 doubleglazed 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 disorders, 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 & Mukherjee, 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).

ORIGIN AND DISTRIBUTION OF BRYOPHYTES

Bryophytes are the first plant group to colonize open ground through the process of adaptive radiation described as terrestrialization and were also among the pioneers of terrestrial photosynthesis (Hanson & Rice, 2014). Among bryophytes,liverworts are resolved as the first divergence of land plants (Stotler & Crandall-Stotler,2016).

The process of terrestrialization is estimated to have begun around 500 million years ago and much is credited to their photosynthetic abilities. The combination of neontology, paleontology, and molecular phylogenetics reveal that bryophytes inherited many physiological traits necessary from terrestrial existence from ancestral algae including spore, body desiccation-resistance, degradation-resistance lignin-like phenolic cell wall polymers (Graham et al., 2014). Transition to land required an interface between water and land and while fossil record is sparse, brackish water seems the most probable origin of land vegetation (Proctor, 2014). More so, bryophytes will require desiccation tolerance alongside other modifications (like size) for the transition and may have been derived from bacterial and algal species that have desiccation tolerant spores or resting stages. Bryophyte lineages: liverworts (Marchantiophyta), hornworts (Anthocerotophyta), and mosses (Bryophyta) may only superficially related due to independent evolution from their green algal ancestor, Charophytes (Qiu et al., 2006; Crandall-Stotler & Bartholomew-Began, 2007). Hornworts and liverworts represent the earliest evolving while mosses are likely the closest sister group to vascular plants (Crandall-Stotler & Bartholomew-Began, 2007; Chang & Graham, 2011; Ligrone et al., 2012). Raven & Edwards (2014) inferred that bryophytes probably evolved from charophycean green algae based on fossil record from spores and resemblance in being desiccation tolerant and poikilohydric. The authors added that homoiohydry in modern-day bryophytes developed much later as a requirement for their subsequent survival since environment, and environmental conditions evolve alongside organism. The relative complex morphologies in their photosynthetic structure enabled them to meet the light harvesting requirements, whereas higher atmospheric CO2 concentrations in the early Phanerozoic era would have permitted higher rates of photosynthesis (Raven & Edwards, 2014).

For organisms that began their existence in aquatic environments, migration to a land or near land habit will require continuous and elaborate adaptations. For instance, on a short-term, within the tropics, some bryophytes thalli may appear greyish, dried and brittle during dry seasons but transform to a bright green colour when supplied with water or at the onset of the rainy season. Thus, on land, bryophytes had to adjust to the reduced surface area to volume ratio and minimize water loss. Earlier in bryophyte evolution, there was a persistent challenge of remaining in the photic zone but on land, water is limiting while the available light and CO2 require elaborate organelles for their absorption and use (Proctor, 2014). Together, the three bryophyte divisions have around 25,000 representative species. The mosses are the most abundant followed by liverworts and then the hornworts. It may be suggested that more bryophyte species are yet to be discovered especially in tropical regions of the world, where taxonomic and general information are rare. The true mosses show several evolutionary advances over the liverworts, hornworts, and other mosses by possessing rhizoids, calyptra, hadrom (single strand conducting hydroids) and leptoms for conducting nutrients and photosynthates. Besides their ecological value, modern representatives of this plant division contain the legacy of adaptations that led to the greening of the Earth (Hanson & Rice, 2014). Epiphytic bryophytes are commonly found on trees. The tree species, management structure, trunk girth and distance to nearest neighbouring trees may be used to explain the observed diversity and variation in bryophyte cover (Whitelaw & Burton, 2015). Forests also provide numerous types of habitat for bryophytes, especially the ground floor (Jiang et al., 2015). Due to their lack of seeds and flowers, they are grouped among other cryptogams or thallophytes. A group that also contains algae, fungi, and ferns. Collection for herbarium storage and other purposes remains paramount. To this end, important floras are Paton's, "The Liverwort Flora of the British Isles (1999)", Smith's, "The Moss Flora of Britain and Ireland (2004)". Others are "Mosses and Liverworts of Britain and Ireland: a field guide" by Atherton et al. (2010), and Hills et al. (2008) Attributes of British and Irish Mosses, Liverworts and Hornworts. Nordic flora is illustrated with photographs and coloured drawings have been published recently and cover, amongst other taxa, Dicranales, Grimmiales, and Pottiales by Hallingbäck et al. (2006; 2008). After collected, in temperate environments, they can be readily processed (by drying indoors) and stored in simple paper packets folded much like an envelope but without any sticky margin (Preston et al., 2012). The method of folding packets is outlined by Rothero & Blackstock (2005) and is described in various handbooks to mosses and liverworts (Preston et al., 2012). The required information on the packets is outlined in Preston et al. (2012). The distribution of bryophyte requires a favorable microhabitat and microclimate for their establishment (Valente et al., 2013). The species composition and richness within bryophyte communities are influenced by external factors, especially water, light, and temperature, hence their roles are biological indicators (Mägdefrau, 1982; Frahm & Gradstein, 1991). More so, their sensitivity to elevational variations have been documented by van Reenen & Gradstein (1983); (1984); Kessler (2000); Frahm (1990); Frahm & Gradstein (1991); Andrew et al. (2003); Grau et al. (2007); Ah-Peng et al. (2007) and suggest that their species richness and distribution may increase, decrease, have humped-back shape or no trend with increasing and decreasing elevations depending on the biogeographic region. As a result, Andrew et al. (2003) suggested the possibility of making reliable generalizations regarding observable changes in bryophyte diversity along latitudinal and altitudinal gradients according to bryophyte distribution. Other environmental factors that influence bryophyte distribution within a geographical location are insolation, frost, fog, temperature, precipitation, lithology, evapotranspiration rate, humidity, thermicity and soil pH. The application of ecological niche modelling to estimate bryophyte species distribution within a location is a viable method (Sergio et al., 2007). Despite having a wider distribution than vascular plants, bryophytes are often excluded in plant diversity surveys and collection due to difficulties in identification, fewer specialists, less taxonomic literatures especially in tropical areas, time consuming and the high financial cost requirements for searching and identifying bryophytes (Andrew et al., 2003; Ah-Peng et al., 2007; Sun et al., 2013).

Classification of Bryophytes according to

Over the last decade, recent advances in DNA sequencing technology and analytical approaches to phylogenetic reconstruction, including the use of ultra-structural, morphological and anatomical data, have enabled unprecedented progress toward our understanding of plant evolution. A growing consensus suggests that the bryophytes possibly represent three separate evolutionary lineages, which are today recognized as: mosses (phylum Bryophyta), liverworts (phylum Marchantiophyta), and hornworts (phylum Anthocerotophyta)

Bryophyte phyla (divisions) Mosses (Bryophyta) The greatest species diversity in bryophytes is found in the mosses, with estimates of the number of species ranging from 10,000 to 15,000. Higher-level classification of the mosses remains unresolved with considerable difference of opinion on the names of the major groups. However, generally four major groups or classes are recognised. These include: Sphagnopsida Andreasopsida Polytrichopsida Bryopsida Peat or Sphagnum moss Rock or Lantern moss Nematodontous mosses Anthrodontous mosses One of the mose ecologically and economically important groups of bryophytes. The majority of these species are found in the southern hemisphere. Very robust gametophyte with upright growth. The largest and most diverse groups within the mosses with over 100 families

Liverworts (Marchantiophyta) The estimated number of liverwort species range from 6000 to 8000. Traditionally, liverworts have been subdivided into two major groups or classes based, partially, on growth form. Class Marchantiopsida Class Jungermanniopsida includes the well-known genera Marchantia, Monoclea, Lunularia, and Riccia, and has a complex thalloid organization. represents an estimated 85% of liverwort species and shows an enormous amount of morphological, anatomical and ecological diversity; plants with leafy shoot systems are the most common growth form in this class, e.g., Frullania,Jubulopsis, Cololejeunea, aand Radula.

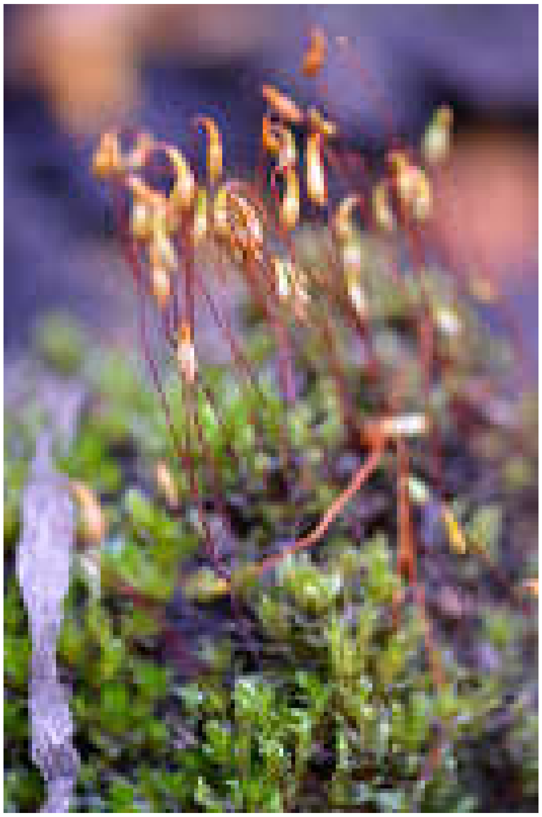
Hornworts (Anthocerotophyta) Hornworts get their name from their long, horn-shaped sporophytes and are the smallest group of bryophytes with only approximately 100 species. Hornworts resemble some liverworts in having simple, unspecialized thalloid gametophytes, but they differ in many other characters. Hornworts differ from all other land plants in having onlyone large, algal-like chloroplast in each thallus cell.

Nothoceros

Symphyogyna pisicolor

Frullania

Sphagnum



Bryum

This classification is taken from: Crandall-Stotler, B., R. E. Stotler & D. G.Long. 2008, 2009. **Morphology and classification of the Marchantiophyta**, pp. 1-54. *In* B. Goffinet & A. J. Shaw (eds.) Bryophyte Biology, 2nd edition. Cambridge University Press, Cambridge. Modifications have been made based upon the more recent publication: Crandall-Stotler, B., R. E. Stotler & D. G. Long. 2009. **Phylogeny and Classification of the Marchantiophyta**, Edinburgh Journal of Botany 66: 155-198.

PHYLUM MARCHANTIOPHYTA Stotler & Crand.-Stotl., in A. J. Shaw & B. Goffinet, Bryoph. Biol.: 63 (2000).

MARCHANTIOPHYTA

The immense morphological diversity among the 377 genera and 6000–8000 species of liverworts has presented significant challenges to systematists (Schljakov, 1972; Schuster, 1984; Crandall-Stotlerand Stotler, 2000). Hepatics have been organized into three groups based on growth form: (1) complex thalloids, (2)simple thalloids, and (3) leafy liverworts. Gametophytes of leafy liverworts range from radially symmetrical with three rows of morphologically similar leaves (isophyllous) to dorsiventral with two rows of lateral leaves and an additional row of reduced (to absent) ventral underleaves or amphigastria (anisophyllous; Simple thalloid (metzgerialean) organizations show less variability, from fleshy undifferentiated thalli to those withprominent midribs and monostromatic wings. Leaflike lobes or lobules in some taxa blur the distinction between leafy and simple thalloid forms. Internal differentiation of water-conducting tissue is restricted to Haplomitrium and certain simple thalloid taxa, whereas conducting parenchyma is widespread among both complex and simple thalloid forms, but not leafy taxa.

CLASS: HAPLOMITRIOPSIDA ,

Stotler & Crand.-Stotl., Bryologist 80: 425 (1977). [including Treubiopsida Stech, J.-P. Frahm, Hilger & W. Frey, Nova Hedwigia 71: 207 (2000)].

SUBCLASS TREUBIIDAE Stotler & Crand.-Stotl., Taxon 57: 290 (2008).

ORDER: TREUBIALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 499 (1972).

Treubiaceae Verd., Man. Bryol. 427 (1932). *Apotreubia* S. Hatt. & Mizut., *Treubia* K. I. Goebel

SUBCLASS HAPLOMITRIIDAE Stotler & Crand.-Stotl., Taxon 57: 290 (2008).

ORDER: Calobryales Hamlin, Rec. Domin. Mus. 7: 315 (1972).

Haplomitriaceae Dedecek, Arch. Naturwiss. Landesdurchf. Böhmen 5(4): 71 (1884). *Haplomitrium* Nees nom. cons.

CLASS: MARCHANTIOPSIDA Cronquist, Takht. & W. Zimm., Taxon 15: 132-133 (1966). ("Marchantiatae").

SUBCLASS: BLASIIDAE He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

ORDER: BLASIALES Stotler & Crand.-Stotl. in A. J. Shaw & B. Goffinet, Bryoph. Biol.: 63 (2000).

Blasiaceae H. Klinggr., Höh. Crypt. Preuss.: 14 (1858). *Blasia* L., *Cavicularia* Steph.

SUBCLASS: MARCHANTIIDAE Engl. [Unterklasse "Marchantiales"] in: A. Engler & K. Prantl, Nat. Pflanzenfam. I (3): 1 (1893).

ORDER: SPHAEROCARPALES Cavers, New Phytol. 9: 81 (1910).

Sphaerocarpaceae Heeg, Verh. K. K. Zool.-Bot. Ges. Wien 41: 573 (1891). *Sphaerocarpos* Boehm., *Geothallus* Campb.

Riellaceae Engl., Syllabus, Grosse Ausgabe: 45 (1892). *Riella* Mont.

ORDER: NEOHODGSONIALES D. G. Long, Edinburgh J. Bot. 63: 258 (2006).

Neohodgsoniaceae D. G. Long, Edinburgh J. Bot. 63: 258 (2006). *Neohodgsonia* Perss.

ORDER: LUNULARIALES D. G. Long, Edinburgh J. Bot. 63: 259 (2006).

Lunulariaceae H. Klinggr., Höh. Crypt. Preuss.: 9 (1858). *Lunularia* Adans.

ORDER: MARCHANTIALES Limpr. in Cohn, Krypt.-Fl. Schlesien 1: 239, 336 (1877).

Marchantiaceae Lindl., Nat. Syst. Bot. (ed. 2): 412 (1836). *Bucegia* Radian, <u>*Marchantia*</u> L., *Preissia* Corda

Aytoniaceae Cavers, New Phytol. 10: 42 (1911). <u>*Asterella*</u> P. Beauv., *Cryptomitrium* Austin ex Underw., *Mannia* Opiz nom. cons., <u>*Plagiochasma*</u> Lehm. & Lindenb. nom. cons., <u>*Reboulia*</u> Raddi nom. cons.

Cleveaceae Cavers, New Phytol. 10: 42 (1911). *Athalamia* Falconer, *Sauteria* Nees, *Peltolepis* Lindb.

Monosoleniaceae Inoue, Bull. Natl. Sci. Mus. Tokyo 9: 117 (1966). <u>*Monosolenium*</u> Griff.

Conocephalaceae Müll. Frib. ex Grolle, J. Bryol. 7: 207 (1972). <u>*Conocephalum*</u> Hill nom. cons.

Cyathodiaceae Stotler & Crand.-Stotl. in A. J. Shaw & B. Goffinet, Bryoph. Biol.: 63 (2000). <u>*Cyathodium*</u> Kunze

Exormothecaceae Müll. Frib. ex Grolle, J. Bryol. 7: 208 (1972). *Aitchisoniella* Kashyap, *Exormotheca* Mitt., *Stephensoniella* Kashyap

Corsiniaceae Engl., Syllabus, Grosse Ausgabe: 44 (1892). *Corsinia* Raddi, *Cronisia* Berk.

Monocarpaceae D. J. Carr ex Schelpe, J. S. African Bot. 35: 110 (1969). *Monocarpus* D. J. Carr

Oxymitraceae Müll. Frib. ex Grolle, J. Bryol. 7: 215 (1972). *Oxymitra* Bisch. ex Lindenb.

Ricciaceae Rchb., Bot. Damen: 255 (1828). *Riccia* L., *Ricciocarpos* Corda

Wiesnerellaceae Inoue, Ill. Jap. Hepat. 2: 192 (1976). *Wiesnerella* Schiffn.

Targioniaceae Dumort., Anal. Fam. Pl.: 68, 70 (1829). *Targionia* L.

Monocleaceae A. B. Frank in Leunis, Syn. Pflanzenk. ed. 2: 1556 (1877). *Monoclea* Hook.

Dumortieraceae D. G. Long, Edinburgh J. Bot. 63: 260 (2006). *Dumortiera* Nees

CLASS: JUNGERMANNIOPSIDA Stotler & Crand.-Stotl., Bryologist 80: 425 (1977).

SUBCLASS: PELLIIDAE He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

ORDER: PELLIALES He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

Pelliaceae H. Klinggr, Höh. Crypt. Preuss.: 13 (1858). *Noteroclada* Taylor ex Hook. & Wilson, *Pellia* Raddi nom. cons.

ORDER: FOSSOMBRONIALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 500 (1972).

SUBORDER: Calyculariineae He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

Calyculariaceae He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006). *Calycularia* Mitt.

SUBORDER: Makinoiineae He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006).

Makinoaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 201 (1943). *Makinoa* Miyake

SUBORDER: Fossombroniineae R.M.Schust. ex Stotler & Crand.-Stotl. in A. J. Shaw & B. Goffinet, Bryoph. Biol.: 63 (2000).

Petalophyllaceae Stotler & Crand.-Stotl., Novon 12: 335 (2002). *Petalophyllum* Nees & Gottsche ex Lehm., *Sewardiella* Kashyap

Allisoniaceae Schljakov, Pecenocnye Mchi, Morfol. Filog. Klassif. [Liverwort morphology, phylogeny, classification]: 119 (1975). *Allisonia* Herzog

Fossombroniaceae Hazsl. nom. cons., Magyar Bir, Moh.-Fl.: 20, 36 (1885). *Fossombronia* Raddi [including *Austrofossombronia* R.M.Schust.]

ORDER: PALLAVICINIALES W. Frey & M. Stech, Nova Hedwigia 81: 64 (2005).

SUBORDER: Phyllothalliineae R. M. Schust., Trans. Brit. Bryol. Soc. 5: 283 (1967).

Phyllothalliaceae E. A. Hodgs., Trans. Roy. Soc. New Zealand, Bot. 2: 247 (1964). *Phyllothallia* E. A. Hodgs.

SUBORDER: Pallaviciniineae R. M. Schust., Phytologia 56: 65 (1984).

Sandeothallaceae R. M. Schust., New Man. Bryol.: 951 (1984). *Sandeothallus* R. M. Schust.

Moerckiaceae Stotler & Crand.-Stotl., Nova Hedwigia Beih. 131: 54 (2007). *Hattorianthus* R. M. Schust. & Inoue, *Moerckia* Gottsche

Hymenophytaceae R. M. Schust., J. Hattori Bot. Lab. 26: 296 (1963). *Hymenophyton* Dumort.

Pallaviciniaceae Mig., Krypt.-Fl. Deutschl., Moose: 423 (1904). *Greeneothallus* Hässel*, Jensenia* Lindb., *Pallavicinia* Gray nom. cons., *Podomitrium* Mitt., *Seppeltia* Grolle, *Symphyogyna* Nees & Mont., *Symphyogynopsis* Grolle, *Xenothallus* R. M. Schust.

SUBCLASS METZGERIIDAE Barthol.-Began, Phytologia 69: 465. (1990[1991]).

ORDER: PLEUROZIALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 505 (1972).

Pleuroziaceae Müll. Frib., Lebermoose 1: 404 (1909). *Pleurozia* Dumort. [including *Eopleurozia* R. M. Schust.]

ORDER: METZGERIALES Chalaud, Ann. Bryol. 3: 41 (1930).

Metzgeriaceae H. Klinggr., Höh. Crypt. Preuss.: 10 (1858). *Metzgeria* Raddi [including *Apometzgeria* Kuwah.
and *Austrometzgeria* Kuwah.], *Steereella* Kuwah., *Vandiemenia* Hewson

Aneuraceae H. Klinggr., Höh. Crypt. Preuss.: 11 (1858). *Aneura* Dumort. [including *Cryptothallus* Malmb.], *Riccardia* Gray nom. cons., *Lobatiriccardia* (Mizut. & S. Hatt.) Furuki, *Verdoornia* R. M. Schust.

Mizutaniaceae Furuki & Z. Iwats., J. Hattori Bot. Lab. 67: 291 (1989). *Mizutania* Furuki & Z. Iwats.

SUBCLASS JUNGERMANNIIDAE Engl. [Unterklasse "Jungermanniales"] in A. Engler & K. Prantl, Nat. Pflanzenfam. I (3): 1 (1893).

ORDER: PORELLALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 505 (1972).

SUBORDER: Porellineae R. M. Schust., J. Hattori Bot. Lab. 26: 229 (1963).

Porellaceae Cavers nom. cons., New Phytol. 9: 292 (1910). *Ascidiota* C. Massal., *Porella* L. [including *Macvicaria* W. E. Nicholson]

Goebeliellaceae Verd., Man. Bryol.: 425 (1932). *Goebeliella* Steph.

Lepidolaenaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 200 (1943). *Gackstroemia* Trevis., *Lepidogyna* R. M. Schust., *Lepidolaena* Dumort., *Jubulopsis* R. M. Schust.

SUBORDER: Radulineae R. M. Schust., J. Hattori Bot. Lab. 26: 229 (1963).

Radulaceae Müll. Frib., Lebermoose 1: 404 (1909). *Radula* Dumort. nom. cons.

SUBORDER: Jubulineae Müll. Frib., Lebermoose 1: 403 (1909).

Frullaniaceae Lorch in G. Lindau, Krypt.-Fl. Anf. 6: 174 (1914). *Frullania* Raddi [including *Amphijubula* R. M. Schust., *Neohattoria* Kamim., *Schusterella* S. Hatt., Sharp & Mizut., and *Steerea* S. Hatt. & Kamim.]

Jubulaceae H. Klinggr., Höh. Crypt. Preuss.: 40 (1858). *Jubula* Dumort. nom. cons., *Nipponolejeunea* S. Hatt.

