

# **CHAPTER 2-6**

## **BRYOPHYTA - ANDREAEOPSIDA, ANDREAEOBRYOPSIDA, POLYTRICHOPSIDA**

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# CHAPTER 2-6

## BRYOPHYTA - ANDREAEOPSIDA, ANDREAEOBRYOPSIDA, POLYTRICHOPSIDA



Figure 1. *Andreaea rupestris* with open capsules. Photo by Michael Lüth, with permission.

### Andreaeopsida – The Granite Mosses

This is a small, cool-climate class of **siliceous**-rock-dwelling mosses (Schofield 1985), again with only one genus, but with approximately 100 species. They are typically **blackish** or **reddish**, **brittle**, and **short** (Figure 1). One can recognize them by rubbing one's hand across them and discovering small fragments stuck to the hand. This no doubt has dispersal potential.

The leaves are but **one cell thick** (Figure 2), but some species have a multiple cell thickness in the center, forming a **costa** (Figure 3). The arrangement of leaves is multi-ranked and the stem typically has colored cell walls (Figure 4). Unlike most mosses, they have a **thalloid protonema**.

Of ecological significance, *Andreaea* is **autoicous** (having male and female reproductive organs in separate clusters on the same plant; Figure 5-Figure 7). This ensures there will be others around to accomplish fertilization.

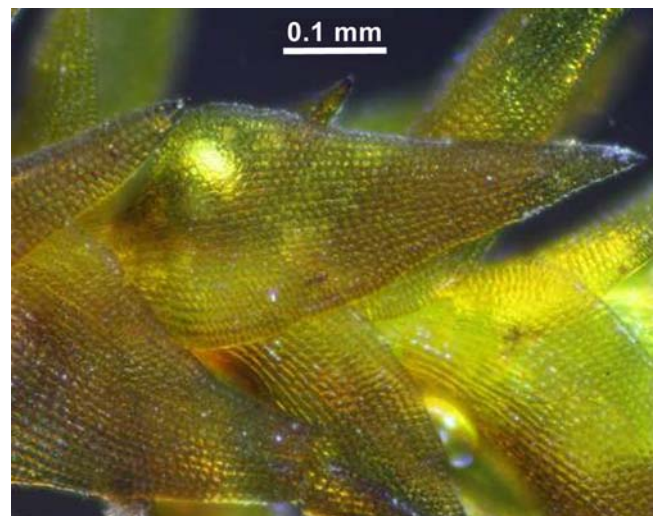


Figure 2. *Andreaea mutabilis* leaves with no costa. Photo by Tom Thekathyl, with permission.



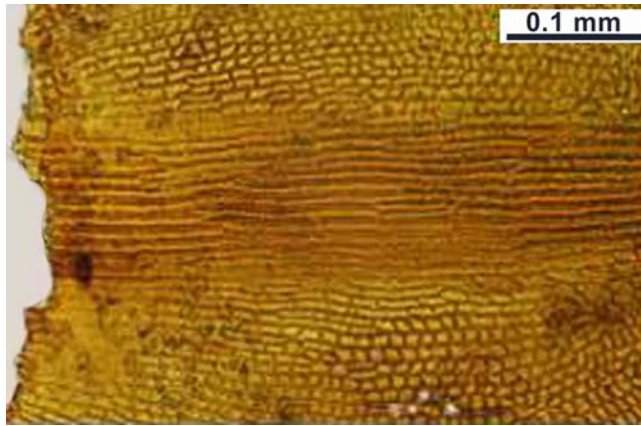


Figure 3. *Andreaaea subulata* leaf showing costa. Photo by Tom Thekathyil, with permission.

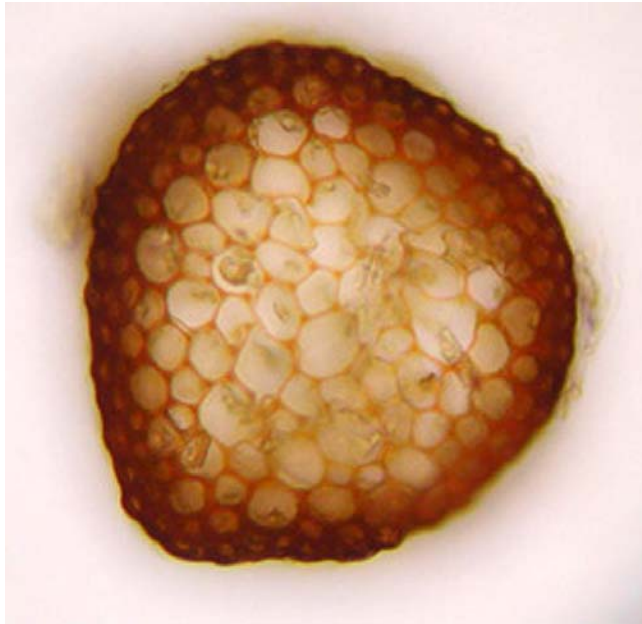


Figure 4. *Andreaaea* stem cross sections. Photo from website of Botany Department, University of British Columbia, with permission.



Figure 5. *Andreaaea nivalis* perigonium. Photo from website of Botany department, University of British Columbia, with permission.



Figure 6. *Andreaaea nivalis* perigonium crushed to reveal paraphyses. Photo from website of Botany Department, University of British Columbia, with permission.

