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# Chapter 4
# Ecological and Economic Significance of Bryophytes

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## ABSTRACT

*With climate change and the massive extinction of biodiversity, this chapter seeks to address the ecological and economic significance of bryophytes. The objective of this chapter is to contribute to the general knowledge of this plant group to spur research and interest in conservation efforts. Ecologically, this chapter x-rays their habit, habitat, distribution, ecophysiology, and reproduction. Bryophytes terrestrialization begun several millions of years ago but is currently threatened by climate change and poor conservation efforts. Economically, this chapter highlights the multifarious uses and applications of bryophytes with a view to promoting diversification, sustainable utilization, and innovative application.*

## INTRODUCTION

Bryophytes are spore-producing, non-vascular land plants that exhibit a clear division of their plant body into photosynthetic and storage zones (Lakna, 2017). They are the second largest division of plants after angiosperms but are less known because of their size (Chandra et al., 2017). Members of this plant division include liverworts (Hepaticopsida or Hepaticae), hornworts (Anthocerotopsida or Anthocerotae) and mosses (Bryopsida or Musci). Bryophytes are considered as the amphibians of the plant kingdom because they inhabit amphibious zones. These plant amphibians were once considered an evolutionary failure due to poor knowledge about inter and intraspecific genetic variations (During & van Tooren, 1987). However, this plant group continuously survived on Earth at least 75 million years before the age of the dinosaurs. Bryophytes are found in diverse habitats (albeit seasonal) as groups of individuals with characteristic features (shape and structure) depending on their family, genus or species (Mägdefrau, 1982). Bryophytes have been found in almost all terrestrial habitats as well as forming biological associations with other organisms. They are mostly found growing in moist, shady places, producing phenolic compounds, which deter herbivores (Lakna, 2017). However, they prefer mesic environments

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that are damp, humid and shaded from excessive sunlight. According to Hanson and Rice (2014), they are often the dominant life form at high latitudes and elevations. They lack specialized lignified vascular tissue, xylem and phloem, which are present in higher and vascular plants. More so, vascular plants differ from bryophytes in possessing two types of apical meristem, those of the shoot and root (Graham et al., 2000). Nonetheless, bryophytes are the main primary producers in different ecosystems globally and influence different biogeochemical activities including nutrient cycling and availability. They are critical to understanding early land plant evolution because bryophytes and pteridophytes – are largely recognized as early grades of land plant evolution (Qui & Palmer, 1999). They possess embryos but lack seeds. They exhibit a distinct alternation of generation between the dominant gametophyte stage and the dependent sporophyte stage. The unbranched sporophyte produces spores, which are mostly wind dispersed and depends on the dominant stage for nourishment. Although they are mostly autotrophs, some bryophytes like liverworts do not contain chlorophyll. Hence, they form a symbiotic relationship with food (Lakna, 2017).

The aim of this chapter is to discuss the ecologic and economic significance of this plant group, which have suffered neglect due to poor knowledge and understanding of their relevance.

## BACKGROUND

Renzaglia et al. (2000) established that extant bryophytes were paraphyletic while the results of Nishiyama et al. (2004) supports monophyly for modern bryophytes based on chloroplast phylogeny, which may represent several lineages along the evolutionary path to vascular plants. However, their exact phylogeny remains unresolved, especially with regard to which group of bryophytes (liverworts, mosses or hornworts) represents the earliest form of land plants (Qiu & Palmer, 1999).

Compared to their vascular counterpart, they are rarely collected and characterized. Hence, many taxonomic gaps continue to exist. Although this group of plants is characteristically small and limited in size, they consist of about 20,000 plant species (Levetin & McMahon, 2012). Climate change is also causing a decline in bryophytes species, which is also heightened the neglect of this plant group in research. This extent of this decline can be ascertained through a comparative assessment of older records (Lockhart et al., 2012) i.e. if such records exist. Bryophyte Flora is not present in many biogeographic regions and where they exist, may not be sufficient. However, it is not too late to collect, document and characterizes these plant groups as a way to checkmate future declines. Mölder et al. (2015) opined that the collection of data on bryophyte distribution has been neglected for so long that it has affected their identification, use, and conservation. The objective of the chapter is to contribute to the knowledge of the plant group and to spur research interests on the group.

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## 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 $CO_2$ 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 $CO_2$ 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

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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).

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## BOTANICAL CLASSIFICATION, DESCRIPTION, AND PHYSICAL CHARACTERISTICS

Bryophytes are macroscopic plants and their size varies from a millimetre tall to several millimeters' long strands. The protonema produced from the germinating spore forms one to several buds, each of which can grow to become an 'individual'. The individuals are thus at the very outset part of an assemblage. Bryophyte assemblages are modified by external conditions to provide the characteristics, which can be described as the life form (Mägdefrau, 1982). Their adaptation to a terrestrial mode of life is considered partial because water remains an indispensable part of their life cycle. This contributed to their reference as the amphibians of the plant kingdom.