Lejeuneaceae Cavers, New Phytol. 9: 291 (1910). *Acanthocoleus* R. M. Schust., *Acantholejeunea* (R. M. Schust.) R. M. Schust., *Acrolejeunea* (Spruce)

Schiffn. nom. cons., *Anoplolejeunea* (Spruce) Schiffn., *Aphanotropis* Herzog, *Archilejeunea* (Spruce) Schiffn., *Aureolejeunea* R. M. Schust., *Austrolejeunea* (R. M. Schust.) R. M. Schust. [including *Nephelolejeunea* Grolle], *Blepharolejeunea* S. W. Arnell, *Brachiolejeunea* (Spruce) Schiffn., *Bromeliophila* R. M. Schust., *Bryopteris* (Nees) Lindenb., *Calatholejeunea* K. I. Goebel, *Caudalejeunea* (Steph.) Schiffn., *Cephalantholejeunea* (R. M. Schust. & Kachroo) R. M. Schust., *Cephalolejeunea* Mizut., *Ceratolejeunea* (Spruce) J. B. Jack & Steph., *Cheilolejeunea* (Spruce) Schiffn. [including *Cyrtolejeunea* A. Evans], *Chondriolejeunea* (Benedix) Kis & Pócs, *Cladolejeunea* Zwick., *Cololejeunea* (Spruce) Schiffn. [including *Aphanolejeunea* A. Evansand *Metzgeriopsis* K. I. Goebel], *Colura* (Dumort.) Dumort., *Cyclolejeunea* A. Evans, *Cystolejeunea* A. Evans, *Dactylophorella* R. M. Schust., *Dendrolejeunea* (Spruce) Lacout., *Dicranolejeunea* (Spruce) Schiffn., *Diplasiolejeunea* (Spruce) Schiffn., *Drepanolejeunea* (Spruce) Schiffn. [including *Capillolejeunea* S. W. Arnell and *Rhaphidolejeunea* Herzog], *Echinolejeunea* R. M. Schust., *Evansiolejeunea* Vanden

Berghen, *Frullanoides* Raddi, *Fulfordianthus* Gradst., *Haplolejeunea* Grolle, *Harp alejeunea* (Spruce)

Schiffn., *Hattoriolejeunea* Mizut., *Kymatolejeunea* Grolle, *Leiolejeunea* A. Evans, *Lejeunea* Lib. nom. cons. [including *Amblyolejeunea* Ast*,* *Amphilejeunea* R. M. Schust., *Crossotolejeunea* (Spruce) Schiffn., *Cryptogynolejeunea* R. M. Schust., *Dactylolejeunea* R. M. Schust., *Dicladolejeunea* R. M. Schust., *Echinocolea* R. M. Schust., *Macrolejeunea* (Spruce) Schiffn., *Neopotamolejeunea* E. Reiner and *Taxilejeunea* (Spruce) Schiffn. nom. cons.], *Lepidolejeunea* R. M. Schust., *Leptolejeunea* (Spruce) Schiffn., *Leucolejeunea* A. Evans, *Lindigianthus* Kruijt & Gradst., *Lopholejeunea* (Spruce) Schiffn. nom. cons., *Luteolejeunea* Piippo, *Macrocolura* R. M. Schust., *Marchesinia* Gray nom. cons., *Mastigolejeunea* (Spruce) Schiffn., *Metalejeunea* Grolle, *Microlejeunea* Steph., *Myriocolea* Spruce, *Myriocoleopsis* Schiffn., *Neurolejeunea* (Spruce) Schiffn., *Odontolejeunea* (Spruce) Schiffn., *Omphalanthus* Lindenb. & Nees, *Oryzolejeunea* (R. M. Schust.) R. M. Schust., *Otolejeunea* Grolle & Tixier, *Phaeolejeunea* Mizut., *Physantholejeunea* R. M. Schust., *Pictolejeunea* Grolle, *Pluvianthus* R. M. Schust. & Schäf.-Verw., *Prionolejeunea* (Spruce) Schiffn., *Ptychanthus* Nees, *Pycnolejeunea* (Spruce) Schiffn., *Rectolejeunea* A. Evans, *Schiffneriolejeunea* Verd., *Schusterolejeunea* Grolle, *Siphonolejeunea* Herz og, *Sphaerolejeunea* Herzog, *Spruceanthus* Verd., *Stenolejeunea* R. M. Schust., *Stictolejeunea* (Spruce)

Schiffn., *Symbiezidium* Trevis., *Thysananthus* Lindenb., *Trachylejeunea* (Spruce) Schiffn. nom. cons. [including *Potamolejeunea* (Spruce) Lacout.], *Trocholejeunea* Schiffn., *Tuyamaella* S. Hatt., *Tuzibeanthus* S. Hatt., *Verdoornianthus* Gradst., *Vitalianthus* R. M. Schust. & Giancotti, *Xylolejeunea* X-L. He & Grolle

ORDER PTILIDIALES Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 501 (1972).

Ptilidiaceae H. Klinggr., Höh. Crypt. Preuss.: 37 (1858). *Ptilidium* Nees

Neotrichocoleaceae Inoue, Ill. Jap. Hepat. 1: 176 (1974). *Neotrichocolea* S. Hatt., *Trichocoleopsis* S. Okamura

Herzogianthaceae Stotler & Crand.-Stotl. in B. Goffinet & A. J. Shaw, Bryoph. Biol. ed. 2: 54 (2009[2008]). *Herzogianthus* R. M. Schust.

ORDER JUNGERMANNIALES H. Klinggr., Höh. Crypt. Preuss.: 16 (1858).

SUBORDER: Perssoniellineae R. M. Schust., J. Hattori Bot. Lab. 26: 229-230 (1963).

Perssoniellaceae R. M. Schust. ex Grolle, J. Bryol. 7: 216 (1972). *Perssoniella* Herzog

Schistochilaceae H. Buch, Commentat. Biol. 3(1): 9 (1928). *Gottschea* Nees ex Mont. [including *Paraschistochila* R. M. Schust.], *Pachyschistochila* R. M. Schust. & J. J. Engel, *Pleurocladopsis* R. M. Schust., <u>*Schistochila*</u> Dumort.

SUBORDER: Lophocoleineae Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 504 (1972). (syn.: Geocalycineae R. M. Schust., J. Hattori Bot. Lab. 36: 397 (1972 [1973]).

Pseudolepicoleaceae Fulford & J. Taylor, Nova Hedwigia 1: 411 (1960). *Archeophylla* R. M. Schust., *Blepharostoma* (Dumort.) Dumort., *Chaetocolea* Spruce, *Herzogiaria* Fulford ex Hässel, *Isophyllaria* E. A. Hodgs. & Allison, *Pseudolepicolea* Fulford & J. Taylor [including *Archeochaete* R. M. Schust. and *Lophochaete* R. M. Schust.], *Temnoma* Mitt.

Trichocoleaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 201 (1943). *Castanoclobus* J. J. Engel & Glenny, *Eotrichocolea* R. M. Schust., *Leiomitra* Lindb., <u>*Trichocolea*</u> Dumort. nom. cons.

Grolleaceae Solari ex R. M.S chust., Phytologia 56: 66 (1984). *Grollea* R. M. Schust.

Mastigophoraceae R. M. Schust., J. Hattori Bot. Lab. 36: 345. (1972 [1973]). *Dendromastigophora* R. M. Schust., *Mastigophora* Nees nom. cons.

Herbertaceae Müll. Frib. ex Fulford & Hatcher, Bryologist 61: 284 (1958). *Herbertus* Gray, *Olgantha* R. M. Schust., *Triandrophyllum* Fulford & Hatcher

Vetaformataceae Fulford & J. Taylor, Mem. New York Bot. Gard. 11: 27 (1963). *Vetaforma* Fulford & J. Taylor

Lepicoleaceae R. M. Schust., Nova Hedwigia 5: 27 (1963). *Lepicolea* Dumort.

Phycolepidoziaceae R. M. Schust., Bull. Torrey Bot. Club 93: 442 (1967). *Phycolepidozia* R. M. Schust.

Lepidoziaceae Limpr. in Cohn, Krypt.-Fl. Schlesien 1: 310 (1877). *Acromastigum* A. Evans, *Amazoopsis* J. J. Engel & G. L. S. Merr., *Arachniopsis* Spruce, *Bazzania* Gray nom. cons., *Chloranthelia* R. M. Schust., *Dendrobazzania* R. M. Schust. & W. B. Schofield, *Drucella* E. A. Hodgs., *Hyalolepidozia* S. W. Arnell ex Grolle, *Hygrolembidium* R. M.

Schust., *Isolembidium* R. M. Schust., *Kurzia* G. Martens, *Lembidium* Mitt. nom. cons., Lepidozia (Dumort.) Dumort. nom. cons., *Monodactylopsis* (R. M. Schust.) R. M. Schust., *Mastigopelma* Mitt., *Megalembidium* R. M. Schust., *Micropterygium* Lindenb., Nees & Gottsche, *Mytilopsis* Spruce, *Neogrollea* E. A. Hodgs., *Odontoseries* Fulford, *Paracromastigum* Fulford & J. Taylor, *Protocephalozia* (Spruce) K. I. Goebel, *Pseudocephalozia* R. M. Schust., *Psiloclada* Mitt., *Pteropsiella* Spruce, *Sprucella* Steph., *Telaranea* Spruce ex Schiffn., *Zoopsidella* R. M. Schust., *Zoopsis* Hook. f. ex Gottsche, Lindenb. & Nees

Lophocoleaceae Vanden Berghen in Robyns, Fl. Gén. Belgique, Bryoph. 1: 208 (1956). *Amphilophocolea* R. M. Schust., *Chiloscyphus* Corda, *Clasmatocolea* Spruce, *Conoscyphus* Mitt., *Cyanolophocolea* R. M. Schust., *Evansianthus* R. M. Schust. & J. J. Engel [including *Austrolembidium* Hässel], *Hepatostolonophora* J. J. Engel & R. M. Schust., *Heteroscyphus* Schiffn. nom. cons. [including *Tetracymbaliella* Grolle], *Lamellocolea* J. J .Engel, *Leptophyllopsis* R. M. Schust., *Leptoscyphopsis* R. M. Schust., *Leptoscyphus* Mitt., Lophocolea (Dumort.) Dumort.

[including *Campanocolea* R. M. Schust.], *Pachyglossa* Herzog & Grolle [including *Invisocaulis* R. M. Schust. nom. inval.], *Perdusenia* Hässel, *Physotheca* J. J. Engel & Gradst., *Pigafettoa* C. Massal., *Platycaulis* R. M. Schust., *Pseudolophocolea* R. M. Schust. & J. J. Engel, *Stolonivector* J. J. Engel, *Xenocephalozia* R. M. Schust.

Brevianthaceae J. J. Engel & R. M. Schust., Phytologia 47: 317 (1981). *Brevianthus* J. J. Engel & R. M. Schust.

Chonecoleaceae R. M. Schust. ex Grolle, J. Bryol. 7: 206 (1972). *Chonecolea* Grolle

Plagiochilaceae Müll. Frib. & Herzog in Müller, Leberm. Eur.: 877 (1956). *Acrochila* R. M. Schust., *Chiastocaulon* Carl, *Dinckleria* Trevis. [? *Proskauera* Heinrichs & J. J. Engel], *Pedinophyllopsis* R. M. Schust. & Inoue, *Pedinophyllum* (Lindb.) Lindb., <u>*Plagiochila*</u> (Dumort.) Dumort. nom. cons. [including *Rhodoplagiochila* R. M. Schust., *Steereochila* Inoue, and *Szweykowskia* Gradst. & E. Reiner], *Plagiochilidium* Herzog, *Plagiochilion* S. Hatt., *Xenochila* R.M.Schust.

SUBORDER: Cephaloziineae Schljakov, Bot. Zhurn. (Moscow & Leningrad) 57: 503 (1972). [syn.: Cephaloziineae R. M. Schust., J. Hattori Bot. Lab. 36: 391. (1972 [1973])].

Adelanthaceae Grolle, J. Hattori Bot. Lab. 35: 327 (1972). *Adelanthus* Mitt. nom. cons. [including *Pseudomarsupidium* Herzog], *Calyptrocolea* R. M. Schust., *Wettsteinia* Schiffn.

Jamesoniellaceae He-Nygrén, Juslén, Ahonen, Glenny & Piippo, Cladistics 22: 27 (2006). *Anomacaulis* (R. M. Schust.) Grolle, *Cryptochila* R.M.Schust., *Cuspidatula* Steph., *Denotarisia* Grolle, *Jamesoniella* (Spruce) Carrington, *Nothostrepta* R. M. Schust., *Pisanoa* Hässel, *Protosyzygiella* (Inoue) R. M. Schust., *Roivainenia* Perss., *Syzygiella* Spruce, *Vanaea* (Inoue & Gradst.) Inoue & Gradst.

Cephaloziaceae Mig., Krypt.-Fl. Deutschl., Moose: 465 (1904). *Alobiella* (Spruce) Schiffn., *Alobiellopsis* R. M. Schust., *Anomoclada* Spruce, *Cephalozia* (Dumort.) Dumort., *Cladopodiella* H. Buch, *Fuscocephaloziopsis* Fulford, *Haesselia* Grolle & Gradst., *Hygrobiella* Spruce, *Iwatsukia* N. Kitag., *Metahygrobiella* R. M. Schust., *Nowellia* Mitt., *Odontoschisma* (Dumort.)

Dumort., *Pleurocladula* Grolle, *Schiffneria* Steph., *Schofieldia* J. D. Godfrey, *Trabacellula* Fulford

Cephaloziellaceae Douin, Bull. Soc. Bot. France, Mém. 29: 1, 5, 13 (1920). *Allisoniella* E. A. Hodgs. [including *Protomarsupella* R. M. Schust.], *Amphicephalozia* R. M. Schust., *Cephalojonesia* Grolle, *Cephalomitrion* R. M. Schust., *Cephaloziella* (Spruce) Schiffn. nom. cons., *Cephaloziopsis* (Spruce) Schiffn., *Cylindrocolea* R. M. Schust., *Gymnocoleopsis* (R. M. Schust.) R. M. Schust., *Kymatocalyx* Herzog [including *Stenorrhipis* Herzog]

Scapaniaceae Mig., Krypt.-Fl. Deutschl., Moose: 479 (1904) [including Chaetophyllopsidaceae R. M. Schust., J. Hattori Bot. Lab. 23: 68. (1960 [1961]), Diplophyllaceae Potemk., Ann. Bot. Fenn. 36: 281 (1999), and Lophoziaceae Cavers, New Phytol. 9: 293 (1910)]. *Anastrepta* (Lindb.) Schiffn., *Anastrophyllum* (Spruce) Steph., *Andrewsianthus* R. M. Schust. [including *Cephalolobus* R. M. Schust.], *Barbilophozia* Loeske, *Chaetophyllopsis* R. M. Schust., *Chandonanthus* Mitt., *Diplophyllum* (Dumort.) Dumort. nom. cons., *Douinia* (C. N. Jensen) H. Buch, *Gerhildiella* Grolle, <u>*Gottschelia*</u> Grolle, *Gymnocolea* (Dumort.)

Dumort., *Hattoria* R. M. Schust., *Isopaches* H. Buch, *Krunodiplophyllum* Grolle, *Lophozia* (Dumort.) Dumort., *Macrodiplophyllum* (H. Buch) Perss., *Plicanthus* R. M. Schust., *Pseudocephaloziella* R. M. Schust., *Scapania* (Dumort.) Dumort. nom. cons., *Scapaniella* H. Buch, *Schistochilopsis* (N. Kitag.) Konst., *Sphenolobopsis* R. M. Schust. & N. Kitag., *Sphenolobus* (Lindb.) Berggr., *Tetralophozia* (R. M. Schust.) Schljakov, *Tritomaria* Schiffn. ex Loeske

SUBORDER: Jungermanniineae R. M. Schust. ex Stotler & Crand.-Stotl. in A. J. Shaw & B. Goffinet, Bryoph. Biol.: 64 (2000).

Myliaceae Schljakov, Novosti Sist. Nizsh. Rast. 12: 308 (1975). *Leiomylia* J. J. Engel & Braggins, *Mylia* Gray

Trichotemnomataceae R. M. Schust., J. Hattori Bot. Lab. 36: 340 (1972 [1973]). *Trichotemnoma* R. M. Schust.

Balantiopsidaceae H. Buch, Mitt. Thüring. Bot. Ges. 1(2-3): 23 (1955). *Anisotachis* R. M. Schust., *Acroscyphella* N. Kitag. & Grolle [≡ *Austroscyphus* R. M. Schust. nom. illeg.], *Balantiopsis* Mitt., *Eoisotachis* R. M. Schust., *Hypoisotachis* (R. M. Schust.) J. J. Engel & G. L. S. Merr., *Isotachis* Mitt., *Neesioscyphus* Grolle, *Ruizanthus* R. M. Schust.

Acrobolbaceae E. A. Hodgs., Rec. Domin. Mus. 4: 177 (1962). *Acrobolbus* Nees, *Austrolophozia* R. M. Schust., *Enigmella* G.A. M.Scott & K. G. Beckm., *Goebelobryum* Grolle, *Lethocolea* Mitt. nom. cons. [including *Neoprasanthus* S. Winkl.], *Marsupidium* Mitt., *Tylimanthus* Mitt.

Blepharidophyllaceae R. M. Schust., Nova Hedwigia Beih. 119: 491 (2002). *Blepharidophyllum* Ångstr., *Clandarium* (Grolle) R. M. Schust.

Arnelliaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 200 (1943). *Arnellia* Lindb., *Gongylanthus* Nees, *Southbya* Spruce, *Stephaniella* J. B. Jack, *Stephaniellidium* S. Winkl. ex Grolle

Jackiellaceae R. M. Schust., J. Hattori Bot. Lab. 36: 395. (1972 [1973]). *Jackiella* Schiffn.

Calypogeiaceae Arnell in Holmberg, Skand. Fl. 2a.: 189 (1928). *Calypogeia* Raddi nom. cons., *Eocalypogeia* (R. M. Schust.) R. M. Schust., *Metacalypogeia* (S. Hatt.) Inoue, *Mnioloma* Herzog

Delavayellaceae R. M. Schust., Bryologist 64: 202 (1961). *Delavayella* Steph., *Liochlaena* Nees

Jungermanniaceae Rchb., Bot. Damen: 256 (1828).[including Mesoptychiaceae Inoue & Steere, Bull. Natl. Sci. Mus. Tokyo, B 1: 62 (1975).] *Eremonotus* Lindb. & Kaal. ex Pearson [including *Anomomarsupella* R. M. Schust.], *Hattoriella* (Inoue) Inoue, *Jungermannia* L., *Leiocolea* (Müll. Frib.) H. Buch, *Mesoptychia* (Lindb.) A. Evans

Solenostomataceae Stotler & Crand.-Stotl., Edinburgh J. Bot. 66: 190 (2009). *Arctoscyphus* Hässel, *Bragginsella* R. M. Schust., *Cryptocolea* R. M. Schust., *Cryptocoleopsis* Amak., *Cryptostipula* R. M. Schust., *Diplocolea* Amak., *Horikawaella* S. Hatt. & Amakawa, *Nardia* Gray nom. cons. [including *Apotomanthus* (Spruce) Schiffn.], *Scaphophyllum* Inoue, *Solenostoma* Mitt. [including *Plectocolea* (Mitt.) Mitt.]

Geocalycaceae H. Klinggr., Höh. Crypt. Preuss.: 34 (1858). *Geocalyx* Nees, *Harpanthus* Nees, *Notoscyphus* Mitt., *Saccogyna* Dumort. nom. cons., *Saccogynidium* Grolle,

Gyrothyraceae R. M. Schust., Trans. Brit. Bryol. Soc. 6: 87 (1970). <u>*Gyrothyra*</u> M. Howe

Antheliaceae R. M. Schust., J. Hattori Bot. Lab. 26: 236 (1963). *Anthelia* (Dumort.) Dumort.

Gymnomitriaceae H. Klinggr., Höh. Crypt. Preuss.: 16 (1858). *Acrolophozia* R. M. Schust., *Apomarsupella* R. M. Schust., *Gymnomitrion* Corda nom. cons., *Herzogobryum* Grolle, *Lophonardia* R. M. Schust., *Marsupella* Dumort., *Nanomarsupella* (R. M. Schust.) R. M. Schust., *Nothogymnomitrion* R. M. Schust., *Paramomitrion* R. M. Schust., *Poeltia* Grolle, *Prasanthus* Lindb.

Moss Classification at the Rank of Genus and Above

(modified from Goffinet, B., W.R Buck and A.J. Shaw, Bryophyte Biology, 2nd ed. Cambridge University Press, 2008; Goffinet 2012: <http://www.eeb.uconn.edu/people/goffinet/Classificationmosses.html>)

PHYLUM BRYOPHYTA

SUBPHYLUM **TAKAKIOPHYTINA** Stech & W. Frey

CLASS **TAKAKIOPSIDA** Stech & W. Frey

ORDER **TAKAKIALES** Stech & W. Frey

FAMILY **TAKAKIACEAE** Stech & W. Frey: *Takakia* S. Hatt. & Inoue

SUBPHYLLUM **SPHAGNOPHYTINA** Doweld

CLASS SPHAGNOPSIDA Ochyra

ORDER SPHAGNALES Limpr.

FAMILY **SPHAGNACEAE** Dumort.: *Sphagnum* L.

FAMILY **FLATBERGIACEAE** A.J. Shaw: *Flatbergium* A.J. Shaw

FAMILY **AMBUCHANANIACEAE** Seppelt & H. A. Crum: *Ambuchanania* Seppelt & H. A. Crum, *Eosphagnum* A.J. Shaw

SUBPHYLLUM ANDREAEOPHYTINA Goffinet, W. R. Buck & A. J. Shaw

CLASS ANDREAEOPSIDA J. H. Schaffn.

ORDER ANDREAEALES Limpr.

FAMILY **ANDREAEACEAE** Dumort.: *Acroschisma* (Hook.f. & Wilson) Lindl., *Andreaea* Hedw.

CLASS ANDREAEOBRYOPSIDA Goffinet & W. R. Buck

ORDER ANDREAEOBRYALES B. M. Murray

FAMILY **ANDREAEOBRYACEAE** Steere: *Andreaeobryum* Steere & B. M. Murray

SUBPHYLLUM BRYOPHYTINA Engler

CLASS OEDIPODIOPSIDA Goffinet & W. R. Buck

ORDER OEDIPODIALES Goffinet & W. R. Buck

FAMILY **OEDIPODIACEAE** Schimp.: *Oedipodium* Schwägr.

CLASS POLYTRICHOPSIDA Doweld

ORDER POLYTRICHALES M. Fleisch.

FAMILY **POLYTRICHACEAE** Schwägr.: *Alophozia* Cardot, *Atrichopsis* Cardot, *Atrichum* P. Beauv., *Bartramiopsis* Kindb., *Dawsonia* R.Br., *Dendroligotrichum* (Müll. Hal.) Broth., *Hebantia* G. L. Sm., *Itatiella* G. L. Sm., *Lyellia* R. Br., *Meiotrichum* (G. L. Sm.) G. L. Sm., *Notoligotrichum* G. L. Sm., *Oligotrichum* Lam. & DC, *Plagioracelopus* G. L. Sm. Merr., *Pogonatum* P. Beauv., *Polytrichadelphus* (Müll. Hal.) Mitt., *Polytrichastrum* G. L. Sm., *Polytrichum* Hedw., *Pseudatrichum* Reimers, *Psilopilum* Brid., *Steereobryon* G. L. Sm.

CLASS TETRAPHIDOPSIDA Goffinet & W. R. Buck

ORDER TETRAPHIDALES M. Fleisch.

FAMILY **TETRAPHIDACEAE** Schimp.: *Tetraphis* Hedw., *Tetrodontium* Schwägr.

CLASS BRYOPSIDA Rothm.

SUBCLASS BUXBAUMIIDAE Doweld

ORDER BUXBAUMIALES M. Fleisch.

