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CHAPTER 3-1
SEXUALITY: SEXUAL STRATEGIES

JANICE M. GLIME AND IRENE BISANG

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CHAPTER 3-1
SEXUALITY: SEXUAL STRATEGIES

Figure 1. Depiction of the ***Marchantia*** sexual life cycle in a chalk drawing by Gerald W. Prescott. Photo by Janice Glime.

Expression of Sex

Understanding sexuality is fundamental to understanding evolution, and by extension, to understanding the ecology of species. The topic of sexual expression has led to interesting discussions for many centuries and still perplexes us. On Bryonet, 14 February 2016, Ken Kellman asked several pertinent questions that remain with incomplete answers. His questions included the role of auxins or other hormones in the **perigonium** (leaves surrounding male reproductive structures) and **perichaetia** (leaves surrounding female reproductive structures) formation. How does **polyploidy** (condition of multiple sets of genes) relate to separate sexes? How many totally asexual species are there? (In California Kellman is aware that only ***Dacryophyllum falcifolium*** is never known to form gametangia). And some species are sexual in Europe, but not in North America, *e.g.* ***Hennediella stanfordensis*** (Figure 2), or male in Europe and female in North America, *e.g.* ***Syntrichia pagorum*** (Figure 3).

Figure 2. ***Hennediella stanfordensis***, a species that is sexual in Europe but not in North America. Photo by Martin Hutten, with permission.

Figure 3. ***Syntrichia pagorum***, a species that is male only in Europe, female only in North America, and both sexes occur in Australia. Photo by Michael Lüth, with permission.

But it turns out that Ken Kellman's example from California is only a drop in the bucket – many species in Europe are not known to reproduce sexually, including ***Bryoerythrophyllum caledonicum***, ***B. ferruginascens*** (Figure 4), ***Bryum dixonii***, ***Campylopus gracilis*** (Figure 5), ***Didymodon maximus*** (Figure 6), ***Ditrichum plumbicola*** (Figure 7), ***Leptodontium gemmascens*** (Figure 8), ***Pohlia scotica***, ***Thamnobryum cataractarum*** (possibly a form of ***T. alopecurum***), and ***Tortella limosella*** (Christopher Preston, Bryonet 15 February 2016). To these, Misha Ignatov (Bryonet 15 February 2016) added ***Limnohypnum muzushimae***, a rare pleurocarpous species in Kamchatka, Kurils, and Japan. Johannes Enroth, Bryonet 16 February 2016) added ***Caduciella mariei***, a species that occurs in eastern Africa, SE Asia, Queensland, and New Britain; it seems to reproduce only by caducous branch leaves. Liverworts include ***Mastigophora woodsii*** (Figure 9), ***Plagiochila norvegica***, ***Riccia rhenana*** (Figure 10), ***Scapania nimbosa*** (Figure 11), ***Herbertus borealis*** (Figure 12), ***H. norenus***, ***Lophozia wenzelii*** (Figure 13-Figure 14), ***Protolophozia herzogiana***, ***Anastrophyllum alpinum*** (Figure 15), and ***Marsupella arctica*** (Jeff Duckett, Bryonet 15 February 2016). But as Nick Hodgetts pointed out (Bryonet 16 February 2016), some may reproduce by sexual union only rarely and "bryologists are unfortunately likely to miss the event!"

Figure 4. ***Bryoerythrophyllum ferruginascens***, a species not known to reproduce sexually. Photo by David T. Holyoak, with permission.

Figure 5. ***Campylopus gracilis*** showing caducous tips by which it reproduces. Sexual plants are unknown. Photo by Michael Lüth, with permission.

Figure 6. ***Didymodon maximus***, a species for which sexual structures are unknown. Photo by Rory Hodd, with permission.

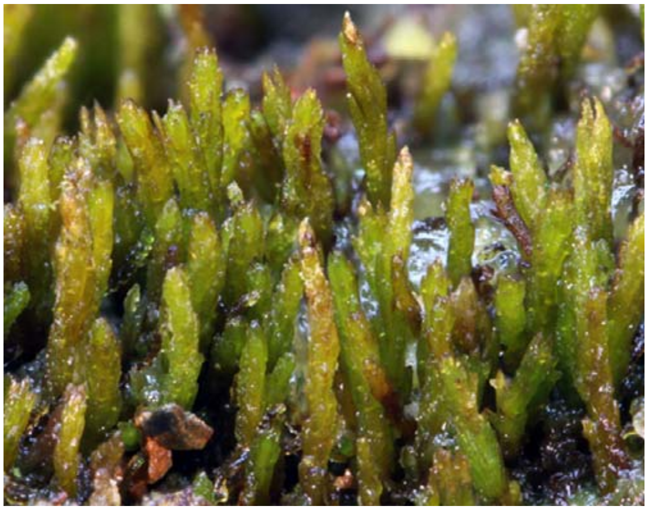

Figure 7. ***Ditrichum plumbicola***, a species for which sexual plants are unknown. Photo by Des Callaghan, with permission.

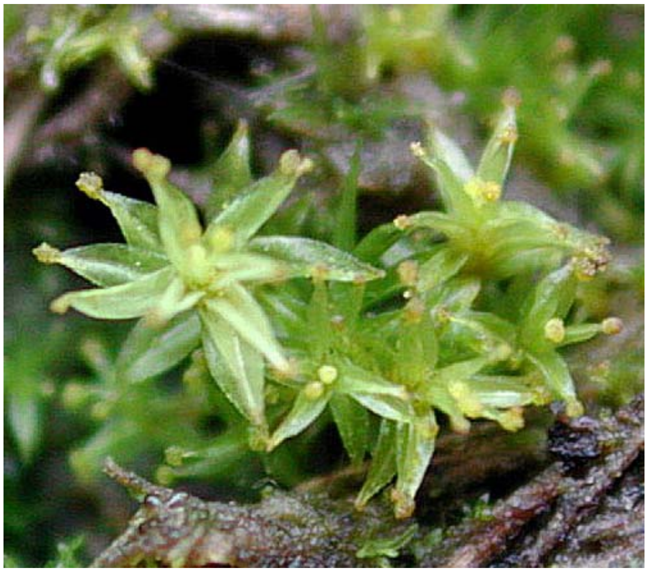

Figure 8. ***Leptodontium gemmascens*** with gemmae, a species with no known sexual plants. Photo by Michael Lüth, with permission.

Figure 9. ***Mastigophora woodsii***, a species for which sexual structures are unknown. Photo by Des Callaghan, with permission.

Figure 10. ***Riccia rhenana***, a liverwort for which there are no known sexual plants. Photo by Štěpán Koval, with permission.

Figure 11. ***Scapania nimbosa***, a species that is unknown in a sexual state. Photo by Michael Lüth, with permission.

Figure 12. ***Herbertus borealis***, a species with no known sexual plants. Photo by Jan-Peter Frahm, with permission.

Figure 13. ***Lophozia wenzelii***, a species with no known sexual plants. Photo by Michael Lüth, with permission.

Figure 14. ***Lophozia wenzelii*** with water trapped in leaves. No sexual plants are known in this species. Photo by Des Callaghan, with permission.

Figure 15. ***Anastrophyllum alpinum***, a species in which sex organs are unknown. Photo by Michael Lüth, with permission.

Unisexual and Bisexual Taxa

Jesson and Garnock-Jones (2012) attempted to provide a single classification of functional sex that could be used for all land plants. They divided the strategies into three categories: sporophyte (and gametophyte) **dimorphic** (having two forms); sporophyte-**cosexual** and gametophyte-dimorphic; gametophyte (and sporophyte) cosexual (having both sexes). Bryophytes exhibit only the latter two of these, always having sporophytes that are cosexual and never dimorphic. The gametophyte is always dimorphic in seed plants. [Note that in seed plants, the female gametophyte is embedded in the sporophyte tissue and the male gametophyte is a pollen grain; hence gametophyte sexes are always on separate gametophyte individuals.] Despite this simplistic approach, Jesson and Garnock-Jones consider that there are many variations within these three categories and that closer examination should reveal that bryophytes have as many variations in strategy as do more complex seed plants.

In bryophytes, it is the gametophyte (1*n*, **haploid**) plant that exhibits the **bisexual** (**monoicous**) trait. To the seed-plant botanist, the terms monoecious and dioecious are familiar, referring to having male and female organs on one sporophytic individual or on separate individuals, respectively, but the terms are legitimately restricted to sporophytes (Magill 1990). The counterpart to these terms for bryophytes, applied to the gametophyte, are **monoicous** and **dioicous**. Nevertheless, the sporophyte terms are often applied, as are the terms leaf and stem, but the oicy terms emphasize important differences in bryophyte sexuality (Zander 1984; Allen & Magill 1987; Magill 1990). Their root words are the same, derived from the Greek μόνος (mónos), single, or δι- (di-), twice, double, and οἶκος (oîkos) or οἰκία (oikía), house. In other words, one house for sperm and egg on one plant (**monoicous**) or two houses for sperm and egg on different plants (**dioicous**).

Bryophytes have an unusually high number of **dioicous** taxa (male and female gametangia on separate individuals) among green land plants. Ramsay and Berrie (1982) reported that about 42% of bryophyte genera are exclusively dioicous, 49% of the genera include both dioicous and monoicous species, and only 9% are exclusively monoicous. Hedenäs and Bisang estimated roughly 60% of all bryophyte species are dioicous. Villarreal and Renner (2013a) estimated 57% in mosses and somewhat higher in liverworts (68%), although McDaniel and Perroud (2012) consider them to be about equal. This may differ somewhat by geographic distribution, but more careful analysis is needed. By contrast, in seed plants only 4-6% of the species are dioecious (Renner & Ricklefs 1995; de Jong & Klinkhamer 2005) and the sex ratio is more likely to be male-biased (Sutherland 1986; Delph 1999; Barrett *et al.* 2010).

Cross fertilization in monoicous **Bryophyta** is insured in many species by having differences in maturity times of male and female gametangia. Other furtherance of outcrossing is accomplished by the placement of gametangia on the plants. Bryophytes exhibit all sorts of arrangements of sexual organs on their **monoicous** species (having male and female gametangia on same individual), providing them with various strategies for outbreeding. These include having male and female gametangia on separate stems or branches and having male gametangia below female gametangia on the same branch or stem. When male and female organs are on separate individuals (Figure 1), outbreeding is ensured whenever sexual reproduction occurs; opportunities for fertilization decrease and opportunities for genetic variation increase.

One of the major problems for dioicous species is that one sex may arrive in a new location without the other, as seems to be the case of ***Syntrichia pagorum*** (Figure 3) in North America (female only) and Europe (male only). ***Didymodon nevadensis*** (Figure 16) is endemic in North America, occurring on the gypsiferous ridges of Nevada and only female plants are known (Zander *et al.* 1995). Llo Stark (pers. comm. 28 March 2023) considers that males have become extinct here. Nevertheless, with a variety of vegetative reproductive means, the species can persist.

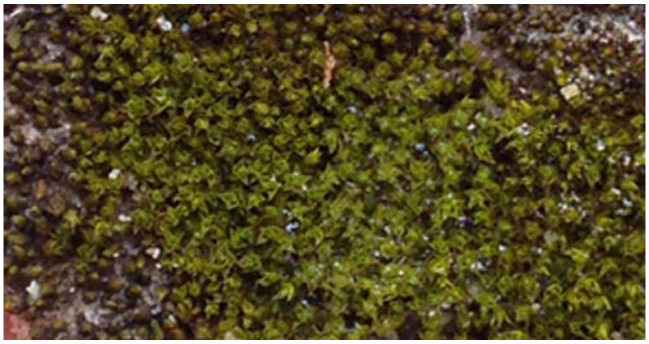

Figure 16. ***Didymodon nevadensis***. Photo by Theresa Clark, with permission.

Among the bryophytes, it is well known that many taxa with separate sexes never produce capsules [*e.g.* ***Sphagnum*** (Cronberg 1991)], presumably due to absence of the opposite sex or to inability of the sperm to reach the female plant and its reproductive structures successfully. For example, in a population of ***Cyathophorum bulbosum*** (Figure 17) in New Zealand, where male plants were located nearly a meter above the females, sporophytes existed in several developmental states, but on a nearby bank the entirely female population was completely barren (Burr 1939). In studies by Grebe (1917) on 207 German mosses and Arnell (1875) on 177 Scandinavian mosses, 200 of the 220 taxa that seldom produced capsules were dioicous. So one must ask what is the genetic mechanism that underlies the sexual differences in these unisexual taxa (taxa having only one sex on an individual; **dioicous**) and just what permits these unisexual taxa to persist?

Sex Chromosomes

Bryologists are the proud discoverers of **X** and **Y** sex chromosomes (Figure 18) in plants (Anderson 2000), first discovered in the liverwort genus ***Sphaerocarpos*** (Figure 19) (Allen 1917, 1919, 1930). And it is fitting that one of the first sex markers in bryophytes was likewise found in ***Sphaerocarpos*** (McLetchie & Collins 2001), although this was predated by identifying the tiny X and Y chromosomes in the female and male liverwort ***Marchantia polymorpha*** (Figure 20-Figure 21) (Okada *et al.* 2000; Fujisawa *et al.* 2001). These researchers have determined that the Y chromosome of the dioicous ***Marchantia polymorpha*** has unique sequences that are not present on the X chromosome or on any autosomes. Note that these individual haploid plants each have only one sex chromosome. To emphasize differences between **haploid** and **diploid** sex determination, the haploid single sex chromosomes have recently been distinguished as **U** (female) and **V** (male) chromosomes (Bachtrog *et al.* 2011; Olsson *et al.* 2013).

