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ARTICLE

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Exploring the intricacies of bryophyte reproduction: life cycles, sexual dynamics, and reproductive strategies

Adaíses S. Maciel-Silva[1], **Kátia C. Pôrto**[2]

1 Laboratório de Sistemática Vegetal, seção Briófitas, Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Brazil
2 Laboratório de Briófitas, Departamento de Botânica, Centro de Ciências Biológicas, Universidade Federal de Pernambuco, Brazil
*Corresponding author: adaisesmaciel@ufmg.br
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Abstract

This review presents a comprehensive examination of bryophyte reproductive biology, an area pivotal to understanding these unique land plants. We delve into the morphological intricacies of both sexual and asexual reproductive structures in bryophytes, underscoring their integral roles in the life cycles of these organisms. Our discussion encompasses the diverse sexual systems observed in bryophytes, ranging from monoicous to dioicous configurations, and investigates the patterns and ecological consequences of sex ratios, particularly the commonly observed female-biased ratios. In detailing reproductive strategies, the review evaluates the reproductive investments, efforts, and costs associated with these ratios in various species. Such analysis provides insights into the evolutionary and ecological dynamics shaping bryophyte populations. We also highlight the primary types of asexual reproductive structures, such as gemmae and leafy propagula, providing examples that illustrate their importance in bryophyte life strategies, especially in terms of dispersal capabilities and habitat colonization. Furthermore, the review juxtaposes the advantages and disadvantages of sexual and asexual reproduction, considering their implications for the distribution, genetic diversity, and conservation of bryophyte species. This comparison sheds light on the adaptive significance of these reproductive modes in response to environmental pressures and habitat variability. To aid in the understanding of specialized terms and concepts, the review includes a brief glossary of key terminology used in bryophyte reproductive biology. This addition makes the paper accessible to a diverse audience, ranging from academic researchers to students and enthusiasts in the field of botany. Overall, this review offers an insightful and thorough exploration of the reproductive strategies of bryophytes, enhancing our understanding of their complex life cycles and the implications for their survival and proliferation in varied ecosystems.

Keywords:liverworts, hornworts, mosses, sexual reproduction, asexual reproduction, plant life cycles, plant life strategies.

Introduction

Bryophytes, comprising three distinct plant lineages - liverworts, mosses, and hornworts - are characterized by life cycles that alternate between haploid and diploid generations, featuring dominant and branched gametophytes. These groups exhibit a notable diversity in both vegetative and reproductive morphologies, surpassing those observed in the gametophytes of other land plants (Vanderpoorten & Goffinet, 2009; Gerrienne & Gonez, 2011).

Their success in colonizing diverse habitats, including tropical and temperate forests, tundra, peat bogs, deserts, and savannas, is attributed to a range of morpho-physiological adaptations such as poikilohydry and desiccation tolerance (Ligrone et al., 2000; Proctor et al., 2007; Renzaglia et al., 2007; Crandall-Stotler et al., 2009; Goffinet et al., 2009; Renzaglia et al., 2009; Goffinet & Buck, 2012). These adaptations, coupled with the structural diversity of their gametophytes and, to a lesser extent, sporophytes, underpin their survival strategies in various environments (Goffinet & Buck, 2012).

Bryophytes demonstrate unique reproductive traits (Maciel-Silva & Pôrto, 2014). For example, the phenomenon of dwarf males, observed in some bryophyte taxa, is exclusive to mosses among land plants and can be either facultative or genetically

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obligatory (Hedenäs & Bisang, 2011; Pichonet & Gradstein, 2012). Une (1985) noted that 2,4-dichlorophenoxyacetic acid stimulates dwarf male formation in isosporous *Macromitrium* species, while anisosporous species produce male gametophytes autonomously. This strategy, whose physiological underpinnings remain largely unknown, effectively shortens fertilization distances in these bryophytes (Rosengren & Cronberg, 2014).

Another intriguing aspect is the occurrence of protonemal neoteny in bryophytes, where a persistent protonema replaces the vegetative gametophyte. This phenomenon manifests in two forms: a rare type with persistent thalloid protonemata in some epiphyllous bryophytes (e.g., *Cololejeunea* and *Radula*) and a more common type with a persistent filamentous protonema found in certain terrestrial mosses and liverworts (Gradstein et al., 2006; Gradstein & Wilson, 2008). Such neoteny is an adaptation for growth in unstable, transient habitats, necessitating rapid maturation and short life cycles.

Despite extensive research, some aspects of bryophyte reproduction remain enigmatic, particularly the physiological and ecological processes underlying observed reproductive patterns. This review revisits key themes in bryology, such as the frequently recorded female bias (Bisang & Hedenäs, 2005; Bisang et al., 2006; Rydgren et al., 2010; contrasted by Alvarenga et al., 2013; Holá et al., 2014), strong field segregation of sexes (Bowker et al., 2000; Stark et al., 2005; Alvarenga et al., 2013), male dwarfism in dioicous mosses (Une, 1985; Hedenäs & Bisang, 2011; Rosengren & Cronberg, 2014), and the trade-offs in male and female reproduction (McLetchie & Puterbaugh, 2000; Bisang et al., 2006; Maciel-Silva et al., 2012; Pereira et al., 2016).

Focusing on their life cycles, reproductive morphologies, sexual parameters, and strategies, along with alternative reproductive paths, this review explores the evolutionary and ecological implications of bryophyte reproductive biology. To assist readers, especially those new to this field, a glossary of reproductive terminology is included.

Life cycles and sexual reproduction in bryophytess

Bryophyte life cycles are marked by unique organizations of life phases and morphologies, despite sharing some steps with other land plants. The gametophyte stage, haploid (n) in nature, is the more enduring generation, typically perennial and photosynthetic, nurturing the comparatively shorter-lived sporophyte (2n) (Longton & Schuster, 1983; Goffinet & Buck, 2012; Glime, 2017a).

Water availability plays a critical role in bryophyte sexual reproduction, similar to lycopods, horsetails, and ferns. The flagellate antherozoids (male gametes) are released into a lipidic matrix and navigate via chemotaxis through a watery film to reach and fertilize the egg within the archegonium (female gametangium) (Paolillo, 1979, 1981; Qiu et al., 2012; Glime, 2017a). This reliance on water for sperm dispersal suggests an adaptation different from that of gymnosperms and angiosperms, which use pollen for fertilization. Yet, studies like those by Cronberg et al. (2006), Cronberg (2012), and Rosenstiel et al. (2012) propose that microarthropod-mediated fertilization in bryophytes, particularly in mosses, might predate animal pollination seen in other plant groups.