FAMILY **BUXBAUMIACEAE** Schimp.: *Buxbaumia* Hedw.

SUBCLASS DIPHYSCIIDAE Ochyra

ORDER DIPHYSCIALES M. Fleisch.

FAMILY **DIPHYSCIACEAE** M. Fleisch.: *Diphyscium* D. Mohr

SUBCLASS TIMMIIDAE Ochyra

ORDER TIMMIALES Ochyra

FAMILY **TIMMIACEAE** Schimp.: *Timmia* Hedw.

SUBCLASS FUNARIIDAE Ochyra

ORDER GIGASPERMALES Goffinet, Wickett, O. Werner, Ros, A.J. Shaw & C.J. Cox

FAMILY **GIGASPERMACEAE** Lindb.: *Chamaeobryum* Thér. & Dixon, *Costesia* Thér., *Gigaspermum* Lindb., *Lorentziella* Müll. Hal., *Oedipodiella* Dixon

ORDER ENCALYPTALES Dixon

FAMILY **BRYOBARTRAMIACEAE** Sainsb.: *Bryobartramia* Sainsb.

FAMILY **ENCALYPTACEAE** Schimp.: *Bryobrittonia* R. S. Williams, *Encalypta* Hedw.

ORDER FUNARIALES M. Fleisch.

FAMILY **FUNARIACEAE** Schwägr.: *Aphanorrhegma* Sull., *Brachymeniopsis* Broth., *Bryobeckettia* Fife, *Clavitheca* O. Werner, Ros & Goffinet, *Cygnicollum* Fife & Magill, *Entosthodon* Schwägr., *Funaria* Hedw., *Funariella* Sérgio, *Goniomitrium* Hook.f. & Wilson, *Loiseaubryum* Bizot, *Nanomitriella* E. B. Bartram, *Physcomitrella* Bruch & Schimp., *Physcomitrellopsis* Broth. & Wager, *Physcomitridium* G.Roth, *Physcomitrium* (Brid.) Brid., *Pyramidula* Brid.

FAMILY **DISCELIACEAE** Schimp.: *Discelium* Brid.

SUBCLASS DICRANIDAE Doweld

ORDER SCOULERIALES Goffinet & W. R. Buck

FAMILY **SCOULERIACEAE** S. P. Churchill in Funk & D. R. Brooks: *Scouleria* Hook., *Tridontium* Hook.f.

FAMILY **DRUMMONDIACEAE** Goffinet: *Drummondia* Hook.

ORDER BRYOXIPHIALES H. A. Crum & L. E. Anderson

FAMILY **BRYOXIPHIACEAE** Besch.: *Bryoxiphium* Mitt.

ORDER GRIMMIALES M. Fleisch.

FAMILY **GRIMMIACEAE** Arn.: *Bucklandiella* Roiv., *Codriophorus* P. Beauv., *Dryptodon* Brid., *Grimmia* Hedw., *Leucoperichaetium* Magill, *Niphotrichum* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, *Racomitrium* Brid., *Schistidium* Bruch & Schimp.

FAMILY **PTYCHOMITRIACEAE** Schimp.: *Aligrimmia* R. S. Williams, *Campylostelium* Bruch & Schimp., *Indusiella* Broth. & Müll. Hal., *Jaffueliobryum* Thér., *Ptychomitriopsis* Dixon, *Ptychomitrium* Fürnr.

FAMILY **SELIGERIACEAE** Schimp.: *Blindia* Bruch & Schimp., *Brachydontium* Fürnr., *Hymenolomopsis* Thér., *Notothamia* R.Ochyra & R.D.Seppelt, *Seligeria* Bruch & Schimp., *Trochobryum* Breidl. & Beck, *Valdonia* Ochyra

ORDER ARCHIDIALES Limpr.

FAMILY **ARCHIDIACEAE** Schimp.: *Archidium* Brid.

ORDER DICRANALES H. Philib. ex M. Fleisch.

FAMILY **FISSIDENTACEAE** Schimp.: *Fissidens* Hedw.

FAMILY **HYPODONTIACEAE** Stech & W. Frey: *Hypodontium* Müll. Hal.

FAMILY **EUSTICHIACEAE** Broth.: *Eustichia* (Brid.) Brid.

FAMILY **DITRICHACEAE** Limpr.: *Astomiopsis* Müll. Hal., *Bryomanginia* Thér., *Ceratodon* Brid., *Cheilothela* Broth., *Chrysoblastella* R. S. Williams, *Cladastomum* Müll. Hal., *Cleistocarpidium* Ochyra & Bednarek-Ochyra, *Crumuscus* W. R. Buck & Snider, *Cygniella* H. A. Crum, *Distichium* Bruch & Schimp., *Ditrichopsis* Broth., *Ditrichum* Hampe, *Eccremidium* Hook.f. & Wilson, *Garckea* Müll. Hal., *Kleioweisiopsis* Dixon, ×*Pleuriditrichum* A. L. Andrews & F. J. Herm., *Pleuridium* Rabenh., *Rhamphidium* Mitt., *Saelania* Lindb., *Skottsbergia* Cardot, *Strombulidens* W. R.

Buck, *Trichodon* Schimp., *Tristichium* Müll. Hal., *Wilsoniella* Müll. Hal.

FAMILY **BRUCHIACEAE** Schimp.: *Bruchia* Schwägr., *Cladophascum* Sim, *Eobruchia* W. R. Buck, *Pringleella* Cardot, *Trematodon* Michx.

FAMILY **RHACHITHECIACEAE** H. Rob.: *Hypnodontopsis* Z. Iwats. & Nog., *Jonesiobryum* B. H. Allen & Pursell, *Rhachitheciopsis* P. de la Varde, *Rhachithecium* Le Jolis, *Tisserantiella* P. de la Varde, *Uleastrum* W. R. Buck, *Zanderia* Goffinet

FAMILY **ERPODIACEAE** Broth.: *Aulacopilum* Wilson, *Erpodium* (Brid.) Brid., *Solmsiella* Müll. Hal., *Venturiella* Müll. Hal., *Wildia* Müll. Hal. & Broth.

FAMILY **SCHISTOSTEGACEAE** Schimp.: *Schistostega* D. Mohr

FAMILY **VIRIDIVELLERACEAE** I. G. Stone: *Viridivellus* I. G. Stone

FAMILY **RHABDOWEISIACEAE** Limpr.: *Amphidium* Schimp., *Arctoa* Bruch & Schimp., *Cynodontium* Schimp., *Dichodontium* Schimp., *Dicranoweisia* Milde, *Glyphomitrium* Brid., *Holodontium* (Mitt.)

Broth., *Hymenoloma* Dusén, *Kiaeria* I. Hagen, *Oncophorus* (Brid.) Brid., *Oreas* Brid., *Oreoweisia* (Bruch & Schimp.) De Not., *Pseudohyophila* Hilp., *Rhabdoweisia* Bruch & Schimp., *Symblepharis* Mont., *Verrucidens* Cardot

FAMILY **DICRANACEAE** Schimp.: *Anisothecium* Mitt., *Aongstroemia* Bruch & Schimp., *Aongstroemiopsis* M. Fleisch., *Braunfelsia* Paris, *Brotherobryum* M. Fleisch., *Bryotestua* Thér. & P. de la Varde, *Camptodontium* Dusén, *Campylopodium* (Müll. Hal.) Besch., *Chorisodontium* (Mitt.) Broth., *Cnestrum* I. Hagen, *Cryptodicranum* E. B. Bartram, *Dicnemon* Schwägr., *Dicranella* (Müll. Hal.) Schimp., *Dicranoloma* (Renauld) Renauld, *Dicranum* Hedw., *Diobelonella* Ochyra, *Eucamptodon* Mont., *Eucamptodontopsis* Broth., *Holomitriopsis* H. Rob., *Holomitrium* Brid., *Hygrodicranum* Cardot, *Leptotrichella* (Müll. Hal.) Lindb., *Leucoloma* Brid., *Macrodictyum* (Broth.) E. H. Hegew., *Mesotus* Mitt., *Mitrobryum* H. Rob., *Muscoherzogia* Ochyra, *Orthodicranum* (Bruch & Schimp.)

Loeske, *Paraleucobryum* (Limpr.) Loeske, *Parisia* Broth., *Platyneuron* (Cardot) Broth., *Pocsiella* Bizot, *Polymerodon* Herzog, *Pseudephemerum* (Lindb.) I. Hagen, *Pseudochorisodontium* (Broth.) C. H. Gao, Vitt, X. H. Fu & T. Cao, *Schliephackea* Müll. Hal., *Sclerodontium* Schwägr., *Sphaerothecium* Hampe, *Steyermarkiella* H. Rob., *Wardia* Harv. & Hook., *Werneriobryum* Herzog

FAMILY **MICROMITRIACEAE** Smyth ex Goffinet & Budke: *Micromitrium* Austin

FAMILY **LEUCOBRYACEAE** Schimp.: *Atractylocarpus* Mitt., *Brothera* Müll. Hal., *Bryohumbertia* P. de la Varde & Thér., *Campylopodiella* Cardot, *Campylopus* Brid., *Cladopodanthus* Dozy & Molk., *Dicranodontium* Bruch & Schimp., *Leucobryum* Hampe, *Microcampylopus* (Müll. Hal.) Fleisch., *Ochrobryum* Mitt., *Pilopogon* Brid., *Schistomitrium* Dozy & Molk.

FAMILY **CALYMPERACEAE** Kindb.: *Arthrocormus* Dozy & Molk., *Calymperes* Sw., *Exodictyon* Cardot, *Exostratum* L. T.

Ellis, *Leucophanes* Brid., *Mitthyridium* H. Rob., *Octoblepharum* Hedw., *Syrrhopodon* Schwägr.

ORDER POTTIALES M. Fleisch.

FAMILY **POTTIACEAE** Schimp.: *Acaulon* Müll. Hal., Acaulonopsis R. H. Zander & Hedd., *Algaria* Hedd. & R. H. Zander, *Aloina* (Müll.Hal) Kindb., *Aloinella* Cardot, *Anoectangium* Schwägr., *Aschisma* Lindb., *Barbula* Hedw., *Bellibarbula* P. C. Chen, *Bryoceuthospora* H. A. Crum & L. E. Anderson, *Bryoerythrophyllum* P. C. Chen, *Calymperastrum* I. G. Stone, *Calyptopogon* (Mitt.) Broth., *Chenia* R. H. Zander, *Chionoloma* Dixon, *Cinclidotus* P. Beauv., *Crossidium* Jur., *Crumia* W. B. Schofield, *Dialytrichia* (Schimp.) Limpr., *Didymodon* Hedw., *Dolotortula* R. H. Zander, *Ephemerum* Schimp., *Erythrophyllopsis* Broth., *Eucladium* Bruch & Schimp., *Ganguleea* R. H. Zander, *Gertrudiella* Broth., *Globulinella* Steere, *Guerramontesia* M.J .Cano, J.A.Jiménez, M.T.Gallego & J.F.Jiménez *Gymnostomiella* M. Fleisch., *Gymnostomum* Nees &

Hornsch., *Gyroweisia* Schimp., *Hennediella* Paris, *Hilpertia* R. H. Zander, *Hymenostyliella* E. B. Bartram, *Hymenostylium* Brid., *Hyophila* Brid., *Hyophiladelphus* (Müll. Hal.) R. H. Zander, *Indopottia* A.E.D.Daniels, R.D.A.Raja & P.Daniels, *Leptobarbula* Schimp., *Leptodontiella* R. H. Zander & E. H. Hegew., *Leptodontium* (Müll. Hal.) Lindb., *Ludorugbya* Hedd. & R.H. Zander, *Luisierella* Thér. & P. de la Varde, *Microbryum* Schimp., *Mironia* R. H. Zander, *Molendoa* Lindb., *Nanomitriopsis* Cardot, *Neophoenix* R. H. Zander & During, *Pachyneuropsis* H.A.Mill., *Phascopsis* I. G. Stone, *Picobryum* R.H.Zander & Hedd., *Plaubelia* Brid., *Pleurochaete* Lindb., *Pottiopsis* Blockeel & A. J. E. Sm., *Pseudocrossidium* R. S. Williams, *Pseudosymblepharis* Broth., *Pterygoneurum* Jur., *Quaesticula* R. H. Zander, *Reimersia* P. C. Chen, *Rhexophyllum* Herzog, *Sagenotortula* R. H. Zander, *Saitobryum* R. H. Zander, *Sarconeurum* Bryhn, *Scopelophila* (Mitt.) Lindb., *Splachnobryum* Müll. Hal., *Stegonia* Venturi, *Stonea* R. H. Zander, *Streptocalypta* Müll.

Hal., *Streptopogon* Mitt., *Streptotrichum* Herzog, *Syntrichia* Brid., *Teniolophora* W. D. Reese, *Tetracoscinodon* R. Br. ter, *Tetrapterum* A. Jaeger, *Timmiella* (De Not.) Schimp., *Tortella* (Lindb.) Limpr., *Tortula* Hedw., *Trachycarpidium* Broth., *Trachyodontium* Steere, *Trichostomum* Bruch, *Triquetrella* Müll. Hal., *Tuerckheimia* Broth., *Uleobryum* Broth., *Vrolijkheidia* Hedd. & R. H. Zander, *Weisiopsis* Broth., *Weissia* Hedw., *Weissiodicranum* W. D. Reese, *Willia* Müll. Hal.

FAMILY **PLEUROPHASCACEAE** Broth.: *Pleurophascum* Lindb.

FAMILY **SERPOTORTELLACEAE** W. D. Reese & R. H. Zander: *Serpotortella* Dixon

FAMILY **MITTENIACEAE** Broth.: *Mittenia* Lindb.

SUBCLASS BRYIDAE Engl.

SUPERORDER **BRYANAE** (Engl.) Goffinet & W. R. Buck

ORDER SPLACHNALES (M. Fleisch.) Ochyra

FAMILY **SPLACHNACEAE** Grev. & Arn.: *Aplodon* R. Br., *Moseniella* Broth., *Splachnum* Hedw., *Tayloria* Hook., *Tetraplodon* Bruch & Schimp., *Voitia* Hornsch.

FAMILY **MEESIACEAE** Schimp.: *Amblyodon* P. Beauv., *Leptobryum* (Bruch & Schimp.) Wilson, *Meesia* Hedw., *Neomeesia* Deguchi, *Paludella* Brid.

ORDER BRYALES Limpr.

FAMILY **CATOSCOPIACEAE** Broth.: *Catoscopium* Brid.

FAMILY **PULCHRINODACEAE** D. Quandt, N.E. Bell & Stech: *Pulchrinodus* B. H. Allen

FAMILY **BRYACEAE** Schwägr.: *Acidodontium* Schwägr., *Anomobryum* Schimp., *Brachymenium* Schwägr., *Bryum* Hedw., *Leptostomopsis* (Müll. Hal.) J. R. Spence & H. P. Ramsay, *Mniobryoides* Hörmann, *Ochiobryum* J. R. Spence & H. P. Ramsay, *Osculatia* De Not., *Perssonia* Bizot, *Ptychostomum* Hornsch., *Rhodobryum* (Schimp.) Limpr., *Roellobryon* R.Ochyra, *Rosulabryum* J. R. Spence

FAMILY **PHYLLODREPANIACEAE** Crosby: *Mniomalia* Müll. Hal., *Phyllodrepanium* Crosby

FAMILY **PSEUDODITRICHACEAE** Steere & Z. Iwats.: *Pseudoditrichum* Steere & Z. Iwats.

FAMILY **MNIACEAE** Schwägr.: *Cinclidium* Sw., *Cyrtomnium* Holmen , *Epipterygium* Lindb., *Leucolepis* Lindb., *Mielichhoferia* Nees & Hornsch., *Mnium* Hedw.,*Orthomnion* Wilson, *Plagiomnium* T. J. Kop., *Pohlia* Hedw., *Pseudobryum* (Kindb.) T. J. Kop., *Pseudopohlia* R. S. Williams, *Rhizomnium* (Broth.) T. J. Kop., *Schizymenium* Harv., *Synthetodontium* Cardot, *Trachycystis* T. J. Kop.

FAMILY **LEPTOSTOMATACEAE** Schwägr.: *Leptostomum* R. Br.

ORDER BARTRAMIALES D. Quandt, N.E. Bell & Stech

FAMILY **BARTRAMIACEAE** Schwägr.: *Anacolia* Schimp., *Bartramia* Hedw., *Breutelia* (Bruch & Schimp.) Schimp., *Conostomum* Sw., *Fleischerobryum* Loeske, *Flowersia* D.

G. Griffin & W. R. Buck, *Leiomela* (Mitt.) Broth., *Neosharpiella* H. Rob. & Delgad., *Philonotis* Brid., *Plagiopus* Brid.

ORDER ORTHOTRICHALES Dixon

FAMILY **ORTHOTRICHACEAE** Arn.: *Cardotiella* Vitt, *Ceuthotheca* Lewinsky, *Codonoblepharon* Schwägr., *Desmotheca* Lindb., *Florschuetziella* Vitt, *Groutiella* Steere, *Leiomitrium* Mitt., *Leratia* Broth. & Paris, *Macrocoma* (Müll. Hal.) Grout, *Macromitrium* Brid., *Matteria* Goffinet, *Orthotrichum* Hedw., *Pentastichella* Müll. Hal., *Pleurorthotrichum* Broth., *Schlotheimia* Brid., *Sehnemobryum* Lewinsky-Haapasaari & Hedenäs, *Stoneobryum* D. H. Norris & H. Rob., *Ulota* D. Mohr, *Zygodon* Hook. & Taylor

ORDER HEDWIGIALES Ochyra

FAMILY **HEDWIGIACEAE** Schimp.: *Braunia* Bruch & Schimp., *Bryowijkia* Nog., *Hedwigia* P. Beauv., *Hedwigidium* Bruch & Schimp., *Pseudobraunia* (Lesq. & James) Broth.

FAMILY **HELICOPHYLLACEAE** Broth.: *Helicophyllum* Brid.

FAMILY **RHACOCARPACEAE** Kindb.: *Pararhacocarpus* Frahm, *Rhacocarpus* Lindb.

ORDER RHIZOGONIALES (M. Fleisch.) Goffinet & W. R. Buck

FAMILY **RHIZOGONIACEAE** Broth.: *Calomnion* Hook.f. & Wilson, *Cryptopodium* Brid., *Goniobryum* Lindb., *Pyrrhobryum* Mitt., *Rhizogonium* Brid.

FAMILY **AULACOMNIACEAE** Schimp.: *Aulacomnium* Schwägr., *Hymenodontopsis* Herzog, *Mesochaete* Lindb.

FAMILY **ORTHODONTIACEAE** Goffinet: *Hymenodon* Hook.f. & Wilson, *Leptotheca* Schwägr., *Orthodontium* Wilson, *Orthodontopsis* Ignatov & B. C. Tan

SUPERORDER **HYPNANAE** W. R. Buck, Goffinet & A. J. Shaw

ORDER HYPNODENDRALES N. E. Bell, A. E. Newton & D. Quandt

FAMILY **BRAITHWAITEACEAE** N. E. Bell, A. E. Newton & D. Quandt: *Braithwaitea* Lindb.

FAMILY **RACOPILACEAE** Kindb.: *Powellia* Mitt., *Powelliopsis* Zanten, *Racopilum* P. Beauv., *Timokoponenia* Zanten.

FAMILY **PTEROBRYELLACEAE** (Broth.) W.R. Buck & Vitt: *Cyrtopodendron* M. Fleisch., *Pterobryella* (Müll. Hal.) A. Jaeger, *Sciadocladus* Lindb. ex Kindb.

FAMILY **HYPNODENDRACEAE** Broth.: *Bescherellia* Duby, *Cyrtopus* (Brid.) Hook.f., *Dendrohypnum* Hampe, *Franciella* Thér., *Hypnodendron* (Müll. Hal.) Mitt., *Mniodendron* Lindb. ex Dozy & Molk., *Spiridens* Nees, *Touwiodendron* N. E. Bell, A. E. Newton & D. Quandt

ORDER PTYCHOMNIALES W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet

FAMILY **PTYCHOMNIACEAE** M. Fleisch.: *Cladomnion* Hook.f. & Wilson, *Cladomniopsis* M. Fleisch., *Dichelodontium* Broth., *Endotrichellopsis* During, *Euptychium* Schimp., *Garovaglia* Endl., *Glyphotheciopsis* Pedersen & A. E. Newton, *Glyphothecium* Hampe, *Hampeella* Müll.

Hal., *Ombronesus* N. E. Bell, Pedersen & A. E. Newton, *Ptychomniella* (Broth.) W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet, *Ptychomnion* (Hook.f. & Wilson) Mitt., *Tetraphidopsis* Broth. & Dixon

ORDER HOOKERIALES M. Fleisch.

FAMILY **HYPOPTERYGIACEAE** Mitt.: *Arbusculohypopterygium* Stech, T. Pfeiffer & W. Frey, *Canalohypopterygium* W. Frey & Schaepe, *Catharomnion* Hook.f. & Wilson, *Cyathophorum* P. Beauv., *Dendrocyathophorum* Dixon, *Dendrohypopterygium* Kruijer, *Hypopterygium* Brid., *Lopidium* Hook.f. & Wilson

FAMILY **SAULOMATACEAE** W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet: *Ancistrodes* Hampe, *Sauloma* (Hook.f. & Wilson) Mitt., *Vesiculariopsis* Broth.

FAMILY **DALTONIACEAE** Schimp.: *Achrophyllum* Vitt & Crosby, *Adelothecium* Mitt., *Beeveria* Fife, *Benitotania* H. Akiyama, T. Yamag. & Suleiman, *Bryobrothera* Thér., *Calyptrochaeta* Desv., *Crosbya* Vitt, *Daltonia* Hook. & Taylor, *Distichophyllidium* M.

Fleisch., *Distichophyllum* Dozy & Molk., *Ephemeropsis* K. I. Goebel, *Leskeodon* Broth., *Leskeodontopsis* Zanten, *Metadistichophyllum* Nog. & Z. Iwats.

FAMILY **SCHIMPEROBRYACEAE** W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet: *Schimperobryum* Margad.

FAMILY **HOOKERIACEAE** Schimp.: *Crossomitrium* Müll. Hal., *Hookeria* Sm.

FAMILY **LEUCOMIACEAE** Broth.: *Leucomium* Mitt., *Rhynchostegiopsis* Müll. Hal., *Tetrastichium* (Mitt.) Cardot

FAMILY **PILOTRICHACEAE** Kindb.: *Actinodontium* Schwägr., *Amblytropis* (Mitt.) Broth., *Brymela* Crosby & B. H. Allen, *Callicostella* (Müll. Hal.) Mitt., *Callicostellopsis* Broth., *Cyclodictyon* Mitt., *Diploneuron* E. B. Bartram, *Helicoblepharum* (Mitt.) Broth., *Hemiragis* (Brid.) Besch., *Hookeriopsis* (Besch.) A. Jaeger, *Hypnella* (Müll. Hal.) A. Jaeger, *Lepidopilidium* (Müll. Hal.) Broth., *Lepidopilum* (Brid.) Brid., *Neohypnella* E. B. Bartram, *Philophyllum* Müll. Hal., *Pilotrichidium* Besch., *Pilotrichum* P.