They lack vascular tissues, true roots, stems, and leaves. Comparative morphology and developmental studies revealed that their meristems are derived from simpler forms but the genetic basis for expressional differences is unknown (Graham et al., 2000).

Their plant body is called the thallus (or thalli), which sometimes appear leafy and is covered by a cutin-like epidermal shield to prevent them from drying up due to water loss. The epidermal shield varies from one species to another as well as from one biogeographic region to another to suit their environmental requirement for survival. The thallus grows prostrate and is attached to a substratum through the hair-like rhizoids. The plant body may be erect in some bryophytes. Their root-like structure is called rhizoid and is mainly used for absorbing substrates and attaching to surfaces. As photosynthetic organisms, bryophytes require water, light, $CO_2$ and other essential chemicals from the environment.

Their multicellular reproductive structures are held in jackets and are still primitive in its water requirement for sexual reproduction. The sperms are often biflagellate while the archegonium houses the female sex organs. The sporogonium is concerned with the production of wind dispensed, non-motile, undifferentiated cutinized homospores, which germinate to give rise to the gametophyte plant directly or indirectly through a protonema. The spores are within the meiospores or gonospores category. The enlarged venter (i.e. the swollen basal region of the archegonium) protects the embryo is called calyptra and it disintegrates as soon as the spores are released.

Asakawa et al. (2013) suggested that bryophytes are taxonomically between algae and pteridophytes. Marchantiophyta. Bryophyte classification has transitioned from morphological based features to a high anatomical examination of very fine morphological detail and cellular structure to molecular-based methods (Australian National Herbarium, 2008). The classification of bryophyte is far from over as many taxonomic revisions are ongoing with immense potentials for new discovery due to advanced technology. The early systems of bryophyte classification is similar to those of other plant groups and are done artificially where grouping was only for convenience based on (observable) evident characters (Asthana, 2006). On this basis, Braun (1864) for the first time introduced the name 'Bryophyta' but at that time Algae, Fungi, Lichen and mosses were also included in this group. Schimper (1879) placed Bryophyta at the level of division and since then it occupies the same rank till date. Eichler (1883) for the first time included two groups Hepaticae and Musci and since then it becomes a tradition to divide Bryophyta into, at least, these two classes. Some bryologists placed liverworts and hornworts (Anthocerotes) in a single class while others placed them into two different classes. Subsequent workers divided the group into three classes: Hepaticae, Anthocerotae and Musci, after raising the order Anthocerotales up to the class level due to many characters which are remarkably different. This system of classification is more natural, placing liverworts, hornworts, and mosses in three different classes: Hepaticae, Anthocerotae, and Musci respectively (Asthana, 2006). Levels of classification above the genus are in such a state of

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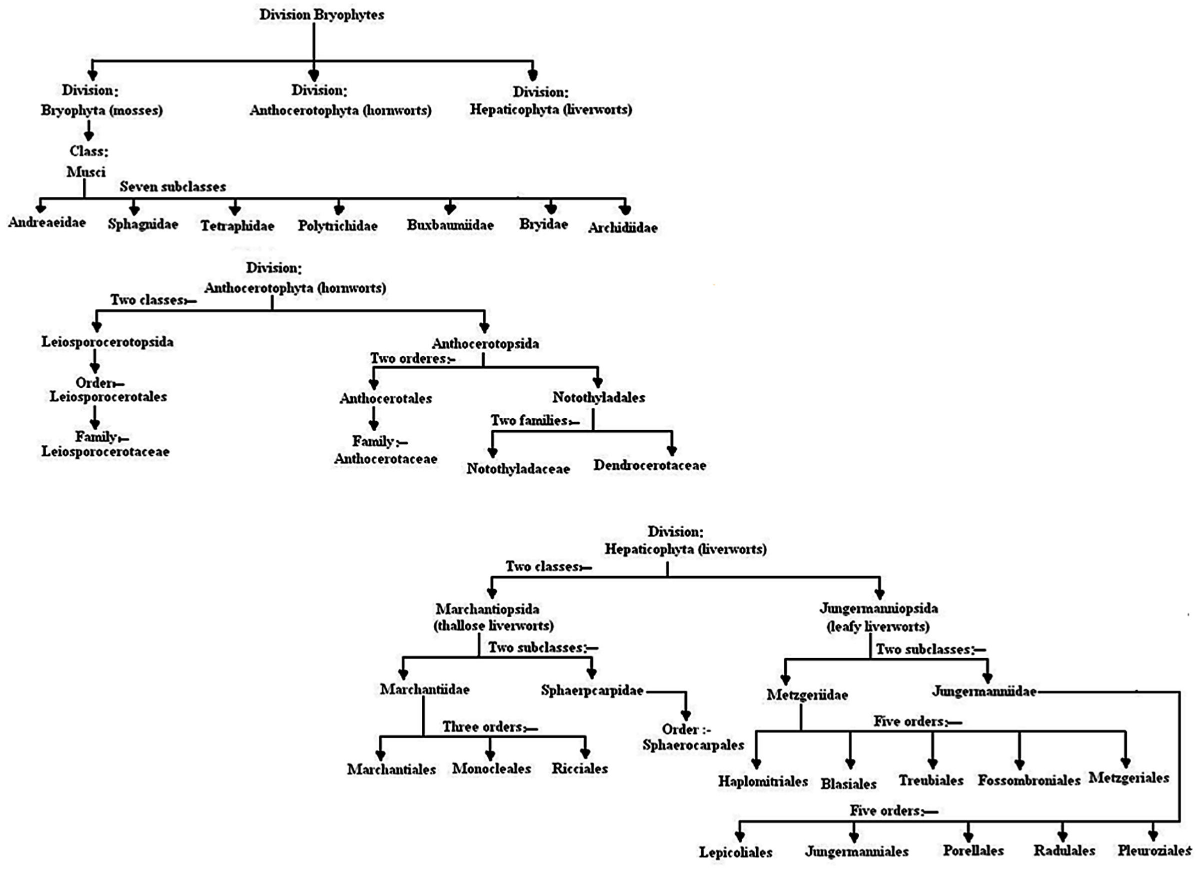
*Figure 1. Bryophyte divisions, their classes, and orders*
*Source: Adapted from Kumar, 2009*




