CHAPTER 3-1
SEXUALITY: ITS DETERMINATION

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CHAPTER 3-1
SEXUAL STRATEGIES

Unisexual and Bisexual Taxa

Jesson and Garnock-Jones (2012) attempted to provide a single classification of functional gender 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 the 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 the more complex seed plants.

In bryophytes, it is the gametophyte (1n, haploid) plant that exhibits the bisexual (monoicous) trait. To the seed-plant botanist, the terms monoeccious 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 mónos (mónos), single, or δί- (di-), twice, double, and οἶκος or οἰκία (oîkos) or oikia, 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, roughly 60% (Hedenäs & Bisang 2011) (57% estimated by Villarreal & Renner 2013a) in mosses and somewhat higher in liverworts (68% estimated by Villarreal & Renner 2013a), 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).

Bryophytes exhibit all sorts of arrangements of sexual organs on their monoicous species (having male and female gametangia on the same individual), providing them with various strategies for outbreeding. When male and female organs are on separate individuals (Figure 1), outbreeding is ensured whenever sexual reproduction occurs; the opportunities for fertilization decrease and the opportunities for genetic variation increase.

One of the major problems for dioicous species is that one gender may arrive in a new location without the other, as in the case of Didymodon nevadensis. On the gypsiferous ridges of Nevada, only female plants are known (Zander et al. 1995). Nevertheless, with a variety of vegetative reproductive means, the species can persist.

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 2) 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 dioecious. 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 3) in plants (Anderson 2000), first discovered in the liverwort genus Sphaerocarpos (Figure 4) (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 5-Figure 6) (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).
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 7-Figure 10), others bisexual (having both sexes on the same individual; monoicous) (Figure 11-Figure 12). Clearly we need more research to discover how some of these determinations are made.

An Unusual Y 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 5-Figure 6), have at least one such gene. This gene is unique and is expressed specifically in the male sex organs.

Figure 6. Marchantia polymorpha females with archegoniophores, the first bryophyte species in which sex markers were found. Photo by Janice Glime.

Figure 7. Clonal colony of male Philonotis calcarea. Note innovation branches below the male splash cups. Photo by Michael Lüth.

Figure 8. A dioecious species, Philonotis calcarea, showing antheridial splash cups. Photo by David T. Holyoak.

Figure 9. Female plants of the dioecious Philonotis calcarea, distinguishable by their sporophytes. Photo by David T. Holyoak.

Figure 10. Colony of non-expressing or female plants of the dioecious Philonotis calcarea. Archegonia are hidden among perichaetal 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.
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**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 13-Figure 15). 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 16) (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 17), 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.

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**Figure 11.** 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.

**Figure 12.** *Funaria hygrometrica* undeveloped and nearly mature capsules on female plant portions. Photo by Robert Klips.

Since that earlier discovery, Yamato *et al.* (2007) have identified 64 genes on the Y chromosome of *Marchantia polymorpha* (Figure 5-Figure 6). 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 Y chromosome are expressed in both male sexual organs and male thalli, suggesting that they have cellular functions unrelated to reproduction.

**Figure 13.** *Orthotrichum pusillum*, an **autoicous** species with capsules. Photo by Robert Klips.

**Figure 14.** *Orthotrichum pusillum*, an autoicous species showing antheridia. Photo by Robert Klips.
In Jungermanniopsida, the antheridia are arranged behind the growing point (Figure 18-Figure 20). In most of the leafy Jungermanniopsida the archegonia occur in perianths (Figure 18, Figure 21) 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 22). In the Marchantiopsida the antheridia occur in clusters on the thallus (Figure 23) or elevated on a stalk (Figure 24), with similar arrangements for archegonia (Figure 24-Figure 25). In Anthocerotopsida the antheridia are imbedded in the thallus (Figure 26-Figure 27) and archegonia are single and surrounded by involucres (Figure 26).

Figure 15. *Orthotrichum pusillum*, an autoicous species showing archegonia. Photo by Robert Klips.