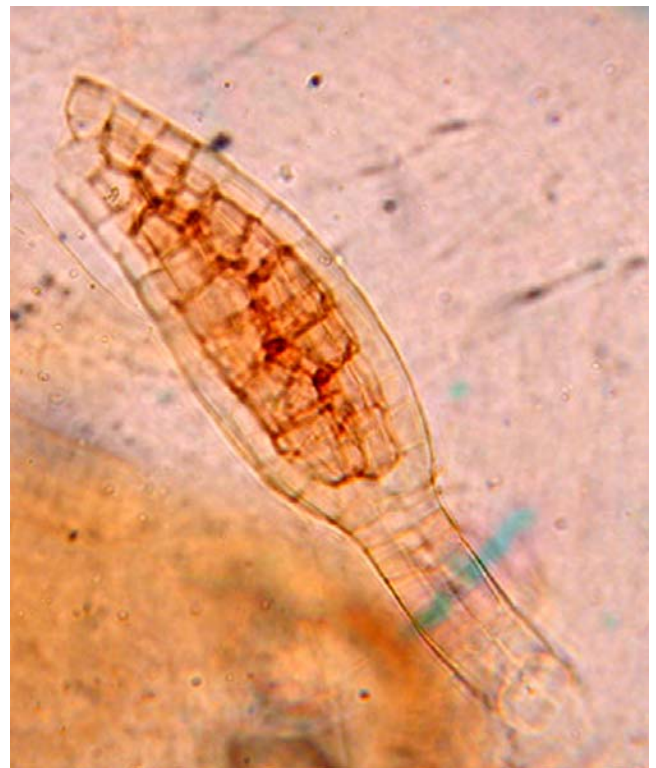


Figure 7. *Andreaaea nivalis* antheridium. Photo from website of Botany department, University of British Columbia, with permission.

The capsule is reminiscent of liverworts, opening in **four valves**, but having the tips remaining **attached** to each other, making it look like those paper lanterns we made as children for Halloween (Figure 8). Unlike the liverworts, it **lacks elaters**. And unlike most liverworts and Bryopsida, it **lacks a seta** and has a gametophyte **pseudopodium**, a character in common with **Sphagnopsida**, a stalk produced at capsule maturity from the gametophyte tissue.



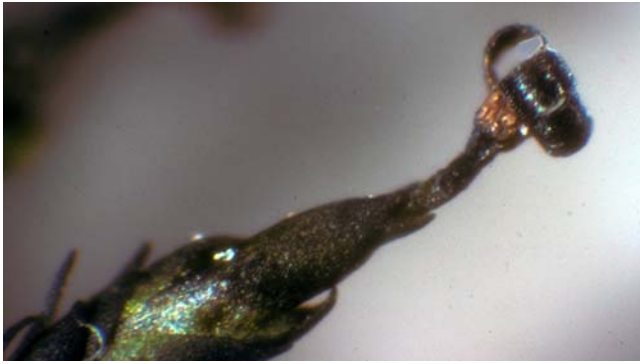


Figure 8. *Andreaea rupestris*, Class **Andreaeopsida**, gametophyte with sporophyte showing four valves of capsule and pseudopodium of gametophyte. Photo by Janice Glime.

## Andreaebryopsida

This class likewise is comprised of a single genus, *Andreaebryum* (Figure 9), which has been considered by most to belong to the Andreaeopsida, but recently separated in the treatment by Buck and Goffinet (2000). It differs in being **dioicous** (having male and female reproductive organs on separate plants) and possessing a **seta**. Its **calyptra** is larger, **covering the capsule**, and the capsule is **valvate**, but unlike the Andreaeopsida, the apex erodes, so the **valves are free**, not joined at the apex. The distribution is narrow, restricted to the northwestern part of Canada and adjacent Alaska, where it grows on calcareous rocks, contrasting with the acidic granite preference of *Andreaea* (**Andreaeopsida**).



Figure 9. *Andreaebryum macrosporum* with valvate capsules. Photo from Biology 321 Course Website, UBC, with permission.

## Polytrichopsida

With bryophytes, the determination of primitive or advanced often depends on the generation being examined. The gametophyte may have changed considerably while some set of characters of the sporophyte remained constant. And of course, the reverse can be true. The **dioicous** condition (male and female reproductive organs on separate plants) that characterizes **Polytrichopsida** is considered to be primitive (Longton & Schuster 1983), with the

**monoicous** condition (male and female reproductive organs on the same plant) that is so frequent in **Bryopsida** typically being derived by doubling of the chromosome number. Likewise, **nematodontous peristome teeth** (having evenly thickened walls and whole dead cells lacking eroded walls; Figure 10) of **Polytrichopsida** would seem to be an earlier development than the **arthrodontous** (having 1-2 rings of separated teeth with differentially thickened walls; Figure 11) condition of **Bryopsida**.

