CHAPTER 2-5
BRYOPHYTA – SPHAGNOPSIDA

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Figure 1. ***Sphagnum papillosum*** with capsules. Photo by Janice Glime.

Class Sphagnopsida – the peat mosses

The class **Sphagnopsida** is very different from other members of **Bryophyta** (*sensu stricto*). It certainly is worthy of its own class, and some agree with Crum (2004) that it is likewise worthy of its own phylum, the **Sphagnophyta**. Certainly its morphological differences play a major role in its unusual ecology. Until recently it was composed of only one genus (***Sphagnum***; Figure 1), but now the family **Ambuchananiaceae** (one genus, ***Ambuchanania***) has been described from Tasmania, and possesses rhizoids. The only other member of **Sphagnopsida** with rhizoids is ***Sphagnum*** (=***Flatbergium***) ***novo-caledoniae*** (Figure 2-Figure 4), an **epiphyte** (Iwatsuki 1986; plants that grow on another plant without deriving nutrients from it) that grows in or near rivers (IUCN 2013).

Figure 2. ***Sphagnum*** (=***Flatbergium***) ***novo-caledoniae***. This species is an endemic to New Caledonia and is the only ***Sphagnum*** species known to produce rhizoids. Photo by Louis Thouvenot, with permission.

Figure 3. ***Sphagnum novo-caledoniae*** showing its habitat that is often on riverbanks. Photo by Juan Larrain, with permission.

Figure 4. ***Sphagnum novo-caledoniae*** rhizoids. Photo by Louis Thouvenot, with permission.

Sphagnaceae

Of all the Bryobiotina, ***Sphagnum*** is best known to the layperson because of its formation of peat and use in horticulture. The class Sphagnopsida is distinguished by **leaves** that are **one cell thick** and mostly possessing two types of cells – **photosynthetic cells** that possess chloroplasts and that form a network arrangement, and **hyaline** (colorless) **cells** that are dead at maturity, have one or more **pores** (giving access to the environment), and hold water (Figure 44). These hyaline cells form transparent patches among the network formed by the photosynthetic cells and may be equal in height to those cells or may surround them on the top (inner leaf surface) or on both surfaces. This arrangement seems to correlate well with the ability to avoid desiccation because the hyaline cells provide a reservoir of water to the photosynthetic cells. Those species typically occupying drier habitats generally have more of the hyaline cell surrounding the photosynthetic cell. These hyaline cells are usually strengthened by bar-like thickenings (**fibrillae**, Figure 44) in the cell walls, making them look superficially like many cells instead of the single long cell that they are. These leaves never possess a **costa** (moss version of a midrib).

The branches in Sphagnopsida occur in **fascicles** (bunches) along the stem, usually with some descending branches close to the stem (helping in capillary movement of water) and some extending outward. The stems have a wood-like cylinder that may be brittle or soft. The most readily distinctive feature is the arrangement of young branches in a tight **capitulum** (Figure 45), the result of branch production and elongation without the elongation of the stem. As older portions of the stem elongate, new branches form and the capitulum is maintained. This gametophyte can reproduce by fragmentation, often bifurcating at the apex to produce two capitula.

This large genus can be divided into two groups based on the large, succulent-looking leaves vs the small leaves on more narrow branches. But this grouping did not work well phylogenetically, so instead nine sections were recognized. These were recently reorganized into subgenera based on 11,704 nucleotide sequences from the nuclear, plastid, and mitochondrial genomes (Shaw *et al*. 2010):

Subgenus *Sphagnum* is characterized by tightly or loosely imbricate, hood-shaped (**cucullate**) branch leaves and large, tongue-shaped (**lingulate**) or fan-shaped stem leaves (> 1 mm long) (Figure 5-Figure 12).

Subgenus *Rigida* is the other group with cucullate branch leaves but is separated by small (< 1 mm long), triangular stem leaves and somewhat (or not) **squarrose** (spreading at right angles) branch leaves (Figure 13-Figure 14).

Subgenus *Cuspidata* has a pronounced difference between hanging branches and spreading branches, usually with hanging branches longer and more slender than spreading branches; stem leaves are much smaller than branch leaves and usually hang downward on the stem; colors vary but are never red; they are typical in wet mineral-rich depressions, submerged or near the water level (Figure 15-Figure 24).