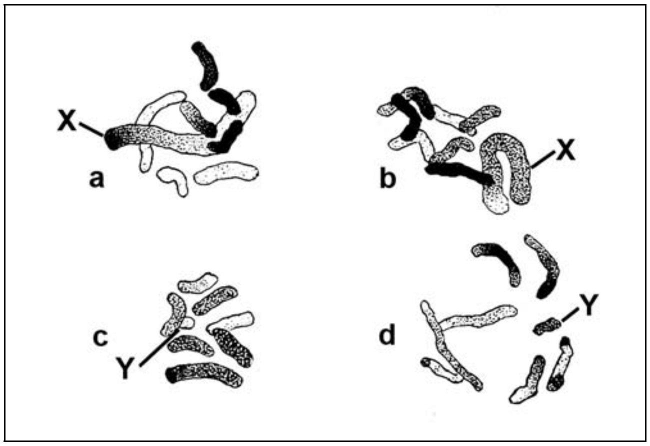

Figure 18. Chromosomes of ***Sphaerocarpos donnellii***. **a** & **b**: Chromosomes from female gametophyte. **c** & **d**: Chromosomes from male gametophyte. From Allen 1919.

Figure 19. ***Sphaerocarpos michelii***, member of the genus where X and Y sex chromosomes were first discovered. Photo by Jan-Peter Frahm, with permission.

Figure 17. ***Cyathophorum bulbosum***, a species that can readily be fertilized when males are above females, but not when females are isolated on a nearby substrate. Photo by Niels Klazenga, with permission.

Figure 20. ***Marchantia polymorpha*** male with antheridiophore, first bryophyte species in which sex markers were found and unique sequences found on males that were not present on females. Photo by David T. Holyoak, with permission.

Figure 21. ***Marchantia polymorpha*** females with archegoniophores, the first bryophyte species in which sex markers were found. Photo by Janice Glime.

But the presence of sex chromosomes does not mean that all bryophytes have separate sexes, or even that all bryophytes have sex chromosomes, so we must ask what determines the sexual differentiation. Ramsay and Berrie (1982) discussed the mechanisms of sex determination in bryophytes, including physiological and genetic regulation of sexuality. They considered that genetic sex is determined at the spore stage, but Bachtrog *et al.* (2011) consider that it is determined at meiosis. Even within the same genus, some bryophytes may be **unisexual** (Figure 22-Figure 25), others **bisexual** (having both sexes on the same individual; monoicous) (Figure 26-Figure 30). Clearly we need more research to discover how some of these determinations are made.

Figure 22. Clonal colony of male ***Philonotis calcarea***. Note innovation branches below the male splash cups. Photo by Michael Lüth, with permission.

Figure 23. A dioicous species, ***Philonotis calcarea***, showing antheridial splash cups. Photo by David T. Holyoak, with permission.

Figure 24. Female plants of the dioicous ***Philonotis calcarea***, distinguishable by their sporophytes. Photo by David T. Holyoak, with permission.

Figure 25. Colony of non-expressing or female plants of the dioicous ***Philonotis calcarea***. Archegonia are hidden among **perichaetial leaves** at the tip of the plant and are often difficult to distinguish without destroying the tip of the plant. Photo by David T. Holyoak, with permission.

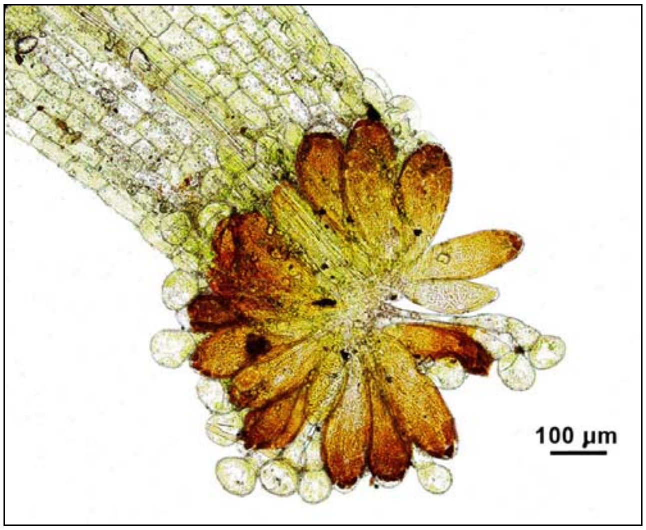

Figure 26. **Antheridia** of ***Funaria hygrometrica***. This is a special case of monoicous termed **autoicous**. Both male and female gametangia are on the same plant, but in separate places. Here the antheridia are at the base of a leaf. The white-knobbed structures with them are **paraphyses**. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Renner *et al*. (2017) reported a different combination of sex chromosomes. In ***Frullania dilatata*** (Figure 28), there are two U chromosomes and one V chromosome. In ***Plagiochila asplenioides*** (Figure 29), there are one U chromosome and two V chromosomes. They discuss the many things we don't understand in bryophyte sexual genetics. There is a lack of high-throughput sequencing, quantification, or *in situ* study of repetitive DNA, organellar DNA, or transposable elements. The causes of size differences in U and V chromosomes is unknown. Even though heterochromatin was first discovered in bryophytes, its role in sex regulation of these organisms remains unknown. The only sequencing of sex chromosomes is that of the V chromosome in ***Marchantia polymorpha*** (Figure 20-Figure 21), a species with 8 autosomes and 1 sex chromosome.

Figure 27. ***Frullania dilatata*** on tree trunk, a species with two U chromosomes and one V chromosome. Photo by Claire Halpin, with permission.

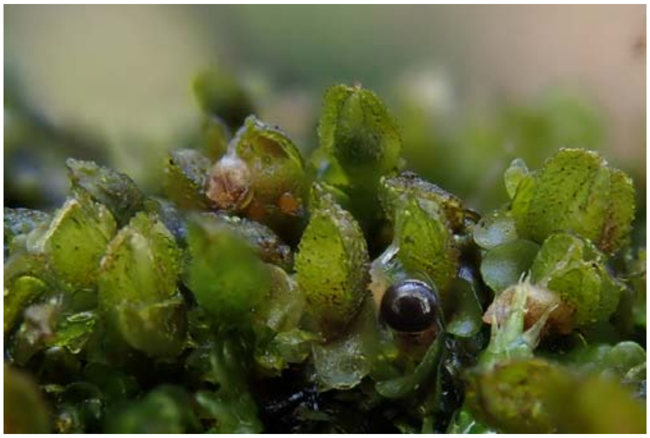

Figure 28. ***Frullania dilatata*** (**lower** with capsules), a species with two U chromosomes and one V chromosome. Photos by Claire Halpin, with permission.

Figure 29. ***Plagiochila asplenioides***, a species with one U chromosome and two V chromosomes. Photos by Claire Halpin, with permission.

An Unusual Y (=V) Chromosome

An active "Y"-chromosome-specific gene has been unknown in plants, although mammals such as humans do have specific genes on the Y chromosomes (Okada *et al.* 2001). But Okada *et al.* found that the bryophytes, or at least ***Marchantia polymorpha*** (Figure 20-Figure 21), have at least one such gene. This gene is unique and is expressed specifically in the male sex organs.

Since that earlier discovery, Yamato *et al.* (2007) have identified 64 genes on the V (male) chromosome of ***Marchantia polymorpha*** (Figure 20-Figure 21). Of these, 14 occur only in the male genome and have been linked exclusively to expression in reproductive organs. Although their individual functions are still not known, this relationship suggests that they participate in the reproductive functions of the male. Additional genes (40 genes) on the V chromosome are expressed in both male sexual organs and male thalli, suggesting that they have cellular functions unrelated to reproduction.

Figure 30. ***Funaria hygrometrica*** with both undeveloped and nearly mature capsules on female plant portions. Photo by Robert Klips, with permission.

Figure 31. ***Orthotrichum pusillum***, an **autoicous** species with capsules. Photo by Robert Klips, with permission.

Gametangial Arrangement

There are multiple configurations of gametangia among the various bryophytes. The monoicous condition of sexuality among mosses can be further divided into **autoicous**, **paroicous**, and **synoicous**. In the **autoicous** condition, the male and female gametangia are in separate clusters, as in ***Orthotrichum pusillum*** (Figure 31-Figure 33). In the **paroicous** condition, the male and female gametangia are in separate groupings but in a single cluster, as they are in a number of species of the liverwort ***Lophozia*** (Figure 34) (Frisvoll 1982). The **synoicous** condition is one in which the male and female gametangia occur intermixed in the same cluster, as in ***Micromitrium synoicum*** (Figure 35), a condition unusual enough to be used in the specific name. Whereas archegonia in acrocarpous mosses are always terminal, pleurocarpous mosses grow horizontally, and the female and male sex organs occur at the apex of specialized short branches, **perichaetia** and **perigonia**, respectively. In dioicous taxa, antheridia of acrocarpous mosses are in various positions, whereas archegonia are terminal. The same arrangements into perichaetia and perigonia is true for both monoicous and dioicous species.

Figure 32. ***Orthotrichum pusillum***, an autoicous species showing antheridia. Photo by Robert Klips, with permission.

Figure 33. ***Orthotrichum pusillum***, an **autoicous** species showing archegonia. Photo by Robert Klips, with permission.

Figure 34. ***Lophozia excisa***, a **paroicous** species. Photo by Michael Lüth, with permission.

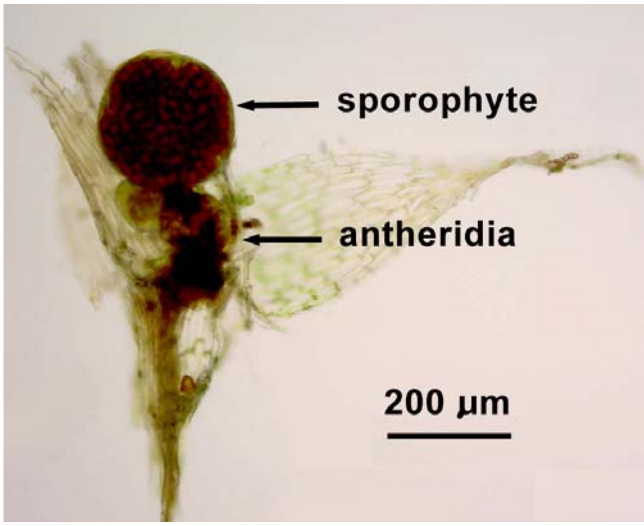

Figure 35. ***Micromitrium synoicum*** with male and female gametangia among the same bracts (**synoicous**). Photo from Duke University, through Creative Commons.

In **Jungermanniopsida**, the antheridia are arranged behind the growing point (Figure 36-Figure 38). In most of the leafy **Jungermanniopsida** the archegonia occur in perianths (Figure 36, Figure 39) that may be terminal on stems and branches or located along these. In the **Metzgeriales** (**Jungermanniopsida**), the archegonia appear along the midrib of the thallus, thus permitting continued apical growth (Figure 40). In the **Marchantiopsida** the antheridia occur in clusters on the thallus (Figure 41) or elevated on a stalk (Figure 42), with similar arrangements for archegonia (Figure 42-Figure 43). In **Anthocerotopsida** the antheridia are imbedded in the thallus (Figure 44-Figure 45) and archegonia are single and surrounded by involucres (Figure 44).

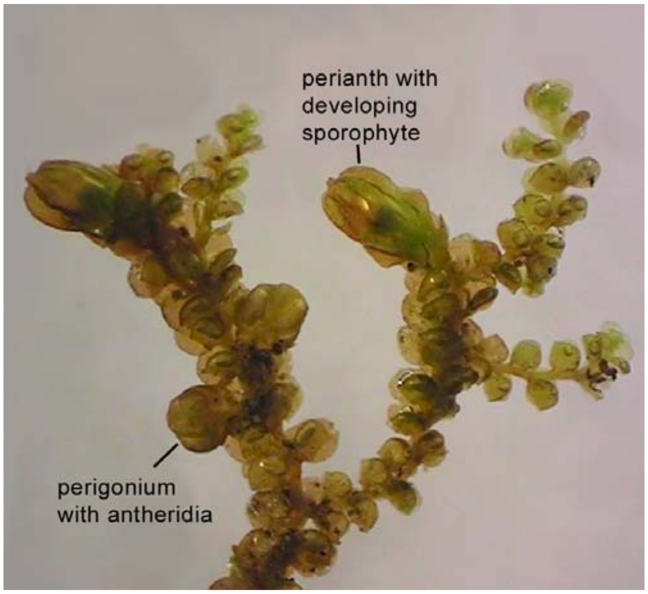

Figure 36. Arrangement of **perianth** with archegonia and **perigonium** with antheridia in the monoicous leafy liverwort ***Frullania oakesiana***. Photo by Paul Davison, with permission.

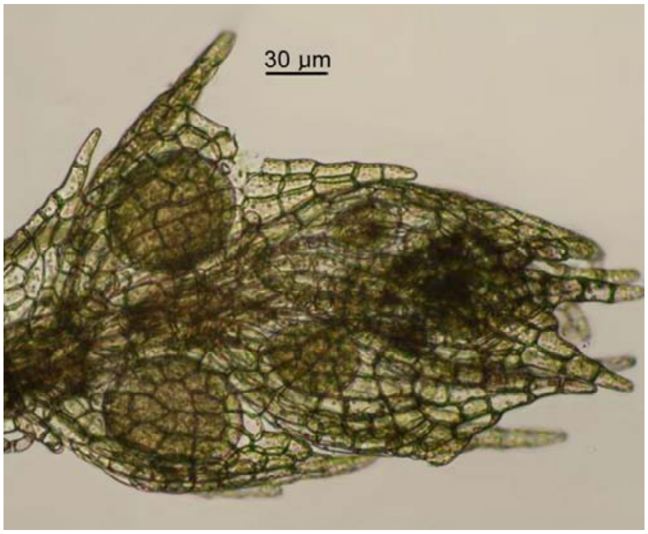

Figure 37. Antheridial arrangement on the leafy liverwort ***Kurzia***. Photo by Tom Thekathyil, with permission.