Mechanisms to minimize fertilization distances in bryophytes challenge the notion of their limited fertilization efficacy due to motile antherozoids. For instance, mosses with splash cups and liverworts like *Conocephalum conicum* with antheridial disks employ strategies to enhance sperm dispersal (Reynolds, 1980; Paolillo, 1981; Shimamura et al., 2008). Similarly, Marchantia's umbrella-shaped archegoniophores facilitate sperm dispersal over water films with low surface tension, extending the reach of the antherozoids (Nakamura et al., 2018; Pressel & Duckett, 2019.

Post-fertilization, the zygote grows into an embryo sustained by the gametophyte through matrotrophy, a process of nutrient and water transfer (Graham & Wilcox, 2000). This embryo develops into a diploid sporophyte with a single sporangium where spore mother cells undergo meiosis, producing haploid spores. These spores, dispersed by wind, animals, or water, germinate upon finding a suitable substrate, marking the commencement of a new gametophyte generation (Goffinet & Buck, 2012; Glime, 2017a, b; Nehira, 1983; Fig. 1). The spores' germination leads to a protonemal phase, varying in form across different bryophyte groups. While leafy bryophytes, mosses, and leafy liverworts develop into diverse forms of protonema, thallose plants experience a shorter protonemal phase, involving germ cell differentiation

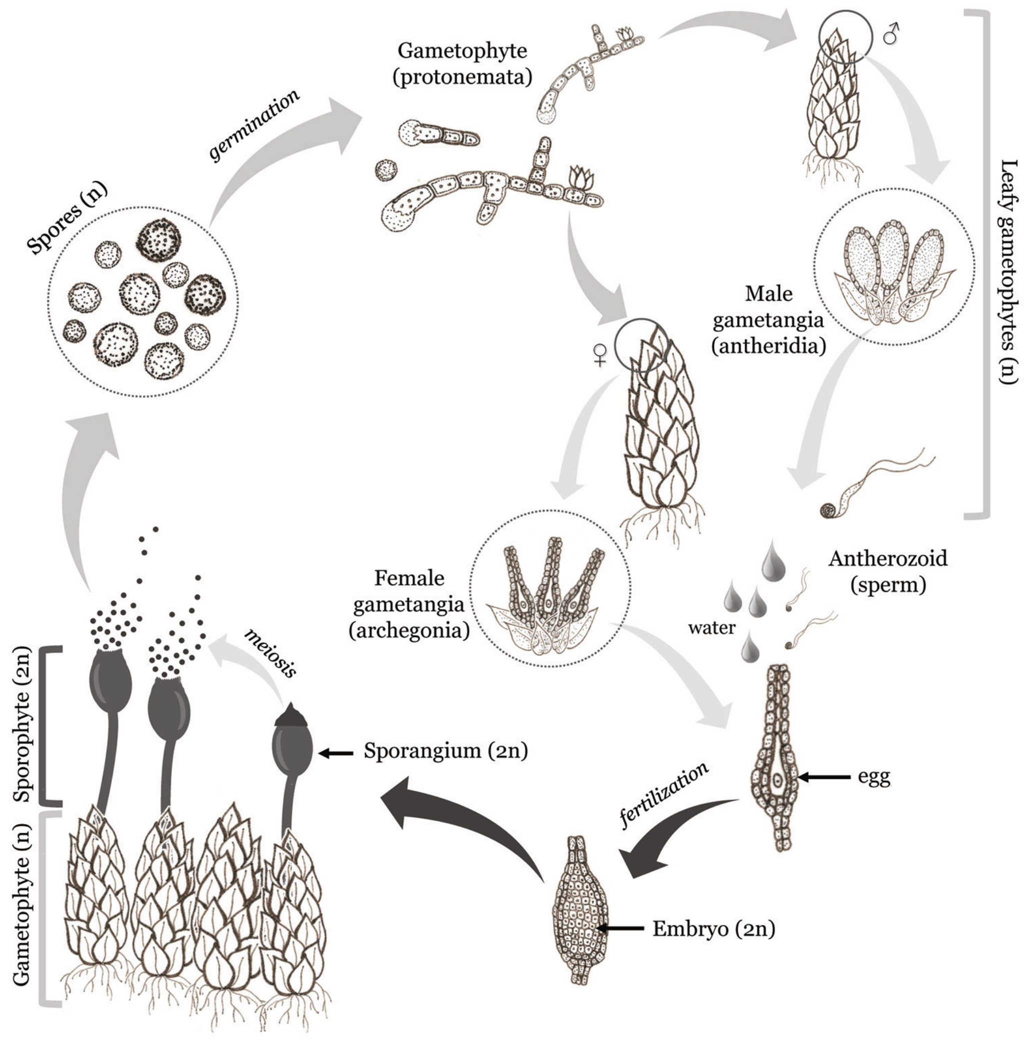

Figure 1: Life cycle of a dioicous moss (gametophytes with separate sexes). Note the gametophyte produces gametes by mitosis. Antheridia release antherozoids that swim toward archegonia, fertilizing egg cells. The sporophyte develops attached to the gametophyte, on which it depends for nutrition. When mature, sporophytes produce spores by meiosis. After dispersal, spores germinate, restarting the life cycle.

(Nehira, 1983). Protonemata can be characterized as filamentous, globular, cylindrical, solid, or discoid structures. In a majority of moss species, particularly those within the Bryopsida and Polytrichopsida classes, protonemata develop into a dense mat of green filaments. Conversely, in most liverwort species, and Sphagnopsida and Andreaeopsida mosses, the protonema transitions into a more thalloid form after undergoing several cell divisions. Moreover, bryophytes can reproduce through alternative methods such as the germination of gemmae and leafy propagula and branching from parent plants.

Variations in sexual reproductive structures

Bryophyte gametangia are differentiated into antheridia (male; Fig 2A) and archegonia (female; Fig 2B). Antheridia produce numerous biflagellate antherozoids, while each archegonium generates a single egg. The antheridia can vary in shape, ranging from globose to rectangular or ovoid, and may possess either short or long stalks (Crandall-Stotler et al. 2009; Goffinet et al. 2009; Renzaglia et al. 2009). Upon maturation, the sterile jacket layer of antheridia absorbs water, swells, and then opens to release both lipids and antherozoids. These antherozoids swim through water to reach a mature, receptive archegonium, which houses the egg cell (Paolillo, 1979; 1981; Glime, 2017a).