Figure 16. *Lophozia excisa*, a paroicous species. Photo by Michael Lüth.

Figure 17. *Micromitrium synoicum* with male and female gametangia among the same bracts (synoicous). Photo from Duke University through Creative Commons.

Figure 18. Arrangement of perianth with archegonia and perigonium with antheridia in the monoicous leafy liverwort *Frullania oakesiana*. Photo by Paul Davison.

Figure 19. Antheridal arrangement on the leafy liverwort *Kurzia*. Photo by Tom Thekathyil.
Figure 20. *Pellia endiviifolia* with antheridia on the thallus in positions not at the apex. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

Figure 21. *Perianth* of the leafy liverwort *Frullania* (*Jungermanniopsida*) in its terminal position. Photo by George Shepherd.

Figure 22. *Symphogyna brasiliensis* (*Metzgeriales*) showing subapical position of archegonia, hidden in this case by fimbriate scales. Photo by George J. Shepherd through Creative Commons.

Figure 23. *Conocephalum conicum* antheridia in clusters on the thallus (arrow). Photo by Malcolm Storey through Creative Commons.

Figure 24. *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.

Figure 25. Arm of archegoniophore head of *Marchantia polymorpha* with archegonia hanging down. Photo by George Shepherd.
Figure 26. *Notothylas orbicularis* (*Anthocerotopsida*) with involucres that surround archegonia and pouches that contain antheridia (see insert). Photo by Paul Davison.

Figure 27. Antheridia in the pocket of a hornwort (*Anthocerotopsida*), expelling sperm. Photo by Hatice Ozenoglu Kiremit.

**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:

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.
7. Monoicous taxa have several means to prevent self-fertilization and may have evolved by hybridization.

This 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 28). They also found that shifts from dioicy to monoicy in that genus occurred multiple times, with some epiphytes having facultative shifts.

Figure 28. *Radula complanata* growing epiphytically and exhibiting numerous sporophytes. Photo by David Holyoak.
Despite the ability to become diploid monoicous gametophytes, we cannot ignore that McDaniel et al. (2013) found that among mosses there are twice as many occurrences from monoicy to dioicy as the reverse. Furthermore, they found that there seem to be higher rates of diversification among the monoicous moss taxa than among the dioicous ones. This is to be expected for those taxa that became monoicous by a doubling of chromosome number through outcrossing or hybridization. McDaniel and coworkers (2013) suggest that dioicy works best when separate sexes derive some advantage in their different morphologies.

One might look for these dioicy advantages in genera such as Diphyscium (Figure 29) 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). 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 evolution of sexual systems will be assessed in a number of studies in the near future, using phylogenetic methods of cladistics and molecular techniques, such as those of McDaniel and Perroud (2012), McDaniel et al. (2013), and Villarreal and Renner (2013a, b).

Figure 29. Diphyscium foliosum females with capsules surrounded by perichaetial leaves and photosynthetic males (green leaves in foreground). Photo by David T. Holyoak.

**Anthocerotophyta and 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 can be explained by the fact that in the hornworts, diversification rates do not correlate with higher ploidy levels as they do in mosses. Rather, in hornworts polyploidy in monoicous taxa is rare, occurring in only one (Anthoceros punctatus, Figure 30-31) of 20 species that have been assessed (Villarreal & Renner 2013a).

Figure 30. Anthoceros punctatus with sporophytes. Photo by Des Callaghan.

Figure 31. Anthoceros punctatus antheridial pit. Note the bluish Nostoc colony to the left of the antheridial pit. Photo by Des Callahan.

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.

**The Monoicous Advantage**

The effects of these dioicy differences on bryophyte ecology and biology are impressive for this gametophyte-dominant group. It means that the monoicous species generally 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 32). Although a much higher percentage (97% compared to 58% in dioicous taxa) of the monoicous group has capsules frequently (Figure 32), 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 33).

Figure 32. 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.

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 34) 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.