Figure 38. ***Pellia endiviifolia*** with antheridia on the thallus in positions not at the apex. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 39. **Perianth** of the leafy liverwort ***Frullania*** (**Jungermanniopsida**) in its terminal position. Photo by George Shepherd, through Creative Commons.

Figure 40. ***Symphogyna brasiliensis*** (**Metzgeriales**) showing subapical position of archegonia, hidden in this case by fimbriate scales. Photo by George J. Shepherd through Creative Commons.

Figure 41. ***Conocephalum conicum*** antheridia in clusters on the thallus (arrow). Photo by Malcolm Storey, through Creative Commons.

Figure 42. ***Marchantia polymorpha*** showing flat-topped antheridiophores with antheridia embedded in them and archegoniophores with fingerlike arms with archegonia on the undersides. Photo by Robert Klips, with permission.

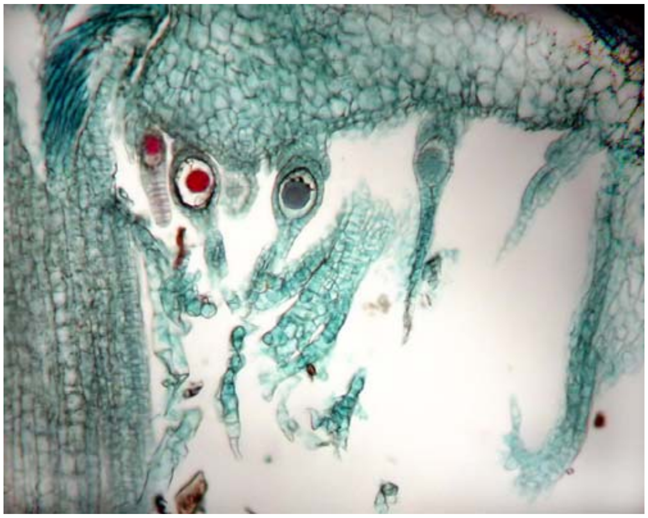

Figure 43. Arm of archegoniophore head of ***Marchantia polymorpha*** with archegonia hanging down. Photo by George Shepherd, through Creative Commons.

Figure 44. ***Notothylas orbicularis*** (**Anthocerotopsida**) with involucres that surround archegonia and pouches that contain antheridia (see insert). Photo by Paul Davison, with permission.

Figure 45. **Antheridia** in the pocket of a hornwort (**Anthocerotopsida**), expelling sperm. Photo by Hatice Ozenoglue Kiremit, with permission.

Origin of Bisexuality in Bryophytes

As already noted, the number of dioicous species of bryophytes is greater than the number of monoicous species (Hedenäs & Bisang 2011), with 68% of liverworts, 57% of mosses, and 40% of hornworts being dioicous (Villarreal & Renner 2013a). Longton and Schuster (1983) recognized 205 liverwort taxa as dioicous, 112 as monoicous in New Zealand. In Guatemala, 161 taxa are dioicous compared to 145 monoicous. Une (1986) found 613 (62.2%) of the bryophyte species in Japan were dioicous and 356 (36.2%) were monoicous. This prevalence of dioicous taxa is an unusual situation among plants and raises questions about its significance. The switch to monoicy has previously been suggested to be a derived character in bryophytes (but see below under Monoicy as a Derived/Advanced Character?), and in many genera it drives speciation through doubling of some or all of the chromosomes. One must then ask, how do so many dioicous taxa survive and spread?

Monoicy as a Derived/Advanced Character?

Ando (1980) suggested seven reasons to consider monoicy as advanced over dioicy in bryophytes, based on concurrent knowledge on bryophyte systematics, distributions, and life histories:

1. Frequently the strain with the haploid chromosome number is dioicous and the monoicous one is diploid.
2. Monoicous taxa seem to have more limited distribution, despite their higher frequency of producing sporophytes and spores.
3. Bryophytes of specialized, more recent habitats such as on decaying wood or living leaves of tracheophytes include many monoicous taxa.
4. Taxa with small gametophytes are more commonly monoicous.
5. Most annual bryophytes are monoicous, e.g. Ephemeraceae, Funariaceae, and Splachnaceae.
6. More advanced groups such as Marchantiales and Anthocerotophyta include many monoicous taxa. [This statement does not fit with 2016 thinking about the phylogenetic position of these groups.]
7. Monoicous taxa have several means to prevent self-fertilization and may have evolved by hybridization.

This suggested direction of evolution is in line with the recent study in hornworts, discussed below, which revealed a transition rate from dioicy to monoicy that was twice as high as in the opposite direction (Villarreal & Renner 2013a, b). Devos and coworkers (2011) consider genetic history in their treatise on the evolution of sexual systems in the mostly epiphytic liverwort genus ***Radula*** (Figure 46). They also found that shifts from dioicy to monoicy in that genus occurred multiple times, with some epiphytes having facultative shifts.

However, recent studies using modern comparative phylogenetic analyses and large scale phylogenies of mosses (McDaniel *et al.* 2013) and liverworts (Laenen *et al.* 2016) found that transitions in sexuality are biased towards dioicy. Furthermore, they found that there seem to be higher rates of diversification among the monoicous moss taxa than among the dioicous ones. In liverworts, bisexuality evolved multiple times. It is nonetheless associated with certain clades in the liverwort tree, which suggests that it might be a response to environmental conditions (Laenen *et al.* 2016). The distinct phylogenetic signal in sexual systems across the liverwort phylogeny contrasts with the high lability of sexual systems in mosses and hornworts. McDaniel and coworkers (2013) suggest that dioicy works best when separate sexes derive some advantage in their different morphologies.

Figure 46. ***Radula complanata*** growing epiphytically and exhibiting numerous sporophytes. Photo by David Holyoak, with permission.

One might look for these dioicy advantages in genera such as ***Diphyscium*** (Figure 47) where males and females have very different morphologies, or in those taxa with **dwarf males** (See Dwarf Males in Chapter 3-3). But even more likely are sexual differences in physiology – phenomena that have barely been explored (see discussions for ***Syntrichia caninervis*** and ***Marchantia inflexa*** in section on Environmental and Geographic Differences in Chapter 3-2).

Figure 47. ***Diphyscium foliosum*** females with capsules surrounded by perichaetial leaves and photosynthetic males (green leaves in foreground). Photo by David T. Holyoak, with permission.

It seems that it still remains for us to unravel the selection pressures and evolutionary processes behind this dioicous phenomenon, but this unravelling is promising with current molecular techniques. It is likely that further phylogenetic analyses as well as the thorough study of genome evolution will shed light on the evolution of sexual systems in bryophytes (Crawford *et al.* 2009; Laenen *et al.* 2016; McDaniel & Perroud 2012; McDaniel *et al.* 2013; Villarreal & Renner 2013a, b).

Multiple Reversals

The hornworts (**Anthocerotophyta**) are unique in many ways, and among these are their sexual systems. Villarreal and Renner (2013a, b) contend that hornworts underwent numerous transitions between dioicy and monoicy, with a transition rate from dioicy to monoicy that was twice that from monoicy to dioicy. But a seemingly strange occurrence is that monoicous groups of hornworts have higher extinction rates. This might be explained by the fact that in the hornworts, diversification rates do not correlate with higher ploidy levels as they do in some mosses (*e.g.* Lowry 1948 for **Mniaceae**). Rather, in hornworts polyploidy in monoicous taxa is rare, occurring in only one (***Anthoceros punctatus***, Figure 48-Figure 49) of 20 species that have been assessed (Villarreal & Renner 2013a). Crawford *et al.* (2009) consider the evidence for simultaneous transitions in chromosome ploidy numbers and sexual systems to be inconclusive in mosses as well. And in liverworts, only about 5% of the species are polyploid whereas 30-40% of the species are monoicous (Fritsch 1991 in Laenen *et al*. 2016).

Figure 48. ***Anthoceros punctatus*** with sporophytes. Photo by Des Callaghan, with permission.

Villarreal and Renner (2013a) examined the sexual systems of 98 of the 200 known species of hornworts. Knowing that a relationship between dioicy and small spores exists in mosses, they looked for a similar relationship in hornworts. Using Bayesian techniques, they found at least a weak support for this correlation in hornworts. More to the point, they showed that the sexual system depends on spore size, but that the reverse relationship is not true. They reasoned that dioicous species would be more successful with small spores by providing dense carpets of gametophytes for reproduction. It would seem that this character also permits them to occupy their disturbed and ephemeral habitats where they can thrive without competition.

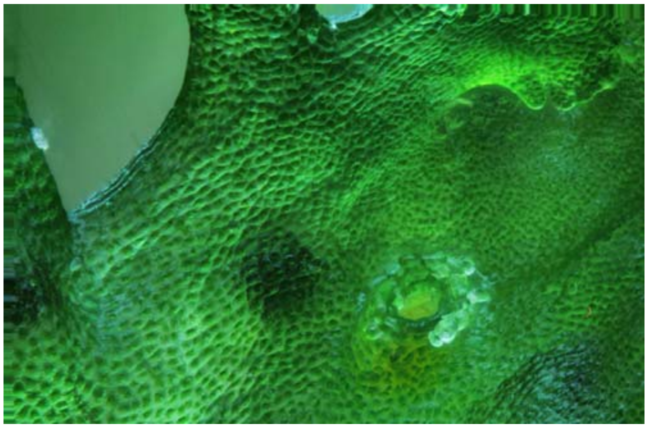

Figure 49. ***Anthoceros punctatus*** antheridial pit. Note the bluish *Nostoc* colony to the left of the antheridial pit. Photo by Des Callaghan, with permission.

The Monoicous Advantage

The effects of these oicy differences on bryophyte ecology and biology are impressive for this gametophyte-dominant group. As in other plants, monoicous species might appear at a competitive advantage, as all individuals in a population can potentially produce offspring. Moreover, monoicous species in general also reproduce by spores more frequently than do dioicous taxa (Longton & Schuster 1983), although this is not always the case. In 1950, Gemmell published vice-county records for the sexual condition of British mosses, using Dixon's The Student's Handbook of British Mosses, and supported the concept that mosses with the monoicous condition are more successful at producing capsules than those of the dioicous condition (Figure 50). Although a much higher percentage (97% compared to 58% in dioicous taxa) of the monoicous group has capsules frequently (Figure 50), presumably because of greater opportunity for fertilization, the dioicous group occupies a greater proportion of the vice-county observations compared to the number of monoicous species (Figure 51).

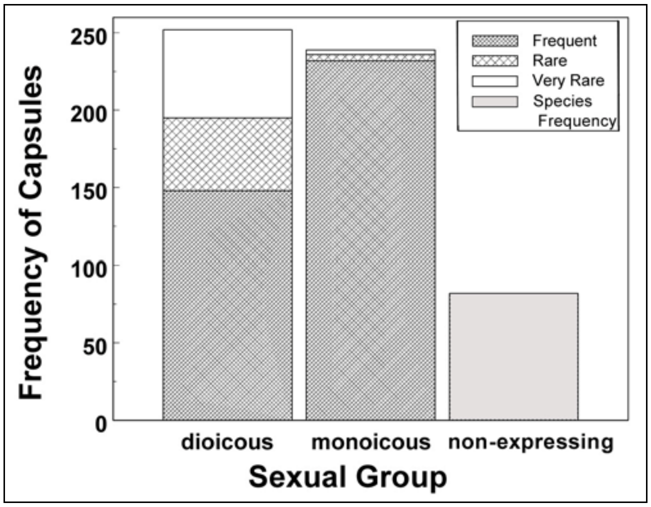

Figure 50. Frequency of producing capsules in dioicous and monoicous mosses and frequency of non-expressing species in vice-counties of Great Britain. The total number of species is 573, and the bars represent the relative frequency of the three types. Based on table in Gemmell 1950.

Heegaard (2001) illustrates the problem of dioicy in ***Andreaea*** (Figure 52-Figure 55). Both monoicous and dioicous species occur in western Norway, permitting us to compare genetically similar sibling taxa from a limited geographic range. The only dioicous species, ***Andreaea blyttii*** (Figure 52), had a lower percent (38%) of sporophytes on cushions bearing **perichaetia** (leaves surrounding archegonia) than did the three monoicous taxa (60-86%). Nevertheless, even among monoicous taxa, ***A. nivalis*** (Figure 53) and ***A. obovata*** var. ***hartmannii*** (Figure 54) rarely produced capsules. The production of capsules in monoicous ***A. rupestris*** var. ***rupestris*** (Figure 55) was highly correlated with the environment, with one group having capsule production that was strongly correlated with altitude and slope, corresponding with **perichaetial** development, and a second group where there was no correlation with perichaetial development, but sporophyte production correlated with gradients of flushing and snow cover. Yet another group produced sporophytes throughout its environmental range. Coordination between the sexes for timing of formation and maturation of the sexual structures, influenced by the environment, could add to the problems of both monoicous and dioicous taxa.

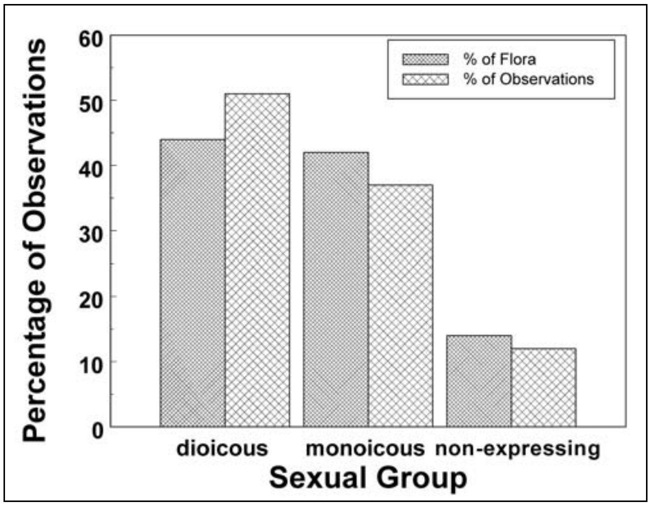

Figure 51. Effect of sexual group on relative frequency of bryophytes in British vice-counties. Total number of species is 573. Percent of flora was obtained by dividing number of species in the category by total number of species. Percent of observations was obtained by dividing total number of vice-county observations by number of species in the category and converting to percent. Based on table in Gemmell (1950).