The archegonium is typically a flask-shaped structure, usually stalked, with a long neck and a dilated base known as the venter, enclosing the egg (Crandall-Stotler et al. 2009; Goffinet et al. 2009; Renzaglia et al. 2009). As the egg cell matures, the central canal cells of the archegonium disintegrate and turn slimy, facilitating sperm navigation. During this time, chemotactic attractants, predominantly

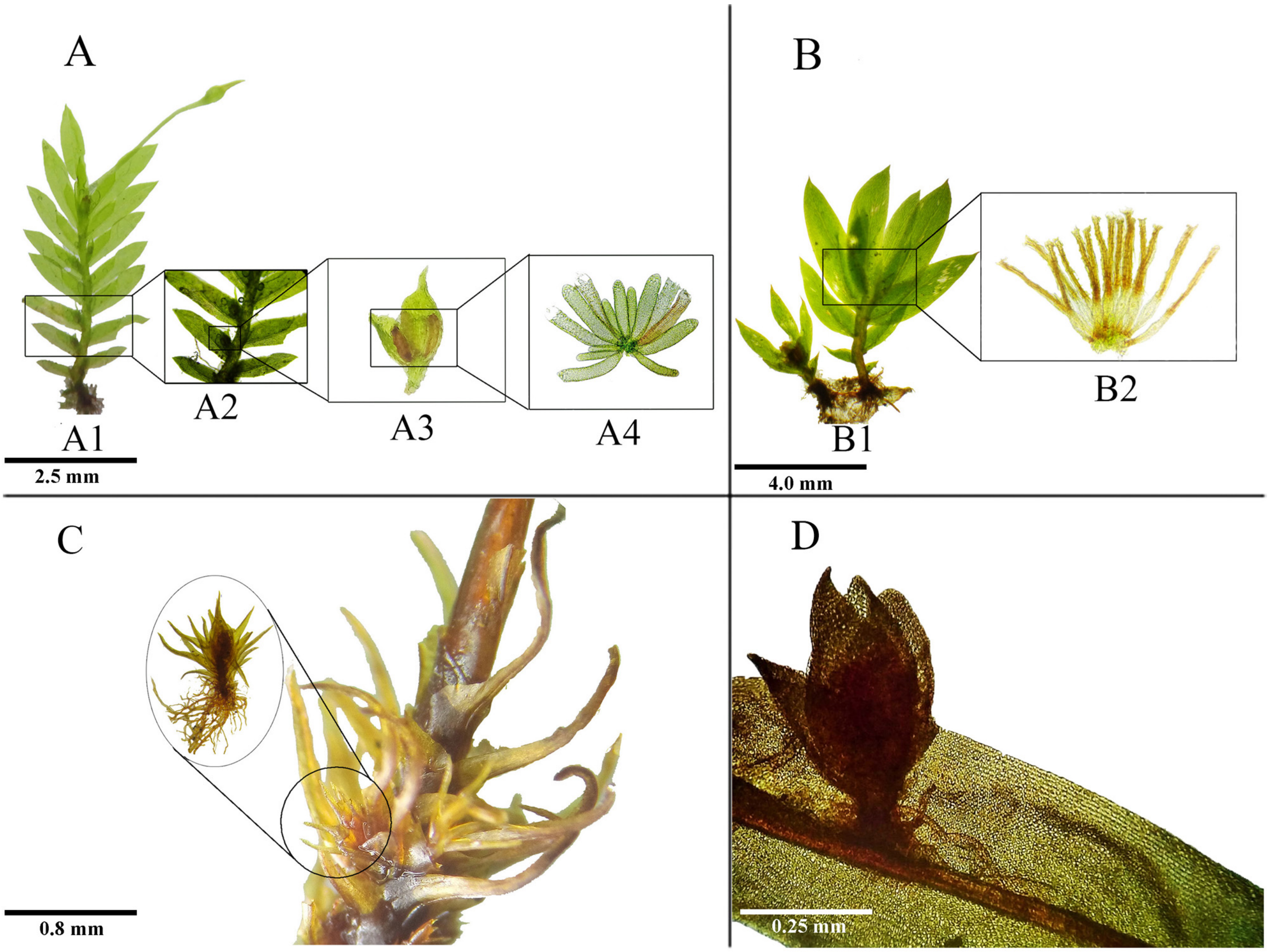

Figure 2: Arrangements of gametangia in bryophytes. A. Gonioautoicous species: *Fissidens submarginatus* Bruch. (A1) sporophytic gametophyte, (A2) perigonia in leaf axils, (A3) perigonia, (A4) antheridia; B. Rhizoautoicous species: *Fissidens scarious* Mitt. (B1) male ramet (right) attached to female ramet (left), (B2) archegonia; C. Pseudoautoicous species: *Holomitrium arboretum* Mitt., dwarf male plant epiphytic on stem of female plant, in detail: dwarf male; D. Phyllodioicous species: *Groutiella apiculata* (Hook.) H.A. Crum & Steere, dwarf male epiphytic on leaf of female plant.

sucrose, are emitted to lure the sperm (Paolillo, 1981; Glime, 2017a).

In leafy bryophytes, gametangia are often encased by modified leaves distinct from the typical vegetative leaves. These clusters of gametangia are termed perigonia or androecia when associated with antheridia and perichaetia or gynoecia with archegonia (Gradstein et al. 2001; Goffinet & Buck 2012). In mosses, paraphyses—hyaline or yellowish sterile filaments—are commonly interspersed among the gametangia, aiding in hydration and protection (Goffinet et al. 2009).

Thalloid bryophytes exhibit diverse arrangements of gametangia: some are borne on specialized branches (e.g., *Marchantia)*, others are dorsally arranged (Pallavicinia), or embedded within the thallus (Riccia, Anthoceros) (Glime, 2017c;d). In complex liverworts, male antheridiophores function as splash-cups to enhance sperm dispersal, while female archegoniophores aid in spore dispersal post-fertilization (Goffinet & Buck 2012).

Bryophyte sporophytes, though nutritionally reliant on the gametophyte, often exhibit photosynthetic activity in their early stages, as observed in hornworts and most mosses (Crandall-Stotler et al. 2009; Goffinet et al. 2009; Renzaglia et al. 2009). These sporophytes consist of a foot, stalk or seta (absent in hornworts), and a single sporangium or capsule. The ontogeny of sporophytes varies among bryophyte lineages. Post-elongation, the young sporophyte's proximal end develops into the foot, penetrating and anchoring within the gametophyte. Subsequent mitotic divisions or cell elongation lead to an elongated stalk elevating the sporangium, which produces spores through meiosis. Transfer cells located at the juncture of the gametophyte and sporophyte play essential roles in the transport of nutrients and water from the gametophyte to the sporophyte (Crandall-Stotler et al. 2009; Goffinet et al. 2009; Renzaglia et al. 2009).