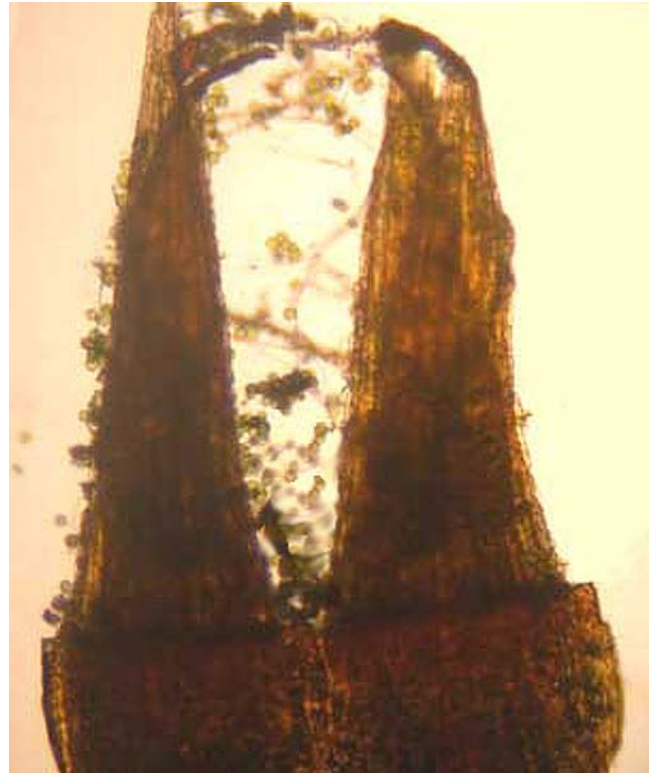


Figure 10. **Nematodontous** peristome teeth of *Tetraxis pellucida* (**Polytrichopsida**). Note the separation at the tips and absence of thickenings. Photo from Biology 321 Course Website, UBC, with permission.



Figure 11. Capsule with **arthrodontous** teeth. Note the projections along the edges. Photo by Laurie Knight, with permission.



All members of the class **Polytrichopsida** possess an elongate sporophyte **seta** (Figure 12), supporting an **operculate peristomate** capsule (Figure 13), and a **columnar columella**, characters that are more advanced than in **Sphagnopsida** but typical in **Polytrichopsida**. Spores are produced by meiosis in a single event in **sporogenous** tissue that surrounds the columella (Figure 14-Figure 15).



Figure 12. *Polytrichum juniperinum* with capsules and seta. Photo by Ralph Foster, through Creative Commons.



Figure 13. *Polytrichum commune* capsules with some showing reddish operculum. Photo by Kristian Peters, through Creative Commons.

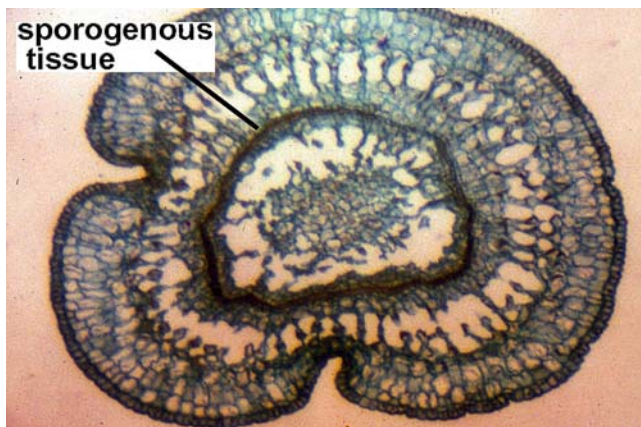


Figure 14. Cross section of immature *Polytrichum* capsule showing sporogenous tissue. Photo by Janice Glime.

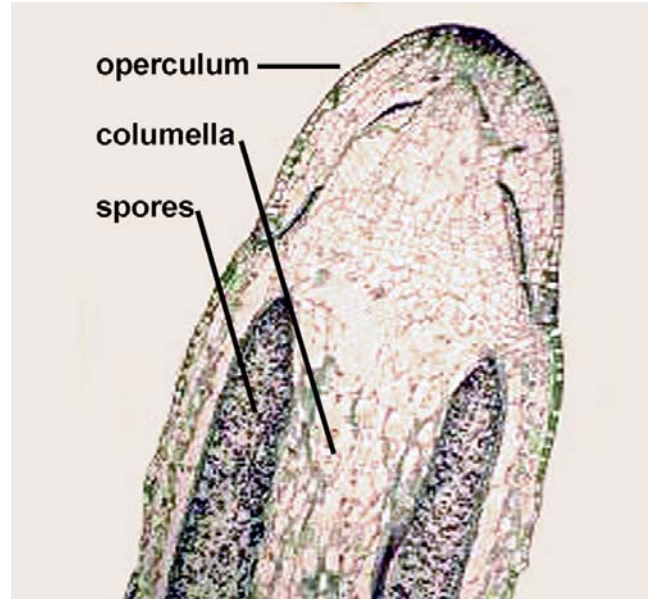


Figure 15. Longitudinal section of *Polytrichum* capsule. Photo by Janice Glime.

The moss gametophyte is often very specialized, being characterized by stems with a **central strand**, reaching its peak in **Polytrichaceae** (Figure 18), with the presence of **hydroids** (water-conducting cells) and **leptoids** (sugar-conducting cells). The leaves of the class are **all costate** (having a midrib-like structure; Figure 16-Figure 17).



Figure 16. *Atrichum undulatum* leaves showing costa. Photo by Bernd Bäuml, through Creative Commons.



Figure 17. *Atrichum undulatum* excised leaves showing costa. Photo by Hermann Schachner, through Creative Commons.



## Polytrichaceae

In many ways, this family looks like a tracheophyte wanna-be. It attains a greater height than the typical moss and can even stand alone to nearly half a meter in the case of *Dawsonia longifolia* (Figure 19). *Polytrichum commune* (Figure 20) likewise attains similar heights, but only with the support of other individuals, forming a hummock. Even in the cold climate of Macquarie Island, *P. juniperinum* reaches hummock heights of 30 cm (Rod Seppelt, pers. comm. 16 March 2007).