Figure 52. ***Andreaea blytii*** at Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.

Figure 53. ***Andreaea nivalis*** in Europe. Photo by Michael Lüth, with permission.

Figure 54. ***Andreaea obovata*** (the dark-colored moss) at Akisko, Sweden. This population lacks capsules, as indicated by the smooth black color. Photo by Dale Vitt, with permission.

Figure 55. ***Andreaea rupestris*** with capsules. Photo by Michael Lüth, with permission.

In comparing taxa that commonly produce capsules, Longton and Schuster (1983) reported only 22 British dioicous mosses, compared to 134 monoicous taxa, commonly have capsules; 154 dioicous taxa rarely or very rarely have capsules, compared to 12 monoicous taxa. It is apparent, then, that factors other than sexual reproduction contribute to the success of dioicous taxa.

Nishimura and Une (1989) examined sporophyte production in **pleurocarpous** mosses (horizontally growing taxa with reproductive organs on short side branches; Figure 56) of the Hiruzen Highlands in Japan. Out of 22 **autoicous** (monoicous with antheridia and archegonia in different clusters) species, 20 produced sporophytes (91%). However, out of 49 dioicous species, including 5 with **dwarf males** (**phyllodioicous** – see Dwarf Males in Chapter 3-2), only 27 produced sporophytes (55%). Studies like this suggest that there is a sexual reproductive advantage to being monoicous. But they still beg the question of better survival.

One possible consequence of being dioicous and spreading to new locations is the total absence of sporophytes for some species in part of their geographic range. This appears to be the case for the entire genus of ***Sphagnum*** in California, USA (Carl Wishner, Bryonet 14 August 2012; Norris & Shevock 2004). McQueen and Andrus (2007), in Flora of North America vol. 27, report that most, if not all, of the species known from California are dioicous. Yet, for the typically dioicous ***Sphagnum russowii*** (Figure 57), Shaw *et al.* (2012) report that some specimens are apparently monoicous. The common presence of sporophytes for some California species [*e.g.* ***S. capillifolium*** (Figure 58), ***S. angustifolium*** (Figure 59)] when they occur elsewhere suggests that there may be a **founder principle** at work (Carl Wishner, Bryonet 14 August 2012) wherein only one sex arrived to colonize a particular location. This was also suggested for ***S. palustre*** (Figure 60) in Hawaii where sporophytes are not known to occur (Karlin *et al.* 2012). But without genetic evidence, we cannot rule out the possibility of a climate that is not suitable for expression of one of the sexes or that makes the two sexes mature at different times.

Herbarium records are frequently the basis for descriptions of bryophytes and frequency of sporophytes. One must view herbarium collection records for such factors as male:female ratios and sporophyte production with caution, however, due to collection bias. As Harpel (2002) demonstrated for bryophytes collections for the western U.S., bryologists are more likely to collect the unusual, creating a bias toward over-collecting the rarer species and those with capsules, while ignoring the common.

Figure 56. ***Plagiothecium denticulatum***. Photo by Bob Klips, with permission.

Figure 57. ***Sphagnum russowii*** in Europe. Photo by Des Callaghan, with permission.

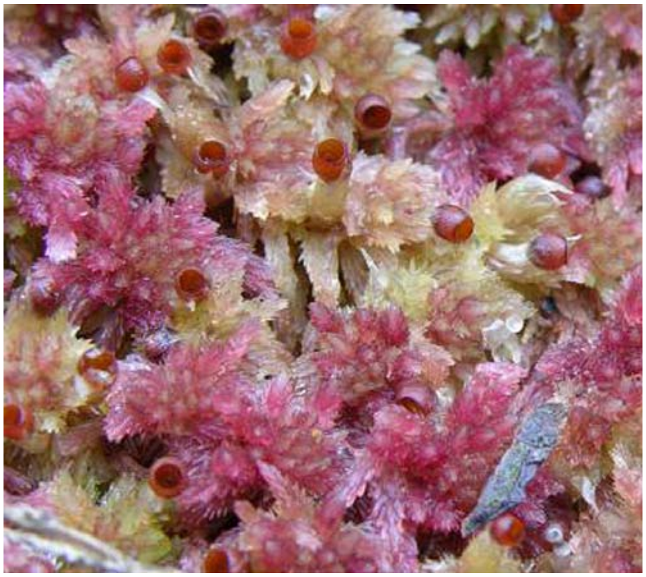

Figure 58. ***Sphagnum capillifolium*** in Chile, showing capsules. Photo by Juan Larrain, with permission.

Figure 59. ***Sphagnum angustifolium*** in Europe. Photo by Michael Lüth, with permission.

Figure 60. ***Sphagnum palustre*** in Europe. Photo by Michael Lüth, with permission.

Stark (1983) suggests that monoicy is advantageous in the desert because of limiting water supplies. However, when he tested the hypothesis in the field in New Mexico, USA, he was unable to support the hypothesis (Stark & Castetter 1987). As found by others, Stark and Castetter found patterns of monoicy correlation with sporophyte production. Nevertheless, Stark considers that at the species level, monoicy provides advantages in the desert habitat.

Or the Dioicous Advantage?

To their potential detriment, monoicous taxa frequently experience **selfing** (being fertilized by sperm from the same plant; see Reproductive Barriers in Chapter 3-4), despite having neighbors that can produce gametes of the opposite sex (Eppley *et al.* 2007). This results in significantly fewer heterozygous fertilizations than that found in dioicous taxa. Furthermore, these monoicous near-neighbors typically belong to the same clone, produced through vegetative reproduction, or have developed from spores from the same parent. This results in a deficiency of heterozygous sporophytes among monoicous taxa. Could it be that the heterozygous condition might itself drive the "mistakes" that result in having two sex chromosomes in one spore, resulting from a misalignment of chromosomes during meiosis? This would drive the bryophytes toward monoicy.

As suggested for the California ***Sphagnum*** species (see The Monoicous Advantage above), total absence of the opposite sex in dioicous taxa can force species to survive vegetatively in many isolated regions and margins of distribution. Because of the success of **vegetative propagation** (reproduction by asexually produced pieces or branches of the plant) (Figure 61-Figure 62), entire single-sex populations of dioicous taxa may exist and expand over large areas without ever producing capsules. Such is often the case with aquatic taxa like ***Fontinalis*** (Figure 63) and in parts of its distribution for ***Pleurozium schreberi*** (Figure 64) (Longton & Greene 1969).

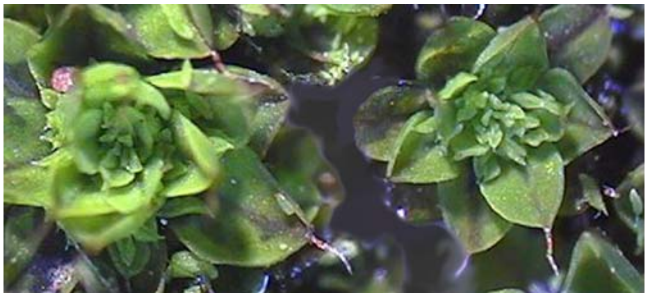

Figure 61. ***Syntrichia pagorum*** exhibiting **gemmae**. These are one means of asexual reproduction. Photo by Paul Davison, with permission.

Figure 62. **Gemma** of ***Syntrichia pagorum***, illustrating its very papillose cells. Photo by Bob Klips, with permission.

Figure 63. ***Fontinalis duriaei*** showing its flowing growth of a single clone. It is unlikely a female in this position would ever get fertilized and produce capsules unless a male clone became intermixed. Photo by Janice Glime.

Figure 64. ***Pleurozium schreberi***, seen here with capsules in Baraga County, Michigan, USA, is barren northward in Ontario where apparently only one sex exists. Photo by Janice Glime.

As a result of being dioicous it may be possible to harbor more genetic variation than that of monoicous species. Both mating systems permit species to reproduce asexually by **ramets** (individual members of clone, arising vegetatively), but the greater percentage of species with asexual diaspores permits those dioicous species to carry non-functional or non-lethal genes as potential pre-adaptations without the selection step that often occurs during failed pairing in meiosis.

Shaw (1991) found that the monoicous moss ***Funaria hygrometrica*** (Figure 30) never had heterozygous sporophytes for 14 allozyme loci, *i.e.*, it had a high level of heterozygote deficiency. The dioicous moss ***Polytrichum juniperinum*** (65), on the other hand, had extremely high levels of heterozygosity based on six allozyme loci (Innes (1990).

In short, monoicous taxa do not always gain the advantages of cross-breeding, although their chances for cross-breeding may in some cases be equal to or greater than that of dioicous taxa. This cross-breeding opportunity assumes that spores of another genotype of a monoicous taxon have equal chances of germinating and growing near that taxon compared to spores of a dioicous taxon growing close enough for fertilization of a plant of the opposite sex of that taxon.

65. ***Polytrichum juniperinum***, a dioicous moss shown here with prolific capsule production. Photo by Daniel Mosquin, through Creative Commons.

In fact, the opportunities for cross fertilization in monoicous taxa should be greater than those of dioicous taxa because any spore of the species that germinates near another of the same species should be able to cross with it, whereas the dioicous taxon must have a pair of sexes. On the other hand, if the archegonia of a monoicous taxon lack any protection against self-fertilization, their own sperm have the greater chance of reaching them due to the shorter distances. Thus, taxa of both mating systems have opportunities for different individuals nearby to fertilize them. At present we do not have enough data to generalize about the numbers of cross-fertilizations that occur in monoicous taxa. Due to the higher number of total successful fertilizations, monoicous taxa have much better dispersal through spores, increasing the possibility of a different genotype nearby and providing it a source of cross-fertilization. The likelihood of cross-fertilization with a different genotype in both sexual strategies is complicated by arrival times, competition, leakage of inhibitory substances, and the degree of self-incompatibility (See Chapter 3-4 in this volume). But dioicous taxa have the advantage of more frequent asexual reproduction and guaranteed mixing of genes when they do reproduce sexually, creating the variability for the species to survive throughout environmental changes.

Origins of Polyploidy

The monoicous condition in mosses may be the result of **polyploidy** (in bryophyte gametophytes, having more than one complete set of chromosomes). Polyploidy is a common occurrence among plants, being rare only among the gymnosperms (Ahuja 2005). Bryophytes seem to have multiple avenues by which to become polyploids. This increase in ploidy is often considered to make the monoicous condition possible by providing an extra set of chromosomes. But in this group where sex chromosomes have been identified in at least some species, the understanding of how all of these possible origins work is complex. See Monoicy as a Derived/Advanced Character? above and examples below.

Sporophytes from Fragments

It is still unclear how the majority of monoicous taxa arose. We know that it is possible in the lab to grow 2*n* (**diploid**) protonemata and leafy gametophores from bits of sporophyte tissue, producing monoicous plants (Crum 2001). Marchal and Marchal (1907, 1909, 1911) grew nineteen species of diploid moss gametophytes from setae in the lab. Since then, many others have succeeded in producing diploid moss gametophytes without spores (Crum 2001). Lorbeer (1934) induced diploid gametophytes from capsules and setae in 52 species of liverworts. But this development of sporophyte tissue into a gametophyte has been observed only once (***Funaria hygrometrica***, Figure 26-Figure 30) in nature (Brizi 1892; Crum 2001).

Sporophytes have also been developed from gametophyte tissues. The first was produced as outgrowths from 2*n* leaves and stem tips of ***Tortula acaulon*** (=*Phascum cuspidatum*) (Marchal & Marchal 1911; Springer 1935). These were initially misinterpreted by Marchal and Marchal as asexual reproductive structures, but later Springer (1935) interpreted them as apogamous sporophytes. These seemed to be the result of altered, mostly dry, conditions. However, these pseudosporophytes failed to produce normal capsules and never produced spores. More recently El-Saadawi *et al.* (2012) discovered what appears to be an apogamous sporophyte – one that lacks any evidence of an archegonium at its base, in ***Fissidens crassipes*** subsp. ***warnstorfii*** (Figure 66). It likewise never produced spores. It originated at the base of the stem, whereas this species normally produces its sporophytes at the apex.

It is unlikely that these vegetative anomalies have contributed much, if any, to the creation of monoicous taxa. On the other hand, the accidental fusion of haploid gametophyte cells other than gametes can result in capsules with at least some viable spores. This suggests that cases might exist where cells join but remain as gametophyte, possibly becoming polyploid monoicous plants.

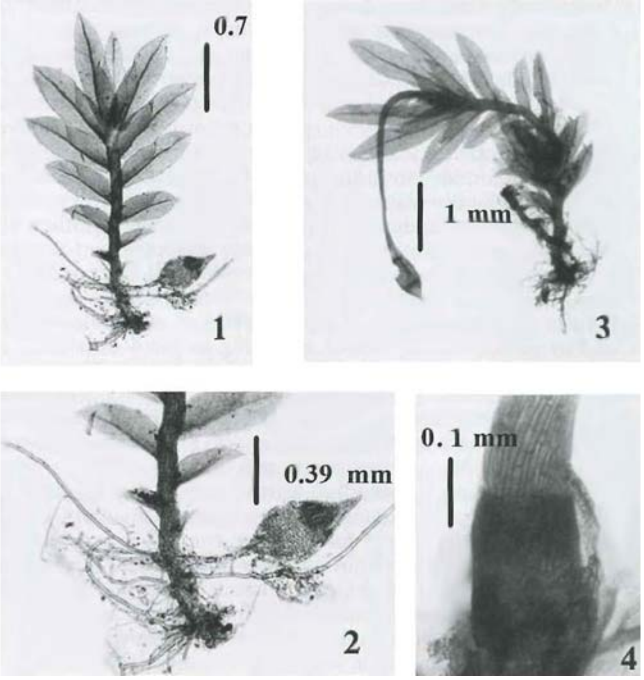

Figure 66. ***Fissidens crassipes*** showing an apogamous sporophyte (**1 & 2**) compared to a normal sporophyte (**3**) and the vaginula at the base of the normal sporophyte (**4**), but absent on the apogamous sporophyte. Photo from El-Saadawi *et al.* (2012). Permission pending.