Diversity of sexual systems

Bryophyte species exhibit a remarkable variety of sexual systems, ranging from dioicous systems, where gametophytes produce either male or female gametangia, to monoicous systems with gametophytes bearing both types of gametangia types. In contrast to seed plants, bryophyte species predominantly exhibit unisexual individuals. About 70% of liverwort species are dioicous, this percentage drops slightly in mosses to 55–60%, and to 40% in hornworts (Wyatt, 1982; 1994; Vanderpoorten & Goffinet, 2009; Villarreal & Renner, 2013). This is a stark contrast to angiosperms, where only 6% of species are dioecious (Renner & Ricklefs, 1995).

The need for a unified terminology for sexual systems across all embryophytes was emphasized by Wyatt (1985). However, terms such as monoicous/ dioicous are often preferred in bryological literature over monoecious/dioecious. This distinction is important as in bryophytes, these terms describe the sexuality of the gametophyte, while in other embryophytes, such as seed plants, they refer to the arrangement of unisexual gametophytes on the sporophyte (Allen & Magill, 1987; Maciel-Silva & Pôrto, 2014).

Moreover, in seed plants, gametophytes are always dioicous, and sporophytes are either monoecious or dioecious. "Dioicy" in this context typically refers to homospory and the production of bisexual or unisexual gametophytes from the same sporangium. In contrast, "dioecy" and "monoecy" of sporophytes relate to heterospory and distinct gametophytes in different sporangia (Zander, 1984). For bryophytes, terms like monoecious and dioecious are not applicable since their sporophytes do not bear gametophytes (Allen & Magill, 1987).

Bryophytes showcase multiple gametangia arrangements. Various schemes and diagrams have been proposed to standardize terminologies for similar sexual phenotypes and functional features (Anderson, 1980; Wyatt, 1985; Mishler, 1988; Cruden et al., 1995; Maciel-Silva & Pôrto, 2014). In monoicous bryophytes, gametangia may be intermixed (synoicy), antheridia may encircle archegonia in the same cluster (paroicy), be located on separate branches (cladautoicy), or perigonia might be bud-like and situated below terminal perichaetia (gonioautoicy), or on short branches attached to female shoots (rhizautoicy), resembling two distinct gametophytes (Wyatt, 1985; Mishler, 1988; Maciel-Silva & Pôrto, 2014; Santos et al. 2020).

In strict dioicous bryophytes, male and female plants are independent. Some species exhibit unique dioicous conditions like dwarf males that are epiphytic on female plants (pseudoautoicy; Fig 2C) or even on gametophytic leaves (phyllodioicy; Fig 2D). Heteroicous species show multiple forms of monoicy on the same plant, whereas polyoicous species have both antheridia and archegonia on the same plant or on different plants of the same species (Wyatt, 1985; Mishler, 1988; Maciel-Silva & Pôrto, 2014). The glossary below provides further explanations of these sexual systems with examples from bryophyte species.

Ecological and evolutionary significance of sexual systems

Multiple studies have established connections between the sexual systems of bryophytes and their modes of reproduction, both sexual and asexual (Longton & Schuster, 1983; Longton, 1992; Löbel et al., 2009; Frey & Kürschner, 2010; Maciel-Silva et al., 2012; Peñaloza-Bojacá et al., 2018). A notable phenomenon in dioicous bryophytes is the infrequent production of sporophytes. This rarity may be attributed to factors such as spatial segregation of sexes, absence or scarcity of one sex, suboptimal conditions on the edges of species' distribution ranges, or an ancestral trait in often non-fruiting dioicous taxa (Longton & Schuster, 1983; Longton, 1992; Korpelainen, 1998; Bisang & Hedenäs, 2005; Stark et al., 2005).

Sexual systems in bryophytes are also linked to dispersal strategies, influencing distribution patterns both locally and globally. In managed or disturbed landscapes, dioicous species often struggle to produce sporophytes before habitat alteration (Snäll et al., 2004; Alvarenga et al., 2009). However, Laenen et al. (2016a) observed that monoicous species generally do not exhibit as broad distribution ranges as dioicous species, and dioicous species do not necessarily compensate for low sporophyte production with increased asexual reproduction.

Island floras tend to have a higher representation of species with asexual diaspores compared to continental bryophyte floras (Patiño et al., 2013). The introduction of sexual and/or asexual diaspores to new environments can trigger speciation events, potentially leading to shifts in reproductive strategies. Examples include the prevalence of asexuality among spore-dispersed monoicous species or the transition from dioicy to monoicy, followed by faster diversification (Patiño et al., 2013; Laenen et al., 2016b).

Environmental constraints may limit sporophyte production in many monoicous species (Longton & Schuster, 1983). Conversely, some dioicous species have developed strategies to reduce fertilization distances and increase the likelihood of sporophyte production, such as microarthropod-mediated fertilization and the presence of dwarf males (Cronberg et al., 2006; Cronberg, 2012; Rosengren & Cronberg, 2014).

Dioicous species sometimes fail to produce sporophytes due to the spatial separation of sexes. In such cases, adaptations like pseudoautoicy and dwarf males become crucial for facilitating sexual reproduction and sporophyte production by minimizing fertilization distances (Rosengren & Cronberg, 2014). However, dwarf males in bryophytes are typically more susceptible to microclimatic changes and have shorter lifespans compared to females, leading to fluctuations in male frequencies across different years (Solli et al., 2000; Rosengren & Cronberg, 2014).

Sex ratios and their dynamics

Despite the expectation of a 1:1 male to female spore ratio within a sporangium post-meiosis, dioicous bryophyte populations often exhibit varying and sometimes strongly female-biased sex ratios, a pattern well-established in bryological studies (Stark et al. 1998; Bisang & Hedenäs 2005; Rydgren et al. 2010; Maciel-Silva et al. 2012; Hugonnot et al. 2014; Maciel-Silva et al. 2016; Pôrto et al. 2016; Peñaloza-Bojacá et al. 2018). However, some species exhibit highly heterogeneous sex ratios over spatial and temporal scales, including populations dominated by non-sex-expressing plants or male-biased populations, such as *Crossomitrium patrisae* in the Brazilian Atlantic Forest and Scapania undulata, an aquatic liverwort (Shaw & Gaughan 1993; Oliveira & Pôrto 2002; Alvarenga et al. 2013; Holá et al. 2014).