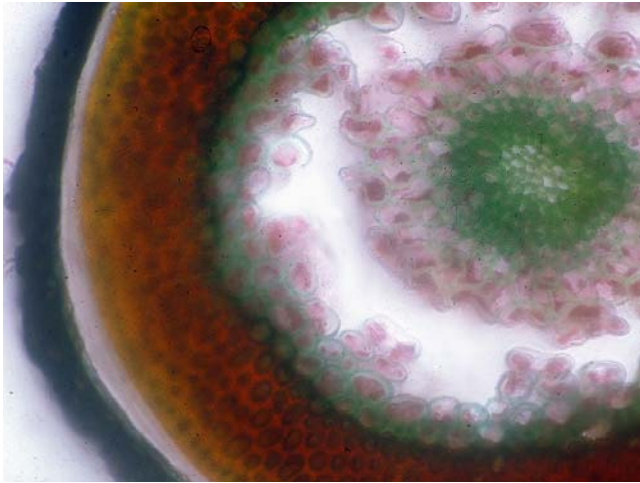


Figure 18. Cross section of a *Polytrichum* stem showing green **hydroids** in center and larger **leptoids** surrounding them. Photo by Izawa Kawai, with permission.



Figure 19. *Dawsonia longifolia* from New South Wales, Australia. Photo by Janice Glime.

The genus *Dawsonia* has many unresolved species, some of which have been moved to a different genus. Even the well known *D. superba* (Figure 19) has been merged into *D. longifolia*. *Dawsonia longifolia* s.l. is a native of New Zealand, Australia, and Papua New Guinea and breaks the height record for upright mosses. It grows up to 48 mm in a year and in this study ranged 6-38 cm tall (Green & Clayton-Greene 1981). This compares well with known growth rates of *Polytrichum commune* of 3-5 cm in one growing season (Figure 21) (Sarafis 1971). It occurs in a temperate climate and its growth tracks available moisture and temperature. Its sperm dispersal is aided by an antheridial splash cup, with sperm known to reach females 1.5-2 m from the males in the field, but experimental tests showed they could splash to heights up to 3.3 m in the lab (Clayton-Greene *et al.* 1977)! Ligrone *et al.* (2002) showed that *Dawsonia* responded differently to antibodies used to label the arabinogalactan proteins in the water conducting cells (WCC), suggesting that their chemical structure differed from that of other mosses tested. On the other hand, *Dendroligotrichum* (Figure 22) and *Polytrichum* demonstrated a strong reaction in the leptoids (Figure 18; Figure 23) of the stem. These three genera differed in other marker reactions as well, supporting the uniqueness of the **Polytrichopsida**.

Antibodies against varied carbohydrate epitopes of arabinogalactan proteins gave different results. The 'arabinogalactan proteins (AGP)' antibody labelled the WCCs in all mosses, except *Dawsonia*, whilst no labelling was observed in hepatics.



Figure 20. *Polytrichum commune* with capsules. Photo by George Shepherd, through Creative Commons.





Figure 21. *Polytrichum commune* 2-year growth in Europe. Photo by Michael Lüth, with permission.



Figure 22. *Dendroligotrichum dendroides*. Photo by Jan-Peter Frahm, with permission.



Figure 23. *Dendroligotrichum dendroides* stem cross section showing hydroids and leptoids. Photo by Juan Larrain, with permission.

The **Polytrichaceae** lead the way to complexity with their unusual leaf structure, possessing vertical **lamellae** (vertical tiers of cells like the pages of an open book; Figure 24-Figure 26) that provide an interior somewhat resembling that of a maple leaf. In fact, in the genus *Polytrichum*, some members have the outer portion of the blade folded over the lamellae (Figure 27-Figure 28), creating an internal chamber resembling palisade mesophyll surrounded with epidermis. The **cuticle** (in this

case, a waxy, water-repellant covering on the outer surface of the leaf; Proctor 1979) of *Polytrichum* is more developed than in most other bryophytes, and *Polytrichum* seems to repel water from its leaves rather than to absorb it (Figure 27), a phenomenon that may prevent the spaces among the lamellae from flooding that would block access of CO<sub>2</sub> to the chloroplasts within. Its rhizoids function not only for anchorage, but also seem to facilitate external water movement.



Figure 24. *Polytrichum ohioense* leaf lamellae in surface view. Photo by John Hribljan, with permission.

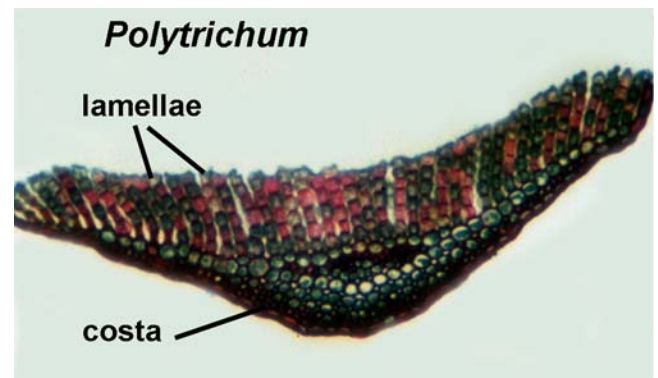


Figure 25. Stained leaf cross section of *Polytrichum* showing vertical lamellae. Photo by Janice Glime.