Genome Doubling in Mosses

Genome doubling seems to occur commonly in mosses [76% polyploidy (Przywara & Kuta 1995)], but seemingly less often so in hornworts (Villarreal & Renner 2013a) and liverworts [10% (Newton 1983); 5% (Fritsch 1991 in Laenen *et al.* 2016) (this can include ancient polyploidism and subsequent chromosome loss). Polyploidy might be coupled with a change in sexual system from dioicous to monoicous, but not necessarily so (Jesson *et al.* 2011). Both **autopolyploidy** (self-doubling of chromosomes within a single bryophyte) and **allopolyploidy** (**hybridization**) are known to be present among bryophytes in nature (Natcheva & Cronberg 2004; see also 3.4, Hybridization).

Autopolyploids – Although **autopolyploidy** was once considered the primary source of polyploidy in mosses (Boisselier-Dubayle & Bischler 1999), this may not be the case. Košnar *et al.* (2012) were able to use genetic markers to demonstrate autopolyploid origin of several lineages in the ***Tortula muralis*** (Figure 67) complex, making them the first group of mosses in which autopolyploidy was demonstrated with molecular markers. Google Scholar, when searched for bryophyte autopolyploidy, listed mostly allopolyploidy references. In one species that does exhibit autopolyploidy, ***Targionia hypophylla*** (Figure 68), its triploidy seems to actually be a combination of autopolyploidy and allopolyploidy (Boisselier-Dubayle & Bischler 1999).

Figure 67. ***Tortula muralis*** with capsules. Photo by Derek Christie, with permission.

Figure 68. ***Targionia hypophylla*** showing black marsupial pouches that house the archegonia and sporophytes. Photo by Martin Hutten, with permission.

Allopolyploids – allopolyploids can be achieved by **hybridization** (crossing of non-identical genomes, as in a different strain or species) and has been demonstrated in a number of bryophyte species. For example, Wyatt *et al.* (1988, 1992) showed that ***Plagiomnium medium*** (**Mniaceae**; Figure 69) arose from a cross between ***Plagiomnium ellipticum*** (Figure 70) and ***Plagiomnium insigne*** (Figure 71-Figure 72), resulting in **allopolyploids** (having two or more complete sets of chromosomes that derive from more than one species). Not only did it happen, but it happened multiple times! ***Plagiomnium cuspidatum*** (Figure 73-Figure 75) is likewise an allopolyploid, but one of its parent species is unknown (Wyatt & Odrzykoski 1998). ***Cinclidium stygium*** (Figure 76) (n=14), also a member of **Mniaceae**, is a monoicous polyploid closely related to ***C. arcticum*** (Figure 77) and ***C. latifolium*** (Figure 78), both having n=7 (Wyatt *et al.* 2013). ***Cinclidium stygium*** appears to have an **allopolyploid** origin from these two close relatives. Also ***Cinclidium subrotundum*** (Figure 79) is a monoicous polyploid (n=14) that exhibits strong evidence for allopolyploidy, having 7 fixed heterozygous loci out of 17 scored (Mogensen 1973).

Figure 69. ***Plagiomnium medium***. Photo by Jan-Peter Frahm, with permission.

Figure 70. ***Plagiomnium ellipticum*** Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.

Figure 71. ***Plagiomnium insigne*** male splash cup. Photo from Botany 321 website, UBC, with permission.

Figure 72. ***Plagiomnium insigne*** female with sporophytes. Photo from Botany 321 website UBC, with permission.

Figure 73. ***Plagiomnium cuspidatum*** females with sporophytes. Photo by Michael Lüth, with permission.

Figure 74. ***Plagiomnium cuspidatum*** showing males with black centers containing antheridia and females with green centers. This arrangement fits the dioicous condition discussed by Andrews (1959), not the more typical synoicous condition known for the species. Photo by Betsy St. Pierre, with permission.

Figure 75. ***Plagiomnium cuspidatum*** showing female reproductive structures on left and male splash cup on right. Photo by Betsy St. Pierre, with permission.

Figure 76. ***Cinclidium stygium*** with capsules, a species with *n*=14. Photo by Misha Ignatov, with permission.

Figure 77. ***Cinclidium arcticum*** (*n*=7), a close relative of ***C. stygium*** (*n*=14). Photo by Michael Lüth, with permission.

Figure 78. ***Cinclidium latifolium*** from Spitzbergen, a species with *n*=7. Photo by Michael Lüth, with permission.

Figure 79. ***Cinclidium subrotundum*** from Spitzbergen. Photo by Michael Lüth, with permission.

In cases when monoicous taxa are polyploids developed from dioicous taxa, we could hypothesize that the monoicous taxa should have more variability and thus better survival. Natcheva and Cronberg (2004) report that the spontaneous hybridization among bryophytes is sufficient to have a significant evolutionary significance, with the many allopolyploid taxa supporting this contention. (See Chapter 3-4, Sexuality: Reproductive Barriers and Tradeoffs).

Relationship of Polyploidy and Monoicy in *Atrichum*

In an ***Atrichum undulatum*** (**Polytrichaceae**, Figure 82) complex from a study in New Brunswick, Canada, monoicous plants were either diploid or triploid, with the number of monoicous individuals increasing as the number of triploids increased (Figure 80; Jesson *et al*. 2011). Many diploid populations, on the other hand, were dioicous (Figure 81). Jesson and coworkers found that male and female gametophytes were represented by haploid, diploid, and triploid individuals (Figure 81). Perley and Jesson (2015) examined the association between polyploidy and sexual system further in the genus, including species of different ploidy-levels. In the haploid state, this genus has either a female **U** chromosome or a male **V** chromosome. Using genetic markers, they determined that certain gene sequences are consistent with independent **allopolyploid** origins of **diploid** (2 sets of chromosomes) and triploid (3 sets of chromosomes) species. In the **triploid *Atrichum undulatum*** (Figure 82-Figure 84), and possibly the diploid ***A. altecristatum*** (Figure 85-Figure 86) as well, hermaphroditism appears to be a result of allopolyploidy. However, in the diploid ***A. crispulum*** (Figure 87), this allopolyploid event did not result in the hermaphrodite condition. This tells us again that the creation of monoicy (hermaphroditism) is more complex than simply doubling the chromosome number. (See more in Chapter 3-4, Reproductive Barriers: Selfing and Hybrids.)

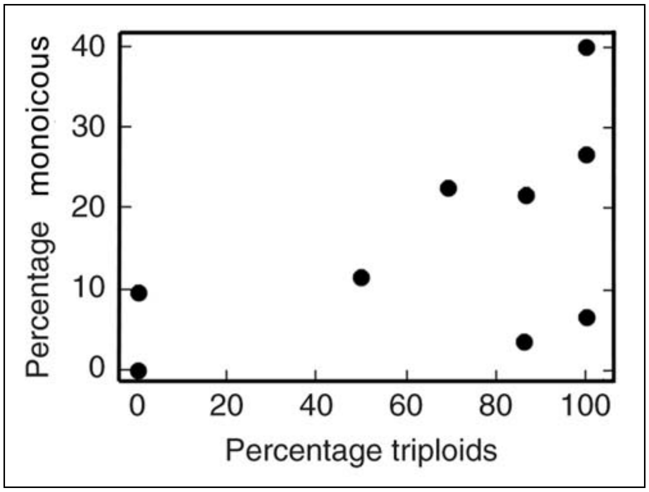

Figure 80. Relationship between percentage of triploid individuals and monoicism in 21 randomly sampled populations of the ***Atrichum undulatum*** complex in New Brunswick, Canada. Five populations were not sampled for ploidy determination. Eight populations exhibited no hermaphrodites and no triploids. Modified from Jesson *et al.* 2011.

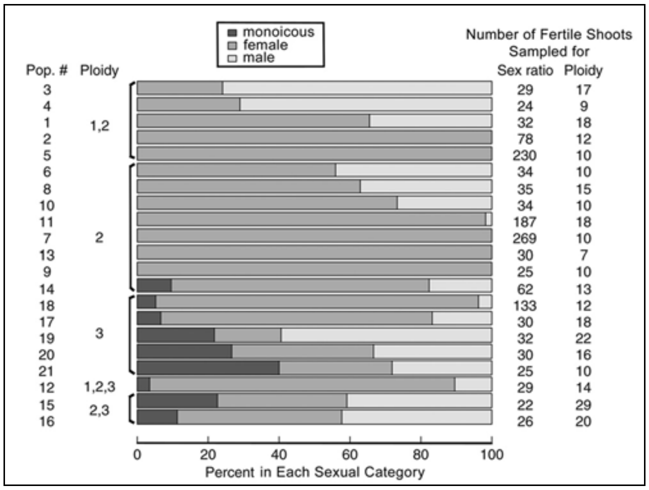

Figure 81. Percentage of individuals in each of three sexual categories in 21 populations of the ***Atrichum undulatum*** complex in New Brunswick, Canada. Column on right indicates the number of individuals in random samples for determining sex ratio and those used for determining ploidy. Modified from Jesson *et al.* 2011.

Figure 82. Female plants representative of the ***Atrichum undulatum*** complex, a group of taxa that may be monoicous or dioicous. Photo by Janice Glime.

Figure 83. ***Atrichum undulatum*** males. Photo by Janice Glime.

Figure 84. ***Atrichum undulatum*** females with capsules. Photo by Andrew Hodgson, with permission.

Figure 85. ***Atrichum altecristatum*** males. Photo by Bob Klips, with permission.

Figure 86. ***Atrichum altecristatum*** capsules. Photo by Bob Klips, with permission.

Figure 87. ***Atrichum crispulum*** capsules. Photo by Robert Klips, with permission.

Pseudodioicy

As its name implies, **pseudodioicy** is a condition which appears to have separate sexes, but in fact they originate from one plant with separate sexual branches. The best known examples of the pseudodioicous condition typically arise when a male branch breaks off or becomes separated by decay. However, that male branch typically remains in proximity of the original plant, which often appears to be only female. The second type is more difficult to observe and can arise when male and female buds from a protonema become separated, causing separate plants to form.

The first record of pseudodioicy I could find is that of Barnes (1887). He noted the condition in ***Fissidens closteri*** (Figure 88), ***F. incurvus*** (Figure 89), and ***F. pallidinervis*** (Figure 90). He described ***F. closteri*** as male gemmiform, attached to the female by rhizoids or separate. For ***F. incurvus***, he writes "male gemmiform, at the base of stems from which they sometimes separate." For ***F. pallidinervis***, he hedges and says "probably pseudodioicous."

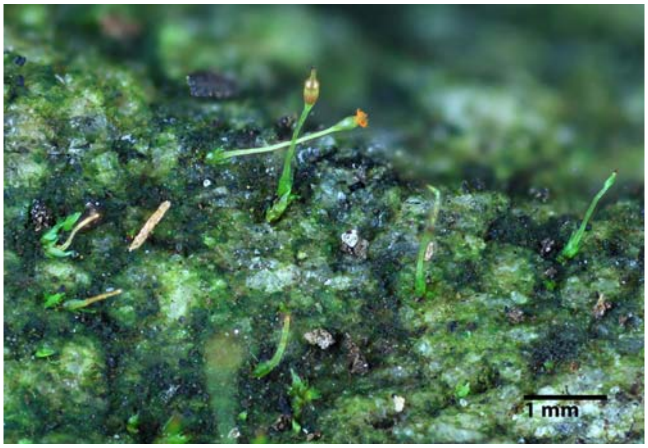

Figure 88. ***Fissidens closteri***, a species with pseudodioicy. Photo by Ken McFarland and Paul Davison, with permission.

Figure 89. ***Fissidens incurvus***, a species with pseudodioicy. Photo by Jan-Peter Frahm, with permission.

Figure 90. ***Fissidens pallidinervis*** with capsules, a species with pseudodioicy. Photo by Frederick B. Essig, with permission.

Fissidens seems to have the most recorded observations of the pseudodioicous condition. Hill (1907) reported that ***F. minutulus*** (Figure 91) had male "flowers" that form little stems among the rhizoids of fertile plants. As the plants age, the connection with the parent plant ceases to exist. Hill suggested that male organs may start in the leaf axils of fertile stems as buds, later becoming independent. Whittier and Miller (1967) described ***Fissidens mangarevensis*** (Figure 92) from the Society Islands as sometimes being pseudodioicous, but they found no antheridia to verify that.

Figure 91. ***Fissidens minutulus***, a species with pseudodioicy. Photo by Jan-Peter Frahm, with permission.

Figure 92. ***Fissidens mangarevensis***, a species with pseudodioicy. Photo by Yang Jia-dong, through Creative Commons.

The fascinating cave moss ***Schistostega pennata*** (Figure 93) likewise can be pseudodioicous (Mežaka *et al.* 2011). Jeff Duckett (pers. comm. 3 December 2019) tells me he has confirmed this in freshly collected material. Hill *et al.* (1994) describe it as pseudodioicous with male and female plants arising separately from the same protonema. Thus, this species fits the second type of pseudodioicy. It is likely that this separation occurs frequently in species with male and female buds on one protonema, but it is difficult to document, and it is likely that these species have been treated as dioicous, as is the case for ***S. pennata*** in Crum's 1983 description.