Subgenus *Subsecunda* has flexuose hanging and spreading branches that are very similar, about the same length, or with few or no branches; stem leaves are much smaller than branch leaves and usually hang downward on stems; plants are various colors but never red (branches and stems sometimes pinkish) (Figure 25-Figure 29).

Subgenus *Squarrosa* has distinctly squarrose branch leaves and large (1-1.5 mm long) lingulate stem leaves (Figure 30-Figure 31).

Subgenus *Acutifolia*

Section *Acutifolia*, like Subgenus ***Cuspidata***, has a pronounced difference between hanging branches and spreading branches, usually with hanging branches longer and more slender than spreading branches; they differ from ***Cuspidata*** in having stem leaves nearly the same size as branch leaves or larger and usually upright on stems; plants are various shades of green, brown, or red (Figure 32-Figure 41).

Section *Polyclada* is monotypic and lacks the cucullate leaf structure, being distinguished by having six or more branches per fascicle and a dense, rounded capitulum (Figure 42).

Section *Insulosa* has toothed branch leaves and pores in hyaline cell ends (Figure 43).

Figure 5. ***Sphagnum divinum*** (Subgenus ***Sphagnum***). Photo by David Holyoak, with permission.

Figure 6. ***Sphagnum centrale*** (Subgenus ***Sphagnum***). Photo by Michael Lüth, with permission.

Figure 7. ***Sphagnum cristatum*** (Subgenus ***Sphagnum***). Photo by Jan-Peter Frahm, with permission.

Figure 8. ***Sphagnum austinii*** (Subgenus ***Sphagnum***). Photo by Des Callaghan, with permission.

Figure 9. ***Sphagnum papillosum*** (Subgenus ***Sphagnum***). Photo by David Holyoak, with permission.

Figure 10. ***Sphagnum imbricatum*** (Subgenus ***Sphagnum***). Photo by Jan-Peter Frahm, with permission.

Figure 11. ***Sphagnum affine*** (Subgenus ***Sphagnum***). Photo by Jan-Peter Frahm, with permission.

Figure 12. ***Sphagnum palustre*** (Subgenus ***Sphagnum***). Photo by Michael Lüth, with permission.

Figure 13. ***Sphagnum compactum*** (Subgenus ***Rigida***). Photo by Jan-Peter Frahm, with permission.

Figure 14. ***Sphagnum strictum*** (Subgenus ***Rigida***). Photo by Jan-Peter Frahm, with permission.

Figure 15. ***Sphagnum riparium*** (Subgenus ***Cuspidata***). Photo by Jan-Peter Frahm, with permission.

Figure 16. ***Sphagnum tenellum*** (Subgenus ***Cuspidata***). Photo by David Holyoak, with permission.

Figure 17. ***Sphagnum pulchrum*** (Subgenus ***Cuspidata***). Photo by Des Callaghan, with permission.

Figure 18. ***Sphagnum fallax*** (Subgenus ***Cuspidata***). Photo by David Holyoak, with permission.

Figure 19. ***Sphagnum angustifolium*** (Subgenus ***Cuspidata***). Photo by Michael Lüth, with permission.

Figure 20. ***Sphagnum majus*** (Subgenus ***Cuspidata***). Photo by Michael Lüth, with permission.

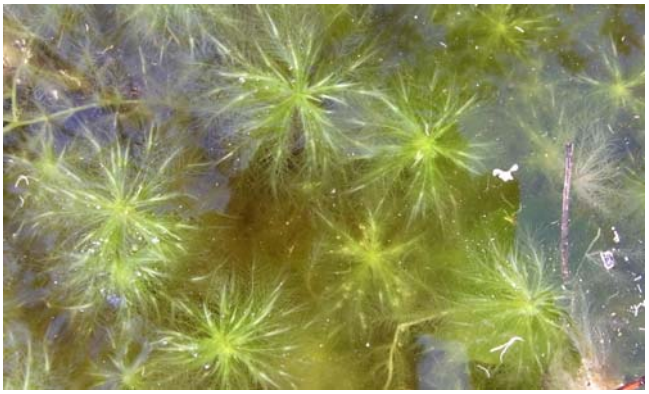

Figure 21. ***Sphagnum trinitense*** (Subgenus ***Cuspidata***). Photo by Blanka Aguero, with permission.

Figure 22. ***Sphagnum mendocinum*** (Subgenus ***Cuspidata***). Photo by Adolf Ceska, with permission.