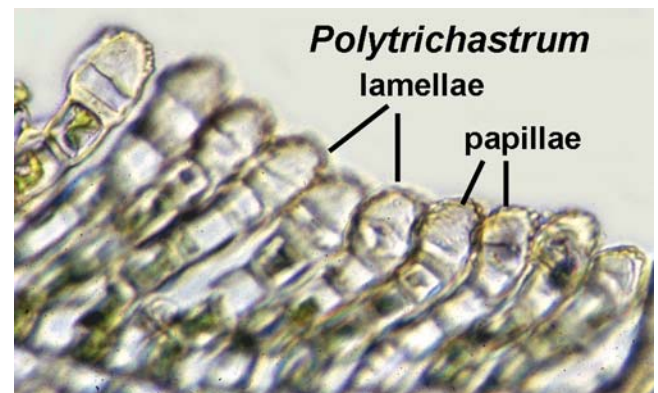


Figure 26. Hand section of *Polytrichastrum alpinum* leaf showing lamellae with papillose terminal cells. Photo by Janice Glime.





Figure 27. *Polytrichum juniperinum* with waxy leaves and lamina that rolls over the lamellae. Photo by Janice Glime.

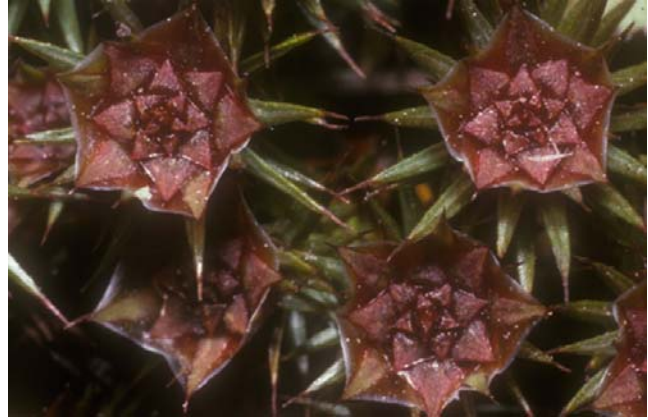


Figure 29. Male plants of *Polytrichum juniperinum* with antheridial splash cups. Photo by Janice Glime.



Figure 28. *Polytrichum juniperinum* leaf cross section showing lamellae and edges of leaf folded over them. Photo by John Hribljan, with permission.

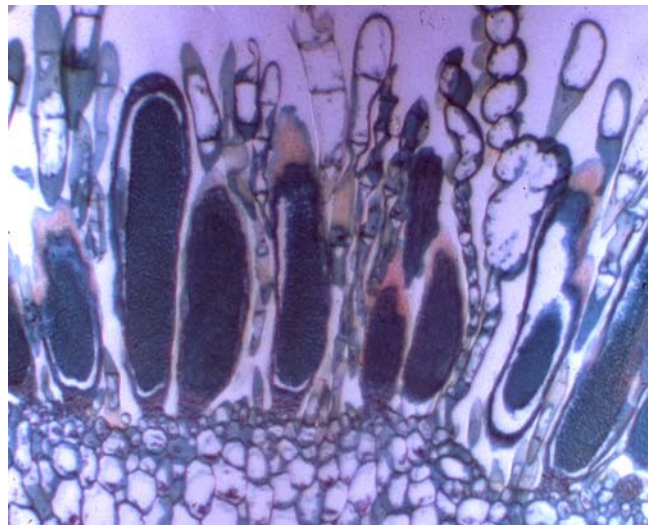


Figure 30. *Polytrichum* antheridial head showing paraphyses and antheridia. Note space where mucilage collects between the dark sperm tissue and the sterile jackets of the antheridia. Photo by Janice Glime.

In some mosses, like *Polytrichum*, the antheridia are in splash **cups** or **platforms** (rosette of leaves from which reproductive units such as sperm, gemmae, or spores can be splashed by raindrops; Figure 29), and when the **sperm** (male reproductive cells; male gametes) are mature, the antheridium (Figure 30) swells and bursts during a rainy period. The bases of the antheridia, in taxa such as *Polytrichum* and *Atrichum* (Figure 37), collect fluid between the sperm tissue and the antheridial jacket (Figure 30) (Bold *et al.* 1987). When the cells at the tip of the sterile jacket open, the antheridial jacket contracts. At this time, the fluid at the bottom acts as a hydraulic ram and forces the sperm out of the antheridium. Once in the open water of the splash cup, the sperm are splashed from the cup. Hopefully, some of these sperm will splash near the tip of a female plant (Figure 31) and will begin swimming toward the archegonium (Figure 32).



Figure 31. Female plants of *Polytrichum ohioense* showing the tight leaves at the apex where archegonia are housed. To the right of the female plants, the yellow swollen tips are male plants with unopened antheridial splash cups. Photo by Janice Glime.