Other cases of pseudodioicy have been reported in both leafy and thallose liverworts. Some of these are guesses, based on finding what appear to be both autoicous and dioicous plants, as in the leafy liverwort ***Lophonardia jamesonii*** (Vána & Watling 2004).

Several thallose liverworts become pseudodioicous when the thallus decays from its base and leaves male and female gametangia in separate thalli. Such is the case for ***Reboulia hemisphaerica*** (Figure 94) (Puglisi *et al.* 2018). In this species the branches can also be easily separated by age, but also during preparation. ***Mannia californica*** (Figure 95) can produce its gynoecia on ventral branches, but at least in Japan, terminal autoicous female branches occur (Borovichev *et al.* 2014). Decaying thallus bases make the species appear to be dioicous, but they are in fact pseudodioicous. Among Canadian specimens of ***Metzgeria conjugata***, Brinkman (1931) found several pseudodioicous specimens in this monoicous species. Borovichev *et al.* (2012) described pseudodioicous plants of ***Sauteria alpina*** (Figure 96) from Russia, earlier described from Greenland by Schuster (1992).

Figure 93. ***Schistostega pennata*** capsules, a species with pseudodioicy. Photo by Martin Hutten, with permission.

Leafy liverworts also exhibit this trait among several species. ***Cephaloziella crassigyna*** can be found in an autoicous or pseudodioicous state (Beveridge *et al.* 2017). Watson (1913) reported that Macvicar considered ***Cephalozia lammersiana*** as pseudodioicous; the taxonomic affinities of the species were unclear, but it does seem to represent the condition in some specimens of ***Cephalozia***.

Figure 94. ***Reboulia hemisphaerica*** male and female reproductive structures. Branches with only one of these can become separated through thallus decay. Photo by Bob Klips, with permission.

Figure 95. ***Mannia californica*** showing thallus fragments with archegoniophores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University (permission from Russ Kleinman & Karen Blisard).

Figure 96. ***Sauteria alpina***, demonstrating decay of older parts of the thallus that can separate branches with female reproductive structures from those of male structures. Photo by Hermann Schachner, through Creative Commons.

Polyploidy and Spore Size

Stebbins (1950) concluded that cell size of constant-form cells such as spores was the best indicator of hybridization and polyploidy in plants. We know from studies in ferns that polyploidy can result in larger cells (Lawton 1932). Subsequent studies indicated a similar relationship in spores size in ferns (Hagenah 1961; Wagner 1966; Schneller 1974). Kott and Britton (1983) suggested that spore size could be used to characterize a species as long as at least 20 spores were measured.

But Britton (1968) found that such a correlation does not seem to exist in the fern genus *Dryopteris*, a finding later corroborated by Wagner (1971) for the same genus. Other factors contribute to selection for spore size, making the ploidy relationship unreliable in at least some cases. For example, Carlquist (1966) demonstrated that small spore size increases likelihood of spore dispersal to greater distances, whereas on islands spore size increases because of absence of suitable habitat at greater distances. Barrington *et al*. (1986) noted the absence of statistical data and statistical analyses in studies of spore size-ploidy relationships. Voglmayr (2000) demonstrated, using 138 different moss taxa, that variation in DNA contents has a much lower range of variation than that of tracheophytes (12-fold compared to 1000-fold). However, the possible correlation of spore size and ploidy level does not seem to be explored in bryophytes.

So what evidence do we have that bryophytes exhibit any relationship of larger spores in polyploid individuals? I decided to examine the possibilities in the **Mniaceae**, a family known to have polyploid species. I was not surprised to find a complicated relationship (Table 1).

Although these data suggest possibilities, they do not supply the necessary link between spore size and chromosome number. Furthermore, as Des Callaghan reminded me, descriptions often fail to indicate true variation. Spore sizes vary a lot; he recommended a mean of 50 spores (10 spores from a capsule and five capsules from different populations).

Table 1. Comparison of spore size with number of chromosomes in several genera of **Mniaceae** in the Great Lakes region of North America (from Crum 1983).

Species	**Spore Size**	**Number of Chromosomes**
Mnium stellare	20-29 µm	n=6 + m, 7
Mnium lycopodioides	19-29 µm	n=6
Mnium marginatum	22-32 µm	n=12
Mnium thomsonii	20-31 µm	n= 6, 8
Mnium spinulosum	28-21 µm	n=8
Plagiomnium cuspidatum	24-31 µm	n=6, 12
Plagiomnium drummondii	18-24 µm	n=6
Plagiomnium affine	26-29 µm	n=6
Plagiomnium medium	24-29 µm	n=12
Plagiomnium rostratum	22-33 µm	n=7, 12, 14, 21
Pseudobryum cinclidioides	31-40 µm	n=6,7
Rhizomnium punctatum	29-41 µm	n=6, 7; 2n=14
Rhizomnium pseudopunctatum	28-48 µm	n=13-14

Variation within a species can be enormous. For example, within ***Cinclidium stygium*** (Figure 76), spore size may range from 31-68 µm within the same capsule, with a ploidy number of n=14 (Crum 1983). Mogensen (1981) demonstrated that multiple spore sizes can occur in the same capsule in mosses, and Glime and Knoop (1986) showed that in ***Fontinalis squamosa*** (Figure 97) two spore sizes can be present in the same capsule (Figure 98-Figure 99), apparently resulting from arrested development and progressive death of spores. The latter phenomenon can make more space for the remaining spores and perhaps permit them to develop to a larger size before leaving the capsule.

This leaves us with little to suggest whether more chromosomes, *i.e.* a higher ploidy number, would result in larger spores in bryophytes, adding this to the many questions still unanswered about bryophytes.

Figure 97. ***Fontinalis squamosa*** at Cwm Idwal National Nature Reserve. Photo by Janice Glime.

Figure 98. ***Fontinalis squamosa*** spores showing healthy, green spores, pale, aborting spores, and small, aborted spores. Photo by Janice Glime.

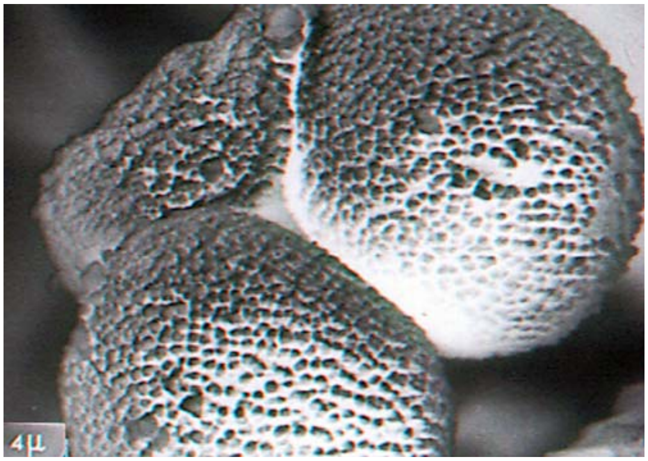

Figure 99. ***Fontinalis squamosa*** tetrad showing abortion already beginning. Photo by Janice Glime.

Cross Fertilization

Certain mixing of genes results from cross fertilization, a condition widely accepted among botanists as providing genetic variability and greater chances for the species to survive changing conditions. For sexual reproduction to be successful, the sperm must reach the egg. For bryophytes, this could be an easy task in **synoicous** taxa (monoicous with antheridia and archegonia in same cluster), but quite difficult in dioicous taxa. (See above in The Monoicous Advantage.)

Some bryophytes can alter their life cycle depending on the density of the population – a strategy reminiscent of maple (*Acer*) trees. The moss ***Tetraphis pellucida*** reproduces asexually with gemmae at low densities and has a female-biased sex ratio (Kimmerer 1991). As the density increases, there is an increase in sexual reproduction and sporophyte production. The proportion of males also increases as the population size increases, but this greater density also causes the onset of senescence. The strategy is beneficial to a species such as this that lives in unstable or short-lived environments.

Sperm Dispersal

Sperm transfer is a problematic aspect of fertilization for bryophytes. It must be accomplished wihin the life of the sperm, keep the sperm hydrated, and find an archegonium of the right species at the right maturity stage. A good release mechanism can start the sperm on their journeys.

The release of sperm in bryophytes is not a simple bursting of the antheridial wall with swimming sperm free to travel their own way. Rather, it typically occurs as the release of **spermatocytes** as a mass (Muggoch & Walton 1942). Meanwhile, as water accumulates at the base of the antheridium, it pushes this mass outward and away from the antheridium. As the spermatocytes reach the air-water interface, they spread apart rapidly to form a regular spaced arrangement on the surface. Muggoch and Walton concluded that this spreading and spacing correlated with the presence of fat from the spermatocyte mass. As the fat lowers the surface tension, the spermatocytes gain their freedom and spread. In some bryophytes, such as ***Sphagnum*** and some liverworts, fats seem to be absent and surface spreading likewise is absent. Muggoch and Walton further concluded that it is the surface spreading that makes the sperm susceptible to dispersal by invertebrates in dioicous taxa – a rather astute observation so long before we had actual proof that invertebrate dispersal occurs.

Once freed, the sperm are able to swim rapidly, and if they are near enough they may be attracted to the female gamete chemotactically. Pfeffer (1884) found chemotaxis involved in sperm locating archegonia of ***Marchantia polymorpha*** (Figure 43) and ***Radula complanata*** (Figure 46). Lidforss (1904) found that the proteins albumin, hemoglobin, and diastase were each able to attract sperm of ***Marchantia polymorpha*** to a capillary tube that contained them. Chemotaxis of sperm still needs clear verification and some studies suggest there is no chemotaxis (Showalter 1928). Diversity among the species is likely, but it leaves us with the question of how the sperm finds the archegonium if no attractant is present.

Walton (1943) observed the spreading of sperm in the monoicous thallose liverwort ***Pellia epiphylla*** (Figure 100-Figure 101). In his observations, archegonia were only 5-10 mm from antheridia. Whereas freed sperm in the dioicous liverwort ***Aneura*** (Figure 102) took several hours to travel only 10 mm, those in many moss and liverwort taxa spread rapidly by surface tension over free water at a rate of ~20 mm per minute. Walton found that ***Pellia epiphylla*** sperm behaved like these fast-moving moss and liverwort sperm, extruding in grey masses into water, breaking apart when they reached the surface, and dispersing over the wet surface rapidly. Once released, they were able to reach archegonial involucres in only ~15 seconds. The more lengthy process was emergence of sperm from spermatocytes, which required ~15 minutes. Walton concluded that if the sperm had to swim it would require several hours, but that the surface tension carried them rapidly to their destination. This leaves us with the question of how transfer is accomplished in dioicous taxa with longer distances to traverse.

Figure 100. ***Pellia epiphylla*** with antheridia (brown). Photo by Des Callaghan, with permission.

Figure 101. ***Pellia epiphylla*** with sporophyte. Photo by Malcolm Storey, through Creative Commons.

Figure 102. ***Aneura pinguis*** with capsules, indicating successful sperm transfer. Photo by Jan-Peter Frahm, with permission.

Sperm Travel Distances

One reason for the observed genetic variability in bryophytes is that cross-fertilization may extend greater distances than we had supposed (Table 2). Anderson and Lemmon (1974) considered the maximum distance for sperm to travel in acrocarpous mosses to be 40 mm, with a median dispersal distance of about 5 mm. Pleurocarpous mosses were assumed to have even shorter dispersal distances due to the total lack of splash cups or platforms (see below under Splash Mechanisms) (Anderson & Snider 1982). But as seen in Table 2, known (implied?) distances range up to 230 cm.

Reynolds (1980) found that splashing water on the platforms of the moss ***Plagiomnium ciliare*** (Figure 103) indicated greater travel distance (50+ cm) than that to the nearest male (5.3 cm). In the thallose liverwort ***Marchantia chenopoda*** (Figure 104), fertilization distances seem to range 0.7-65 cm (Moyá 1992), a range that suggests microhabitat factors may play a role in dispersal distance. Differences in dispersal mechanisms can account for wide ranges. Earlier chapters on **Marchantiophyta** and **Bryophyta** have discussed these mechanisms, including splash cups and platforms, flowing water, and arthropods.

Table 2. Maximum known distances for sperm dispersal. Those in bold have splash cups or splash platforms. Distances mostly from Crum 2001.

Splachnum ampullaceum	5-15 mm	Cameron & Wyatt 1986
Breutelia arcuata	2.5 cm	Bedford 1940
Weissia controversa	4 cm	Anderson & Lemmon 1974
Climacium dendroides	7 cm	Bedford 1938
Pleurozium schreberi	10 cm	Longton 1976
Plagiomnium affine	10 cm	Andersson 2002
Atrichum angustatum	11 cm	Wyatt 1977
Abietinella abietina	12 cm	Bisang *et al.* 2004
Anomodon viticulosus	25 cm	Granzow de la Cerda 1989
Hylocomiadelphus triquetrus	34 cm	Bisang *et al.* 2004
Plagiomnium ciliare	50 cm	Crum 2001
Polytrichastrum ohioense	60 cm	Brodie 1951
Marchantia chenopoda	65 cm	Moyá 1992
Polytrichum juniperinum	75 cm	Longton 1976
Ptychostomum (=*Bryum*) *capillare*	200 cm	Gayet 1897
Dawsonia longifolia	230 cm	Crum 2001
epiphytes	2-5 m	Longton & Schuster 1983
Marchantia polymorpha	9 m	Pressel & Duckett 2019

Figure 103. ***Plagiomnium ciliare*** showing male splash cups and horizontal (plagiotropic) branches. Photo by Robert Klips, with permission.