Beauv., *Stenodesmus* (Mitt.) A. Jaeger, *Stenodictyon* (Mitt.) A. Jaeger, *Thamniopsis* (Mitt.) M. Fleisch., *Trachyxiphium* W. R. Buck

ORDER HYPNALES (M. Fleisch.) W. R. Buck & Vitt

FAMILY **RUTENBERGIACEAE** M. Fleisch.: *Neorutenbergia* Bizot & Pócs, *Pseudocryphaea* Broth., *Rutenbergia* Besch.

FAMILY **TRACHYLOMATACEAE** W. R. Buck & Vitt: *Trachyloma* Brid.

FAMILY **FONTINALACEAE** Schimp.: *Brachelyma* Cardot, *Dichelyma* Myrin, *Fontinalis* Hedw.

FAMILY **Climaciaceae** Kindb.: *Climacium* F. Weber & D. Mohr, *Pleuroziopsis* E. Britton

FAMILY **AMBLYSTEGIACEAE** G. Roth: *Amblystegium* Schimp., *Anacamptodon* Brid., *Bryostreimannia* Ochyra, *Campyliadelphus* (Kindb.) R.S. Chopra, *Campylium* (Sull.) Mitt., *Conardia* H. Rob., *Cratoneuron* (Sull.) Spruce, *Cratoneuropsis* (Broth.) M. Fleisch., *Drepanocladus* (Müll. Hal.) G.

Roth, *Gradsteinia* Ochyra, *Hygroamblystegium* Loeske, *Hygrohypnella* Ignatov & Ignatova, *Hygrohypnum* Lindb., *Hypnobartlettia* Ochyra, *Koponenia* Ochyra, *Leptodictyum* (Schimp.) Warnst., *Limbella* (Müll. Hal.) Müll. Hal., *Limprichtia* Loeske, *Ochyraea* Váňa, *Palustriella* Ochyra, *Pictus* C. C. Towns., *Pseudoamblystegium* Vanderpoorten & Hedenäs, *Pseudo-calliergon* (Limpr.) Loeske, *Pseudocampylium* Vanderpoorten & Hedenäs, *Pseudohygrohypnum* Kanda, *Sanionia* Loeske, *Sasaokaea* Broth., *Sciaromiella* Ochyra, *Sciaromiopsis* Broth., *Scorpidium* (Schimp.) Limpr., *Sinocalliergon* Sakurai, *Serpoleskea* (Limpr.) Loeske, *Vittia* Ochyra

FAMILY **CALLIERGONACEAE** Vanderpoorten, Hedenäs, C. J. Cox & A. J. Shaw: *Calliergon* (Sull.) Kindb., *Hamatocaulis* Hedenäs, *Loeskypnum* H. K. G. Paul, *Straminergon* Hedenäs, *Warnstorfia* Loeske

FAMILY **Helodiaceae** Ochyra: *Actinothuidium* (Besch.) Broth., *Bryochenea* C. H. Gao & K. C. Chang, *Helodium* Warnst.

FAMILY **LESKEACEAE** Schimp.: *Claopodium* (Lesq. & James) Renauld & Cardot, *Fabronidium* Müll. Hal., *Haplocladium* (Müll. Hal.) Müll. Hal., *Hylocomiopsis* Cardot, *Leptocladium* Broth., *Leptopterigynandrum* Müll. Hal., *Lescuraea* Bruch & Schimp., *Leskea* Hedw., *Leskeadelphus* Herzog, *Leskeella* (Limpr.) Loeske, *Lindbergia* Kindb., *Mamillariella* Laz., *Orthoamblystegium* Dixon & Sakurai, *Platylomella* A. L. Andrews, *Pseudoleskea* Bruch & Schimp., *Pseudoleskeella* Kindb., *Pseudoleskeopsis* Broth., *Ptychodium* Schimp., *Rigodiadelphus* Dixon, *Rozea* Besch., *Schwetschkea* Müll. Hal.

FAMILY **THUIDIACEAE** Schimp.: *Abietinella* Müll. Hal., *Boulaya* Cardot, *Cyrto-hypnum* (Hampe) Hampe & Lorentz, *Fauriella* Besch., *Pelekium* Mitt., *Rauiella* Reimers, *Thuidiopsis* (Broth.) M. Fleisch., *Thuidium* Bruch & Schimp.

FAMILY **REGMATODONTACEAE** Broth.: *Regmatodon* Brid., *Yunnanobryon* Shevock, Ochyra, S.He & D.G.Long

FAMILY **STEREOPHYLLACEAE** W. R. Buck & Ireland: *Catagoniopsis* Broth., *Entodontopsis* Broth., *Eulacophyllum* W. R. Buck & Ireland, *Juratzkaea* Lorentz, *Pilosium* (Müll. Hal.) M. Fleisch., *Sciuroleskea* Broth., *Stenocarpidium* Müll. Hal., *Stereophyllum* Mitt.

FAMILY **BRACHYTHECIACEAE** G. Roth: *Aerobryum* Dozy & Molk., *Aerolindigia* M. Menzel, *Brachytheciastrum* Ignatov & Huttunen, *Brachythecium* Schimp., *Bryhnia* Kaurin, *Bryoandersonia* H. Rob., *Cirriphyllum* Grout, *Clasmatodon* Hook.f. & Wilson, *Donrichardsia* H. A. Crum & L. E. Anderson, *Eriodon* Mont., *Eurhynchiadelphus* Ignatov & Huttunen, *Eurhynchiastrum* Ignatov & Huttunen, *Eurhynchiella* M. Fleisch., *Eurhynchium* Bruch & Schimp., *Flabellidium* Herzog, *Frahmiella* Ignatov, Y.F.Wang & Vanderpoorten, Hedenaesia Huttunen & Ignatov, Hedenasiastrum Ignatov & Vanderpoorten, *Helicodontium* Schwägr., *Homalotheciella* (Cardot) Broth., *Homalothecium* Schimp., *Juratzkaeella* W. R. Buck, *Kindbergia* Ochyra, *Lindigia* Hampe, *Mandoniella* Herzog, *Met* *eoridium* (Müll. Hal.) Manuel, Microeurhynchium Ignatov & Vanderpoorten , *Myuroclada* Besch., *Nobregaea* Hedenäs, *Okamuraea* Broth., *Oxyrrhynchium* (Schimp.) Warnst., *Palamocladium* Müll. Hal., *Plasteurhynchium* Broth., *Platyhypnidium* M. Fleisch., *Pseudopleuropus* Takaki, Pseudorhynchostegiella Ignatov & Vanderpoorten , *Pseudoscleropodium* (Limpr.) M. Fleisch., *Remyella* Müll. Hal., *Rhynchostegiella* (Schimp.) Limpr., *Rhynchostegium* Bruch & Schimp., *Sainthelenia* Ignatov & M. Wigginton, *Schimperella* Thér., *Sciuro-hypnum* (Hampe) Hampe, *Scleropodium* Bruch & Schimp., *Scorpiurium* Schimp., *Squamidium* (Müll. Hal.) Broth., *Stenocarpidiopsis* M. Fleisch., *Tomenthypnum* Loeske, *Zelometeorium* Manuel

FAMILY **METEORIACEAE** Kindb.: *Aerobryidium* M. Fleisch., *Aerobryopsis* M. Fleisch., *Barbella* M. Fleisch., *Barbellopsis* Broth., *Chrysocladium* M. Fleisch., *Cryptopapillaria* M. Menzel, *Diaphanodon* Renauld & Cardot, *Duthiella* Renauld, *Floribundaria* M.

Fleisch., *Lepyrodontopsis* Broth., *Meteoriopsis* Broth., *Meteorium* (Brid.) Dozy & Molk., *Neodicladiella* W. R. Buck, *Neonoguchia* S. H. Lin, *Pseudospiridentopsis* (Broth.) M. Fleisch., *Pseudotrachypus* P. de la Varde & Thér., *Sinskea* W. R. Buck, *Toloxis* W. R. Buck, *Trachycladiella* (M. Fleisch.) M. Menzel & W. Schultze-Motel, *Trachypodopsis* M. Fleisch., *Trachypus* Reinw. & Hornsch.

FAMILY **MYRINIACEAE** Schimp.: *Austinia* Müll. Hal., *Macgregorella* E. B. Bartram, *Merrilliobryum* Broth., *Myrinia* Schimp., *Nematocladia* W. R. Buck

FAMILY **FABRONIACEAE** Schimp.: *Dimerodontium* Mitt., *Fabronia* Raddi, *Ischyrodon* Müll. Hal., *Levierella* Müll. Hal., *Rhizofabronia* (Broth.) M. Fleisch.

FAMILY **HYPNACEAE** Schimp.: *Acritodon* H. Rob., *Andoa* Ochyra, *Austrohondaella* Z.Iwats., H.P.Ramsay & Fife, *Bardunovia* Ignatov & Ochyra, *Breidleria* Loeske, *Bryocrumia* L. E. Anderson, *Buckiella* Ireland, *Callicladium* H. A.

Crum, *Calliergonella* Loeske, *Campylophyllopsis* W. R. Buck, *Campylophyllum* (Schimp.) M. Fleisch., *Caribaeohypnum* Ando & Higuchi, *Chryso-hypnum* (Hampe) Hampe, *Crepidophyllum* Herzog, *Ctenidiadelphus* M. Fleisch., *Cyathothecium* Dixon, *Dacryophyllum* Ireland, *Ectropotheciella* M. Fleisch., *Ectropotheciopsis* (Broth.) M. Fleisch., *Ectropothecium* Mitt., *Elharveya* H. A. Crum, *Elmeriobryum* Broth., *Entodontella* M. Fleisch., *Eurohypnum* Ando, *Foreauella* Dixon & P. de la Varde, *Gammiella* Broth., *Giraldiella* Müll. Hal., *Gollania* Broth., *Hageniella* Broth., *Herzogiella* Broth., *Homomallium* (Schimp.) Loeske, *Hondaella* Dixon & Sakurai, *Horridohypnum* W. R. Buck, *Hyocomium* Bruch & Schimp., *Hypnum* Hedw., *Irelandia* W. R. Buck, *Isopterygiopsis* Z. Iwats., *Leiodontium* Broth., *Leptoischyrodon* Dixon, *Macrothamniella* M. Fleisch., *Mahua* W. R. Buck, *Microctenidium* M. Fleisch., *Mittenothamnium* Henn., *Nanothecium* Dixon & P. de la Varde, *Orthothecium* Bruch & Schimp., *Phyllodon* Bruch & Schimp., *Plagiotheciopsis* Broth., *Platydictya* Berk., *Platygyriella* Cardot, *Podperaea* Z. Iwats. & Glime, *Pseudohypnella* (M. Fleisch.)

Broth., *Pseudotaxiphyllum* Z. Iwats., *Ptilium* De Not., *Pylaisia* Schimp., *Rhacopilopsis* Renauld & Cardot, *Rhizohypnella* M. Fleisch., *Sclerohypnum* Dixon, *Stenotheciopsis* Broth., *Stereodon* (Brid.) Mitt., *Stereodontopsis* R. S. Williams, *Syringothecium* Mitt., *Taxiphyllopsis* Higuchi & Deguchi, *Taxiphyllum* M. Fleisch., *Vesicularia* (Müll. Hal.) Müll. Hal., *Wijkiella* Bizot & Lewinsky

FAMILY **CATAGONIACEAE** W. R. Buck & Ireland: *Catagonium* Broth.

FAMILY **PTERIGYNANDRACEAE** Schimp.: *Habrodon* Schimp., *Heterocladium* Bruch & Schimp., *Iwatsukiella* W. R. Buck & H. A. Crum, *Myurella* Bruch & Schimp., *Pterigynandrum* Hedw., *Trachyphyllum* A. Gepp

FAMILY **HYLOCOMIACEAE** M. Fleisch.: *Ctenidium* Mitt., *Hylocomiastrum* Broth., *Hylocomium* Bruch & Schimp., *Leptocladiella* M. Fleisch., *Leptohymenium* Schwägr., *Loeskeobryum* Broth., *Macrotha* *mnium* M. Fleisch., *Meteoriella* S. Okamura, *Neodolichomitra* Nog., *Orontobryum* M. Fleisch., *Pleurozium* Mitt., *Puiggariopsis* M. Menzel, *Rhytidiadelphus* (Limpr.) Warnst., *Rhytidiopsis* Broth., *Schofieldiella* W. R. Buck

FAMILY **RHYTIDIACEAE** Broth.: *Rhytidium* (Sull.) Kindb.

FAMILY **SYMPHYODONTACEAE** M. Fleisch.: *Chaetomitriopsis* M. Fleisch., *Chaetomitrium* Dozy & Molk., *Dimorphocladon* Dixon, *Symphyodon* Mont., *Trachythecium* M. Fleisch., *Unclejackia* Ignatov, T. Kop. & D. Norris

FAMILY **PLAGIOTHECIACEAE** M. Fleisch.: *Plagiothecium* Bruch & Schimp., *Struckia* Müll. Hal.

FAMILY **ENTODONTACEAE** Kindb.: *Entodon* Müll. Hal., *Erythrodontium* Hampe, *Mesonodon* Hampe, *Pylaisiobryum* Broth.

FAMILY **PYLAISIADELPHACEAE** Goffinet & W. R. Buck: *Aptychella* (Broth.) Herzog, *Brotherella* M.

Fleisch., *Clastobryopsis* M. Fleisch., *Clastobryum* Dozy & Molk., *Heterophyllium* (Schimp.) Kindb., *Isocladiella* Dixon , *Isopterygium* Mitt., *Mastopoma* Cardot, *Platygyrium* Bruch & Schimp., *Pterogonidium* Broth., *Pseudotrismegistia* H. Akiyama & Tsubota, *Pylaisiadelpha* Cardot, *Taxitheliella* Dixon, *Taxithelium* Mitt ., *Trismegistia* (Müll. Hal.) Müll. Hal., *Wijkia* H. A. Crum, *Yakushimabryum* H.Akiyama, Y.Chang, Yamagushi & B.C.Tan.

FAMILY **SEMATOPHYLLACEAE** Broth.: *Acanthorrhynchium* M. Fleisch., *Acroporium* Mitt., *Allioniellopsis* Ochyra, *Aptychopsis* (Broth.) M. Fleisch., *Chionostomum* Müll. Hal., *Clastobryella* M. Fleisch., *Clastobryophilum* M. Fleisch., *Colobodontium* Herzog, *Donnellia* Austin, *Hydropogon* Brid ., *Hydropogonella* Cardot, *Macrohymenium* Müll. Hal., *Meiotheciella* B. C. Tan, W. B. Schofield & H. P. Ramsay, *Meiothecium* Mitt., *Papillidiopsis* (Broth.) W. R. Buck & B. C. Tan, *Paranapiacabaea* W. R. Buck & Vital, *Potamium* Mitt., *Pterogoniopsis* Müll. Hal., *Piloecium* (Müll. Hal.) Broth., *Radulina* W. R. Buck & B. C. Tan, *Rhaphidostichum* M.

Fleisch., *Schraderella* Müll. Hal., *Schroeterella* Herzog, *Sematophyllum* Mitt., *Timotimius* W. R. Buck, *Trichosteleum* Mitt., *Trolliella* Herzog, *Warburgiella* Müll. Hal.

FAMILY **CRYPHAEACEAE** Schimp.: *Cryphaea* D. Mohr, *Cryphaeophilum* M. Fleisch., *Cryphidium* (Mitt.) A. Jaeger, *Cyptodon* (Broth.) M. Fleisch., *Cyptodontopsis* Dixon, *Dendroalsia* E. Britton, *Dendrocryphaea* Broth., *Dendropogonella* E. Britton, *Pilotrichopsis* Besch., *Schoenobryum* Dozy & Molk., *Sphaerotheciella* M. Fleisch.

FAMILY **PRIONODONTACEAE** Broth.: *Prionodon* Müll. Hal.

FAMILY **LEUCODONTACEAE** Schimp.: *Antitrichia* Brid., *Dozya* Sande Lac., *Eoleucodon* H. A. Mill. & H. Whittier, *Leucodon* Schwägr., *Nogopterium* Crosby & W.R.buck, *Pterogoniadelphus* M. Fleischer, *Scabridens* E. B. Bartram

FAMILY **PTEROBRYACEAE** Kindb.: *Calyptothecium* Mitt., *Cryptogonium* (Müll. Hal.) Hampe, *Henicodium* (Müll. Hal.)

Kindb., *Hildebrandtiella* Müll. Hal., *Horikawaea* Nog., *Jaegerina* Müll. Hal., *Micralsopsis* W. R. Buck, *Muellerobryum* M. Fleisch., *Neolindbergia* M. Fleisch., *Orthorrhynchidium* Renauld & Cardot, *Orthostichidium* Dusén, *Orthostichopsis* Broth., *Osterwaldiella* Broth., *Penzigiella* M. Fleisch., *Pireella* Cardot, *Pseudopterobryum* Broth., *Pterobryidium* Broth. & Watts, *Pterobryon* Hornsch., *Pterobryopsis* M. Fleisch., *Renauldia* Müll. Hal., *Rhabdodontium* Broth., *Spiridentopsis* Broth., *Symphysodon* Dozy & Molk., *Symphysodontella* M. Fleisch.

FAMILY **PHYLLOGONIACEAE** Kindb.: *Phyllogonium* Brid.

FAMILY **ORTHORRHYNCHIACEAE** S. H. Lin: *Orthorrhynchium* Reichardt

FAMILY **LEPYRODONTACEAE** Broth.: *Lepyrodon* Hampe

FAMILY **NECKERACEAE** Schimp.: *Alleniella* S.Olsson, Enroth & D. Quandt,*Baldwiniella* M. Fleisch., *Bryolawtonia* D. H. Norris & Enroth, *Caduciella* Enroth, *Circulifolium* S. Olsson, Enroth &

D.Quandt, *Crassiphyllum* Ochyra, *Cryptoleptodon* Renauld & Cardot, *Curvicladium* Enroth, *Dixonia* Horik. & Ando, *Dolichomitra* Broth., *Echinodiopsis* S.Olsson, Enroth & D. Quandt, *Exsertotheca* S.Olsson, Enroth & D. Quandt,*Handeliobryum* Broth., *Himantocladium* (Mitt.) M. Fleisch., *Homalia* (Brid.) Bruch & Schimp., *Homaliodendron* M. Fleisch., *Hydrocryphaea* Dixon, *Isodrepanium* (Mitt.) E. Britton, *Metaneckera* Steere, *Neckera* Hedw., *Neckeropsis* Reichardt, *Neomacounia* Ireland, *Noguchiodendron* Ninh & Pócs, *Orthostichella* Müll. Hal., *Pendulothecium* Enroth & S. He, *Pinnatella* M. Fleisch., *Porotrichodendron* M. Fleisch., *Porotrichopsis* Broth. & Herzog, *Porotrichum* (Brid.) Hampe, *Shevockia* Enroth & Ji, *Thamnobryum* Nieuwl., *Thamnomalia* S.Olsson, Enroth & D. Quandt,*Touwia* Ochyra

FAMILY **ECHINODIACEAE** Broth.: *Echinodium* Jur.

FAMILY **LEPTODONTACEAE** Schimp.: *Alsia* Sull., *Forsstroemia* Lindb., *Leptodon* D. Mohr, *Taiwanobryum* Nog.

FAMILY **LEMBOPHYLLACEAE** Broth.: *Acrocladium* Mitt., *Bestia* Broth., *Camptochaete* Reichardt, *Dolichomitriopsis* S. Okamura, *Fallaciella* H. A. Crum, *Fifea* H. A. Crum, *Isothecium* Brid., *Lembophyllum* Lindb., *Looseria* (Thér.) D. Quandt, S. Huttunen, Tangney & Stech, *Neobarbella* Nog., *Pilotrichella* (Müll. Hal.) Besch., *Rigodium* Schwägr., *Tripterocladium* (Müll. Hal.) A. Jaeger, *Weymouthia* Broth.

FAMILY **MYURIACEAE** M. Fleisch.: *Eumyurium* Nog., *Myurium* Schimp., *Oedicladium* Mitt., *Palisadula* Toyama

FAMILY **ANOMODONTACEAE** Kindb.: *Anomodon* Hook. & Taylor, *Bryonorrisia* L. R. Stark & W. R. Buck, *Chileobryon* Enroth, *Curviramea* H. A. Crum, *Haplohymenium* Dozy & Molk., *Herpetineuron* (Müll. Hal.) Cardot, *Schwetschkeopsis* Broth.

FAMILY **Miyabeaceae** Enroth, S. Olsson, Buchbender, Hedenäs, Huttunen & D. Quandt: *Bissetia* Broth., *Homaliadelphus* Dixon & P. de la Varde, *Miyabea* Broth.

FAMILY **THELIACEAE** M. Fleisch.: *Thelia* Sull.

FAMILY **MICROTHECIELLACEAE** H. A. Mill. & A. J. Harr.: *Microtheciella* Dixon

FAMILY **SORAPILLACEAE** M. Fleisch.: *Sorapilla* Spruce & Mitt.

Bryophyte Classification

The roughly 18,000 species of bryophytes are generally classified into three coordinate phyla, the Marchantiophyta (liverworts), Bryophyta (mosses) and Anthocerotophyta (hornworts). Phylogenetic analyses such as those of Mishler et al. (1994) and Qiu et al. (2006) suggest that these phyla do not form a monphyletic group, but rather represent a grade in embryophyte evolution. In most recent analyses liverworts are resolved as the first divergence of land plants (embryophytes).

Hornwort Classification at the Rank of Genus and Above

PHYLUM (DIVISION) **ANTHOCEROTOPHYTA** Stotl. & Crand.-Stotl. Bryologist 80: 425. 1977.

CLASS **LEIOSPOROCEROTOPSIDA** Stotl. & Crand.-Stotl., Bryologist 108: 24. 2005

ORDER **LEIOSPOROCEROTALES** Hässel, J. Hatt. Bot. Lab. 64: 82. 1988.

FAMILY **LEIOSPOROCEROTACEAE** Hässel, J. Bryol. 14: 255. 1986.

Leiosporoceros Hässel, J. Bryol. 14: 255. 1986.

CLASS **ANTHOCEROTOPSIDA** Jancz. ex Stotl. & Crand.-Stotl., Bryologist 108: 24. 2005.

In noother branch of the green tree of life does extension of each sporophyte involve continuous,presumably indeterminate, basipetal growth of a single elongated sporangium. All stages ofspore development, from undifferentiated cells through pre-meiotic/meiotic spore mother cells to sequentially more mature spores, can be found in a single hornwort sporangium. A constant production of spores therefore ensures dispersal through-out the growing season for as long as the gametophyte persists.This mode of sporophyte development has no counterpart in other plant groups, thus obscuring the phylogenetic positionof hornworts among green plants. Twelve genera of hornworts have been named, ***Anthoceros, Dendroceros, Folioceros, Notothylas, Megaceros,Phaeoceros, Aspiromitus, Hattorioceros, Leiosporoceros,Nothoceros, Mesoceros, and Sphaerosporoceros***, of whichonly the first six are widely recognized.