flux that the most useful indicator of the taxonomic extent of the bryophytes can be gained from approximate numbers of genera and species (Miller, 1982). Although renewed interest in bryophyte and training of future bryologist will be handy for meeting this challenge. Liverwort contains metabolites that are valuable for their chemotaxonomic classification (Asakawa et al., 2013).

There are three main taxonomic bryophyte divisions: mosses (Bryophyta), liverworts (Marchantiophyta or Hepatophyta) and hornworts (Anthocerotophyta) with different sub taxonomic representatives (Figure 1, Kumar, 2009).

Mosses have erect or creeping stem-like structures with tiny leaf-like outgrowths, but hornworts and some liverworts have only a flat thallus and no leave-like protrusions. They are generally small but very conspicuous as extensive mats or cushions on walls, rocks and tree trunks, and as pioneer colonists of disturbed habitats.

Specialized tissue in some moss gametophytes includes chlorenchyma, parenchyma, epidermis, water-conducting hydroids, and sugar-conducting leptoids. The sporophyte and gametophyte have very different morphologies (heteromorphic generations) and the sporophyte is usually partly dependent on the gametophyte.

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General characteristics of bryophytes include:

1. Dominant homothallic or heterothallic gametophyte (n) stage that is morphologically different from the dependent sporophytic stage (2n) (i.e. heteromorphic generations).
2. Small photosynthetic plants with no vascular differentiation, cuticle, and stomata.
3. Presence of thalloid, rhizoids, caulalia and phyllids.
4. Female and male reproductive structures are called archegonium and antheridium respectively.
5. Ovum is nonmotile and remains in the archegonium while the spermatozoids are motile.
6. Reproduction requires water or chemical.
7. The sporophytic plant is produced from meiosis and possess a basal foot, elevating seta and a capsule (sporangium).

Division - Bryophyta (Mosses)

1. Bryophyta contains approximately 15,000 species. Common examples are granite mosses, peat mosses, dung mosses, true mosses, *Mnium*, and *Sphagnum*.
2. Mosses are mostly terrestrial and often epiphytic.
3. Dominant gametophyte (n) with erect of the prostrate thallus and spirally arranged, variable shaped phyllids (leaf-like structures) and rhizoids for attachment to the substratum and for absorption. Rhizoid are absent in except *Takakia* and *Sphagnum.*
4. Some family (e.g. Polytrichaceae) possess hydroids (tissue hydrom), for water and mineral conduction and leptoids (tissue leptom) for conducting photosynthates conduction.
5. They have a sporic (diplohaplontic) life cycle, which is oogamous. Most spore germination may be exosporic but also endosporic as in *Andreaea*, *Drummondia*, and *Leucodon.*
6. Mosses have radial symmetry, in that a cut down the long axis of an individual gives two similar halves.
7. Phyllids consist of a single cell layer that is traversed by a midrib and toothed or rounded margins. The phyllids of Mnium may be a single cell thick, but with a midrib with hydroids and leptoids while that of Polytrichum have layers of cells and filamentous strands of photosynthetic cells. The phyllids may be isophyllous or anisophyllous.
8. Hydroids are used for conducting water and leptoids for conducting sugars, which are similar to the xylem and phloem of vascular plants respectively.
9. Short-lived, highly branched and uniserate protonema are formed after spore germination gives rise to caulonema (plastid rich cells for nutrient absorption) and chloronema (chloroplast rich cells for photosynthesis).
10. The Moss stem consists of an epidermal layer, a cortex, and a central strand of thin-walled, hydrolyzed water-conducting cells, called hydroids.
11. The male and female gametangia may be on the same thallus (homothallic or monoecious) or on separate gametophytes (heterothallic or dioecious) with jacketed antheridium and archegonium for protection against desiccation. Spore dispersal is controlled by hygroscopic movement of peristome teeth or spore capsule but members of Splachnaceae e.g. *Tayloria gunnii* (Figure 2) rely on insects (Goffinet et al., 2004; Gallenmüller et al., 2018).