Figure 34. Plagiothecium denticulatum. Photo by Bob Klips.

Heegaard (2001) illustrates the problem of dioicy in Andreaea (Figure 35-Figure 38). 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 35), 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 36) and A. obovata var. hartmannii (Figure 37) rarely produced capsules. The production of capsules in monoicous A. rupestris var. rupestris (Figure 38) 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 genders 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.
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 39), 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 40), S. angustifolium (Figure 41)] when they occur elsewhere suggests that there may be a founder principle at work (Carl Wishner, Bryonet 14 August 2012) wherein only one gender arrived to colonize a particular location. This was also suggested for S. palustre (Figure 42) 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.
Figure 41. *Sphagnum angustifolium* in Europe. Photo by Michael Lüth.

Figure 42. *Sphagnum palustre* in Europe. Photo by Michael Lüth.

Herbarium records are frequently the basis for descriptions of bryophytes and frequency of sporophytes. One must view herbarium collection records for such factors a male:female ratios and sporophyte production with caution, however, due to collection bias. As Harpel (2002) demonstrated for bryophyte 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.

**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 43-Figure 44), 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 45) and in parts of its distribution for *Pleurozium schreberi* (Figure 46).

Figure 43. *Syntrichia laevipila* exhibiting *gemmae*. These are one means of asexual reproduction. Photo by Paul Davison.

Figure 44. *Gemma* of *Syntrichia laevipila* (=*Tortula pagorum*), illustrating its very papillose cells. Photo by Bob Klips.

Figure 45. *Fontinalis duriae* 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 Gliome.
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 12) never had heterozygous sporophytes for 14 allozyme loci, i.e., it had a high level of heterozygote deficiency. The dioicous moss Polytrichum juniperinum (Figure 47), 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. 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 works 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 2n (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 gametophyte has been observed only once (Funaria hygrometrica, Figure 11-Figure 12) in nature (Brizi 1892; Crum 2001).

Sporophytes have also been developed from gametophyte tissues. The first was produced as outgrowths from 2n 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. warnstorffii (Figure 48). It likewise never produced spores. It originated at the base of the stem, whereas this species normally produces its sporophytes at the apex.

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 49) complex, making them the first group of mosses in which autopolyploidy was demonstrated with molecular markers. Cinclidium subrotundum (Figure 50) is a monoicous polyploid (n=14) that exhibits strong evidence for allopolyploidy, having 7 fixed heterozygous loci out of 17 scored. And Google Scholar, when searched for bryophyte autopolyploidy, listed mostly allopolyploidy references. In one species that does exhibit autopolyploidy, Targionia hypophylla (Figure 51), its triploidy seems to actually be a combination of autopolyploidy and allopolyploidy (Boisselier-Dubayle & Bischler 1999).

Genome Doubling in Mosses

It appears that becoming monoicous is actually much simpler than producing sporophytes from fragments. Genome doubling is a common method by which mosses [76% (Przywara & Kuta 1995)] and liverworts [10% (Newton 1983)], but seemingly not hornworts (Villarreal & Renner 2013a), become monoicous (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).
Chapter 3-1: Sexuality: Its Determination

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 52) arose from a cross between *Plagiomnium ellipticum* (Figure 53) and *Plagiomnium insigne* (Figure 54-Figure 55), 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 56-Figure 58) is likewise an allopolyploid, but one of its parent species is unknown (Wyatt & Odrzykoski 1998). *Cinclidium stygium* (Figure 59) \((n=14)\), also a member of Mniaceae, is a monoicous polyploid closely related to *C. arcticum* (Figure 60) and *C. latifolium* (Figure 61), both having \(n=7\) (Wyatt et al. 2013). *Cinclidium stygium* appears to have an allopolyploid origin from these two close relatives.
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 62) 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 63; Jesson et al. 2011). Many diploid populations, on the other hand, were dioicous (Figure 64). Jesson and coworkers found that male and female gametophytes were represented by haploid, diploid, and triploid individuals (Figure 64). (See more in Chapter 3-4, Reproductive Barriers: Selfing and Hybrids.)