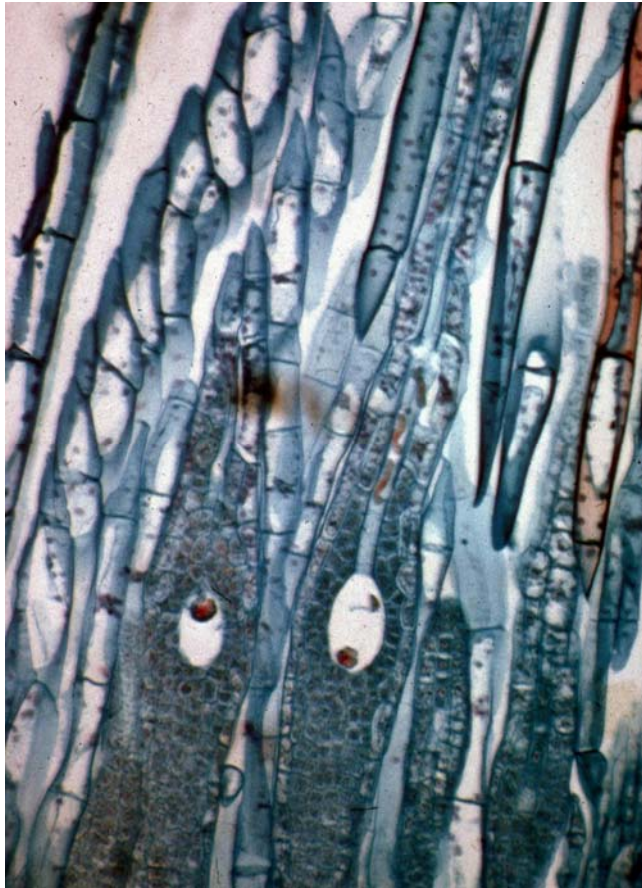


Figure 32. Archegonia nestled among terminal leaves of *Polytrichum*. Photo from Michigan State University botany collection, with permission.

But it appears that the sperm of *Polytrichum commune*, and perhaps others, may have some help in this process from another source (Harvey-Gibson & Miller Brown 1927). A variety of invertebrates visit the male splash cups once they are fertile and get the mucilage with sperm stuck on their bodies. While visiting the plants, the insects lap up the mucilage and lick the saline crystals that form on the margins of the perichaetial leaves. The same insects, bodies and limbs smeared with mucilage in which sperms were abundant and motile, likewise appear on female plants. Now, can someone show whether the red color of splash cups (Figure 29) in several members of this family have the ability to attract any dispersal agents?

After fertilization, the zygote divides to form an **embryo** within the **archegonium**. Eventually this sporophyte embryo tissue forms a **foot**, **seta**, and **capsule**. The capsule develops within the **calyptra** (Figure 33-Figure 35), which is the expanded archegonium. The calyptra is essential for normal development in most mosses, and a split on one side can cause asymmetrical development. In the case of *Polytrichum*, the calyptra is very hairy (Figure 35), earning the moss the name of haircap moss or goldilocks moss. If it is removed early in development, the capsule will not develop properly.

Eventually the **calyptra** (Figure 35) is shed, exposing the capsule. Then the **operculum** (lid) must come off to permit spore dispersal. In this family the capsule has 64 short teeth joined by a membrane (**epiphragm**) that covers

the capsule like skin on a drum (Figure 36). These small spaces permit spores to escape the capsule a few at a time, providing maximum chances for some escaping under the right conditions for dispersal and establishment.



Figure 33. *Polytrichum piliferum*. Young sporophyte with calyptra (old archegonium) on top. Photo by Janice Glime.



Figure 34. **Seta** (stalk) of sporophyte with calyptra removed, showing that the capsule has not yet begun to develop. Photo by Janice Glime.



Figure 35. Capsules of *Polytrichum* at maturity, still covered with the calyptra. Photo by Janice Glime.





Figure 36. Epiphragm of *Polytrichum*. Photo by Laurie Knight <<http://www.flickr.com/photos/laurie-knight>>, with permission.



Figure 37. *Atrichum undulatum* with antheridial splash cups, another member of the **Polytrichaceae**. Photo by Janice Glime.

### Tetraphidaceae

*Tetraphis* (Figure 38), also in the **Polytrichopsida**, looks more like a typical moss than do other **Polytrichopsida**, with thin, 1-cell-thick leaves and a costa (Figure 38-Figure 39). *Tetraphis* is unique among mosses in having **gemmae** (Figure 40-Figure 42) arranged in splash cups at the tips of the stems when sexual reproduction is not in season, arguably a primitive remnant. These gemmae are asexual bits of plant material that can grow into a new plant. Its most unusual character is that its protonemata are not threads, but rather flaps (Figure 43). Antheridia are borne terminally on the leafy plants (Figure 44), as are the archegonia. The capsule (Figure 45) has only four long, unjoined, nematodontous teeth (Figure 10, Figure 46).



Figure 38. *Tetraphis pellucida* showing thin leaves with a costa. Photo by Des Callaghan, with permission.



Figure 39. *Tetraphis pellucida* leaf cross section showing 1-cell-thick lamina and multicellular costa. Photo from botany website, University of British Columbia, with permission.



Figure 40. Leafy gametophytes of *Tetraphis pellucida* with gemmae cups on top. Photo by Janice Glime.





Figure 41. Gemma cup with gemmae of *Tetraphis pellucida*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.



Figure 42. *Tetraphis pellucida* gemmae, asexual means of reproduction. Photo by Jessica Budke, with permission.