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*Figure 2. Tayloria gunnii ([Wilson] J.H. Willis, Splachnaceae, Splachnales)*
*Source: Australian National Herbarium (2008)*

*Figure 3. New Zealand leafy liverwort Leiomitra lanata ([Hook] R.M. Schust, Trichocoleaceae)*
*Source: Australian National Herbarium (2008)*

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*Figure 4. Hornworts, Phaeoceros carolinianus ([Michx] Prosk., Notothyladaceae)*
*Source: Asakawa et al. (2013)*

## Division - Hepatophyta (Liverworts)

1. Liverworts contain approximately 8000 species. Common ones are *Marchantia*, *Conocephalum,* and *Porella*.
2. Small liver-shaped plants found in diverse environments.
3. Leafy filaments less than 0.02 in (0.5 mm) in diameter, to plants exceeding 8 in (20 cm) in size.
4. Liverworts are made up of flat, lobed thalli.
5. The plant body may be thallose and leafy.
6. Stalked, multicellular, flask-shaped archegonia consisting of an elongated upper portion called neck and lower swollen portion -venter.
7. The neck consists of jacketed rows of cells, which encloses a larger egg cell or the ovum and the smaller ventral canal cell just above the egg.
8. Antheridia consist of rounded structure mass of cells called the androcytes that gives rise to the antherozoids.
9. Using *Leiomitra lanata* (Figure 3) De Lucia et al. (2003) emphasized the contribution of bryophytes to carbon exchange within temperate forests.

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*Table 1. Differences between the three bryophyte divisions*

| Feature | Bryophyta | Hepaticophyta | Anthocerotophyta |
|---|---|---|---|
| Protonema | Filamentous, forming many buds | Globose, forming one bud | Globose, forming one bud |
| Gametophyte | Leafy shoot | Leafy shoot or thallus; either simple or with air chambers | Simple thallus |
| Growth of sporophyte | Apical | Apical | Grows continuously from a basal meristem |
| Arrangement and form of leaf-like structures | Spiral, undivided with a midvein | In three rows; divided into two lobes with no midveins | Not applicable |
| Branches | Developing from stem epidermis | Developing from leaf initial cells or inner stem cells, rarely stem epiderma | Not applicable |
| Gemmae | Common on leaves, stems, rhizoid or protonema | Common on leaves | Not applicable |
| Paraphyses | Usually associated with antheridia and archegonia | Usually lacking but they often have mucilaginous filaments | Not applicable |
| Special organelles | None or simple, small oil bodies | Oil bodies | Single plastids with pyrenoids |
| Water-conducting cells | Present in both generations | Present in a few thalloid forms | Absent |
| Rhizoids | Brown and multicellular | Hyaline and one-celled | Hyaline and one-celled |
| Gametangial position | Apical clusters | Apical clusters (sometimes leaf-like) or on the upper surface of the thallus | Sunken in thallus and scattered |
| Stomates | Present in sporophyte capsule | Absent in both generations | Present in both generations |
| Seta | Photosynthetic and emergent from the gametophyte early in the development | Hyaline, elongating just prior to spore release | Absent |
| Capsule | Fixed sized and complex with an operculum, theca, and neck | Undifferentiated, spherical or elongated (also of fixed size) | Undifferentiated, horn-shaped, growing continuously from a basal meristem |
| Sterile cells in the capsule | Columella | Spirally thickened elaters | Columella and pseudoelaters |
| Calyptra | Ruptures and persist at the apex of seta and capsule. It influences the capsule shape | Ruptures and persist at the apex of seta and capsule. It influences the capsule shape | Not applicable |

Source: Adapted from Kumar (2009); Crandall-Stotler (1996); Gradstein et al. (2001)

## Division – Hornworts

1. Hornworts contains approximately 1,000 species common example is Anthoceros.
2. Irregular lobed or branching thalli with guard cells on the underside.
3. Characteristic long and slender horn-like or needle-like sporangia produced by the sporophyte stage, hence the name hornworts.
4. The sporophyte is separated into a capsule and foot. Seta is absent and sometimes the capsule also. The capsule is cylindrical ‘horn’ like and is not determinate in growth.
5. Dominant gametophyte form is a flat, green-bodied plant with embedded reproductive organs.
6. The rhizoids are unicellular, smooth walled and simple.