Several hypotheses have been proposed to explain these biased sex ratios, particularly the female bias in liverworts and mosses. These include meiotic sex ratio variations (Norrell et al. 2014), differential spore germination rates and mortality (Newton 1972; McLetchie 1992; 2001), sexual dimorphism with higher male sensitivity to environmental stress (Benassi et al. 2011; Hugonnot et al. 2014; Rosengren & Cronberg 2014), and differences in reproductive costs between sexes (Stark et al. 2000; Rydgren et al. 2010). Further reviews by Glime & Bisang (2017a; b) and Bisang & Hedenäs (2005) delve deeply into these factors.

The underlying causes of skewed sex distributions in bryophyte populations are complex, often involving a combination of life history traits, genetic factors, and environmental conditions that result in fluctuating sexual biases (Shaw & Beer 1999; Hugonnot et al. 2014). Conservation efforts, particularly for dioicous bryophytes with strong sex biases, need to consider these dynamics (Hugonnot et al. 2014; Peñaloza-Bojacá et al. 2018).

Bryologists acknowledge that multiple factors contribute to observed sex ratio biases, including species' phylogenetic histories (Bisang & Hedenäs, 2005; Bisang et al. 2014). However, generalizations should be approached with caution due to the limited scope of studies on populations, species, and ecosystems (Glime & Bisang, 2017a).

Furthermore, the absence of sexual expression in bryophytes does not imply sterility McLetchie 1992; Shaw & Gaughan 1993; Shaw & Beer 1999; Oliveira & Pôrto 2002; Stark et al. 2010; Norrell et al. 2014; Maciel-Silva et al. 2016; Santos et al. 2023c), as external conditions can influence the activation of sexual traits in both sexes (Hugonnot et al. 2014). Additionally, the development of antheridia often lags behind that of archegonia, leading to asynchronous production of male and female gametangia (Stark, 1983; 1997; Stark & Castetter, 1995; Milne, 2001; Maciel-Silva & Válio, 2011).

Investments, efforts, and costs of sexual reproduction

To understand the reproductive biology of bryophytes, it's essential to define some key terms frequently used in plant reproductive studies (Obeso, 2002; Ehrlén et al., 2000; Stark et al., 2009). In bryophytes, with their dominant gametophyte generation, these concepts are typically measured at the gametophytic level.

'Reproductive allocation' or 'investment' refers to the proportion of resources a plant allocates to reproduction, typically estimated as a static measure. 'Reproductive effort' is the proportion of total resources derived from the vegetative plant devoted to reproduction, often calculated as RE = Ir/(Ir+Is) or RE = Ir / Is, where Ir represents resources allocated to reproduction, and Is to vegetative parts. 'Reproductive costs' denote the losses in future plant performance due to current reproductive investments, calculated as (Bn – Br)/R, where Bn is the biomass of non-reproductive plants, Br the biomass of reproductive plants, and R the biomass of reproductive structures (Ehrlén et al., 2000; Bisang et al., 2006).

In bryophytes, fertilized females or bisexual plants bearing sporophytes often incur higher reproductive costs than non-fertilized plants. This difference is particularly notable in dioicous species, where males and females may have varying reproductive costs over their lifespans, particularly in terms of resource allocation to gametangia, gametes, and sporophytes (Rydgren et al., 2010).

Although several studies have explored trade-offs between sexual reproduction and other functions in bryophytes, experimental investigations monitoring resource allocation are relatively few (Stark et al., 2009). Notable findings include the cost of reproduction in female *Dicranum polysetum* plants, where sporophyte maturation negatively impacted subsequent annual biomass accumulation (Ehrlén et al., 2000), and observations that maternal plants with young sporophytes showed reduced clonal growth compared to those with abortive sporophytes (Stark et al., 2009).

Differential reproductive allocations, efforts, and costs between sexes in bryophytes have been proposed (Bowker et al., 2000; Horsley et al., 2011; Holá et al., 2014), potentially contributing to the observed sexual dimorphisms in dioicous bryophytes (Rydgren & Økland, 2002; Pohjamo & Laaka-Lindberg, 2004; Stark et al., 2009; Holá et al., 2014; Hedenäs & Bisang, 2011; Slate et al., 2017). These dimorphisms are also present in some monoicous species, such as the rhizoautoicous moss Fissidens flaccidus Mitt. (Santos et al., 2018). However, these sexual dimorphisms don't fully account for the sex ratios commonly seen in bryophyte populations (Bisang et al., 2006; et al., 2017), leaving room for further research in this area.

Moreover, individual reproductive variations, shaped by both environmental and genetic factors (Brzyski et al., 2014), underscore the need to monitor natural variations in reproductive parameters across different species' spatial and temporal distributions. In a compelling example, Santos et al. (2020) compared two species of the moss *Fissidens*, discovering that rhizoautoicy (occasionally, functional dioicy) leads to reduced gametangia expression compared to gonioautoicy, yet still achieves equivalent reproductive success more efficiently. Remarkably, rhizoautoicous *Fissidens* species allocates more energy to reproduction, particularly in males compared to females, as opposed to genuinely monoicous species in the same genus (Santos et al., 2023a,b). This study (Santos et al., 2023b) also unveiled trade-offs between sexual reproductive allocation and asexual gemma production, highlighting the crucial role of female ramets in the asexual reproduction of *Fissidens scariosus*. Furthermore, there appears to be a habitat preference between the sexes, as male ramets predominantly occupy high-density patches and are often located beneath female ramets, suggesting a strategic avoidance of direct sunlight by male ramets (Santos et al., 2023b).

Asexual reproduction: a common phenomenon in bryophytes

Asexual reproduction is a vital reproductive strategy in bryophytes, playing an essential role in their lifecycle. The mature gametophyte, which represents the dominant phase, has the capacity for vegetative reproduction through a variety of asexual structures, detailed further below. Moreover, bryophytes demonstrate additional asexual reproduction methods, such as the formation of new gametophytes directly from sporophyte tissue without the involvement of spores—a process termed apospory—and the creation of sporophytes without the fertilization of gametes, known as apogamy.