ORDER **ANTHOCEROTALES** Limpricht in Cohn, Krypt. Fl. von Schlesien: 239, 345. Breslau. 1877.

FAMILY **ANTHOCEROTACEAE** Dumort., Analys. Fam. Pl. 68-69. Tournay. 1829.

Anthoceros L., Sp. Plt.: 1139. Stockholm. 1753.

Folioceros D. C. Bharadwaj, Geophytology 1: 9. 1971.

Sphaerosporoceros Hässel, J. Hattori Bot. Lab. 64: 79. 1988.

ORDER **NOTOTHYLADALES** Hyvönen & Piippo, J. Hatt. Bot. Lab. 74: 117. 1993. "Notothylales".

FAMILY **NOTOTHYLADACEAE** (Milde) Müll. Frib. ex Prosk., Phytomorphology 10: 10. 1960.

SUBFAMILY **NOTOTHYLADOIDEAE** Grolle, J. Bryol. 7: 215. 1972.

Notothyas Sull. ex A. Gray, Amer. J. Sci. Arts, ser. 2, 1: 74. 1846.

SUBFAMILY **PHAEOCEROTOIDEAE** Hässel, J. Hatt. Bot. Lab. 64: 81. 1988.

Hattorioceros (Hasegawa) Hasegawa, J. Hattori Bot. Lab. 76: 32. 1994.

Mesoceros Piippo, Acta Bot. Fenn. 148: 30. 1993.

Phaeoceros Prosk., Bull. Torrey Bot. Cl. 78: 346. 1951.

Phymatoceros Stotler, W. T. Doyle & Crand.-Stotl., Phytologia 87: 113. 2005.

FAMILY **DENDROCEROTACEAE** (Milde) Hässel, J. Hatt. Bot. Lab. 64: 82. 1988.

SUBFAMILY **DENDROCEROTOIDEAE** R. M. Schust., Phytologia 63: 195, 200.

Dendroceros Nees in Gottsche, Lindenberg & Nees, Syn. Hep.: 579. 1846.

SUBFAMILY **MEGACEROTOIDEAE** Stotl. & Crand.-Stotl., Bryologist 108: 24. 2005.

Megaceros Campb., Ann. Bot. (London) 21: 484. 1907.

Nothoceros (R. M. Schust.) Hasegawa, J. Hatt. Bot. Lab. 76: 32. 1994. "*Notoceros*"

SOURCE:

Stotler, R. E. & B. Crandall-Stotler. 2005. A revised classification of the Anthocerotophyta and a checklist of the hornworts of North America, north of Mexico. Bryologist 108: 16-26.

Division Bryophyta, or mosses, include about 10000 species

Evolution Of Sporophytes.

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.The sporophytic phase begins with the formation of a diploid zygote within the venter of the archegonium. In the simplest form of sporophyte (e.g., Riccia) the entire zygote is taking part in the formation of stelile capsule wall and the central sporogenous cells. In complex forms, zygote differentiates and sporogenous cells form more sterile tissues.This theory was advocated by Bower (1908- 35) and supported by Cavers (1910) and Campbell (1940). According to this theory, the primitive sporophyte of bryophytes was simple and most of the sporogenous tissue was fertile (e.g., *Riccia*) and from such a sporophyte, the more complex sporophytes (e.g., mosses) have been evolved by the progressive sterilisation of potential sporogenous tissue. This theory is also known as “theory of sterilisation”. The 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) differentiates into spores with a very few sterile nurse cells, possibly the forerunners of elaters.

Second stage:

In this stage, the zygote divides transversely to form a hypobasal and an epibasal cells. A small foot is formed from the hypobasal cell. The epibasal cells differentiates into an outer amphithecium and inner 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 endothecial 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, Riccarclia*, 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 retrogressive theory, and supported by several scientists like Church (1919), Kashyap (1919), Goebel (1930) and Evans-(19391 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, Plagiochasma, Riccia*) by reduction.

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

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

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

Evolution of Gametophytes in Bryophytes:

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

There are two opposing theories regarding the nature of the vegetative structure of the primitive bryophytic gametophyte and its subsequent evolution:

1. The upgrade or the progressive evolution theory, and

2. The downgrade or the regressive evolution theory.

1. The upgrade or the progressive evolution theory:

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

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

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

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

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

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

2. The downgrade or the regressive evolution theory:

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

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

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

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

(a) Reduction in the number of involucre:

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

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

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

(c) Simplification of Pores:

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

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

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

Mehra (1969) proposed the above hypothesis. In *Marchantia*, the antheridia and archegonia are borne terminally on the stalked gametophores. In *Preissia quadrata* and *Plagiochasma articulatum*, the stalk is initially terminal, but becomes dorsal by the further growth of the thallus. A further downward shifting of the stalk is observed in *Corsinia* and *Boschia*, where the female receptacle almost becomes sessile by the elimination of the stalk .

ORIGIN OF ALTERNATION OF GENERATION (HOMOLOGUS AND ANTITHETIC THEORY

The late-nineteenth/early-twentieth century debate over homologous versus antithetic alternation of generations is reviewed. Supporters of both theories, at first, used *Coleochaete* as a model for the origin of land-plant life cycles. The early debate focused on the morphological interpretation of the sporophyte and on whether vascular cryptogams had bryophyte-like ancestors. The terms of the debate shifted after the discovery that the alternation of morphological generations was accompanied by an alternation of chromosome number. Supporters of homologous alternation now promoted a model in which land plants had been derived from an algal ancestor with an isomorphic alternation of haploid and diploid generations whereas supporters of antithetic alternation favored a model in which land plants were derived from a haploid algal ancestor with zygotic meiosis. Modern evidence that embryophytes are derived from charophycean green algae is more compatible with an updated version of the antithetic theory. For more than a century, theories of the 'antithetic' origin of sporophytes have been juxtaposed with theories of their 'homologous' origin. During this same period, there have been profound changes in our knowledge of the phylogeny of land plants and of mechanisms of inheritance. The opposing theories have not remained static but have been reformulated in the light of new discoveries and as implicit assumptions changed. Although *alternation of generations* initially referred to the alternation of sexual and asexual forms in animals, the term is now almost exclusively associated with the life cycles of plants, specifically with the alternation of haploid gametophytes and diploid sporophytes. Hofmeister (1862) wrote that mosses and ferns "exhibit remarkable instances of a regular alternation of two generations very different in their organization. The first generation—that from the spore—is destined to produce the different sexual organs … The object of the second generation is to form numerous free reproductive cells—the spores—by the germination of which the first generation is reproduced." Hofmeister's synthesis was pre-Darwinian (the German version of his treatise appeared in 1851) and he did not view the correspondences that he had identified among the life cycles of bryophytes, ferns and gymnosperms as evidence of common descent (Goebel, 1926; p. 60). Hofmeister's investigations were also 'pre-cytological'. Chromosomes were not identified until the 1880s. Thus, Hofmeister was unaware that the alternation of morphological generations was associated with an alternation of chromosome number. Bower (1890) derived his concept of 'antithetic alternation of generations' from Celakovsky (1874). Scott (1895) ascribed his hypothesis of 'homologous alternation' to Pringsheim (1876b). Celakovsky proposed that the spore-producing asexual bionts and egg-producing sexual bionts of algae are morphologically similar because they obey the same growthlaws. Therefore, these generations are *homologous*. By contrast, the asexual and sexual generations of mosses and vascular cryptogams obey quite different growth-laws.

Therefore, these generations are *antithetic* (Celakovsky, 1874; pp. 31-32). life cycle of *Coleochaete*, an alga whose life cycle had been described by Pringsheim (1860). Coleochaetes were freshwater algae that grew as epiphytes on other plants. Multicellular thalli developed from zoospores (*Schwärmsporen*). A thallus could be asexual, and produce zoospores; could be a sexual male, and produce sperm (*Samenkörper*); or be a sexual female, and produce oogonia (*Oogonien*). After fertilization of an oogonium, the resulting oospore was retained on the female thallus and underwent a number of cell divisions to produce a multicellular ‘fruit’. In some coleochaetes, the female thallus produced a cellular ‘rind’ that grew around and enclosed the fruit. All cells derived from the oospore then transformed into zoospores that dispersed to establish new thalli (Pringsheim, 1860). This life cycle was characterized by a succession of asexual thalli interspersed with occasional sexual thalli. *Coleochaete* was thought by many to exhibit a close analogy, and perhaps homology, to the life cycle of land plants. Celakovsky believed that *Coleochaete* exhibited *both* antithetic and homologous alternation. That is, *Coleochaete* possessed three kinds of generations that succeeded each other in the order *A*, *B*, *C*. Generation *A* was represented by vegetative asexual bionts that produced zoospores; generation *B* by vegetative sexual bionts that produced oospores; and generation *C* by a rudimentary antithetic generation that developed from the fertilized oospore. Asexual generation *A* and sexual generation *B* followed the same growth-law and were thus homologous, whereas asexual generation *C* (the 'fruit') followed a different growth-law and was thus antithetic to *A* and *B*Bower (1890) viewed the alternation of generations of archegoniates as arising from the adaptation of an initially aquatic organism for the land. That is, the life cycle could "be distinguished as an *amphibious alternation*, which finds its morphological expression in the difference of external form and internal structure between the more ancient gametophyte and the more recent sporophyte." In his view, the sporophyte arose by the "*interpolation* of a new development between successive gametophytes." Bower (1890) suggested that this could be styled *alternation by interpolation*. Bower (1890) defined *antithetic alternation* as an alternation "of two generations phylogenetically distinct, i.e., where a new stage (sporophyte) has been interpolated between pre-existing generations (gametophytes)." By contrast, he defined *homologous alternation* as an alternation "of two or more generations phylogenetically similar to one another, but differing in the presence or absence of sexual organs." Antithetic alternation, he believed, had probably arisen independently in several distinct phyla, including the Archegoniatae, the green Confervoideae (a taxon that included *Coleochaete*), the Florideae (red algae), and the Ascomycetous Fungi. Homologous alternation occurred in most thallophytes and "might be described as a mere differentiation—often a very slight one—of successive gametophytes."

Nineteenth-century botanists distinguished asexual (spore-producing) generations from sexual (gamete-producing) generations. From a 21st-century perspective, the category 'asexual generation' grouped together haploid individuals producing haploid spores by mitosis, diploid individuals producing diploid spores by mitosis, and diploid individuals producing haploid spores by meiosis. The category 'sexual generation' encompassed haploid individuals producing gametes by mitosis and diploid individuals producing gametes by meiosis.

The discovery of an alternation of nuclear phase shifted the debate on the alternation of morphological generations and, in particular, changed the way in which the homologous theory was presented. This shift can be illustrated with the example of *Coleochaete*. Celakovsky (1874) had recognized three generations in the life cycle of *Coleochaete*: zoospore-producing thalli (*A*); gamete-producing thalli (*B*); and the multicellular body produced from the fertilized oospore (*C*). Celakovsky (1874) and Bower (1890) believed generation *C* was an antithetic generation intercalated into the life cycle,

whereas Pringsheim (1876b) and Scott (1895) believed generation *C* was merely a reduced version of generation *A* (Figure 1). After Strasburger's (1894) description of the alternation of nuclear ploidy, it was soon realized that generations *A* and *B* probably had the same (reduced) number of chromosomes. Therefore, asexual generation *A* could not correspond cytologically to the asexual generation (sporophyte) of land plants. However, if it were assumed that chromosome reduction occurred immediately before the production of zoospores by generation *C*, then generation *C* would be analogous, perhaps even homologous, to the sporophyte of mosses (i.e., a multicellular body with the doubled number of chromosomes growing attached to a sexual generation with the reduced number of chromosomes). Thus, the alternation of chromosome numbers was initially seen as strengthening the antithetic theory. Supporters of the homologous theory, however, were soon able to invoke cytological discoveries in algae to booster their own theory but, in the process, they abandoned *Coleochaete* as an exemplar of homologous alternation. Williams (1904) reported that the brown alga *Dictyota dichotoma* underwent an isomorphic alternation between tetrasporeproducing individuals (with 32 chromosomes) and gamete-producing individuals (with 16 chromosomes). The former developed from fertilized eggs, the latter from tetraspores. Thus, *Dictyota* provided an example of a regular alternation between a haploid sexual and diploid asexual generation that were "in all morphological respects … perfectly similar to one another" (Scott, 1908).

Soon after, Lang (1909) presented an *ontogenetic theory of alternation* that he believed placed the relation of the two generations in a new light. He regarded gametophytes and sporophytes “as homologous, in that they correspond to regularly succeeding individuals (sexual and asexual), developed from germ-cells which are similar in their morphogenetic powers.” In his view, the spore and fertilized egg had the same developmental potential but produced different plant-bodies because they developed under different environmental influences. Spores develop free, in direct contact with soil, water and light, whereas the fertilized eggs of archegoniates develop enclosed within cells of the preceding sexual generation. Lang believed that the descent of land plants could “fairly be assumed to have been from forms in which a sexual (haploid) and asexual (diploid) generation of similar form alternated regularly.” The change from a dispersed to a retained egg probably accompanied the transition to land. “Once the dependent relation of the diploid generation was established, profound and probably sudden changes might be expected to follow, resulting in the difference in the body form between sporophyte and gametophyte.”

Lang presented these ideas at a meeting of the Linnean Society of London (February 18th, 1909) at which Bower and Scott (among others) were present (Lang et al., 1909).

In response, Bower argued that the most stringent criterion of homology was identical phyletic history. He wished to “retain the old idea of the historical distinctness of the two alternating phases” and he did not “feel prepared to concede the full morphogenetic unity of the spore and zygote.”

Scott, on the other hand, believed that Lang had merely restated the homologous doctrine “as it had taken shape … since the discovery of the cytological facts in *Dictyota*.

These discoveries had shown that cytological differences did not preclude the two generations being homologous, and had thus completely removed the value of the cytological distinction as supporting the antithetic theory.” The homologous theory had assumed the form in which it is best known today: land plants had descended from an alga with isomorphic alternation of haploid and diploid thalli.

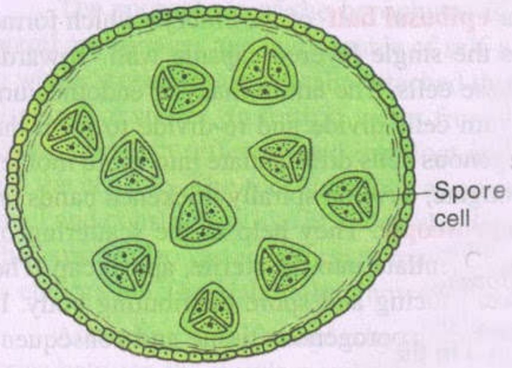
The green alga *Ulva* replaced the brown alga *Dictyota* as the favored algal exemplar of the homologous theory (Graham, 1985; Blackwell, 2003) after Föyn (1929) and Hartmann (1929) described isomorphic alternation of generations in *Ulva* and *Enteromorpha*. It should be noted, however, that Föyn and Hartmann considered they had demonstrated *antithetic* alternation of generations because haploid sexual plants and diploid asexual plants differed in inner constitution although they resembled each other in outward form. Clearly, one botanist’s antithetic alternation was another botanist’s homologous alternation. Celakovsky (1874) introduced a distinction between homologous and antithetic alternation of generations. In Celakovsky's scheme, two generations were homologous if they obeyed the same growth-law but were antithetic if they obeyed different growthlaws. Thus, *Coleochaete* possessed both forms of alternation: gamete-producing (sexual) and zoospore-producing (asexual) thalli were homologous, whereas the multicellular (asexual) body that developed from the zygote was antithetic to these generations. With respect to archegoniates, Celakovsky considered the asexual generation (sporophyte) to be antithetic to the sexual generation (gametophyte). Pringsheim (1876b) rejected the distinction between homologous and antithetic alternation. He interpreted the 'fruit' of *Coleochaete* as a rudimentary asexual thallus that developed while attached to the previous sexual thallus. In his view, the 'fruit' and a freeliving, zoospore-producing thallus were different manifestations of an asexual generation that was homologous to the gamete-producing sexual generation. The life cycle of a moss could be derived from a life cycle resembling that of *Coleochaete* by the suppression of all except the first asexual generation. Bower (1890) believed that the sporophyte was a fundamentally new structure that had been *interpolated* into the life cycle between successive gametophytes. He borrowed Celakovsky's terminology and called this antithetic alternation of generations. Scott (1895), by contrast, believed that the sporophyte had been derived from an asexual algal thallus. He called this homologous alternation of generations. Scott favored independent algal origins of bryophytes and vascular cryptogams. The homologous theory can be considered to have had an early and a late version. In the early version, *Coleochaete* was used as a model for the algal ancestor of land plants. *Coleochaete* was considered to show an isomorphic alternation of sexual and asexual thalli. The first asexual thallus differed from the others because it developed while attached to a sexual thallus. The life cycle of archegoniates could be derived from such a life cycle by suppressing all except the first asexual generation. The discovery that the alternation of generations in land plants was accompanied by an alternation of chromosome number (Strasburger, 1894) weakened this version of the homologous theory because it accentuated the distinctiveness of gametophytes and sporophytes. In the late version of the homologous theory, first *Dictyota*, then *Ulva*, replaced *Coleochaete* as the model for the algal ancestor of land plants. This version of the theory proposed that land-plants were derived from an alga with an isomorphic alternation of haploid and diploid generations. *Dictyota* (unlike *Coleochaete*) disperses its eggs. Therefore, this version of the theory assumed that the diploid generation was initially free-living, rather than retained on the haploid maternal plant. The early and late versions of the homologous theory mark a shift in the debate over homologous versus antithetic alternation. In the early debate, the proponents of both theories could use *Coleochaete* as a model for the algal ancestor of archegoniates. Their disagreement was not about the nature of this algal ancestor but about the morphological interpretation of the sporophyte (as something new or something modified) and about the evolutionary relationship between the ‘parasitic’ sporogonium of bryophytes and the freeliving sporophyte of pteridophytes. In the later debate, the two theories proposed different kinds of algal ancestor for archegoniates. This shift in the terms of the debate partially reflected a shift in emphasis from questions of morphology to questions of phylogeny. We now know that embryophytes were derived from within the charophycean green algae, and that the closest extant relatives of embryophytes possess a multicellular haploid body but lack a multicellular diploid body. Therefore, the sporophyte has been interpolated into a basically haploid life cycle. One could interpret this conclusion as a vindication of the antithetic theory championed by Bower (1908) and as a rejection of the late version of the homologous theory. However, debate continues about whether the sporophyte originated from a dispersed zygote or from a zygote that was retained on a maternal gametophyte.

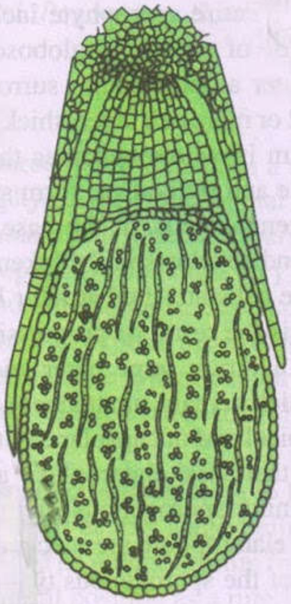
Bower's outlook

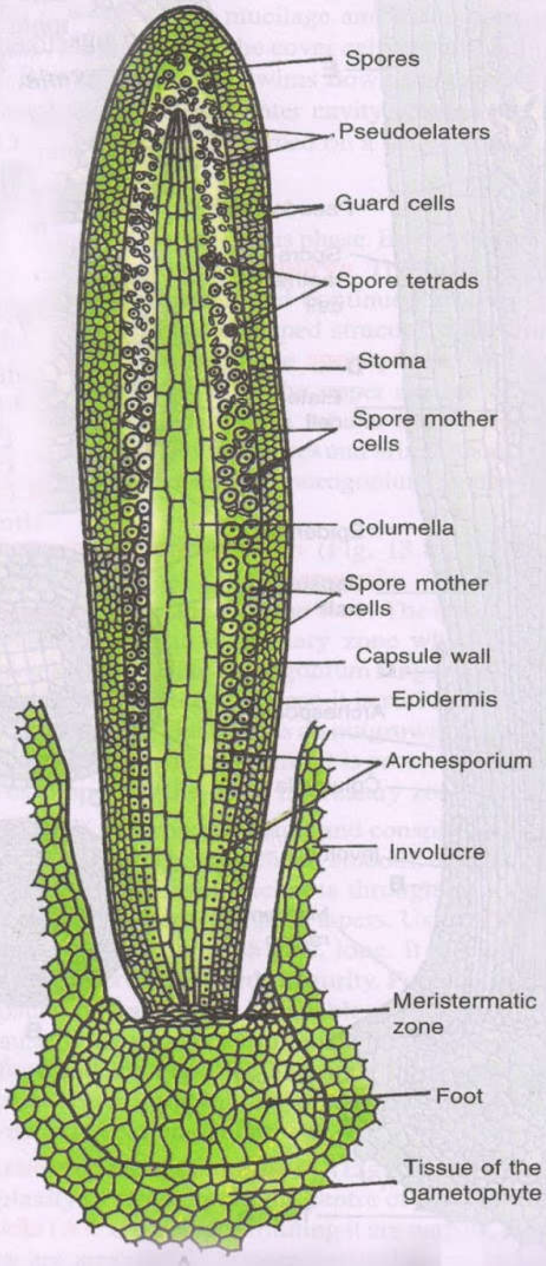
Archegoniate Plants, was recognised as having been fixed and perpetuated in accordance with the adaptation of aquatic organisms to a Land Habit." Tbe essence of this theory is tbat not only the sporogonium or fruit-body of the Bryophytes, but also the sporophyte or leafy plant of the Pteridophytes has arisen as a new intercalated phase in tbe life-history of a hypothetical gameto
pbytic ancestor whicb did not possess such a phase, by gradual elaboration of the oospore or fertilised egg.