Figure 104. ***Marchantia chenopoda***, with males on **left** and females on **right**. Female archegoniophores elongate after fertilization. Photos by Janice Glime.

Maggot and Walton (1942) demonstrated experimentally that some bryophyte sperm can move 0.1-0.2 mm per second and continue movement for several hours, suggesting they could swim for 35 cm. Rosenstiel and Eppley (2009) and Shortlidge *et al.* (2012) provided further evidence of the possibility of greater sperm dispersal distances based on longevity (see below under Sperm Longevity).

Explosive Help in Thallose Liverworts

As discussed in Chapter 2-3 on **Marchantiophyta**, ***Conocephalum conicum*** (Figure 105) releases its sperm into a mist that makes them airborne (Benson-Evans 1950; Shimamura *et al.* 2008; see Chapter 2-3), suggesting that this could result in greater dispersal distances. Benson-Evans (1950) describes her experience with dried males of this species in the lab, the result of a hot week-end. Upon rewetting, the plants emitted a fine mist. She paid little attention to this until she noticed that "the mist was being emitted from the antheridial heads in regular puffs. Removal into direct sunlight increased the activity and the particles which were being ejected were visible to the naked eye, so that the puffs were obviously composed of distinct granules." A similar "explosion" is known from a number of other Marchantiales taxa (Peirce, 1902; Cavers 1903, 1904a, 1904b; Andersen 1931; Benson-Evans 1950).

Figure 105. ***Conocephalum conicum*** antheridia. Photo by Janice Glime.

Sperm Dispersal Vectors – After Release

Water has been presumed to be the primary dispersal vector in bryophytes. But interesting mechanisms accompany this water dispersal and still others rely on other organisms to accomplish the task.

I have suggested (Glime 1984) that species of the dioicous aquatic moss ***Fontinalis*** could accomplish fertilization when females are wet but above the water level in streams or lake margins. In streams, this would typically be on emergent rocks, and emergent rocks can create water spray. Once released the sperm could then travel in these drops of water to land on the moist female plants. The timing of their gametangial maturation in autumn when plants are often emergent supports this hypothesis. And if splash from the stream is not effective, autumn rains splashing on emergent males could accomplish the mission.

Splash Mechanisms

Bryologists have been interested in the use of splash mechanisms in bryophytes for dispersal of sperm. Clayton-Greene *et al.* (1977) found that both field studies and lab tests support the hypothesis that antherozoids of ***Dawsonia longifolia*** (= *D. superba*; Figure 106) are dispersed by a splash mechanism. They found that females up to 1.5 m from males were fertilized, a distance only slightly less than the distance travelled by water drops released at 3.3 m above the splash cups.

Figure 106. ***Dawsonia longifolia*** male plant with splash cup. Photo by Allan Fife, with permission.

Andersson (2002) used a more sophisticated approach by making a video of splashes of rain on the splash platforms of the moss ***Plagiomnium affine*** (Figure 107). He discovered that a crown forms upon impact of water. Small droplets are propelled away from the rim of this crown. For this to be effective, the diameter of the drop should be 1 mm or less to permit the crown to form, a size common in most showers. Upon impact of the drop, the antheridia rupture. Water fills the capillary spaces between the antheridia and the paraphyses, permitting the spermatozoids to reach the bottom of the splash cup. When the crown forms, it incorporates water from the bottom of the splash cup and hence includes the spermatozoids. These entrapped spermatozoids are ultimately released from the splash cups as the small droplets propel away from the splash cups. Such droplets are known to travel more than 100 mm, fertilizing most of the females within an 80 mm radius.

Among the best known splash platforms among bryophytes is that of ***Marchantia polymorpha*** (Figure 20-Figure 21). But Duckett and Pressel (2009) inform us that the widely told dispersal story is not entirely correct. Traditional description since the accounting by Goebel (1905) has been that fertilization occurs when the archegoniophore stalks are still young and short, at which time the archegonial necks still point upward. The antheridiophores, developing first, tower over these, permitting sperm to travel downward by splashing or dripping during rainfall. But it is likely that the sperm actually disperse as they do in ***Conocephalum conicum*** (Figure 105), discharging into the air up to 15 cm above the antheridial heads (see Sperm Dispersal by the Bryophyte above). This can explain why both Parihar (1970) and Crum (2001) reported that the archegonia continued to be fertilized after the stalk elongated. Furthermore, when female thalli were placed in dye, the coloring reached archegonial heads in 30-60 minutes (Duckett & Pressel 2009), suggesting that capillary action and surface tension movement could carry the water and accompanying sperm from the antheridial splash cups upward to the archegonial heads and archegonia.

Figure 107. ***Plagiomnium affine*** showing splash platforms of male plants. Photo by Janice Glime.

The splash mechanism in the dioicous ***Fontinalis*** (Figure 108) requires a suitable location within a rapid stream. When female plants are elevated above the water and male plants or their rock substrate are obstructing flow to create splash, sperm may be able to go about 2 m (personal estimate based on distance between male plants and females with capsules) in a rocky stream. This takes advantage of the splashing of rapid water, whereas when the antheridia and archegonia are under water, the highly diluted sperm will be swept away, most likely never being able to enter the neck of an archegonium (Goebel 1905).

Figure 108. ***Fontinalis dalecarlica*** with immature, green capsules. This clump is located in a rapid stream where rocks are covered with this species. Photo by Janice Glime.

Invertebrate Dispersal

Clayton-Greene *et al.* (1977) reported on the use by Gayet (1897) of netting over ***Rosulabryum capillare*** to demonstrate that some outside force was needed for fertilization. With fine nets over the plants, fertilization failed, but when the netting was removed, fertilization occurred over distances of 2 m. Although this may suggest that invertebrates were denied access, hence being prevented from fertilizing the females, it does not eliminate the possibility of the netting affecting the splashing of raindrops.

As early as 1927, Harvey-Gibson and Miller-Brown found that the paraphyses (Figure 26) of both males and females in ***Polytrichum commune*** (Figure 109) exuded a mucilage, but that mucilage did not contain any sugars. Nevertheless, **oribatid mites**, **springtails** (**Collembola**), **midges** (**Diptera**), **leaf hoppers** (**Cicadellidae**), **aphids**, and **spiders** visited these structures and lapped up the mucilage. Their body parts carried the mucilage, and thus they might easily have carried the sperm. But this possibility seemed to be ignored by most bryologists until recently.

Figure 109. ***Polytrichum commune*** with capsules. Photo by David Holyoak, with permission.

Cronberg *et al.* (2006) experimentally demonstrated that **springtails** and **mites** were able to transport sperm over distances of up to 4 cm, but it is possible that under the right circumstances transport could be much farther. Rosenstiel *et al.* (2012) also described one of the more remarkable cases of sperm dispersal in the mosses ***Bryum argenteum*** (Figure 110-Figure 111) and ***Ceratodon purpureus*** (Figure 112). These species can have their sperm dispersed from male to female by the springtail ***Folsomia candida*** (Figure 112). Rosenstiel and coworkers showed that the springtails chose significantly more female mosses than male mosses in ***Ceratodon purpureus*** (Figure 113) and that their presence facilitated fertilization (Figure 114). This preference was supported by verifying that the volatile compounds differed between the two sexes in ***C. purpureus*** (Figure 115-Figure 116).

Figure 110. ***Bryum argenteum*** mixed females and males. Note the open brown tips where antheridia are located. Photo by George Shepherd, through Creative Commons.

Figure 111. ***Bryum argenteum*** perigonium, a collection of antheridia that attract invertebrates to facilitate transfer of sperm. Photo by George J. Shepherd, through Creative Commons.

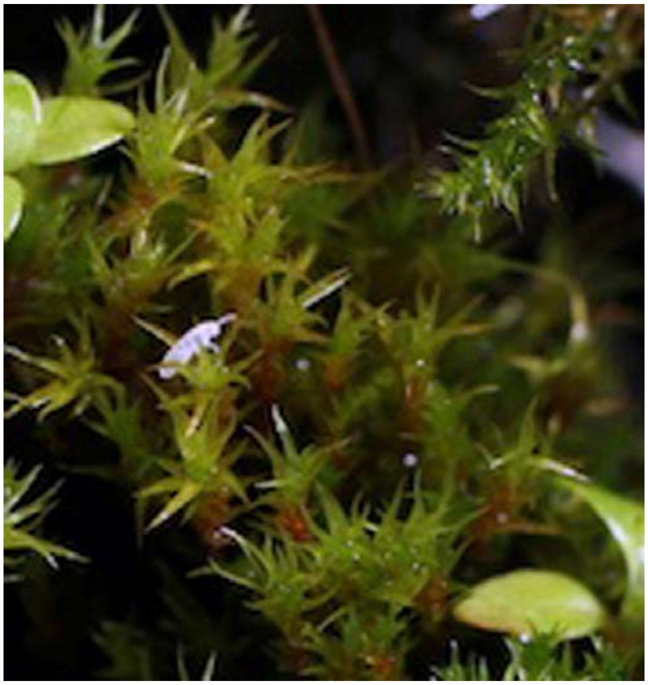

Figure 112. Springtail ***Folsomia candida*** on ***Ceratodon purpureus***, possibly bringing sperm to the archegonia. Photo by Erin Shortlidge, with permission.

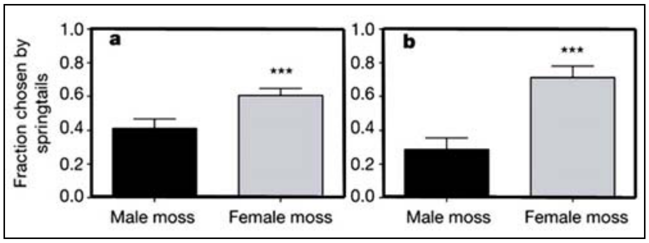

Figure 113. Visits to ***Ceratodon purpureus*** males and females by the springtail ***Folsomia candida***, a showing mean and error bars. n=24 assays, 491 springtails. b represents male vs female samples in an olfactometer; n=10 assays; ***P<0.0001. Redrawn from Rosenstiel *et al.* 2012.

Sperm Longevity

Few studies have included the life of the sperm or experimented with conditions necessary for their survival. It has always been assumed that sperm had a short life span and were unable to survive desiccation. However, Rosenstiel and Eppley (2009) experimented with sperm from geothermal populations of the **paroicous** (having reproductive organs beside or near each other) moss ***Pohlia nutans*** (Figure 117-Figure 118) and found that this is not the case, at least for this ubiquitous species. Sperm in this species were not affected by temperatures between 22 and 60°C and only showed increased mortality at temperatures above 75°C. Dilution also contributed to their mortality (Figure 119), suggesting that they might protect each other. Moreover, within their safe temperature range 20% survived for more than 200 hours (Figure 120). If this trait has been retained in a paroicous moss, we are likely to find some surprisingly tolerant and long-lived sperm in dioicous bryophytes.

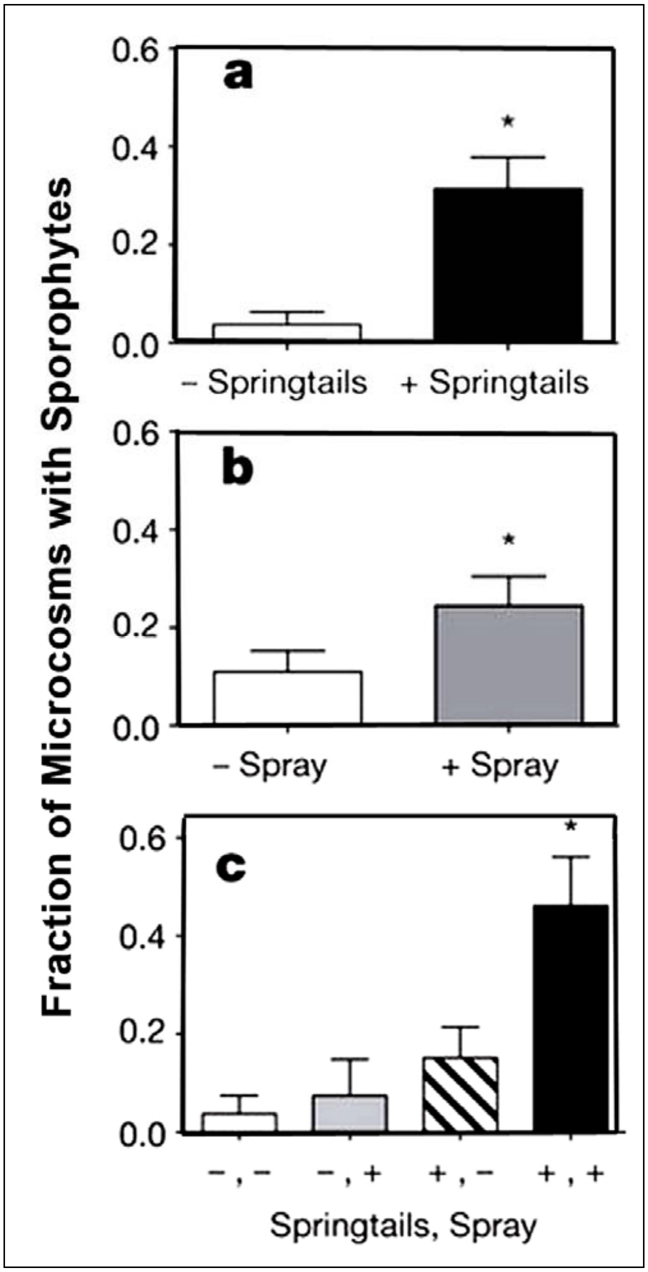

Figure 114. Effect of spray and the springtail ***Folsomia candida*** presence on sporophyte production in ***Ceratodon purpureus*** / ***Bryum argenteum*** microcosms, showing mean and error bars. + and – represent presence or absence of **springtails** or water spray; n=108 microcosms; *P<0.05. Redrawn from Rosenstiel *et al.* 2012.