Particularly in dioicous species, even producing sporophytes and spores, asexual reproduction is often a key strategy due to frequent challenges in completing sexual reproduction processes (Longton & Schuster, 1983; Laaka-Lindberg et al., 2003; Frey & Kürschner, 2010; Maciel-Silva, 2016). Asexual structures like gemmae and vegetative propagula are crucial in the dynamic population processes of bryophytes (During, 1979; Söderström & During, 2005; Löbel et al., 2009).

The main types of asexual structures in bryophytes, including their dispersal vectors, have been summarized in several studies (Longton & Schuster, 1983; Imura & Iwatsuki, 1990; Imura, 1994; Laaka-Lindberg et al., 2003; Frey & Kürschner, 2010; Maciel-Silva & Pôrto, 2014; Glime, 2017e; Glime, 2017f). These structures are often classified as propagula or gemmae based on the presence or absence of an apical cell, with classifications ranging from narrow to broad interpretations (Imura, 1994; Laaka-Lindberg et al., 2003) (Tab. 1; Figure 3A-H).

Bryophytes can also replicate their colonies through less specialized methods (Frey & Kürschner, 2010; Glime, 2017e). For instance, older gametophyte

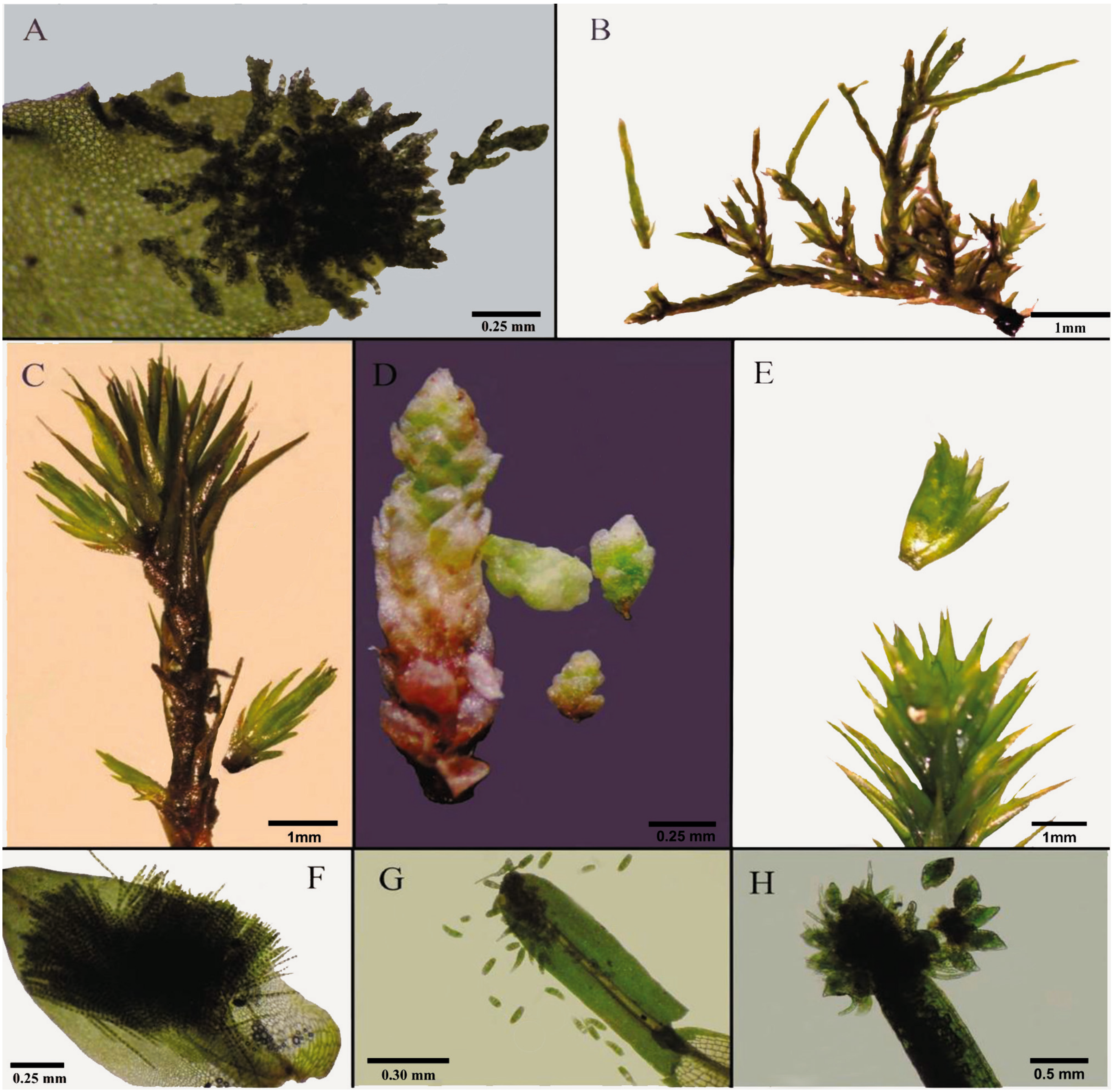

Figure 3: Asexual structures in bryophyte species. A. Plantlets on leaf in *Plagiochila corrugata* (Nees) Nees & Mont., B. Deciduous flagelliferous branches in *Wijkia flagellifera* (Broth.) H. A. Crum.; C. Deciduous branches in *Campylopus pilifer* Brid.; D. Bulbils in Bryum argenteum Hedw.; E. Deciduous apex in *Campylopus pilifer*; F. Gemmae on leaf in *Syrrhopodon parasiticus* (Sw. ex Brid.) Besch.; G. Gemmae produced on leaf apex in *Syrrhopodon ligulatus* Mont.; H. Gemmae on leaf apex in *Ochrobryum gardneri* (Müll. Hal.) Mitt.

sections in *Riccia* spp. decay, leading to the separation and growth of younger parts. Gametophyte fragmentation is common in species like *Lejeunea laetevirens*, and rhizoautoicous species such as *Fissidens scariosus* often develop multiple shoots from subterranean axes (Fig. 2B). Some mosses, like *Octoblepharum albidum*, grow gametophytes from aerial rhizoids, and most mosses produce multiple gametophores from buds on protonema after spore germination.

Vegetative diaspores in bryophytes, typically originating exogenously from gametophytes, exhibit a wide variety of shapes, sizes, germination types, and abscission modes (Duckett & Ligrone, 1992; Glime, 2017e). For example, moss diaspores often employ specialized abscission mechanisms involving tmema cells, as seen in the leaf gemmae of *Calymperes* and the axillary gemmae of *Zygodon* (Edwards, 1978; Duckett & Ligrone, 1992).