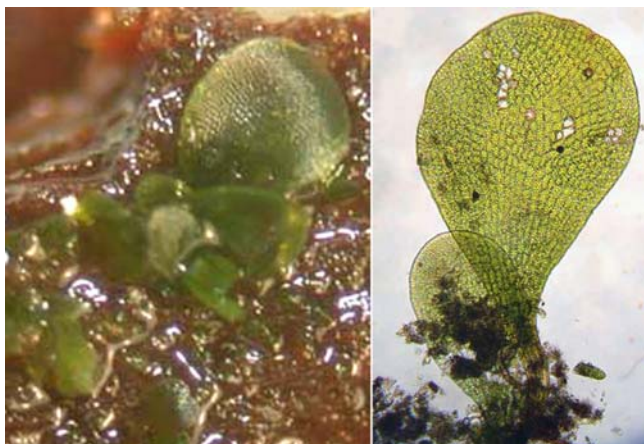


Figure 43. Protonemal flaps of *Tetraphis pellucida*. Photos from University of British Columbia Biology 321 Course Website, with permission.

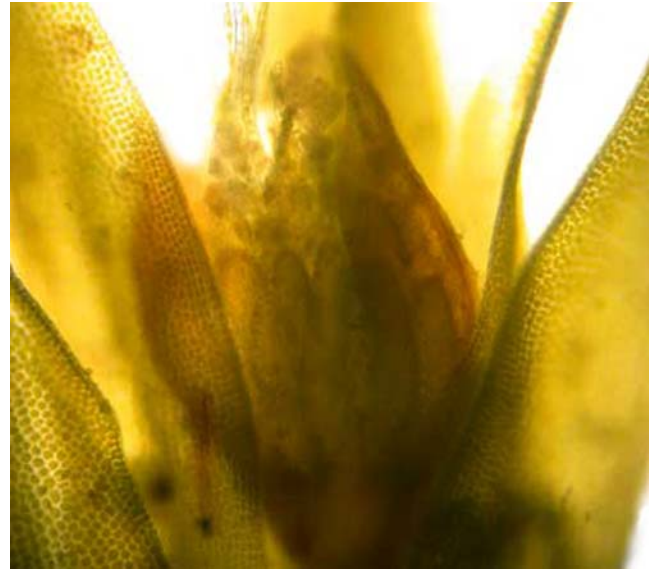


Figure 44. Leaves and antheridia of *Tetraphis pellucida*. Photo from UBC Biology 321 Course Website, with permission.



Figure 45. Capsules of *Tetraphis pellucida* showing calyptra with capsule exposed in the lower third. Photo by Janice Glime.

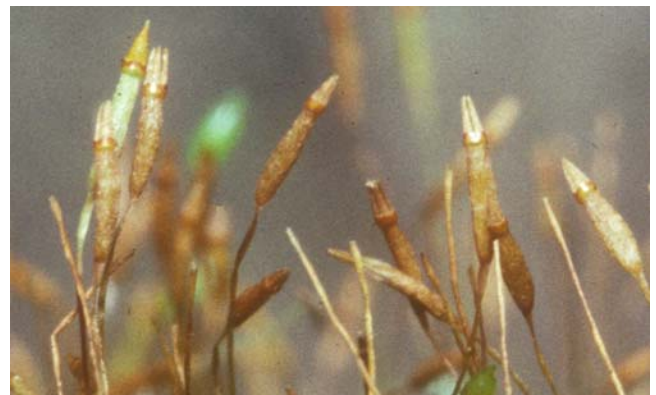


Figure 46. Capsules of *Tetraphis pellucida*, lacking calyptra and operculum (lid), exposing the 4 peristome teeth. Photo by Janice Glime.



### Buxbaumiaceae – Bug on a Stick

*Buxbaumia* (Figure 47-Figure 51) is one of the strangest of all mosses. It lacks any leafy stem at all (Figure 47). Its archegonia and antheridia arise directly from the protonema. Hence, its capsules (Figure 49) arise directly from this persistent protonema (Figure 47). They all tend to orient in the same direction (Taylor 1972), most likely in response to the predominant direction of light. Its capsules, although possessing teeth (Figure 50), more typically split across their broad, flattened surface, hence exposing the spores (Figure 51) (Koch *et al.* 2009). Koch and coworkers demonstrated that in *Buxbaumia viridis* (Figure 47) this capsule surface is covered with "massive" wax layers that have embedded and superimposed platelets and granules on them. When these waxy layers peel back, the epidermis peels with them.



Figure 47. *Buxbaumia viridis* sporophyte and protonema. Photo by Bernd Haynold, through Wikimedia Commons.

The *Buxbaumia* capsule interior is chambered and spongy, somewhat like a spongy mesophyll of Magnoliophyta. It typically occurs with tiny, black leafy liverworts such as *Cephalozia* (Figure 52). Campbell (1918) had considered this moss to be saprophytic, exhibiting almost no chlorophyll, but Mueller (1975) demonstrated dense chlorophyll in the protonema and considered that to be the primary photosynthetic organ, one that persists throughout the life of the moss. The protonema is not a good competitor, so you can find it after forest fires, on soil banks, on roadsides, and other places that are not very hospitable to plants that could easily overgrow the photosynthetic protonemata. The capsule (Figure 47-Figure 49) is rather unusual, with its broad, flattened side and a rounded side. This strange shape has earned it a number of common names, including humpbacked elves, elf-cap moss, Aladdin's lamp, and bug on a stick.



Figure 48. *Buxbaumia aphylla* on a soil bank with all capsules pointing the same direction. It has been suggested that common habit is advantageous to maximize light absorption by the photosynthetic capsule. Photo by Janice Glime.