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7. The thallus may be compact or spongy with no air chambers and pores.
8. The epidermal cells usually have single, large, plate-like chloroplast with conspicuous pyrenoid bodies.
9. Endothecium forms from the central sterile portion-columella but are sometimes absent as in *Notothylas* species.
10. Gametangia are located inside the thallus.
11. Nitrogen-fixing cyanobacteria may live symbiotically with hornworts.
12. Unlike the typical black or brown spores of *Anthoceros*, members of the genus *Phaeoceros* (Figure 4) have unique yellow horn and spores.

The major distinction between the bryophyte divisions is presented in Table 1.

## 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.

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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).

## 2. Bryophyte Reproduction and Propagation

Bryophyte cultivation may be required for physiological and biochemical research. More so, some bryophyte species add to the beauty of gardens, front and backyards as well as landscapes. Schneider et al. (1967) developed standard substrates for cultivating liverwort, *Marchantia polymorpha* using vermiculite, perlite, glass cloth, nutrient agar, and nutrient solution. The authors added that selected culture conditions and vessels are specially adapted to each substrate. Shaw (1986) also outlined other methods for cultivating some economically important bryophytes.

Mosses can be established easily into diverse environments through transplanting or blending moss fragments in a blender. Fragmentation is common and occurs when they are naturally broken by storm or animals (e.g. *Papillaria flavolimbata*) or artificially when lawn mowing result in fragments been cut. Thus, fragmentation is a form of vegetative reproduction in bryophytes. Many bryophytes contain zones of weakness that may easily fragment. The most preferred site for moss establishment would be those with moss already on it, shady and most areas. Watering is required until moss germinates, which could be approximately five weeks after transplanting fragments. When managing orchards, managers should proactively consider bryophyte community characteristic for the benefit of biodiversity since they are useful indicators of habitat quality and structure (Davies et al., 2007; Whitelaw & Burton, 2015).

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Bryophytes have dioecious and monoecious representatives on the basis of their sexual mode of reproduction. About 70% of liverworts species are dioecious, 55 - 60% of moss species whereas in hornworts monoecy is dominant (Wyatt 1982, 1994; Vanderpoorten & Goffinet, 2009). Out-crossing occurs in dioecious species, hence establishment from spores hardly ever results directly in gametophores occurring close enough in time and space whereas self-fertilization dominates monoecious species (During & van Tooren, 1987; Maciel-Silva & Pôrto, 2014). According to Maciel-Silva & Pôrto (2014), self-fertilization in monoicous bryophytes can be prevented through protandry (*i.e.* through the maturation of antheridia before the archegonia on the same plant) and protogyny (*i.e.* through the maturation of archegonia before the antheridia). Gamete dispersal distances are also very low. Self-incompatibility has not yet been shown to occur in bryophytes, but several less absolute mechanisms promoting outbreeding have been found, mostly involving temporal separation of the sexes (Wyatt, 1982). Many species that do not possess such specialized propagula show indeterminate growth and branching followed by a gradual falling apart of the ramets (*i.e.* a clonal offshoot and can be called genets) (During & van Tooren, 1987).

Bryophytes lack the complexities associated with vascular plant reproduction. Reproduction occurs through spores borne on the gametophytes often as a 'headdress'. These spores require water for formation (for the movement of sperms to fertilize the eggs) and wind for dispersal. Spore capsules (and sometimes a stalk called seta) are produced after the sperm has fertilized the eggs. Fertilization of gametes forms the gametophyte with the spore capsules called sporophyte. Gametophytes may bear propagules on the rhizoids, on short specialized rhizoids on the stem, on leaf lamina or Costa, on leaf tips, even on specialized 'splash-cup' Gemma heads as in *Tetraphis pellucida* (During & van Tooren, 1987).

Generally, bryophytes can reproduce asexually when sporophytes release spores and sexually when gametes fuse to form a zygote. The latter involves the mixing of the genes of two independent parents while in the former, there is no such mixing and each new plant is derived from just one parent plant. The gametophytes of mosses and leafy liverworts are the stems and leaves while in hornworts and thallose liverworts, it is the flattish sheet (Australia National Botanical Garden, 2012). These are responsible for the production of gametes. The spores are antheridia (male organ *i.e.* produces sperm) and archegonia (female organ *i.e.* produces eggs), which appear like umbrellas on the gametophytic plant in *Marchantia polymorpha*. Spores germinate to give rise to the gametophyte.