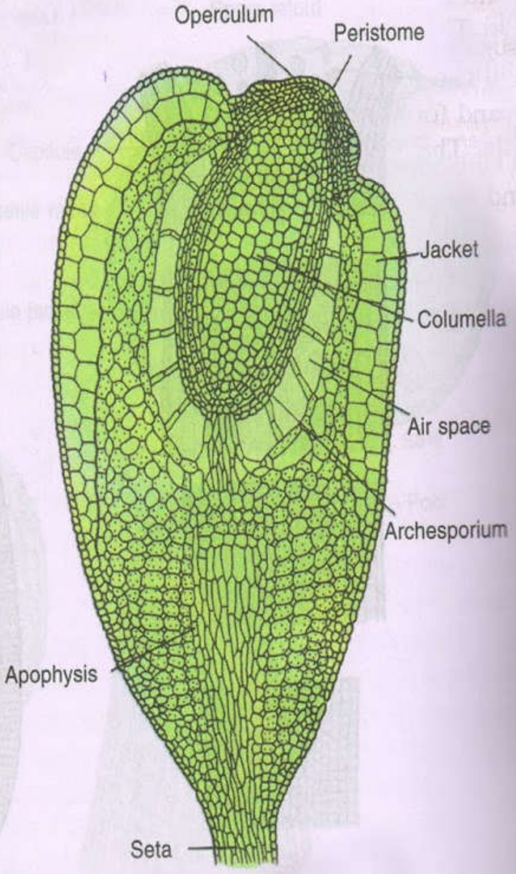
The origin of the sporophyte in land plants represents a fundamental phase in the plant evolution. Today this subject is controversial and, in my opinion, scarcely considered in our textbooks and journals of botany, in spite of its importance. There are two conflicting theories concerning the origin of the alternating generations in land plants: the "antithetic" and the "homologous" theory. These have never been fully resolved. 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. By contrast, 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. In this context, a very important question concerns the possible ancestor or ancestors of the land plants. Considerable evidences at morphological, cytological, ultrastructural, biochemical and, especially, molecular level, strongly suggest that the land plants or Embryophyta (both vascular and non-vascular) evolved from green algal ancestor(s), similar to those belonging to the genus Coleochaete, Chara and Nitella, living today. Their organism is haploid for most of their life cycle, and diploid only in the zygote phase (haplontic cycle). On the contrary, the land plants are characterized by a diplo-haplontic life cycle. Several questions are implied in these theories, and numerous problems remain to be solved, such as, for example, the morphological difference between gametophyte and sporophyte (heteromorphism, already present in the first land plants, the bryophytes), and the strong gap existing between these last with a sporophyte dependent on the gametophyte, and the pteridophytes having the gametophyte and sporophyte generations independent. On the ground of all of the evidences on the ancestors of the land plants, the antithetic theory is considered more plausible than the homologous theory. Unfortunately, no phylogenetic relationship exists between some green algae with diplontic life cycle and the land plants. Otherwise, perhaps, it should be possible to hypothesize another scenario in which to place the origin of the alternating generations of the land plants. In this case, could the gametophyte be formed by gametes produced from the sporophyte, through their mitoses or a delayed fertilization process?

Owing to their perishable nature, the simpler green Algze and Bryophytes have left very meagre fossil rem-iains, so that their geological history is very imperfect, and we are perforce driveln to a study of the living forms, as practically our only means of tracing the ancestry of the higher plant forms. Of the vascular plants there are abundant fossil remains which throw much light upon the relationship of the Pteridophytes and seed-plants, and the succession of forms in geologic times, but help but little in determining the lower forms from which the former originated. It has been urgecl that inasmuch as ferns, and even seedplants, can be traced back to the Devonian, and possibly even further, it is hopeless to expect the secret of the origin of the vascular plants can ever be solved. However, as many extremely primitive forms have undoubtedly survived to the present time, we can learn very much from a comparative study of these with the higher plants, which must have come from forms very similar to them. Of the forms which are of special importance in this connection are the simpler green Algae, and the generalized liverworts. According to the antithetic theory of alteration, the ferns have originated from forms very similar to the simpler existing liverworts, the leafy sporophyte being an elaboration of the nonsexual sporophyte. The homologous theory maintains that Bryophytes and Pteridophytes have nothing to do with each other, the latter arising quite independently from algal ancestors. The latter hypothesis was first suggested by the alga-like protonem-a of the mosses, and the somewhat similar prothallia of certain ferns, especially Trichomanes. The structure of the archegonium and spores is identical throughout, and the early stages of the sporophyte agree very closely, this being especially true of the more primitive types of Pteridophytes. In these the young sporophyte remains very much longer dependent upon the gametophyte and the external organs which characterize the Pteridophytes, are relatively late in making their appearance. Both of these facts point to a nearer approach to the bryophytic type in the lower Pteridophytes, a fact which is not readily explicable on the assumption that they are in no way connected with the Bryophytes. In a number of the lower Pteridophytes, e. P., Marattia Lycopoclium, Botrychium, the young sporophyte may remain attached to the gametophyte for months, or even years, long after it has passed beyond the embryonic stage If we compare the gametophyte and sporophyte of any typical Archegoniate, we note a very significant difference in their relation to the water-supply. The gametophyte is always, to a greater or less degree, an aquatic organism, never quite emancipating itself from the life conditions of its algal ancestors. The sporophyte, on the contrary, at least in its earlier stages, is never exposed directly to the water, although a few groups of Pteridophytes have developed, secondarily, aquatic sporophytes. Almost from the first the sporophyte is provided with a special massive absorbent organ, the foot, which is later superseded by the true roots of the Pteridophytes, a much more efficient means of obtaining water than is provided by the rhizoids of the gametophyte; and the unlimited capacity for growth of the true roots of the vascular plants allows the development of a root system to keep pace with the growth of the aerial part of the sporophyte. There is thus developed for the first time a plant-body strictly terrestrial in its character, and capable of independent growth. The gradual elaboration of the sporophyte is easily traced in the liverworts from the simple capsule of Riccia to the large and almost independent sporophyte of Anthoceros, or in another direction to the elaborate sporophyte of the true mosses.


Spore cell




Spores
Pseudoelaters
Guard cells
Spore tetrads
Stoma
Spore mother cells
Columella
Spore mother cells
Capsule wall
Epidermis
Archesporium
Involucre
Meristermatic zone
Foot
Tissue of the gametophyte


Operculum
Peristome
Jacket
Columella
Air space
Archesporium
Apophysis
Seta

Origin of Bryophytes from Gametophyte, Algae, Pteridophytes and Sporophyte

Origin of the Gametophyte:

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

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

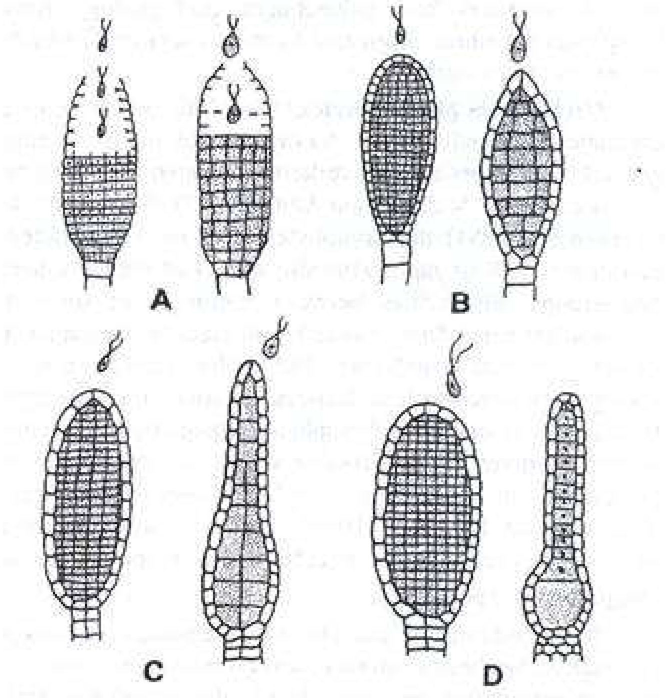


Fig. 19.2. Origin of bryophytes. Diagrams (A-D) illustrating the hypothatical origin of the antheridium and archegonium from the plurilocular sporangium of certain Phaeophyceae (*Ectocarpus*).

Origin from algae:

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

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

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

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

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

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

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

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

Origin from pteridophytes:

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

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

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

Origin of the Sporophyte:

It is an established fact now that an alternation of independent gametophytic and sporophytic generations has been evolved in several independent lines among aquatic algae. It is also thought that a migration from an aquatic to a land habit is not essential for the appearance of an alternation of generations. The algae have both isomorphic and heteromorphic alternation of generations.

Different views have been proposed concerning the origin of the sporophytes of bryophytes. There are two main theories — 1. Modification (homologous) theory and 2. Intercalation (antithetic) theory. According to modification or homologous theory the sporophyte is a direct modification of the gametophyte. The supporters of this theory advocate that the sporophyte is to be interpreted as a neutral generation and its primary function is the production of spores.

The facts which support this theory are – the presence of isomorphic alternation in some algae; photosynthesis in sporophytes of bryophytes; presence of tracheids in gametophytes of pteridophytes; apogamy and apospory. Supporters of the modification theory (Church, 1919; Fritsch, 1945; Zimmermann, 1932) are of the opinion that the two generations were isomorphic, independent and of a complex external structure. They think that in time the sporophyte became permanently attached and partially dependent upon the sporophyte and resulted in a reduction in the complex structure of the sporophyte.

According to intercalation or antithetic theory the sporophyte has been interpreted as a entirely new structure intercalated between two successive gametophytic generations. This theory further supports that the bryophytics sporophyte did not make its appearance until after a gametophyte had evolved an archegonium.

The zygote found in the venter of archegonium divided mitotically forming a number of diploid (2n) cells, each of which divided meiotically to form four haploid (n) spores. Thus a rudimentary type of sporophyte was developed in which all cells were sporogenous.

Further evolution of the sporophyte took place as a result of sterilization of sporogenous tissue and foot, seta and capsule were differentiated. According to this theory there was a progression from a simple to a more complex sporophyte by a progressive sterilization of sporogenous tissue.

Extra write up or explanations

Alternation of generations is a dramatic and familiar evolutionary trend in the plant kingdom. It is a notable feature of land plants, important in studies of phylogenies and evolution of the diploid sporophyte. Alternation can be defined simply as the two phases that normally occur in the life cycle of a plant, one haploid (gametophyte) the other diploid (sporophyte).Knowledge of plant life cycles and the study of land plant origins have grown significantly over the past century. Likewise, ideas on the origin of alternation have flourished. However, the traditional theories devised to explain alternation have languished, first in dispute, later in disregard because of confusing terminology and definitions that have not kept pace with changes in knowledge as it grew.The homologous and antithetic theories were first described as different morphological patterns of reproduction homologous alternation meaning a cycle of similar forms in algae, vs. antithetic alternation, that seen in the regular pattern of differing phases in bryophytes and ferns. The theories soon came to mean opposing methods by which the sporophyte originated, thus resulting in alternation of generations. Prior to 1900 the homologous theory derived the sporophyte by a change in reproductive mode of the gametophyte, a transfer of function, from production of gametes to producing spores for dissemination. This notion developed before the significance of the chromosome cycle and meiosis were realized or even known. The antithetic theory, on the other hand, maintained that the sporophyte was an interpolated phase resulting from vegetative growth of the zygote. This theory was described as such well before the correlative event of meiosis was known, yet that phenomenon fit nicely with the idea of interpolation.The discovery of isomorphic algae further confirmed the genetic homology of the phases that some botanists had long advocated, but it also clouded the issue as to the origin of the sporophyte. It resulted in equating isomorphic phases with the homologous theory, thus making that notion more attractive to its proponents. Since about 1910, however, the homologous theory has generally been assumed to derive the sporophyte by a delay in zygotic meiosis, the same way as the antithetic theory. Botanists adopted the notion of interpolation from the antithetic theory to use for the basic tenet of the homologous theory, taking the main premise of the former to support the latter, without realizing that in doing so they had combined the two theories into one. Curiously, however, many botanists did not recognize the significance of this change in the homologous theory, or even that it had happened. Even supporters of the antithetic theory did not recognize the extent to which the homologous view had co-opted their own. That is probably because by then the emphasis in meaning of the theories had shifted to the morphology of the phases rather than the origin of the sporophyte. The dispute over which theory was right for the origin of alternation continued, however, even though both derived the sporophyte by the same method. For nearly a century the only real difference between the two embattled theories has been whether ancestral sporophytes were isomorphic or heteromorphic. In a sense the old theories have returned to their original meanings, i.e., only suggesting different morphological outcomes of alternation.

Two somewhat conflicting theories (the homologous theory and antithetic theory) of the origin of alternating generations, specifically the origin of the sporophyte, in embryophytes (land plants) have had respective supporters for approximately a century. The question of initial sporophyte development in the land-plant life cycle resides at a much more fundamental level than the question of whether to interpret the sporophytes we observe today as fundamentally "axial" or "phytonic" structures (Wardlaw, 1968). Although one theory or the other of sporophyte origin (homologous vs. antithetic) has at times been favored by various authors (some authors remaining "neutral"), any real resolution of this question (i.e., which theory should actually be considered correct) has not been overwhelmingly apparent. This seeming indecision, or lack of clarity, has continued in spite of the accumulation of much pertinent knowledge (cytological, ultrastructural, biochemical, molecular-genetic) during the last four decades on the particular group of Chlorophyta, namely the Charophyceae, thought to be most representative of immediate land-plant ancestors. Green algae (chlorophytes) s.l., including charophytes, and green plants make up the large but generally related lineage "Viridiplantae" (Cavalier-

Smith, 1981; Blackwell & Powell, 1995; Nakayama et al., 1998).There is convincing evidence that, among Chlorophyta (s.l.), members of the Charophyceae (e.g., Coleochaete, Nitella, Chara) possibly offer critically important clues to landplant origin (Prescott, 1968; Graham, 1984, 1993); some authors (e.g., Bold et al., 1987) recognize the Charophyceae as "Charophyta," a division distinct from Chlorophyta, perhaps more closely related to embryophyte plants (than other green algae). In any event, in the context of an improved knowledge of putative land-plant ancestors, we may now appropriately ask again the question, which theory of alternation of generations (and sporophyte origin) in land plants is more plausible, the homologous theory or the antithetic theory? Based on an increased knowledge and/or further scrutiny of the morphology, cytology, biochemistry, and life cycle of charophycean algae (in particular), only the antithetic theory may be considered presently tenable--that is, still both logically and evidentially supported (as discussed herein).

The Alternating Generations of a Land Plant. Alternating generations (the sexual plant or gametophyte, and the spore-producing plant or sporophyte) in the life cycle of land plants has been appreciated since the work of Hofmeister (1851); see the discussions in Wardlaw (1952), Cronquist (1961), and Kaplan (2001). This alternation occurs in all major groups of land plants (i.e., in groups of nonvascular plants and in groups of vascular plants), although the "balance" (comparative dominance in the life cycle) of the two generations may vary greatly among groups (cf. Bold et al., 1987; Niklas, 1997). A land-plant life cycle may be viewed as encompassing what actually amounts to "two types of organisms" (Niklas, 1994): one promoting sexual reproduction and genetic diversity; the other, organismal proliferation and dissemination via asexual, olden one-celled, propagules (spores). Since, in evolution, the development of sex surely preceded alternation of generations, the gametophyte generation is considered, necessarily, to be older than the sporophyte generation (cf. Scagel et al., 1984; South & Whittick, 1987). The gametophyte generation, through most of plant (including land-plant) evolution, was tied into an aquatic environment, or at least the presence of water for a motile sperm (angiosperms and some gymnosperm groups being exceptions, cf. Bold et al., 1987). The sporophyte in most land plants, by contrast, effects aerial dispersal, and the development of this generation is thus the "key" to terrestrial plant development (Niklas, 1997). These statements concerning alternating generations are relatively noncontroversial. The bone of contention has been, just how, precisely, might the sporophyte generation have originated in the land-plant life cycle?

IV. **Putative Origins of the Sporophyte**. A. **HOMOLOGOUS THEORY**.Pringsheim (1878) proposed the "homologous" theory (later called the "transformation" or "modification" theory) for the origin of alternating generations, that is, fur the occurrence of the sporophyte, in the land-plant life cycle (Fig. 1). In this interpretation, the sporophyte is considered to be a direct modification of the gametophyte, in effect a "transformed" gametophyte with the specific function of spore production. The gametophytes and sporophytes of certain algae (e.g., Ulva) are similar (isomorphic), obviously related, structures. Such gametophytes and sporophytes are thus considered "homologous," the sporophyte being a kind of "diploid" version of the "haploid" gametophyte. (Since various levels of ploidy may be encountered, it is perhaps more accurate to say, simply, that the sporophyte usually has twice the chromosome number of the gametophyte.) Algal ancestors are considered to have given rise to land plants, with both a gametophyte and a sporophyte already present in the ancestral algal life cycle (meiosis already being sporic) prior to land invasion. Actually, algae with either isomorphic or heteromorphic generations have been given attention in theorizing land-plant origins, but the greater consideration has gone to algae with isomorphic alternation--in alleged corroboration of the homologous theory. The homologous theory of sporophyte origin in land plants found support in the writings of Goebel (1930), Eames (1936), Bold (1948), and Ditmer (1964).

ANTITHETIC THEORY. In "The Origin of a Land Flora," Bower (1908) suggested an alternative hypothesis for the origin of the sporophyte of land plants (Fig. 2.). In his "antithetic" theory, as in the homologous theory of other authors, algal ancestors of land plants were also envisioned (but not the same kinds of algae in the antithetic theory as in the homologous theory and not the same kind of algal life cycle). In algal ancestors, suggested in the antithetic theory by Bower, only the gametophyte was thought to have been present initially in the algal life cycle, the sporophyte arising subsequently and in correspondence with (or soon after) land occupancy by the gametophyte. Bower suggested that the sporophyte appeared in the life cycle by "amplification of the zygote," i.e., by delay of meiosis, during which a series of mitotic divisions produced a mass of cells (the new sporophyte). Meiosis would thus shift naturally with this new development, from a zygotic "position" to a sporic "position" in the life cycle. The main point is that, in this theory, the sporophyte is viewed as something "new," added or intercalated into the life cycle. Bower later (1935), wishing to downplay some of the connotation of "antithetic" (i.e., as something truly "different" or "foreign" in the life cycle), preferred to refer to the "antithetic theory" as the "interpolation theory," indicating that the sporophyte was indeed "added" to the life cycle, but not that it need be envisioned as something profoundly different from the gametophyte. Smith (1938), Campbell (1940), and Haupt (1953) were among those who supported Bower's antithetic theory of sporophyte origin in land plants. Some have looked at the question of sporophyte origin with different conclusions, or else without deciding in favor of one theory or the other. In a somewhat novel idea (though not accepted as a whole at present), Frisch (1916) suggested that the bryophyte sporophyte originated antithetically but that the sporophyte of pteridophytes ("higher" plants) was of homologous origin. This is confusingly referred to as Frisch's "pseudo-homologous" alternation theory (cf. Graham, 1993). Brown (1935) favored independent origins of alternating generations "in various lines," his meaning being somewhat elusive. Brown (1935: 657-658) clearly believed, however, that "it is doubtful if any alternation of generations ... in any ... algae has any relationship to the Bryophyta and other land plants," seeming in this statement to favor an antithetic origin of the land-plant sporophyte but (perhaps overzealously) ruling out the role any alga might have played in this. Land-plant origins have in fact been viewed as monophyletic (e.g., Zimmerman, 1930) or decidedly polyphyletic (e.g., Church, 1919; see also the discussion in Wardlaw, 1952). At least as numerous as those taking sides, a number of authors have been "on the fence" of the issue; such authors have usually just presented the ideas of both the homologous theory and antithetic theory, without apparent preference (e.g., Smith, 1938; Wardlaw, 1955; Foster & Gifford, 1959; Burns, 1974; Delevoryas, 1977; Gifford & Foster, 1989). Bold, though earlier (e.g., 1948, 1957) favoring the homologous theory, in later writings (e.g., Bold et al., 1987), gave equal credence to the homologous theory and to the antithetic theory. Graham first (1984, 1985) supported the antithetic origin of the land-plant sporophyte but later wavered to an extent by stating, "it is evident that consensus has not yet been reached among plant scientists regarding the origin of plants and their life cycle" (1993: 38). Questions of logical content and consistency of theories of land-plant origin should be addressed before a posteriori (evidential) arguments. A priori arguments are important because of the matter of scientific plausibility and coherence of theories, and are advisedly taken into account prior to the launching of such into the literature of science. The theories of sporophyte origin should (until now, perhaps) have been regarded as "hypotheses," rather than "theories," because of their relatively limited scope (compared with evolution as a whole) and lack of confirmation (cf. Sattler, 1986). Regardless, in the homologous theory the assumption is made that both alternating generations of an algal ancestor would be carried over, essentially intact, to land, that both would adapt (the sporophyte having presumably the greater adaptative burden), and that the sporophyte would become (at least to an extent) dependent (structurally and physiologically) on the gametopbyte (this, given our knowledge of the dependent or semidependent nature of extant sporophytes of bryophytes and, in initial stages, vascular cryptogams). No real mechanism has been suggested in the homologous theory per se for exactly how all of this would occur or for how motile spores of the algal sporophyte would become nonmotile and adapted to aerial (often wind) dispersal. It is instructive here to think of ontogenetic possibilities (Arber, 1950). Whether the origin and certain changes in the sporophyte occurred before, during, or after invasion of land, it would seem reasonably patent that such changes would necessarily involve altered development of the zygote; if so, then one is actually suggesting an antithetic mechanism, that is, theory reduction (cf. Ruse, 1988) to the antithetic theory, for incipient sporophytes. A further complication is that two lines of subsequent land-plant evolution (cf. Cronquist, 1961) would be required in the homologous theory. Postulated are both a "downgrade" and a limited "upgrade" development sequence leading to bryophyte (s.l.) sporophytes (some bryophyte sporophytes are inexplicably much more complex, or "less reduced," than others); by contrast, a significantly "upgrade" sequence is envisioned as leading to vascular plant sporophytes. Thus, both reduction and elaboration sequences of the sporophyte are enigmatically proposed in the homologous theory (even within one group, e.g., the Hepatophyta), occurring in what was probably the same, or a very similar, environment (again, without a defining mechanism to account for the two different paths). To this scenario, Bold et al. (1980) added the questionable speculation that homworts (e.g., Anthoceros) evolved (devolved?) by reduction from Psilophyte sporophytes and (without explanation of "how"), in the process, lost useful land-plant adaptations (including vascular tissue)--hence, a putative "downgrade," after an "upgrade," development. A speculation such as that by Bold et al. plays into the larger question, long debated (cf. Minkoff, 1983), as to whether the tracheophyte and bryophyte sporophytes actually had any direct connection to one another. In contrast to the homologous theory, the antithetic theory presents none of the theoretical difficulties discussed so far in this section, because all bryophyte and vascular plant sporophyte patterns (and assumptions about these) are based on a progressive, "vegetative" development (i.e., by mitosis) of the zygote, retained on the gametophyte, with meiosis obviously delayed. Over time (many generations), a subsequent, generally "upgrade," evolutionary development would be envisioned to take place, by which one could (eventually) account for virtually any land-plant sporophyte type (see Zimmerman, 1952; Niklas, 1992). Bower's (1908, 1935) antithetic (interpolation) theory thus projects both a definite ontogenetic mechanism and a plausible phylogenetic sequence. In not necessarily requiring major morphological reductions (reversals), the antithetic theory is a much more parsimonious interpretation of land-plant evolution (i.e., the evolutionary development of the sporophyte) than is the homologous theory. **ALGAE WITH ISOMORPHIC GENERATIONS**.An argument often put forward in favor of the homologous theory of alternation of generations (and sporophyte origin) is the alleged "evidence" of algae with isomorphic (morphologically identical or very similar) gametophytes and sporophytes, such as Ulva, Cladophora suhriana, Chaetomorpha (cf. Bold, 1957; Bold & Wynne, 1985; Lee, 1999). The sporophyte is so obviously related to the gametophyte in these algae that it has been regarded merely as a "modified gametophyte" (Bold, 1957); gametophyte and spornphyte appear to be homologous structures. From this has come the extrapolation that it must be so with all sporophytes (e.g., Bold, 1957), including those of land plants. Although green algae are related to green plants (in combination, the "Viridiplantae"; cf. Sluiman, 1985), evidence reviewed in some of the lettered headings in this section (VI), and in other sections of this article (e.g., section VIII), indicates that algae with isomorphic life cycles (isomorphic alternating generations) are definitely not among those green algae most closely related to land plants. Rather, it is charophytes (e.g., Coleochaete, Chara, Nitella) that are closely related to land-plant (embryophyte) ancestors (cf. Graham, 1993). In none of the closest living (or fossil, as far as we know) algal relatives of land plants does alternation of generations (i.e., a sporophyte) actually occur; advanced charophytes are gametophytic plants. Thus, it is a moot point (to the origin of land plants) whether other kinds of algae--Ulva or members of the Cladophorales, tbr example--have alternating generations (or whether these generations are isomorphic).