Sperm Dispersal by the Bryophyte

Sperm transfer is a problematic aspect of fertilization for bryophytes. 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.

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 the archegonia of Marchantia polymorpha (Figure 25) and Radula complanata (Figure 28). 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).

Walton (1943) observed the spreading of sperm in the monoicous thallose liverwort Pellia epiphylla (Figure 65-Figure 66). In his observations, the archegonia were only...
5-10 mm from the antheridia. Whereas freed sperm in the liverwort *Aneura* (Figure 67) 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. *Pellia epiphylla* behaved like these mosses and liverworts, 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 the archegonial involucres in only ~15 seconds. The more lengthy process was emergence of the sperm from the 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.

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 1). 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 1, known (implied?) distances range up to 230 cm.

Reynolds (1980) found that splashing water on the platforms of the moss *Plagiomnium ciliare* (Figure 68) indicated greater travel distance (50+ cm) than that to the nearest male (5.3 cm). In the thallose liverwort *Marchantia chenopoda* (Figure 69), 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>
<thead>
<tr>
<th>Species</th>
<th>Distance</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Splachnum ampullaceum</em></td>
<td>5-15 mm</td>
<td>Cameron &amp; Wyatt 1986</td>
</tr>
<tr>
<td><em>Breutelia arcuata</em></td>
<td>2.5 cm</td>
<td>Bedford 1940</td>
</tr>
<tr>
<td><em>Weissia controversa</em></td>
<td>4 cm</td>
<td>Anderson &amp; Lemmon 1974</td>
</tr>
<tr>
<td><em>Climacium dendroides</em></td>
<td>7 cm</td>
<td>Bedford 1938</td>
</tr>
<tr>
<td><em>Pleurozium schreberi</em></td>
<td>10 cm</td>
<td>Longton 1976</td>
</tr>
<tr>
<td><em>Plagiomnium affine</em></td>
<td>10 cm</td>
<td>Andersson 2002</td>
</tr>
<tr>
<td><em>Atrichum angustatum</em></td>
<td>11 cm</td>
<td>Wyatt 1977</td>
</tr>
<tr>
<td><em>Abietinella abietina</em></td>
<td>12 cm</td>
<td>Bisang <em>et al.</em> 2004</td>
</tr>
<tr>
<td><em>Anomodon viticulosus</em></td>
<td>25 cm</td>
<td>Granzow de la Cerda 1989</td>
</tr>
<tr>
<td><em>Rhytidialesplus triquetrus</em></td>
<td>34 cm</td>
<td>Bisang <em>et al.</em> 2004</td>
</tr>
<tr>
<td><em>Plagiomnium ciliare</em></td>
<td>50 cm</td>
<td>Crum 2001</td>
</tr>
<tr>
<td><em>Polytrichastrum ohioense</em></td>
<td>60 cm</td>
<td>Brodie 1951</td>
</tr>
<tr>
<td><em>Marchantia chenopoda</em></td>
<td>65 cm</td>
<td>Moyá 1992</td>
</tr>
<tr>
<td><em>Polytrichium juniperinum</em></td>
<td>75 cm</td>
<td>Longton 1976</td>
</tr>
<tr>
<td><em>Ptychostomum (=Bryum)</em></td>
<td>200 cm</td>
<td>Gayet 1897</td>
</tr>
<tr>
<td><em>Dawsonia longifolia</em></td>
<td>230 cm</td>
<td>Crum 2001</td>
</tr>
<tr>
<td>epiphytes</td>
<td>2-5 m</td>
<td>Longton &amp; Schuster 1983</td>
</tr>
</tbody>
</table>
Figure 68. *Plagiomnium ciliare* showing male splash cups and horizontal (plagiotropic) branches. Photo by Robert Klips.

Figure 69. *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 70) 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).

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.

**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 71) 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 70. *Conocephalum conicum* antheridia. Photo by Janice Glime.