Frey & Kurschner (2011) suggested that asexual reproduction in bryophyte occur:

1. Dioeciously through regeneration from specialized caducous organs or by the production of specialized propagules like gemmae and protonemal cells.
2. By the fragmentation of their plant body.
3. Clonally (i.e. self-cloning due to the endogenous mechanism or forced cloning due to external influences). That results in ramets (independent daughter plants also called merriments).

Asexual reproduction is also capable of occurring through structures like gemmae, propagules, and regeneration of fragments that are able to form new plants (Maciel-Silva & Pôrto, 2014). The process of germination begins in the capsule, mother cells of spores (sporocytes), which split meiotically into tetrads of haploid spores. These are dispersed and germinate into a filamentous phase called protonema with chloronema, caulonema, and Rhizoids cells. In leafy liverworts, the gametophyte possesses rhizoids, caulid (stem), and phyllids (leaves). Sexual reproduction in bryophytes involves the release of motile male gametes into the environment and requires successful navigation of these naked cells from the male to the female sex organs via an external water source (Shaw & Enzaglia, 2004).

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*Figure 5. The lifecycle of a typical moss*
*Source: Krempels (1996)*

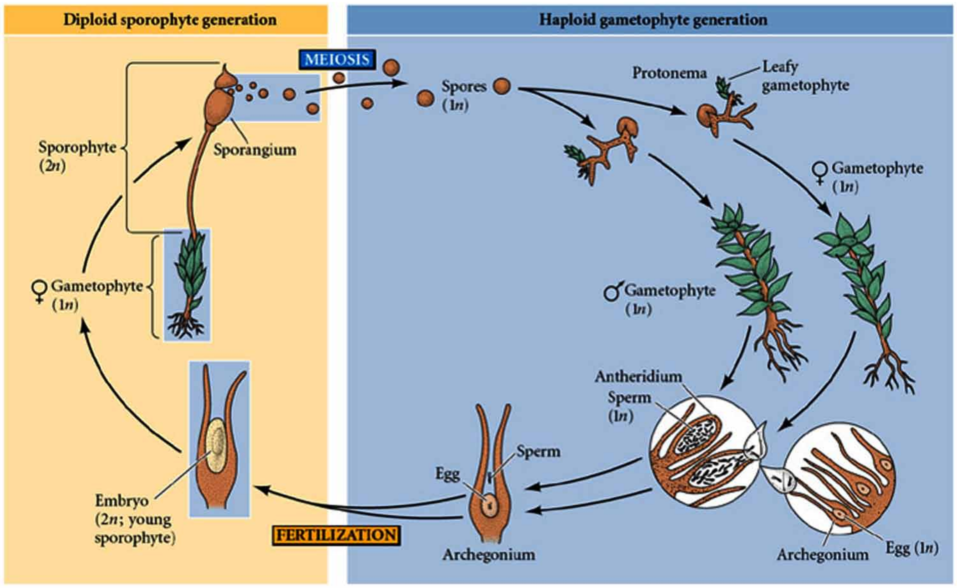


*Figure 6. The lifecycle of Marchantia (Liverworts)*
*Source: Krempels (1996)*

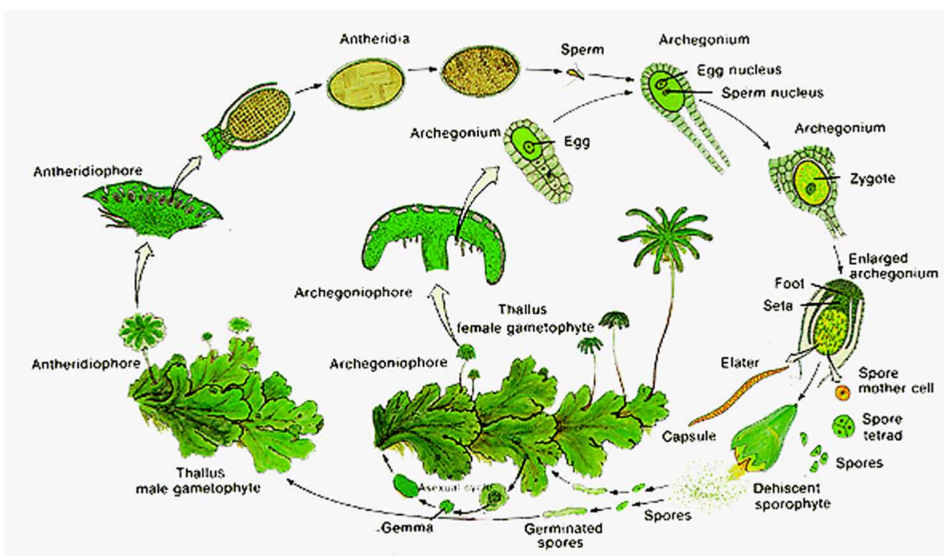

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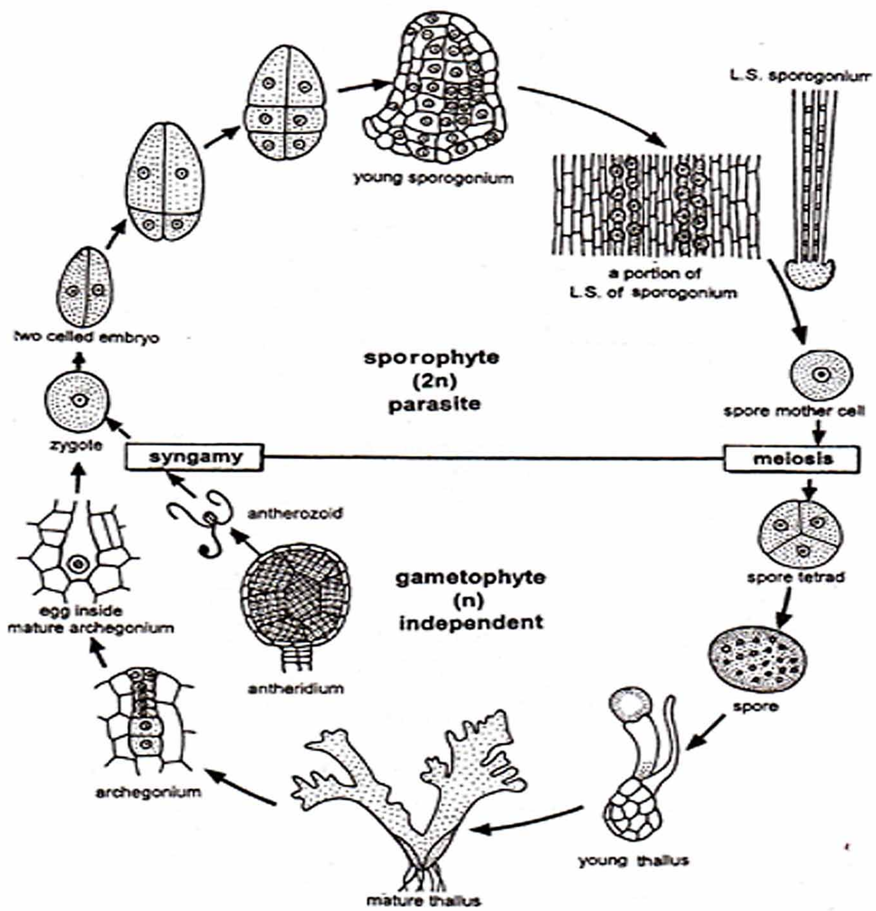
*Figure 7. The lifecycle of Anthocero (Hornwort)*




Spore output per sporophyte is in the range of 50,000-600,000 in many moss species with small spore size whereas, in mosses with somewhat larger spores, numbers are in the range 5,000-10,000 per sporophyte. Among hepatics (liverworts), spore output is low in many Marchantiales (Longton & Schuster, 1983; During & van Tooren, 1987). Although bryophytes maintain their populations mostly through asexual reproduction, sexual