APOGAMY AND APOSPORY. Apogamy ("without gametes") and apospory ("without spores") are, to an extent, misnomers, because in some instances gametes and spores are still produced in the life cycle when these phenomena occur; the chromosome complement of the apogamously tbrmed sporophyte and aposporously produced gametophyte is, however, sometimes other than the usual for these generations (for example, both gametophyte and sporophyte in the life cycle may be found to be diploid). Apogamy and apospory are rather well known in bryophytes (s.l.) and ferns, with apogamy perhaps being the more common phenomenon in nature (Bold et al., 1987); apomixis in angiosperms constitutes forms of apogamy (cf. Stuessy, 1990, re "apogameon"). **Apogamy,** by definition, is the formation of a sporophyte by (cells of) the gametophyte, without fertilization (without sexual union of gametes). Apospory is the formation of a gametophyte by the sporophyte, without the function of actual melospores. Apogamy and apospory have been alleged as evidence for the homologous theory of alternating generations (e.g., Bold, 1957; Bold et al., 1987), since in some cases gametophyte and sporophyte seem rather readily interconvertible. However, because the gametophyte and sporophyte of a plant necessarily share a large percentage (or all) of a genome, it is probably more accurate to state, simply, that the gametophyte and the sporophyte may be expected on occasion to exhibit a fundamental (genetic) relationship (Niklas, 1997) and even the capacity for interconversion. Because of significant genomic overlap, this genetic relationship would be true regardless of whether the sporophyte originated in a homologous manner or an antithetic manner. There is, thus, no special reason to prefer either the homologous theory or the antithetic theory based on observed phenomena of apogamy/apospory.

REVERSION OF VEGETATIVE TO SPOROGENOUS TISSUE

The land sporophyte generation is thought of by some as a neutral generation, not concerned with sex and genetic diversity but "introduced" into the life cycle for the primary "purpose" of producing (often large numbers of) spores for asexual propagation and (perhaps rapid) spread in a terrestrial environment; its function is thus quite different from that of the gametophyte (cf. Niklas, 1997). In an "antithetic view" of sporophyte origin, the only view well suited to this particular "asexual scenario," the sporophyte is seen as a generally upgrade development, progressively coping with distribution in a dynamic, often harsh, land-based environment; it is seen as derived from original sporophytes that were probably little more than small masses of spores (sporophytes represented in appearance perhaps by those of such liverworts as Riccia and Ricciocarpus). This antithetic view holds that more elaborate sporophytes developed by progressive sterilization, and further vegetative development, of originally almost totally sporogenous tissues. One support for this (development by sterilization) assumption is the observation of occasional "reversions," in Porella and some other liverworts, of vegetative tissues of the sporophyte (e.g., of the seta and foot) to sporogenous tissue (Smith, 1938)--an indication of an original, more completely sporogenous state. A more general interpretation is that cells of these rather simple plants retain a similar genetic potential, regardless of the usual course of cell differentiation.

PRESENCE OF LIMITED CHLOROPHYLL IN SIMPLE (REDUCED OR PRIMITIVE?)SPOROPHYTES. Bold (1948, 1957) interpreted the finding of a modicum of chlorophyll in the small, simple, ball-like sporophyte of the liverwort Ricciocarpus as evidence of a relic remaining from the reduction of a formerly more elaborate chlorophyll-producing sporophyte derived according to the homologous theory of sporophyte origin. This represents a possibly spurious, and contradictory, interpretation of Rieciocarpus as having a relatively primitive (i.e., thallose) gametophyte but a highly reduced (derived!) sporophyte (Bold, 1957). There is no substantial basis for interpreting either the gametophyte or the sporophyte of Ricciocarpus as anything other than relatively primitive, although the gametuphyte in this case is not the simplest among Hepatics (cf. Schofield, 1985; Bold et al., 1987). The fact is that the vast majority of land-plant sporophytes, of all groups of land plants (excepting certain bryophytes), are heavily chlorophyll bearing, a major autotrophic adaptation evident in a virtually unbroken sequence. The presence of limited chlorophyll in Ricciocarpus, rather than being regarded as relictual, could just as well be regarded as part of a relatively primitive (inchoate) condition of a protected (more or less enclosed), antithetically developed sporophyte--representative, perhaps, of a relatively early stage in an elaboration sequence leading to the much more abundantly chlorophyllose sporophytes of some bryophytes and most tracheophytes.

DEPENDENCY OF SPOROPHYTES OF EMBRYOPHYTES

Sporophytes of bryophytes (liverworts, hornworts, mosses) are at least partially dependent upon gametophytes for nutrition in the life cycle; that is, total sporophyte independency is not attained in the Bryophyta (s.l.). In vascular cryptogams (psilophytes, lycopods, sphenophytes, ferns), the sporophyte, though usually becoming independent, nonetheless has early stages that are heavily dependent on the gametophyte. Only a very limited dependency of the sporophyte is retained in gymnosperms and angiosperms, and only during the embryonic stages of development; by contrast, the microscopic gametophytes of seed plants have, in reversal of fortune, established complete dependency on the sporophyte. In any case, overwhelmingly, the sporophytes of embryophytes do not closely resemble the gametophytes on which they depend. Although one could conjure various scenarios for these facts, it is actually difficult to explain them logically with any other than the antithetic theory of sporophyte origin (Wardlaw, 1955); if the homologous theory (deriving the generations from isomorphic precursors) were true, we would expect a greater similarity (and independence) than is observed, at least in some lower groups of embryophytes.

OCCURRENCE OF MOTILE (FLAGELLATED) CELLS IN PLANTS

Flagellated sperm occur in bryophytes, vascular cryptogams, and some groups of gymnosperms (cf. Sporne, 1965; Bold et al., 1987), but not in angiosperms. The apical biflagellation of bryophytes and most lycopods is perhaps traceable to a similar pattern in green algae (Bold & Wynne, 1985; Gifford & Foster, 1989; Van den Hoek et al., 1995), including members of the Charophyceae. Flagellation of sperm in land plants is a trait retained to achieve fertilization in aquatic (or past aquatic) environments. Many algae, such as Ulva, in addition to biflagellate gametes, exhibit flagellated zoospores (quadriflagellate in the case of Ulva) produced by the sporophyte. If the homologous theory of origin of the land-plant sporophyte were true, we would expect to find some evidence (in lower land plants) of either motile meiospores or of spores that exhibit (cytologically) a remnant of former flagellation. In fact, no flagellation, or remnant of flagellation, is found in spores of land plants. On the other hand, if the land-plant sporophyte developed antithetically, in response to (initiated in) a terrestrial environment, one would not necessarily expect to find spore flagellation (or even residual evidence of same). It is quite possible that flagella were present on spores of earliest land plants but were lost relatively soon after the incursion onto land--with little or no evidence of former flagellation remaining. The loss of flagella does not represent a special morphogenetic hurdle, since flagella are readily retracted in a number of kinds of flagellated algae, as a natural part of their cell cycles (cf. Beech et al., 1991). This question (of why we do not observe residual evidence of flagellation in land-plant spores), however, should cause us to consider carefully which charophytes might be most representative of algae that were land-plant ancestors. Was it those with flagellated spores (e.g., forms such as Coleochaete) or those forms, such as Nitella and Chara, that produce no spores at all (flagellated or otherwise)? Could not only the sporophyte but also spores of land plants have been an innovation associated with land invasion? It is quite possible that the land-plant spore (even in primitive land plants) represents a structure which is rather different from the spores of any algal group; at a minimum, there is a significant difference in appearance, in both internal and external features (cf. Gray, 1985; Bold et al., 1987; Taylor & Taylor, 1993).

PALEOBOTANICALEVIDENCE . Fossil material provides useful evidence for understanding plant evolution. However, compared with sporophytes, gametophytes are less commonly preserved. Some ancient fossil gametophytes are quite different from their respective sporophytes, as is the case in land plants today (Taylor & Taylor, 1993)--such information tentatively supports the antithetic theory. Other fossil gametophytes, however, are more similar to sporophytes in structure (Remy & Remy, 1980; Remy & Hass, 1986), a fact that has been claimed in support of the homologous theory (see the discussion in Graham, 1993). The Devonian garnetophytes discussed by Remy and Remy and Remy and Hass are, however, some 40 50 million years too recent in the geologic record to provided clues as to the appearance of the earliest land-plant gametophytes. As Niklas (1997) suggested, a repertory of ancient forms (sporophytes and gametophytes) probably occurred (but it is unlikely that we will ever know of all of them). In speculation, gametophytes and sporophytes, which were either similar or dissimilar to each other, could be projected from either the homologous theory (i.e., isomorphic vs. heteromorphic life cycles) or the antithetic theory (especially as reinterpreted by Bower, 1935). Thus, Ordovician, Silurian, and Devonian gametophytes have not yet offered special help in choosing between the homologous theory and the antithetic theory. A possible exception, the Silurian genus Parka, is parenchymatous and padlike (Taylor & Taylor, 1993) and, if eventually demonstrated to be a gametophyte, may be concluded to resemble

Coleochaete (Charophyceae). If Parka is eventually shown to have a relationship to Coleochaete. this finding would lend support to the antithetic theory (since charophytes are thought to be most representative of the algal progenitors of land plants; cf. Graham, 1984, 1993). Fossil representatives of the Charales (though not entirely the equivalent of modern genera such as Chara and Nitella) have great antiquity in the fossil record, as exemplified by finds of "gyrogonites" (fossil oogonia); such structures are known from the early Devonian (cf. Croft, 1952; Taylor & Taylor, 1993).

CYTOLOGICALEVIDENCE. Since 1970 a great deal of evidence on cell structure and ultrastructure has accumulated, shedding light on ancestry of land plants. The starlike, flagellar transition zone (as seen in cross-section; cf. Dodge, 1973) possessed by green algae (Chlorophyta) was clearly carried over to motile cells (sperm) of land plants (cf. Mishler & Churchill, 1985). Pinning the (green algal) ancestry of land plants down further, vegetative cells of advanced charophytes (e.g., Chara, Nitella, and Coleochaete) have plasmodesmata, as do land plants. Similarly, these advanced charophytes exhibit a distinctly land-plant ("embryophytic") pattern of mitotic and cytokinetic events, including, an open mitosis with a persistent, interzonal spindle (the daughter mitotic nuclei remaining separated at a distance) and a phragmoplast (spindle fiber remnants perpendicular to the cytokinetic plane and associated golgi-derived vesicles; el. Wolfe, 1983). A cell plate is formed, which often begins centrally and progresses centrifugally. Advanced charophytes thus exhibit a land-plant type of vegetative cell division or "desmoschisis" in which the "parental wall forms part of the wall of the cellular progeny" (Bold & Wynne, 1985: 649). While this definition of desmoschisis (of vegetative cell division, pro parte) is correct insofar as it goes, Groover and Bold (1969) and Bold and Wynne (1985) actually employed "desmoschisis" in the limited context of packets of cells formed by chlorosarcinalean algae (which are chlorophycean, not charophycean, algae; cytokinetic details of the two groups are typically different). The context of Groover and Bold is a concept of cell division actually traceable back to Fritsch (1935). The more demanding and inclusive concept of the land-plant type of vegetative cell division discussed above (presence of phragmoplast, persistent spindle, cell plate, etc.) is in Pickett-Heaps (1975, 1976), Stewart and Mattox (1975), and Mattox and Stewart (1984). Smith (1950) actually used "vegetative cell division" in the "loosest" sense, implying simply cell division that resulted in vegetative (i.e., other than reproductive) cells. Thus, confusingly perhaps, vegetative cell division is used differently by different authors and also is not entirely the equivalent of "desmoschisis."

Returning to motile cells, the flagellated cells of charophytes have a unilateral (asymmetrical) flagellar rootlet system. There are usually two distinct roots, a larger root and a smaller root (and these are sometimes rather closely spaced; cf. Mattox & Stewart, 1984). The larger flagellar root is a "band" with many microtubules (perhaps 60 or so) and is associated (toward the base) with a distinctive multilayered structure (MLS) composed of microtubules and laminate plates; this composite structure is similar to that found in sperm of embryophytes (cf. Van den Hock et al., 1995; Lee, 1999). The ultrastructure of the motile cell of charophytes, particularly the rootlet structure, is in fact quite suggestive of land-plant motile-cell ultrastructure (Melkonian, 1982; Bold & Wynne, 1985; Mishler & Churchill, 1985). Motile cells of" green algae other than charophytes (e.g., Ulvophyceae and Chlorophyceae), by contrast, tend to have a "cruciate" (symmetrical) flagellar root system (i.e., four equally spaced rootlets) and lack the larger root with the MLS (Mattox & Stewart, 1984; Bold & Wynne, 1985).

BIOCHEMICAL AND MOLECULAR--GENETIC EVIDENCE

Biochemical. Green algae s.l. (Chrorophyta and Charophyta) share the same types of chlorophylls (a and b) and carotenoids (e.g., lutein, beta-carotene) with embryophytes and, associatedly, similar chloroplast structure and thylakoid arrangement (Van den Hock et al., 1995). The storage product is the same (starch) as higher plants and is similarly stored within plastids; most algal groups other than chlorophytes and charophytes (e.g., chrysophytes, xanthophytes, phaeophytes), exhibit extraplastidal storage of photosynthate (cf. Lee, 1999). The cell-wall composition of green algae and higher plants is similar as well (Green, 1962). Comparing chlorophytes and charophytes, biochemically, Frederick et al. (1973), Al-Houty and Syrett (1984), and Syrett and Al-Houty (1984) determined that charophytes and embryophytes (bryophytes and tracheophytes) utilize the enzyme glycolate oxidase in their photorespiratory pathway; chlorophytes (meaning green algae other than charophytes) utilize glycolate dehydrogenase instead. A further distinction was found in the systematic distribution of the specific urea-utilizing enzyme (Al-Houty & Syrett, 1984; Syrett & Al-Houty, 1984); Charophyceae and land plants possess Urease; Chlorophyceae and Ulvophyceae have urea amidolyase (UAL-ase). Al-Houty and Syrett (1984) found such biochemical (enzymatic) information useful in confirming taxonomic alignment of certain genera; for example, placement of Klebsormidium Silva et al. (1972) with the Charophyceae was affirmed with enzymatic evidence.

Molecular-Genetic evidence Small subunit ribosomal RNA and DNA sequences (e.g., Nakayama et al., 1998; Katana et al., 2001) support the general lineages of algae outlined by Mattox and Stewart (1984)--chlorophytes, ulvophytes, charophytes, etc. and basal groups ofprasinophytes leading to some of these lineages (Nakayama et al., 1998). Mattox and Stewart's (1984) revised classification of green algae (s.l.) has received support (though perhaps limited) from some authors of phycology texts (e.g., Bold & Wynne, 1985). However, a detraction from the Mattox and Stewart (1984) proposals was their consideration (in a "phylogenetic tree") of Charophyceae as a "primitive" group among green algae, based on structure of "swarmers" (motile cells), a mistaken conclusion that could have been avoided through application of sound cladistic methodology to ultrastructural and biochemical data (as discussed by Bremer, 1986). Work on tRNA introns (Manhart & Palmer, 1990), on SSU rRNA gene sequences (Kranz et al., 1995), and rbcl sequences (cf. Graham & Wilcox, 2000) all point to charophytes (of one type or another) as the group of extant "algae" most closely related to land plants.

CLADISTIC INTERPRETATIONS. A number of cladistic analyses, based on multiple sorts of information, have examined the question of the lineage order of Viridiplantae (green algae and green plants): e.g., Bremer and Wanntorp (1981a, 1981b), Mishler and Churchill (1984, 1985), Bremer (1985), Sluiman (1985), Bremer et al. (1987), and Theriot (1988). Many characters, of various kinds, have been included in these analyses, viz., morphological, ultrastructural and biochemical (cf. Mishler & Churchill, 1985). Some minor disagreements have occurred, as in Theriot's (1988) criticism of Sluiman's (1985) failure to resolve grouping relationships of Coleochaete, other charophytes, bryophytes and tracheophyes (all arising in Sluiman's work as a sort of polychotomy). Generally, however, the filiation sequence has been relatively clear: chlorophytes, then charophytes, then either liverworts or hornworts, then mosses, and finally, tracheophytes (cf. Theriot, 1988; Niklas, 1997). Some authors (e.g., Niklas, 1997; Purves et al., 1998) considered liverworts to have preceded hornworts in evolution; others (e.g., Theriot, 1988; Renzaglia & Vaughn, 2000) thought hornworts to have the more primitive assemblage of traits and/or to have arisen first. Solomon et al. (2002) considered the matter equivocal. Regardless, the Viridiplantae are considered by virtually all authors to represent generally related groups of organisms, some details not withstanding; in most cladistic analyses it seems clear that, among algae, charophytes place the closet to lower embryophytes.

Is there further evidence (characters), so far largely overlooked, amid the many characters used in cladistic analysis, and recently in molecular genetic analysis, that might be brought to bear on the question of relative filiation "position" of hornworts (anthocerophytes) and liverworts (marchantiophyes)? One such piece of evidence, not found to be a part of cladistic data sets reviewed, might be found in something as seemingly relatively simple and straightforward as chromosome number. As pointed out by Schofield (1985: 274), "there is considerable uniformity in the chromosome number of hepatics (n = 8, 9, or 10) and hornworts (n = 4, 5, or 6) with secondary polyploidy occurring relatively infrequently." Bold et al. (1987) noted that the usual number for hornworts is, in fact, n = 5. In any event, I assume here that, with such a low number, n is the equivalent of x (one chromosome set). Schofield (1985) further indicated that, among hepatics, fully three-fourths (with known chromosome numbers) have n = 9. This last fact is potentially enlightening, because (for example) of Mandal and Ray's (2001) cytotaxonomic study of the genus *Nitella* (Charophyceae), in which a uniform chromosome number of n = 18 was found. If this (n = 18) in *Nitella* were actually considered a "diploid" number (the zygote being in effect tetraploid at 36), it would be very difficult to derive a haploid number to match the usual hornwort n (i.e., n = 5); "polyploids" of the hornwort number would probably be 10 or 20, for example, not 18. However, a "haploid" of the 18 number would, of course, be n = 9, matching perfectly the most prevalent n found in the Hepatophyta. This idea is put forward not as any sort of definitive answer to the charophyte--liverwort-hornwort filiation sequence but, rather, as another source of evidence of a possible charophyte--hepatophyte connection--which could be carried further by detailed, karyotype analysis (as initiated by Mandal & Ray, 2001). In short, the limited chromosome number evidence available so far suggests, given scenarios available, the filiation sequence of charophytes, then liverworts, and then hornworts (i.e., prior to reaching the moss clade).

Plant Life Cycles, Morphology, and Habitats: Keys to the Kingdom (and to the Land-Plant Sporophyte). Considerable evidence exists, some presented herein, that the plant kingdom, Plantae or Viridiplantae (cf. Cavalier-Smith, 1981; Blackwell & Powell 1995, 1999; viz., green algae and green plants) is a sizable but relatively coherent phylogenetic lineage (i.e., a large clade). There is, as discussed, strong evidence from cytology and biochemistry that links green algae, especially charophytes, to higher plants. Perhaps surprisingly, some of the most compelling evidence comes from study of morphology and life cycles (and, in association, habitat); this is, in fact, evidence that has been available for a long time. The selection of the flattened-spheroidal, sometimes parenchymatous Coleochaetae as possibly representative of the putative ancestor of embryophytes (particularly thallose liverworts) is not a new idea and was clearly suggested by Bower (1908) and later supported by Campbell (1940). Wardlaw (1955) and Jeffrey (1962) mentioned charophytes as an algal group possibly involved in land-plant origins. Among more recent students of green algae-green plants, some authors (e.g., Graham, 1984; Scagel et al., 1984) have more apparently credited these past insights and suggestions than have other authors (e.g., Mattox & Stewart, 1984).