Figure 49. Unopened capsule of *Buxbaumia aphylla*, illustrating flat side with beaked operculum that has earned it the common names of bug-on-a-stick and Aladdin's lamp moss. Note the absence of a leafy gametophyte, but the presence of other mosses. Photo by Adam Gordon through Creative Commons.





Figure 50. *Buxbaumia piperi* capsule showing diminished peristome teeth. Photo from botany website at the University of British Columbia, with permission.



Figure 51. *Buxbaumia aphylla* (Class Polytrichopsida) showing flat side of capsule peeled back to expose the spores and spongy interior. Photo by Janice Glime.



Figure 52. *Cephalozia bicuspidata*, member of a genus of tiny liverworts that often occur with *Buxbaumia aphylla*. Photo by Kristian Peters, through Wikimedia Commons.

In *Buxbaumia aphylla*, Hancock and Brassard (1974a) found that almost all elements that occurred in the protonema also occurred in the sporophyte, suggesting they were transported internally. Hancock (1973) also suggested that its protonemata were perennial. In northern climates, this is advantageous because the capsules are very susceptible to mortality from sudden early frosts. Normally, the capsules form in fall and overwinter as green capsules (Hancock & Brassard 1974b). They complete development and disperse their spores early in spring, then disappear.

### Diphysciaceae

*Diphyscium* (Figure 53-Figure 60) is distributed mostly in the northern hemisphere (Milne & Klazenga 2012). Its three genera have been reduced to one (Magombo 2002; Goffinet 2012), which has an asymmetrical capsule (Figure 57-Figure 60) of similar shape to that of *Buxbaumia* and lacks a leafy female stem except for perichaetial leaves (Figure 60), but the male plant of this genus has large, strap-shaped leaves and leads an independent and separate existence (Figure 53-Figure 56). The capsule opening is quite small and the teeth extrude like a wisp of hairs (Figure 60). The perichaetial leaves are unusual, having a long, excurrent costa and often being fimbriate on the margins (Figure 59-Figure 60). As in *Buxbaumia*, the capsule shape is responsible for several common names – nut moss, powder gun moss, grain of wheat moss. It shares the phototropic behavior of *Buxbaumia* by having its capsules all oriented in one direction with their flat sides facing the direction of the light (Figure 57-Figure 59).



Figure 53. Male plant of *Diphyscium foliosum* showing strap-shaped leaves. Photo by Hermann Schachner, through Creative Commons.



Figure 54. Leaf of male plant of *Diphyscium foliosum* showing weak costa and rows of cells. Photo by Hermann Schachner, through Creative Commons.





Figure 55. Male plant of *Diphyscium foliosum* showing antheridia. Photo modified from botany website and University of British Columbia, with permission.



Figure 56. Cross section of leaf of male plant of *Diphyscium foliosum* showing multiple layers and extensive papillae. Photo by Hermann Schachner, through Creative Commons.



Figure 57. *Diphyscium foliosum* female plants with young sessile capsules surrounded by perichaetial leaves. These are clumped here among male plants with green, strap-shaped leaves. Photo by Janice Glime.



Figure 58. **Upper:** *Diphyscium foliosum* female plants with young sessile capsules among male plants. Photo by Janice Glime. **Lower:** Mature female *Diphyscium foliosum* plants with capsules showing peristome teeth. Photo by Michael Lüth, with permission.



Figure 59. Capsules and perichaetial leaves of *Diphyscium foliosum*. Photo by Michael Lüth, with permission.



Figure 60. *Diphyscium foliosum* female plant with perichaetial leaves and capsule showing small opening and peristome teeth. Photo by Jan-Peter Frahm, with permission.



## Summary

Bryophyta can be considered to have six classes: Takakiopsida, Sphagnopsida, Andreaeopsida, Andreaobryopsida, Polytrichopsida, and Bryopsida, differing most consistently in capsule structure. Gametophores of **Andreaeopsida**, **Andreaobryopsida**, and **Polytrichopsida** produce **archegonia** and/or **antheridia** at the apex and the **embryo** develops within the archegonium.

**Sporophytes** remain attached to the **gametophyte** and produce **spores** by **meiosis**. These classes, and all Bryophyta, produce spores from the sporophyte only once.

**Takakiopsida**, **Andreaeopsida**, and **Andreaobryopsida** have capsules that **split** into valves, but lack elaters. **Sphagnopsida** lacks valves and has an **operculum** that is shed at dispersal time, but lacks peristome teeth. In capsules of **Polytrichopsida** and **Bryopsida**, an **operculum** usually covers **peristome** teeth that often aid dispersal, contrasting with liverworts wherein the capsule splits into four valves with elaters that possibly facilitate spore movement. **Polytrichopsida** have **nematodontous** peristome teeth; **Bryopsida** have **arthrodontous** peristome teeth. All other classes of Bryobiotina lack peristomes. **Andreaobryopsida** is **dioicous** (two sexes on separate plants) and possesses a **seta** (stalk of capsule), whereas **Andreaeopsida** is **monoicous** (both sexes on same plant) and lacks a seta.

## Acknowledgments

I appreciate the comments and suggestions of Karla Werner, who offered a beginner's perspective. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and helped with the proof reading. Heino Lepp alerted me to the invertebrate dispersal of sperm by his 3 September 2006 contribution to Bryonet. Llo Stark provided valuable suggestions on the chapter.

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