Bryophyte gemmae and leafy propagula can be dispersed via wind, gravity, water, and animals, including earthworms, various arthropods, slugs, amphibians, migratory birds, and even flying foxes (Glime, 2017f). While spores are typically associated with long-distance dispersal in bryophytes, recent studies have highlighted the significant roles played by asexual structures in this process (Pohjamo et al., 2006; Parsons et al., 2007; Lewis et al., 2014; Laenen et al., 2016a).

Sexual and asexual reproduction: advantages and disadvantages

In bryophytes, reproduction can be classified as either sexual, developing from a spore that resulted from cross-fertilization and meiosis, or asexual, where the new plant develops from a mitotically produced cell without cross-fertilization (Mishler, 1988).

Sexual reproduction in bryophytes allows genetic material sharing between individuals, enhancing genetic diversity. Although it requires significant resources and energy, this mode of reproduction is advantageous for potentially increasing offspring survival under environmental change (Obeso, 2002). Asexual reproduction, conversely, produces genetically identical clones, limiting genetic variability and evolution, which may lead to increased susceptibility to environmental changes (Frey & Kürschner, 2010; Glime, 2017g). However, it is a faster and less energetically demanding process, common in various bryophyte species (Glime & Bisang, 2017a, b).

Table 1. Classification of main types of asexual reproduction presented in bryophytes (after Imura and Iwatsuki 1990; Imura 1994; Laaka-Lindberg, Korpelainen and Pohjamo 2003; and Maciel-Silva and Pôrto 2014). |

Type of asexual structure	Description	Examples
Propagula	*vegetative diaspores with an apical cell; grow directly into a leafy shoot (or thallus), if the apical cell is reactivated*	
deciduous shoot apices	terminal portions of stems	*Campylopus* spp. (Fantecelle et al. 2017; Peñaloza-Bojacá et al. 2018)
deciduous flagelliform shoots	slender branches with suppressed leaves	*Wijkia flagellifera* (Fantecelle et al. 2017; Peñaloza-Bojacá et al. 2018)
caducous branchlets	branch-like structures with minute leaves	*Campylopus* spp.; *Plagiochila corrugata* (Fantecelle et al. 2017; Peñaloza-Bojacá et al. 2018)
bulbils	bud-like branches with leaf-like projection	*Pohlia bulbifera, Bryum arachnoideum, B. argenteum,* (Frey and Kürschner 2010; Fantecelle et al. 2017; Peñaloza-Bojacá et al. 2018)
Gemma	*vegetative diaspores with no apical cell; a protonemal phase precedes the production of the leafy shoots (or thallus)*	
gemma (*sensu stricto*)	specialized structures with no leaves or leaf primordia; usually multicellular and ranging from filaments to globose	*Metzgeria* spp., *Calymperes* spp., *Syrrhopodon*, spp., *Ochrobryum gardneri*, *Octoblepharum albidum* (Fantecelle et al. 2017; Peñaloza-Bojacá et al. 2018)
tubers	type of gemmae spherical or ovoid, produced on rhizoids or thallus margin	*Rosulabryum bilardieri*, *Bryum atenense* (Fantecelle et al. 2017; Peñaloza-Bojacá et al. 2018; Fernandes Oliveira unpublished data)
protonemal gemma	type of filamentous gemmae produced on filamentous protonema of some mosses	*Schistostega pennata*, *Lepidopillum muelleri*, (Edwards 1978; Maciel da Silva, Pôrto and Simabukuro 2006)
caducous leaves	normal vegetative, or reduced leaves produced on special branches	*Campylopus fragilis*, *Leucoloma serrulatum*, *Leucobryum clavatum*, *Bazzania phyllobola* (Frey and Kürschner 2010; Maciel-Silva 2016)
fragile leaves	parts of leaves, commonly apices, detached from parent shoots	*Octoblepharum pulvinatum*, *Syntrichia fragilis* (Allen 1991; Frey and Kürschner 2010)

In some bryophytes, sexual and asexual reproduction are balanced, offering short-term vegetative growth benefits in young or low-density colonies and long-term genetic diversity benefits in older or high-density colonies (During, 1979; Kimmerer, 1991a). Asexual reproduction is favored in transient or unpredictable habitats, while sexual reproduction seems to prevail in stable environments (Mishler, 1988).

During (1979) categorized bryophyte species based on their life-history traits, proposing a range of life strategies from fugitive to perennial species. The balance between sexual and asexual reproduction, reproductive effort, spore size and number, and annual production, was used to classify these species. For example, fugitive species like *Funaria hygrometrica* exhibit high sexual reproductive effort with no asexual reproduction, while colonist species such as *Bryum argenteum* may invest heavily in both modes, and perennial stayer species as *Phyllogonium viride* tend to invest minimally in reproduction.

Longton & Schuster (1983) suggested a correlation between reproductive modes and sexual systems in bryophytes, where dioicous species are hypothesized to produce asexual propagula more frequently than monoicous species. However, studies have shown no significant statistical correlation between dioicy and asexual reproduction (Crawford et al., 2009; Laenen et al., 2016a), indicating complex interactions between sexual systems and reproductive modes.

The sexual systems of bryophytes have implications for their reproduction. Dioicous species tend to produce sporophytes less frequently than monoicous ones (Longton, 1992; Longton & Schuster, 1983; Maciel-Silva et al., 2012). In dioicous species, mandatory outcrossing increases the likelihood of gene recombination, whereas in monoicous species, the probability of self-fertilization is higher, leading to homozygous sporophytes (McDaniel & Perroud, 2012; Haig, 2016). This process of haploid selfing in monoicous bryophytes can be seen as a form of asexual reproduction with sexual underpinnings.

Self-fertilization initially increases inbreeding depression levels, but over time, deleterious alleles may be purged, making selfing an adaptive strategy (Taylor et al., 2007; Charlesworth & Willis, 2009). This phenomenon is more observable in dioicous than in monoicous species (Taylor et al., 2007).

Sexual and asexual diaspores play distinct roles in bryophyte life histories. Asexual diaspores, usually larger and heavier, are crucial for local population establishment and maintenance. Spores, being smaller and lighter, are more suited for long-distance dispersal and colonization of new habitats (Newton & Mishler, 1994; Kimmerer, 1991b; Laenen et al., 2016a). The short-range dispersal limitation of asexual diaspores can be compensated by their high establishment likelihood (Löbel et al., 2009).