Regardless, summaries of recent evidence (Graham, 1993; Niklas, 1997), and information presented herein, generally support the ideas of Bower, Campbell, Wardlaw, and Jeffrey. What can be said, morphologically, is that algae belonging to the Charophyceae, particularly forms like Coleochaete. are now thought (based on considerable evidence) to resemble (i.e., be representative of) putative land-plant ancestors. But if we allow that the land-plant (embryophyte) lineage is traceable to charophycean forms (i.e., to these sorts of algae), does this help us decide which theory of alternating generations, and sporophyte origin, to adopt? The answer is, yes, most definitely it does. First then, a brief, but necessary, digression to consider algal (and plant) life cycles. Anyone who has studied either Bold's morphology texts or his phycology texts (in their various editions) has become familiar with the three basic life cycles in algae. To simplify, these are (as per Bold's editions of Morphology of Plants (and Fungi), up through the fourth edition, 1980, with or without coauthors): 1. Haplobiontic, Haploid: one type of generation (i.e., the gametophyte) only, in the life cycle, the only "diploid" cell usually being the zygote; meiosis is therefore zygotic; many simple green algae such as Chlamydomonas and Ulothrix exhibit this type of life cycle. 2. Haplobiontic, Diploid: gametophyte only, but the gametophyte is diploid and meiosis is gametic (e.g., the genus Codium, a member of the green algae). As an aside it may be noted that animals generally are diploid organisms, with gametic meiosis.3. Diplobiontic: alternating generations present, gametophyte (haploid) and sporophyte (diploid); the sporophyte and gametophyte may be similar (isomorphic), as in Ulva and some Cladophora species (both genera being members of the Chlorophyta), or dissimilar (heteromorphic), as in a species of Bryopsis (Chlorophyta) and in Laminaria (belonging to the Phaeophyta); meiosis is sporic in diplobiontic life cycles. A diplobionitic type of life cycle (sporic meiosis) is typically found in land plants, but this land-plant life cycle cannot necessarily be extrapolated to have been derived from algae which are/were diplobiontic (a point discussed a number of times in this article). Since the terms haplobiontic and diplobiontic actually refer to the number of generations in the life cycle and not chromosome number per se, these terms came to be viewed as potentially confusing. Thus, in the fifth edition of his morphology text (1987), Bold and his coauthors switched to the terms "monobiontic" (haploid), "monobiontic" (diploid), and "dibiontic," respectively, for the three types of life cycles. Other authors have used still different terminology for these three life cycles: "haplontic,'" "diplontic," and "diplohaplontic" (Pritchard & Bradt, 1984). However, it is simpler to refer to these life cycles by the timing or "position" of meiosis in the life cycle, respectively, "zygotic," "'gametic," and "'sporic," as did South and Whittick (1987). South and Whittick (p. 246) presented an easy-to-follow "flow diagram" of the evolution of meiosis, life cycles, alternation of generations, and so forth; their tracings led first to eukaryotes (after the development of mitosis and meiosis), and then to several major eukaryotic lineages and sublineages, including land plants based on the timing of meiosis in the life cycle and the supposed development of alternating generations. South and Whittick (1987) rightly saw land plants as possessing sporic meiosis (since they do!) but envisioned this lineage as arising from ancestors with preexisting alternation of generations, for which there is no substantive evidence (only speculation), as I have discussed and will continue to discuss. South and Whittick speculated that this alternation of generations in algae, connecting to land-plant origins, would be heteromorphic (they did not name a specific group of algae). This thesis of heteromorphic precedence (of land plants) is a more plausible proposition, but less common, than an isomorphic hypothesis (since extant land-plant lifecycle generations are indeed overwhelmingly heteromorphic); but even a heteromorphic hypothesis is not truly plausible, because there is no evidence for algae that were already in possession of alternating generations, as being among those leading directly to land plants. The less plausible, but seemingly more common, suggestion has been that green algae with isomorphic alternating generations, such as Ulva (Bold, 1957; Tippo & Stern, 1977), were land-plant progenitors. However, in Ulvophyceae the furrowing type of somatic cytokinesis, the cruciate, flagellar roots of the motile cell, and the fact that not only male but also female gametes of Ulva are motile (the gametes being isogamous or anisogamous) would all but preclude the direct involvement of ulvophytes in land-plant origins (cf. Mattox & Stewart, 1984). Also, Ulva and relatives are marine organisms. It is likely that land plants originated in amphibious environments involving fresh water (and land; cf. Niklas, 1997), regardless of the past counterspeculations of a few (cf. Church, 1919). Fritschiella, a terrestrial green alga (sometimes found on tree bark), with a growth form varying from filamentous to parenchymatous, has also been postulated as a land-plant progenitor (Cronquist, 1961). However, Fritschiella (a chaetophoracean or ulotrichacean form) does not develop a phragamoplast during cytokinesis but, rather, has a more primitive, "phycoplast" configuration (cf. Lee, 1999)--again virtually eliminating it as a possible direct land-plant ancestor. Concerning other types of algae, there is little point in considering algae not related to the green-plant lineage (cf. Wardlaw, 1952; Cavalier-Smith, 1981 ; Blackwell & Powell, 1995, 1999). For example, Ectocarpus and Laminaria (Phaeophyceae, i.e., brown algae) exhibit, respectively, fundamentally isomorphic and heteromorphic alternations of generations. Regardless of the appealing and instructive nature of their life cycles, these brown algae are not only marine organisms but Stramenopiles (cf. Blackwell & Powell, 2000), relatively unrelated to Viridiplantae (cf. Blackwell & Powell, 1995). The alternating life cycles of brown algae are thus best interpreted as parallel (not related) developments to any such life cycles in green algae (e.g., Ulva, Derbesia).

The Coleochaete Connection (or Is the Connection with *Nitella*, or Klebsormidium, or Something Else?) Given greatly improved knowledge of the relationships of particular algal groups to land plants (i.e., to embryophytes), as discussed throughout this article, the focus need now be primarily on those groups of algae clearly related to embryophytes (in attempting to account for land-plant origins). It is specifically from the morphology and life cycle of these algae, with a close and certain connection to land plants, that one should hope to solve the riddle of the homologous versus antithetic origin of the land-plant sporophyte. A review and development of a considerable body of evidence has indicated the phylogenetic significance of Charophyceae to land-plant origins. The discussion, thus, will necessarily proceed to an analysis of the life cycle of this particular group of algae.

COLEOCHAETE. As discussed, along several lines of evidence, advanced charophytes provide the best insight into land-plant origins. Singled out among charophytes as possibly morphologically representative of very primitive land plants has often been the small, freshwater, sometimes filamentous, sometimes flattened and padlike (depending on the species) genus Coleochaete. Coleochaete indeed appears to offer developmental clues to embryophyte origins (Graham, 1984). The parenchymatous thallus and more or less circular shape of certain species of Coleochaete (e.g., C. scutata, C orbicularis; cf. Graham, 1982) are consistent with forms postulated for primitive land plants (Niklas, 1992). Such a "dorsiventral bifacial" thalloid structure is considered probable in the ancestry of land plants, according to some theories of land-plant origin (cf. Sattler, 1998: 784). While establishing an essential bipolarity in development (Haberlandt, 1914; Smith, 1938; Wardlaw, 1952), portions of the gametophytes of liverworts and some vascular plants (Equisetum. lycopods, certain terns) retain a similar pattern of parenchymatous growth (cf. Bold et al., 1987). Graham (1982) mentioned that the branching pattern of one species of Coleochaete in particular, C. soluta, suggests a possible "pathway" to land-plant patterns. Features of morphology, life cycle, cytology, ultrastructure, and biochemistry have combined to provide a focused viewpoint on the possible significance of Coleochaete. and other advanced charophytes, in phylogenetic interpretation. In understanding Coleochaete as possibly representative of land-plant progenitors, illuminating is the work of Marchant and Pickett-Heaps (1973) and Pickett-Heaps (1975, 1976) on cell division (including cell-plate formation), indicating a land-plant pattern of cell division in Coleochaete. The parenchymatous (tissue-like) thallus of some species of Coleochaete has struck certain workers (e.g., Bower, 1908) as being similar to thalli of simple embryophytes (e.g., thallose liverworts). Comparing species of

Coleochaete, a transition from filamentous to parenchymatous may be outlined (Graham, 1982, 1984), suggestive of a conversion of algal thallus to a thallus type possibly suitable for land existence. The thallus of Coleochaete is gamete producing (i.e., is a gametophyte). The apically biflagellate sperm of Coleochaete, formed in small but distinct antheridial cells, are consistent with sperm of land plants. A single-celled oogonium (not a multicellular archegonium, as found in embryophytes) surrounds the single egg cell; however, the nonmotile female gamete, and oogamous reproduction, are similar to embryophytes. Unlike most algae, the zygote of Coleochaete remains attached to the gametophyte, becoming surrounded by a layer of protective cells (of gametophytic origin). These cells surrounding the enlarging zygote (see the discussion of "spermocarp" in Smith, 1950) may develop invaginations indicative of nutrient transfer, as in the archegonial venter cells of lower embryophytes (cf. Graham & Wilcox, 1983; Niklas, 1997); such invaginated, "placental" cells (cf. Graham & Wilcox, 1983) may provide evidence of archegonial origins. The zygote divides initially by meiosis, and a small mass of biflagellate zoospores is produced (Bold & Wynne, 1978, 1985). In the original terminology of Bold (1957), the life cycle of Coleochaete is "haplobiontichaploid," the zygote being the only diploid stage; meiosis is, thus, zygotic. As discussed, we may refer to the life cycle of Coleochaete as, simply, "zygotic" (South & Whittick, 1987). If it is convincing that

Coleoehaete is similar to the algal ancestor of primitive embryophytes (cf. Graham, 1984, 1993), and if Coleoehaete and other advanced charophytes (e.g., Nitella, Chara) have only a zygotic type of life cycle (are only gametophytes), then consideration should be given to how this rather simple type of life cycle could have been modified into that of a land plant with a diplobiontic life cycle and sporic meiosis. In this consideration, it is the putative beginning stages of sporophyte development that require initial and primary attention, not all the subsequent (and also important, of course) land-plant adaptations, such as rhizoids, stomata, cuticles, nonflagellated, aerial spores, distinct organs, and, eventually, vascular tissue. Bower (1908) provided an answer (in his antithetic theory) for such sporophytic beginnings when he suggested that a delay in zygotic meiosis, with mitotic divisions of the zygote added to the life cycle (to produce a mass of cells), just prior to the occurrence (or potential occurrence) of meiosis, is primarily what would be necessary to add or intercalate a sporophyte into the life cycle. Without a great deal of morphological modification, thus, a multicellular structure (a sporophyte produced by zygotic, mitotic divisions) could be "interpolated" (Bower, 1935) in the life cycle and would presumably be retained on the gametophyte (cf. Scagel et al., 1984) as, for example, the zygote of Coleochaete is observed to be (no sporophyte, however, is developed in Coleochaete itself).

There is no supposition, or really even viable possibility, of a preexisting sporophyte in Bower's (1908, 1935) antithetic (interpolation) theory of origin of alternating generations; nor, for that matter, would such be expected based on careful scrutiny of the life cycle of Coleoehaete and other advanced charophytes (Chara, Nitella, etc.). As has been emphasized, advanced charophytes do not exhibit alternating generations; they possess only the gametophyte stage (no sporophyte is present). Thus, as Bower suggested, the sporophyte stage must have been something subsequently added to the life cycle, as an adaptation to a land-based existence. If this is so, the land-plant sporophyte is to be viewed as a structure "different" from the sporophytes of any algae. Graham (1984) made a case for the antithetic theory but, as discussed, later vacillated to an extent (1993) in the direction of the homologous theory--perhaps in response to paleobotanical evidence of a similarity of some early vascular plant gametophytes to sporophytes (see the discussion in section VI.G). The total paleobotancial evidence, though, as previously discussed, does not support either theory of alternation of generations conclusively; put another way, the existing evidence could be argued to support both theories more or less equally. The soundest approach, perhaps, is to appreciate and understand the extensive evidence available for advanced charophyte--land-plant relationships and then to examine carefully the life cycles of these charophytes for the potential evolutionary insights they may bring (i.e., into the mechanism of origin of the land-plant sporophyte). From the understanding of morphological possibilities afforded by such life cycles, we may pursue the most logical and parsimonious path to the probable origin of a land-plant sporophyte. Only the antithetic theory (of sporophyte origin), not the homologous theory, is actually tenable given the possibilities offered by the life cycles of Nitella, Chara, and Coleochaete (as representative of forms ancestral to land plants). We also note that not only living but also fossil charophytes (of. Taylor & Taylor, 1993) show no evidence of alternating generations (do not exhibit, or left no evidence of, a sporophyte stage). It is, thus, likely that algal ancestors of primitive embryophytes possessed only the gametophyte stage in the life cycle. The first (probably antithetically generated) sporophytes were, in all likelihood, "attempted" in amphibious habitats. Over time, intermittent periods of drying probably selected for the gene mutations and recombinations involved in incipient sporophyte development (Campbell et al., 1999), including the adaptation of desiccation-resistant, nonmotile spores. In the subsequent colonization of land by plants, a generally upgrade development (elaboration) of the sporophyte (by progressive sterilization of sporogenous tissues and subsequent diversification of vegetative tissue produced) occurred, in what were, often perhaps, increasingly drier environments. The sporophyte and gametophyte of land plants were thus cast upon different, though intimately related, courses (Niklas, 1997). Considering a possible ancestral form, perhaps represented by Coleochaete, loss of spore motility (flagellar reduction and loss) and development of a protective spore wall (with sporopollenin) probably occurred quite early in the process of land-plant adaptation (cf. Campbell et al., 1999). In the case of Chara and Nitella, these charophytic algae produce only gametes (do not produce spores); hence, spore flagellar loss need not even be contemplated in the case of these two advanced charophytes; in others words, it is possible that earliest land-plant spores were never flagellated. **OTHER CHAROPHYTES**. Questions remain as to which charophycean algae (e.g., Coleochaete, Klebormidium, Nitella. Chara. etc.) are actually the closest, genetically, to bryophytes and other land plants (e.g., lycopods, ferns). Some mildly conflicting results are apparent in recent literature, in some cases related, perhaps, to how well the gene trees are "resolved." Regardless of the explanation, small differences in alignment of charophycean taxa are to be found. In Katana et al. (2001), based on nuclear SSU rDNA sequences, the placement of Coleochaete and Klebsormidium is somewhat closer to primitive land plants than is that of Nitella (and Chara); some of their results from chloroplast SSU rRNA genes, in fact, place Klebsormidium closer to land plants than even Coleochaete (echoed in the maximum likelihood tree based on combined data). On the other hand, the work of Nakayama et al. (1998), utilizing nuclear-encoded SSU rRNA sequences, illustrates a nice "bootstrap resolution," with Chara and Nitella more closely connected to land plants than are Coleochaete or Klebsormidium. However, there seems to be little doubt in these types of studies that charophytes (generally) are the group of algae representative of those leading to land plants (cf. Kranz et al., 1995). Although it may eventually be determined which charophyte is "closest" to primitive land plants, in terms of molecular-genetic data, we must bear in mind that we are looking, in all these forms, at extant plants (as representatives of ancestral forms), not at the actual ancestors of land plants. As Campbell et al. (1999) pointed out, modern land plants and modern charophytes both probably evolved from a common ancestor. It is possible that this ancestor had a combination of traits that we see in modern charophyte genera; or, it may have differed, to an extent, from all of them. Given the morphology of marchantioid liverworts, Coleochaete may be the most plausible morphological counterpart of this ancestor. However, Coleochaete has flagellated spores. Nitella and Chara, as discussed, do not produce spores and are compelling to consider in a putative antithetic development of the land-plant sporophyte; spores of primitive land plants show no evidence of flagellation, or even residual flagellation. Also, the multicellular sex organs of Chara and Nitella are suggestive of land-plant gametangia (cf. Bold & Wynne, 1985; Bold et al., 1987). An interesting phylogenetic diagram is in Lee (1999: 186), which infers that Coleochaete may be more along the path to liverworts and hornworts, than to mosses--Nitella and Chara being more aligned with mosses and vascular land plants. This diagram is consistent with Niklas's (1997) diagram and view of mosses and tracheophytes as sharing a "last common ancestor." Lee's (1999) conception is based in part on the work of Okuda and Brown (1992), showing a close relationship between the cellulose-synthesizing complex of Coleochaete scutata and that of hornworts, for example, but not those of mosses and tracheophytes--the cellulose-synthesizing complexes of mosses and tracheophytes being more similar to such complexes in Nitella and Chara. Lee (1999) also cited McCourt's (1995) analysis of a compilation of molecular-genetic results (e.g., small and large subunit rRNA sequences and the corresponding, encoding rDNA) that indicated a more direct relationship of embryophytes (which, not specified) with the Charales (e.g., Chara, Nitella) than with Coleochaete, Klebsormidiales, or the Zygnematales. This close relationship of members of the Charales (several genera considered) and land plants was supported by further molecular-phylogenetic analyses (Karol et al., 2001). Thus, it is questionable whether, among charophytes s.1., Coleochaete is genetically as close to some groups of land plants as are characeans such as Chara, Nitella, and Tolypella. Graham and Wilcox (2000), however, maintained the position of a close relationship of the Coleochaetales with Embryophyta. Whatever the precise answer, the life cycles, morphology, and biochemistry of charophytes (s.1.) should be examined for clues to land origins. It seems reasonably certain that

the origin of land plants occurred at fresh (at most, brackish) water--land interfaces, since it is very doubtful that even fossil charophytes were marine organisms (cf. Taylor & Taylor, 1993). **Conclusions :**
A review of historical and recent opinions concerning alternation of generations in land plants has led to the conclusion that there still has been no clear decision (i.e., approaching unanimity) as to which theory of land-plant sporophyte origin to accept, the homologous theory or the antithetic theory. The crux of the issue has centered on the exact mode of origin of the structure that was to eventually become the terrestrial sporophyte. The conclusions of the present article, as to land-plant sporophyte beginnings, are based on philosophical-analytic (logistic) considerations and on a corpus of evidence that has grown considerably over the past several decades; of particular interest is evidence bearing directly upon which group of algae is the most closely related to embryophytes. Logistic (essentially a priori) assessments concern, specifically, questions of the feasibility of sporophyte origin by two (or more) different alleged processes. The homologous theory of alternation of generations presents certain problems of logical content. By definition, the homologous theory is based on the idea of homology and the belief in a fundamental similarity, or essential "equality," of gametophyte and sporophyte generations (the sporophyte being considered in this theory as basically a "transformed" gametophyte). This "similarity," in turn, is

based, again almost by definition, on the observation of types of presumed precursor organisms (i.e., types of green algae, represented possibly by Ulva) with isomorphic (morphologically almost identical) gametophytes and sporophytes. The homologous theory (of land-plant sporophyte origin) thus predicts the preexistence of independent sporophytes and gametophytes in the ancestral algal life cycle and accounts for the existence of these alternating generations in embryophytes by a carryover of both generations to a primitive land-plant cycle. There is the further improbable suggestion (at least implied) of the subsequent establishment of dependency (or additional dependency) of this sporophyte (on the gametophyte); how this was supposed to have occurred has not been made clear in the literature. If, in fact, one is going to attempt to invoke preexisting sporophytes (and gametophytes) in an algal lineage leading to embryophytes, a better guess (since land-plant sporophytes are virtually always different in appearance from gametophytes) would, perhaps, be that some type of green alga with distinctly heteromorphic alternation was ancestral. However, no such heteromorphic algal candidates have been clearly suggested, and such "heteromorphism" in ancestry seems at least somewhat contrary to the concept of the fundamental similarity of generations so strongly emphasized in the homologous (transformation) theory. In any case, no specific mechanism has been proposed for the establishment of sporophyte dependency on the gametophyte, in accounts of the homologous theory, other than the following: An intercalative ontogenetic mechanism would seem to be the only plausible explanation (i.e., retention of the zygote on the gametophyte, the zygote thereupon developing in situ into an attached sporophyte) for the origin of a sporophyte that is completely or largely dependent on the gametophyte and dissimilar in form from the gametophyte. If so, then, by theory reduction, is it not the case that the homologous theory defaults at least in part to the theory with which it has been for so long in competition; that is, the antithetic (interpolation) theory? A further problem with the homologous theory includes the presumption of (at least the likelihood of) separate origins of the sporophyte in bryophytes (s.1.) and vascular plants, both presumably taking place in the same or essentially the same environments. These environments were generally marshy, at least with abundant moisture for migration of the flagellated sperm produced by gametophytes; but intervals of drying probably occurred commonly, no doubt promoting adaptations leading to land-plant development. In any event, the point is that these early "amphibious" environments were similar! So, if logic is invoked, why expect two different patterns of sporophyte development (bryophytic and tracheophytic) to develop, in concurrence, in virtually identical environments? Also problematical in the homologous theory is that both upgrade and downgrade series of sporophyte development were "required" according to the tenets of this theory, even within one group of plants (such as the liverworts).

The antithetic theory does not presuppose the existence of a sporophyte in the initial land-plant ancestral life cycle; only the gametophyte of an alga (like *Chara*, for example, which is only a gametophyte) need be preexistent (i.e., be present in the land-plant ancestor). This antithetic (interpolation) theory suggests that the development of a land-plant sporophyte occurred in situ, specifically in response to an increasingly terrestrial habitat, as a "novel" innovation in land-plant existence. Suited to sounder logic than is the homologous theory, a definite ontogenetic mechanism for the antithetic theory is proposed; that is, a delay in meiosis by the zygote, during which a mass of sporogenous (or potentially sporogenous) tissue is developed (by zygotic mitosis). In this way, a small sporophyte, attached to the gametophyte, may be rather readily intercalated into the life cycle (of what was formerly primarily a gametophytic life cycle). Furthermore, independent origins of sporophytes in bryophytes and vascular plants were not necessary (i.e., are not necessary to postulate); and a primarily upgrade evolutionary development of the sporophyte ("progressing" from bryophytes through major groups of vascular plants) is envisioned, leading to eventual sporophyte dominance and independence. Arguments of parsimony lie clearly on the side of the antithetic theory; reversible phenomena on any large scale, at least, are not required. The antithetic theory thus is rather clearly the one considered more plausible given the preponderance of all of the evidence, and logic, discussed in this article. The homologous theory, by contrast, falls short on basic questions, "Was it really feasible?" and "How did it happen?" The homologous theory does not measure up well against the antithetic theory as to the precise mechanism of occurrence; if the ontogenetic mechanism of the homologous theory is in fact the same as the antithetic theory (interpolation by zygotic mitosis), then we are talking basically about the same theory (the only difference in the two theories then being whether the sporophyte originated before or after land occupancy). In addition to questions of logical content of the above theories of land-plant origin, a range of factual information has been reviewed herein, relating (directly or indirectly) to which theory to accept. Much of the previous so-called evidence for the homologous theory does not point clearly to either the homologous or the antithetic theory as correct. This is particularly true, as discussed, of such often hailed points (allegedly supporting the homologous theory) as apogamy/ apospory and the presence of limited chlorophyll in allegedly reduced hepatophyte sporophytes (such as those of Ricciocarpus). On the other hand, such points as sporophyte dependency on the gametophyte in bryophytes and (to a lesser extent) in vascular cryptogams, the occasional reversion of vegetative to sporogenous tissue, and the usually striking dissimilarity of the gametophyte and the sporophyte in the life cycle of a given plant are seemingly more cogent arguments--and these arguments rather plainly suggest an antithetic origin of sporophytes of land plants. Paleobotanical evidence, though interesting and still promising, has not yet offered a definitive verdict on sporophyte origins (i.e., on theory preference). Continued paleobotanical investigation of the very earliest land plants could perhaps eventually provide valuable data and insights. The strongest evidence at present (and the beginnings of resolution of the question of the initiation of alternating generations in land plants) comes to light when we understand which algal group, generally, is most probable as representative of forms involved in embryophyte origin. As has been reviewed rather thoroughly in this manuscript, strong evidence from morphology, cytology (particularly mitosis/cytokinesis and ultrastructure of motile cells), biochemical evidence (e.g., glycolate oxidase), and a variety of molecular-genetic data (often based on rRNA) supports Charophytes, particularly "advanced" forms (Coleochaete. Chara, Nitella, etc.), as the group of algae most related to land plants. Since these advanced charophyceans are fundamentally gametophytic organisms, with simple, haplontic life cycles (and zygotic meiosis)--no sporophyte being present in their life cycles--we should strongly suspect that the sporophyte was developed (in very early land plants originating from charophyte-like predecessors) antithetically, as an addition to the life cycle (by mitosis of a zygote retained on the gametophyte) and in response to newly available terrestrial (at least amphibious) habitats. This being true, the "interpolated" land-plant sporophyte has no palpable connection to the sporophyte per se of any known alga; however, the sporophytes of bryophytes and tracheophytes are evolutionarily related to each other, an idea recently endorsed by a number of authors. An understanding of the life cycle of advanced members of the Charophyta is thus key to selection of the antithetic (interpolation) theory of land sporophyte origin over the homologous (transformation) theory. Although Charophytes have clearly been shown to be the algal group most closely related to land plants, opinions still differ as to exactly which Charophytes are most representative of embryophyte ancestors.