Shortlidge *et al.* (2012) demonstrated that in ***Bryum argenteum*** (Figure 110-Figure 111), ***Campylopus introflexus*** (Figure 121), and ***Ceratodon purpureus*** (Figure 112) some of the sperm were able to survive environmental desiccation for extended periods of time. The tolerance seemed to be independent of both species and dehydration conditions. Furthermore, the addition of sucrose during drying improved their recovery. Despite the lack of variation among species, there was considerable variability among individuals within a species.

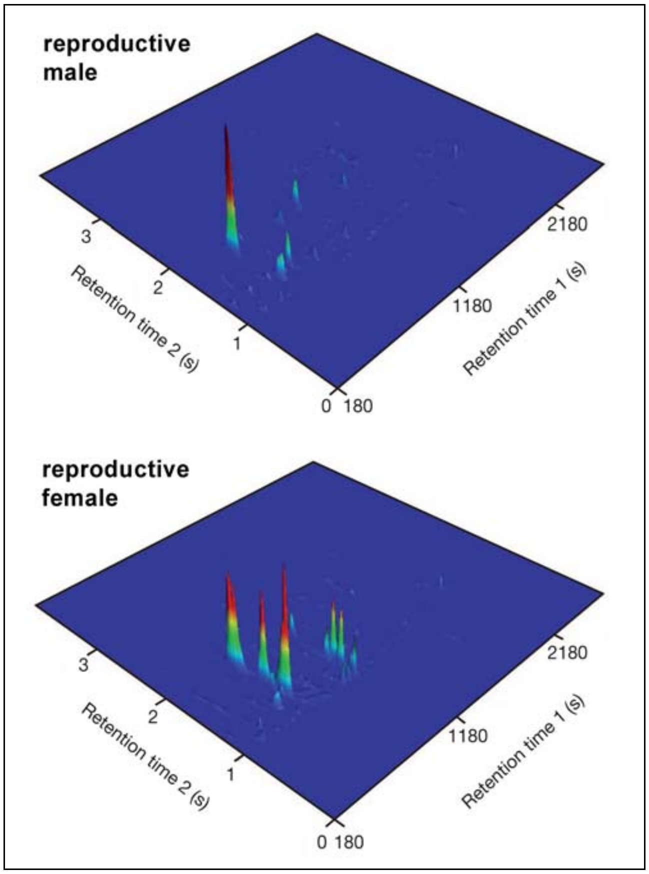

Figure 115. Comparison of profiles (two-dimensional GC3GC–TOFMS chromatograms) of volatile compounds in a male and a female shoot of reproductive ***Ceratodon purpureus***. Colors indicate relative measures of compound abundance; red indicates compounds that are greater than 50% of the largest individual peak area. Modified from Rosenstiel *et al.* 2012.

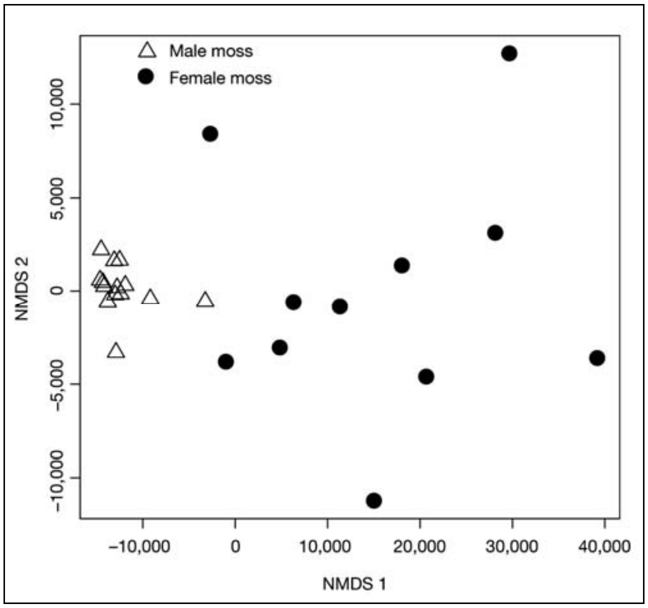

Figure 116. Differences in volatile gas composition from reproductive male and female individuals of the moss ***Ceratodon purpureus*** using non-metric multidimensional scaling (NMDS). This graph shows that there are significant sex-specific differences in VOC composition (P=0.001). Each symbol represents one individual moss plant. Modified from Rosenstiel *et al.* 2012.

Figure 117. ***Pohlia nutans*** plants showing apex where antheridia and archegonia occur together. Photo by Petri Kuhno, through Creative Commons.

Figure 118. ***Pohlia nutans*** in the Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.

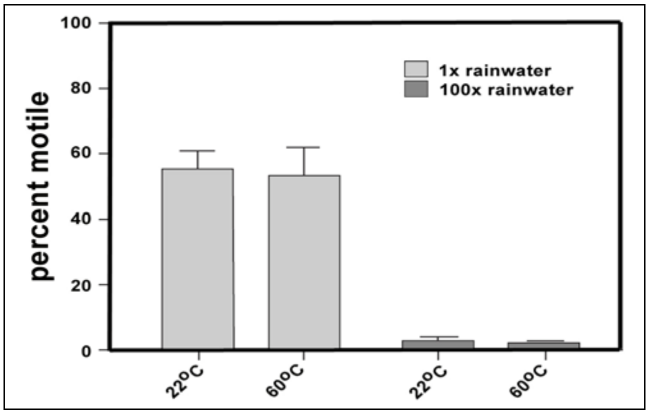

Figure 119. The mean percent of motile (live) ***Pohlia nutans*** sperm vs dilution in rainwater for 96 hours at 1x (no dilution) and 100x dilution at 22°C and 60°C. Redrawn from Rosenstiel and Eppley 2009.

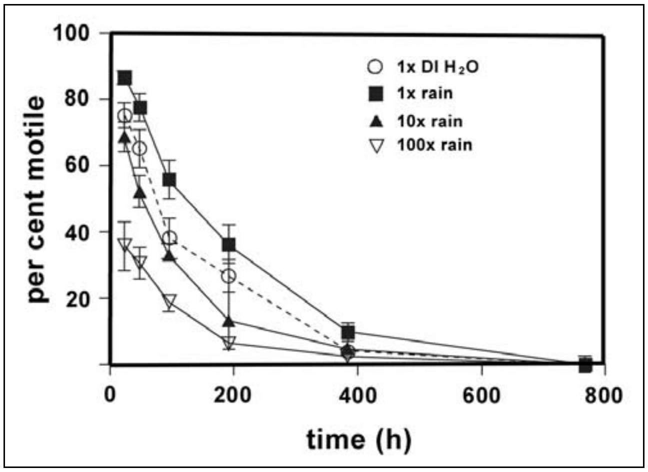

Figure 120. The percent of motile (live) ***Pohlia nutans*** sperm in 40 µl DI or rainwater as they diminish through time. Rainwater created a series of dilutions. Open circles, 1x DI H2O; filled squares, 1x rain; filled triangles, 10x rain; inverted triangles, 100x rain. Redrawn from Rosenstiel and Eppley 2009.

Figure 121. ***Campylopus introflexus*** with water drops. Such drops can greatly aid fertilization. Photo by Michael Lüth, with permission.

Stark *et al.* (2016) revealed that moss antheridia are desiccation tolerant. Noting that free-living sperm are partially desiccation tolerant, they hypothesized that the mature antheridia should also be tolerant. They further hypothesized that rehydration to partial turgor or full turgor before immersion in water is required for full recovery from the damaging effects of desiccation. They cultured ***Bryum argenteum*** until it produced mature perigonia with antheridia, then dried them slowly over ~36 hours, equilibrating them with 50% relative humidity. To test their hypothesis, they prehydrated them in a saturated atmosphere or rehydrated them in saturated media in a range of times from 0 to 1440 minutes. Following these treatments they immersed them in sterile water. When they were prehydrated for at least three hours before their immersion, the antheridia functioned like those of the controls that had not been dried. They found that prehydration did not improve on the recovery compared to rehydration. After three hours of rehydrating before immersion, the antheridia have full recovery.

Factors for Successful Fertilization

Multiple factors contribute to the successful fertilization of bryophytes, including sex expression of both sexes, distance to nearest mate, suitable sperm dispersal mechanism (see above), and appropriate weather conditions, especially temperature and water availability. But assessing the relative importance of multiple factors in a single study has rarely been done. Rydgren *et al.* (2006) used generalized linear modelling (GLM) to assess three factors for the dioicous perennial moss ***Hylocomium splendens*** (Figure 122). They found that most sporophytes (up to 85%) were located within 5 cm of a male, with the longest distance measured being 11.6 cm. But year was an even better predictor of success than distance, attesting to the importance of weather and probably past history, although female segment size as well as distance to closest male were both highly significant. They emphasized the importance of using multiple factors as predictors of reproductive success.

Figure 122. ***Hylocomium splendens*** with capsules. This dioicous species forms colonies with only one sex, hence not producing sporophytes from fertilization by its neighbors. Photo by Janice Glime.

Bisang *et al.* (2004) took the distance question further to see if increasing the availability of mates would increase the success of fertilization. They selected two dioicous pleurocarpous mosses, ***Hylocomiadelphus triquetrus*** (=*Rhytidiadelphus triquetrus*; Figure 123) and ***Abietinella abietina*** (Figure 124) and transplanted individual male shoots into non-sporophyte-bearing female colonies.

Figure 123. ***Hylocomiadelphus triquetrus*** with capsules. Photo by David T. Holyoak, with permission.

Figure 124. ***Abietinella abietina*** in Europe. Photo by Michael Lüth, with permission.

They determined that the number of sporophytes produced depended on the distance from the male mate, *i.e.* spermatozoid source. Furthermore, differences between species were evident, with ***Hylocomiadelphus triquetrus*** (Figure 123) being more successful than ***Abietinella abietina*** (Figure 124). They estimated that in ***H. triquetrus*** the maximum fertilization distance was 34 cm, considerably more than the 3-6 cm previously reported (Riemann 1972). Bisang *et al.* (2004) found that in ***H. triquetrus*** the number of female reproductive branches significantly affected the number of sporophytes. By contrast, in ***A. abietina*** the number of female reproductive branches per plot did not affect sporophyte production. Both species were mate limited.

As one might expect, for both species, when male plants were uphill from female branches, the number of sporophytes was significantly greater than when their positions were reversed, presumably because the sperm were able to travel farther, possibly carried or splashed down the slope by rain (Bisang *et al.* 2004). In ***Hylocomiadelphus triquetrus*** (Figure 123), a mean of 40 sporophytes per plot (n=25 plots) occurred on sloping substrata compared to 22 on horizontal surfaces. Upslope distances for this species had a mean of 6.2 cm above transplanted males (max=16 cm) and 10.2 cm downslope (max=34 cm). In ***Abietinella abietina*** (Figure 124), the downslope distances (mean=3.3 cm) were also significantly greater than upslope (mean=1.9 cm) distances, but in this species both the distance travelled and the successful production of sporophytes (mean=2.4 per plot) were considerably less than in ***H. triquetrus***. Genes matter.

Figure 125. ***Anomodon viticulosus*** in a seepage area of England. Photo by Janice Glime.

Granzow de la Cerda (1989) demonstrated movement of sperm in seepage water by transplanting male ***Anomodon viticulosus*** (Figure 125) to a position at least 25 cm above female plants, a move that resulted in production of sporophytes.

Multiple Fertilizations

Wyatt *et al.* (2022) used isozyme markers to estimate incidence of multiple paternity in the dioicous, haploid, leafy liverwort ***Porella platyphylloidea*** (Figure 126). They found that 12.6% of the plants were non-sex-expressing, 13.4% were females without sporophytes, 31.9% were males, and 42% were females with sporophytes. The sex ratio was female biased at 1.74:1. Using the criterion that only females with two or more sporophytes with different genotypes had experienced multiple paternity, they estimated 57% of female plants had been fertilized more than once. Plants on the lower parts of trees were significantly larger, but the larger size of females seemed to account for this difference.

Figure 126. ***Porella platyphylloidea***, a species in which a female can be fertilized by multiple males. Photo by Suzanne Cadwell, through Creative Commons.

Summary

The liverwort genus ***Sphaerocarpos*** was the first genus in which sex chromosomes were known in plants. Many bryophytes possess sex chromosomes (**X** & **Y** chromosomes, or designated **U** & **V** to refer to their haploid condition) which may play a role in sex determination. Bryophytes can be **monoicous** (bisexual) or **dioicous** (unisexual). Gametangia in monoicous bryophytes can be **autoicous** (♂ & ♀ gametangia in separate clusters), **paroicous** (♂ & ♀ gametangia in separate groupings but one cluster), or **synoicous** (♂ & ♀ gametangia intermixed in same cluster). **Monoicy** may have arisen through **hybridization** and **polyploidy**. Transitions from monoicy to dioicy and vice versa have happened multiple times. There seem to have been more changes from monoicy to dioicy than the reverse in mosses, whereas the opposite was the case in hornworts, but this pattern appears to depend on those taxa included in the study and is not a settled relationship. McDaniel *et al.* suggested that dioicy works best when there are advantages to both sexes for being separate.

At least some antheridia can tolerate desiccation, but survival is improved by rehydration before submersion. Sperm dispersal begins with bursting of the antheridium, often accompanied by movement with surface tension of water drops. In thallose liverworts, sperm are often expelled explosively into the air. Sperm dispersal is usually accomplished by movement through a water film or by splashing and is sometimes aided by gravity. But some species have their sperm dispersed by invertebrates, including insects and mites. Dispersing sperm are known to survive as much as 200 hours and travel distance is known up to 230 cm. Travel distance and weather seem to be the most important factors in determining the success of fertilization in bryophytes.

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