reproduction result in the production of numerous spores but their subsequent establishments may be difficult (During & van Tooren, 1987). Asexual reproduction enables bryophytes propagules to rapidly colonize an area following disturbance, thereby reducing the chances of extinction. Regarding genetic and population variations, the remarkable rapid fine-scale dynamics found in many bryophyte populations contribute ole in the maintenance and determination of community diversity (During & van Tooren, 1987).

A typical moss sporophyte is produced by the fusion of gametes. The terminal disk-shaped antheridium in mosses consists of a spore-containing capsule on a stalk (seta, may be absent), a sterile jacket, and spermatogenic tissue. Through meiosis, the sporophyte produces haploid spores, which develops into the next generation of gametophyte plants. By mitotic division of haploid spermatogenic tissues, the flagellated chemotactic sperms are developed and at the right time swim through water to the eggs

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in the archegonium. The antheridia also have filamentous cells called paraphyses, which swell up with water and squeeze the antheridia to help expel sperm. The peristome becomes visible with spaces through which the spores escape. The composite cells produced by mitosis in the archegonium consists of a stalk, a venter surrounds the egg, and a long neck filled with canal cells. The neck disintegrates while the ventral canal cells provide chemicals involved in sperm chemotaxis to fuse with the egg. After fusion of egg and sperm zygote is formed which diploid.

Gametophyte plant is produced by the germination of a haploid spore. As a spore germinates, it produces a mostly ephemeral branched filament of photosynthetic cells called a protonema. This branching filament is similar to a green alga. The protonema produces a caulonema filament which can produce either a leafy moss gametophyte or a hard, dry bulbil for asexual reproduction. The moss gametophyte produces male and female gametangia. The typical moss lifecycle is presented in Figure 5.