Figure 71. *Dawsonia longifolia* male plant with splash cup. Photo by Allan Fife.

Andersson (2002) used a more sophisticated approach by making a video of splashes of rain on the splash cups of the moss *Plagiomnium affine* (Figure 72). 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 5-Figure 6). 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 70), 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.

The splash mechanism in the dioecious *Fontinalis* (Figure 73) 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).

**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 11) of both males and females in *Polytrichum commune* (Figure 74) 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.
Cronberg et al. (2006) experimentally demonstrated that springtails and mites were able to transport sperm over distances of up to 4 cm. Rosenstiel et al. (2012) also described one of the more remarkable cases of sperm dispersal in the mosses *Ceratodon purpureus* (Figure 77) and *Bryum argenteum* (Figure 75-Figure 76). These species can have their sperm dispersed from male to female by the springtail *Folsomia candida* (Figure 77). Rosenstiel and coworkers showed that the springtails chose significantly more female mosses than male mosses in *Ceratodon purpureus* (Figure 78) and that their presence facilitated fertilization (Figure 79). This preference was supported by verifying that the volatile compounds differed between the two genders in *C. purpureus* (Figure 80-Figure 81).
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 the geothermal moss *Pohlia nutans* (Figure 82) and found 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 temperature effects above 75°C. Dilution contributed to their mortality (Figure 83). Moreover, within their safe temperature range 20% survived for more than 200 hours (Figure 84).

Figure 82. *Pohlia nutans* in the Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth.

Figure 83. 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.

Shortlidge *et al.* (2012) demonstrated that in *Bryum argenteum* (Figure 75-Figure 76), *Campylopus introflexus* (Figure 85), and *Ceratodon purpureus* (Figure 77) 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.
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 86). 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.

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, *Rhytiadiadelphus triquetrus* (Figure 87) and *Abietinella abietina* (Figure 88) and transplanted individual male shoots into non-sporophyte-bearing female colonies.

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 *R. triquetrus* being more successful than *A. abietina*. They estimated that in *R. triquetrus* the maximum fertilization distance was 34 cm, considerably more than the 3-6 cm previously reported...
considerably less than in production of sporophytes (mean=2.4 per plot) were species both the distance travelled and the successful greater than upslope (mean=1.9 cm) distances, but in this England. Photo by Janice Glime.

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 Rhytidiadelphus triquetrus (Figure 87), 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 88), 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 R. triquetrus. Genes matter. Granzow de la Cerda (1989) demonstrated movement of sperm in seepage water by transplanting male Anomodon viticulosus (Figure 89) to a position at least 25 cm above female plants, a move that resulted in production of sporophytes.

Figure 89. Anomodon viticulosus in a seepage area of England. Photo by Janice Glime.

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 gender determination. Bryophytes can be monoicous (bisexual) or dioicous (unsexual). 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). Monoic frequently has arisen through hybridization and polyploidy. Transitions from monoic to dioicy and vice versa have happened multiple times. There have been more changes from monoicy to dioicy than the reverse in mosses, whereas the opposite was the case in hornworts. McDaniel et al. suggested that dioicy works best when there are advantages to both sexes for being separate.

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.

Acknowledgments

We greatly appreciate the numerous comments and suggestions of Lars Hedenäs who provided a critical review of an earlier draft of the chapter and gave me encouragement. Heinjo During asked probing questions, challenged me to do more, and provided me with references to do it. Karla Werner offered a beginner's perspective and suggested the internal summaries. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and helped with the proof reading of a very early draft. Bryonetters have been especially helpful in providing examples and observations to answer questions arising during the preparation of this chapter. As always, many people have contributed images, as noted in the captions.

Literature Cited


Villarreal, J. C. and Renner, S. S. 2013b. Transitions from monoicy to dioicy are more likely in hornwort species with
small spores, supporting findings from mosses, but with no role for polyploidy. Conference of the International Association of Bryologists, 15-19 July 2013 at Natural History Museum, London, UK.