In dynamic or temporary environments, both sexual and asexual reproduction are vital strategies. However, in stable environments, sexual reproduction may be necessary for survival (Longton, 2006; Alvarenga et al., 2013). Asexual reproduction could be the only viable option for maintaining populations in extreme conditions, fragmented populations, or when historic events result in isolated or sex-dominated patches (Frey & Kürschner, 2010; Löbel et al., 2009; Peñaloza-Bojacá et al., 2018).

Final remarks

Bryophytes represent the second largest group of land plants, unique in their dominance of a haploid life cycle, a trait not shared with other terrestrial plants. Their gametophytes exhibit a diverse range of morphologies and complex trade-offs, presenting both clear and subtle distinctions recognized by bryologists. Found across the globe, bryophytes are integral to ecosystems ranging from polar to tropical regions. However, many species are sparsely distributed, making their reproductive life history traits critical considerations in conservation efforts.

Presently, the richness and genetic diversity of bryophytes face significant threats, primarily due to deforestation, habitat fragmentation, and environmental degradation (Hallingbäck & Hodgetts, 2000). This situation is particularly alarming for dioicous species that exhibit less frequent sexual reproduction, as they are at an increased risk of sexual extinction, potentially surviving only through asexual means. Furthermore, in the face of global change, reproductive success might become increasingly challenging, favoring only certain opportunistic bryophyte species (Casanova-Katny et al., 2016).

The impact of climate change, deforestation, and habitat loss on bryophytes raises important questions about future distribution patterns. It remains uncertain whether these factors will predominantly favor sporophyte-prolific species capable of wide dispersal. One thing is clear: the world a century from now will likely present a very different reality for the bryophyte species we study today. Understanding and mitigating these changes are crucial for preserving the rich diversity and ecological functions of these ancient plant lineages and vital components of terrestrial biomes.

Glossary

- Androecia – perigonia, male inflorescence.
- Autoicous, a subtype of monoicous; antheridia and archegonia produced on separate branches (or chambers) on the same plant. e.g., the liverwort *Lejeunea flava* (Sw.) Nees; the moss *Octoblepharum albidum* Hedw.; and the hornwort *Phaeoceros carolinianus* (Michx.) Prosk.
- Antheridiophore – a specialized antheridium-bearing branch.
- Archegoniophore – a specialized archegonia-bearing branch.
- Bisexual – monoicous species with gametophytes producing both gametangia (female and male).
- Brood bodies – a general term for asexual reproductive structures.
- Cladautoicous – a subtype of autoicous; androecia and gynoecia are terminal on distinct elongated branches of the same plant; e.g., the moss *Fissidens radicans* Mont.
- Diaspores – dispersal agents; any structure that becomes detached from a parent plant and gives rise to a new individual. They can be sexually produced in bryophytes as spores or asexually produced as gemmae, tubers, etc.
- Dioicous – antheridia and archegonia are produced on separate gametophytes; e.g., the liverwort *Lejeunea laetevirens* Nees & Mont.; the moss *Fissidens polypodioides* Hedw.; and the hornwort *Phaeoceros laevis* (L.) Prosk. The term "dioecious" is commonly used to characterize sporophytes among seed plants.
- Gemma (pl. gemmae) – a unicellular, or usually multicellular, structure for vegetative reproduction.
- Genets – individuals (all ramets) that arise from a single spore.
- Gonioautoicous – with perigonia small, gemmiform, and axillary below at the terminal perichaetia. e.g., *Fissidens submarginatus* Bruch. (Figure 2A).
- Gynoecia – perichaetia, the female inflorescence.
- Heteroicous – occurrence of male and female gametangia in separate inflorescences or in mixed inflorescences on a same plant. e.g., the moss *Gyroweisia monterreia* R.H. Zander & F.J. Herm. with inflorescences variable with only archegonia, only antheridia or synoicous.
- Inbreeding depression – is the reduced biological fitness in a given population as a result of inbreeding, or breeding of related individuals.
- Monoicous – antheridia and archegonia are produced on the same gametophyte; e.g., the liverwort *Frullania platycalyx* Herzog; the moss *Sematophyllum subpinnatum* (Brid.) E. Britton; and the hornwort *Dendroceros crispus* (SW.) Nees. The term "monoecious" is frequently used for seed plants.
- Outcrossing – the egg and sperm originate from two separate gametophytes.
- Paraphysis (pl. paraphyses) - sterile filaments of cells that often grow associated with the antheridia and archegonia of mosses.
- Paroicous – antheridia and archegonia in the same perichaetium, although the antheridia are naked in the axils and located below the perichaetial leaves. e.g., the liverwort *Cheilolejeunea compacta* (Steph.) M.E. Reiner; the moss *Trichostomum perligulatum* (Flowers) R.H. Zander.
- Perichaetia – the female inflorescence (commonly used to designate the female branches of mosses).
- Perigonia – the male inflorescence (commonly used to designate the male branches of mosses).
- Phyllodioicous – with dwarf male plants epiphytic on the leaves of female plants. e.g., *Groutiella apicullata* (Hook) H.A. Crum & Steere. (Figure 2D).
- Poikilohydry – defined as the inability of an organism to control its hydration state, i.e., their water potential is in equilibrium with the environment.
- Polyoicous – with antheridia and archegonia on the same plant, or sometimes on different plants of the same species. e.g., the liverwort *Frullania kunzei* (Lehm & Lindenb.) Lehm & Lindenb.
- Propagule or propagulum (pl. propagules or propagula) – a diaspore used in vegetative reproduction; they are small, easily detached plantlets

or deciduous shoot apices, caducous branchlets, flagella, or bulbils, etc.; they differ from gemmae by the presence of an apical cell that can grow directly into a leafy shoot without passing through a protonema stage.

- Pseudoautoicous – dwarf male plants epiphytic on female plants. e.g., *Holomitrium arboreum* Mitt. (Figure 2C).
- Ramets – an individual member of a genetically identical population (genet). See also "genets"
- Rhizoautoicous – perigonia on short shoots attached to female shoots (in general, longer) by rhizoids. e.g., the moss *Fissidens scariosus* Mitt. (Figure 2B).
- Synoicous – both antheridia and archegonia occur mixed in the same gametoecium. e.g., the liverwort *Cololejeunea desciscens* Steph.; the moss *Pilotrichum bipinnatum* (Schwägr.) Brid.
- Tmema – a small cell that forms a weak link and permits the abscission of a protonema.
- Unisexual – dioicous species with gametophytes producing either male or female gametangia.

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