In liverworts, spores from the sporophyte develop into gametes (*i.e.* longer gametophyte stage) that are later fertilized to produce a zygote and then the sporophyte. The antheridiophores (male stalk) contain the sperm-generating antheridia while the archegoniophores (female stalk) contain the ovum-bearing archegonia. The antheridia release sperm, which swims up the archegoniophore and into the archegonium. Fertilization occurs in the archegonium, and the resulting zygote then grows into a sporophyte on the archegoniophore. The sporophyte grows a single sporangium, within which meiosis takes place to produce spores that will be released into the environment. The release spore germinates to produce the gametophyte and the cycle begins all over again (Figure 6).

Hornworts begin its lifecycle as a haploid spore with a germ tube. The germ tube divides to form the thalloid, which becomes the gametophyte (Figure 7).

## 3. Management of Bryophytes

Bryophyte control may be required after heavy infestations on the soil-substrate surface may cause irrigation water and liquid fertilizers to leach (Svenson, 1997; 1998; Svenson et al., 1997). Therefore, more water, fertilizers, and pesticides may be required. Regulating bryophyte population reduces the potential for environmental pollution due to the use of excess polluting chemicals.

More so, liverworts may provide refuge for fungus gnats, which are proven to damage roots and spread crop diseases. Liverworts cannot be effectively controlled chemically by using conventional herbicides except by using a cinnamon oil extract treatment (with a cinnamic aldehyde as the active ingredient, which must be used with caution because it is generally phytotoxic) and Mogeton (active ingredient: quinoclamine). These chemicals are not effective against moss. Meadowfoam seed meal (left over after the crop's oil has been extracted) can be used for effective liverwort and moss control. The seed meal is a natural product and may provide less environmental risk. Another product that is routinely effective is vinegar (acetic acid). The cost to remove bryophytes by hand is extremely time-consuming. Some fungus that grows on liverworts is currently been tested for use as a potential biocontrol agent. In the case of bryophyte infestation;

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1. Do not overwater. Rather allow the surface of the growing medium to dry between irrigation cycles or switch to sub-irrigation systems.
2. Do not apply excess nitrogen or phosphorus fertilizers.
3. Surface applications of slow-release iron sulphate and/or copper sulphate help prevent liverwort infestations. Zinc sulphate or zinc chloride fertilizers can help control liverworts, but the amount applied to kill the liverwort is often toxic to nursery crops.
4. Liverworts generally die if the crop's canopy will provide sufficient shade to the surface of the growing medium.

## 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 double-glazed windows, balls, and dolls (Thomas & Jackson 1985; Pant & Tewari 1990; Glime, 2017b). *Neckera complanata*, a species that has been used in bedding in Europe while Sphagnum is used in America as an absorbent to serves as an insulator to keep warm, dry or cool (Glime, 2017b). Sphagnum has been implicated in making clothes, soap, and ointment for dressing wounds. A number of mosses make ideal lamp wicks including *Dicranum elongatum*, *Racomitrium lanuginosum,* and *Sphagnum* (Glime, 2017b). Tribal people use these plants to cure various ailments in their daily lives including to cure hepatic 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-

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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).

## CONCLUSION

Due to their sensitivity to environmental change, bryophytes have been implicated in many studies where they are used as indicator species to monitor climate change. Only a few studies have considered the impacts of climate change on bryophytes despite obvious vulnerabilities to their diversity and the ecosystem. Global climate modellers are realizing that massive peatlands make substantial contributions to the modification of global temperatures and water movement. In future, the exploration of bryophyte ecophysiology in the changing climatic conditions will be required to provide new information that will assist bryophyte conservation. The reproductive biology of bryophyte is a relatively unexplored area with many species and ecosystems unexplored especially in the tropics as well as studies on their natural history that will identify and characterize interesting systems for research.

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Bryophytes diversity and distribution are related to environmental factors, which is helpful in understanding the ecological niche of various bryophytes. Nature reserve, especially in the humid environment, is an important area of biodiversity conservation and is a vital ecological region that preserves a large number of ground bryophytes. IUCN distribution criteria such as population reduction, the geographic range within occurrence area, declining population size, population restrictions and quantitative analysis are critical for the evaluation of bryophyte threatened status with a view to promoting their conservation. A major advantage of working on bryophytes compared to many other groups of plants is the ease of preparing and examining herbarium specimens. Apart from ethnomedicinal uses, some bryophytes possess against different cancer cell lines and this property of bryophytes needs to be more focused on the future. There is a need to investigate how bryophyte species respond to climate change. Since their diversity and distribution is threatened by global climate variabilities.

In conclusion, several unexplored topics with regards to understanding salient aspects of bryophytes. The group will benefit from extended surveys and collection. This group continues to adapt to changing global conditions and may hold the key to future survival on planet earth.

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