Figure 23. ***Sphagnum cuspidatum*** (Subgenus ***Cuspidata***). Photo by Michael Lüth, with permission.

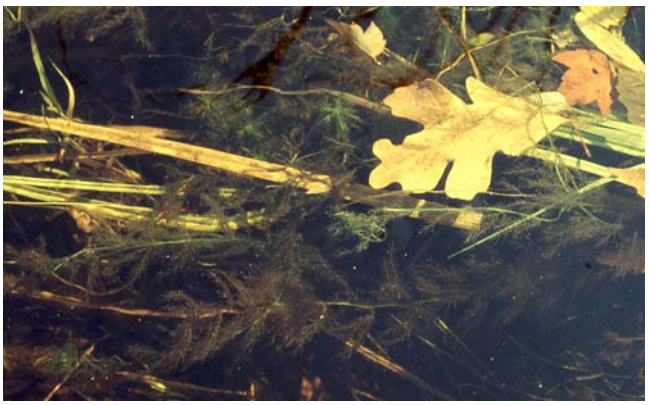

Figure 24. ***Sphagnum torreyanum*** (Subgenus ***Cuspidata***). Photo by Janice Glime.

Figure 25. ***Sphagnum pylaisii*** (Subgenus ***Subsecunda***). Photo by Jan-Peter Frahm, with permission.

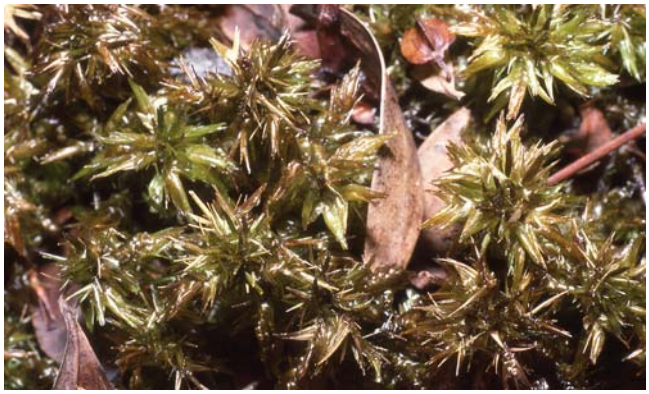

Figure 26. ***Sphagnum macrophyllum*** (Subgenus ***Subsecunda***). Photo by Janice Glime.

Figure 27. ***Sphagnum subsecundum*** (Subgenus ***Subsecunda***). Photo by Michael Lüth, with permission.

Figure 28. ***Sphagnum contortum*** (Subgenus ***Subsecunda***). Photo by Michael Lüth, with permission.

Figure 29. ***Sphagnum platyphyllum*** (Subgenus ***Subsecunda***). Photo by Michael Lüth, with permission.

Figure 30. ***Sphagnum squarrosum*** (Subgenus ***Squarrosa***). Photo by Dick Haaksma, with permission.

Figure 31. ***Sphagnum teres*** (Subgenus ***Squarrosa***). Photo by Michael Lüth, with permission.

Figure 32. ***Sphagnum quinquefarium*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Sphagnum fimbriatum*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Jan-Peter Frahm, with permission.

Figure 34. ***Sphagnum girgensohnii*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Janice Glime.

Figure 35. ***Sphagnum russowii*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Michael Lüth, with permission.

Figure 36. ***Sphagnum arcticum*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Michael Lüth, with permission.

Figure 37. ***Sphagnum meridense*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Jan-Peter Frahm, with permission.

Figure 38. ***Sphagnum warnstorfii*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). This species can turn blue in a basic *p*H. Photo by Michael Lüth, with permission.

Figure 39. ***Sphagnum fuscum*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Michael Lüth, with permission.

Figure 40. ***Sphagnum balticum*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by Michael Lüth, with permission.

Figure 41. ***Sphagnum capillifolium*** (Subgenus ***Acutifolia***, Section ***Acutifolia***). Photo by David Holyoak, with permission.

Figure 42. ***Sphagnum wulfianum*** (Subgenus ***Acutifolia***, Section ***Polyclada***). Photo by Jan-Peter Frahm, with permission.

Figure 43. ***Sphagnum aongstroemia*** (Section ***Insulosa***). Photo by Dale Vitt, with permission.

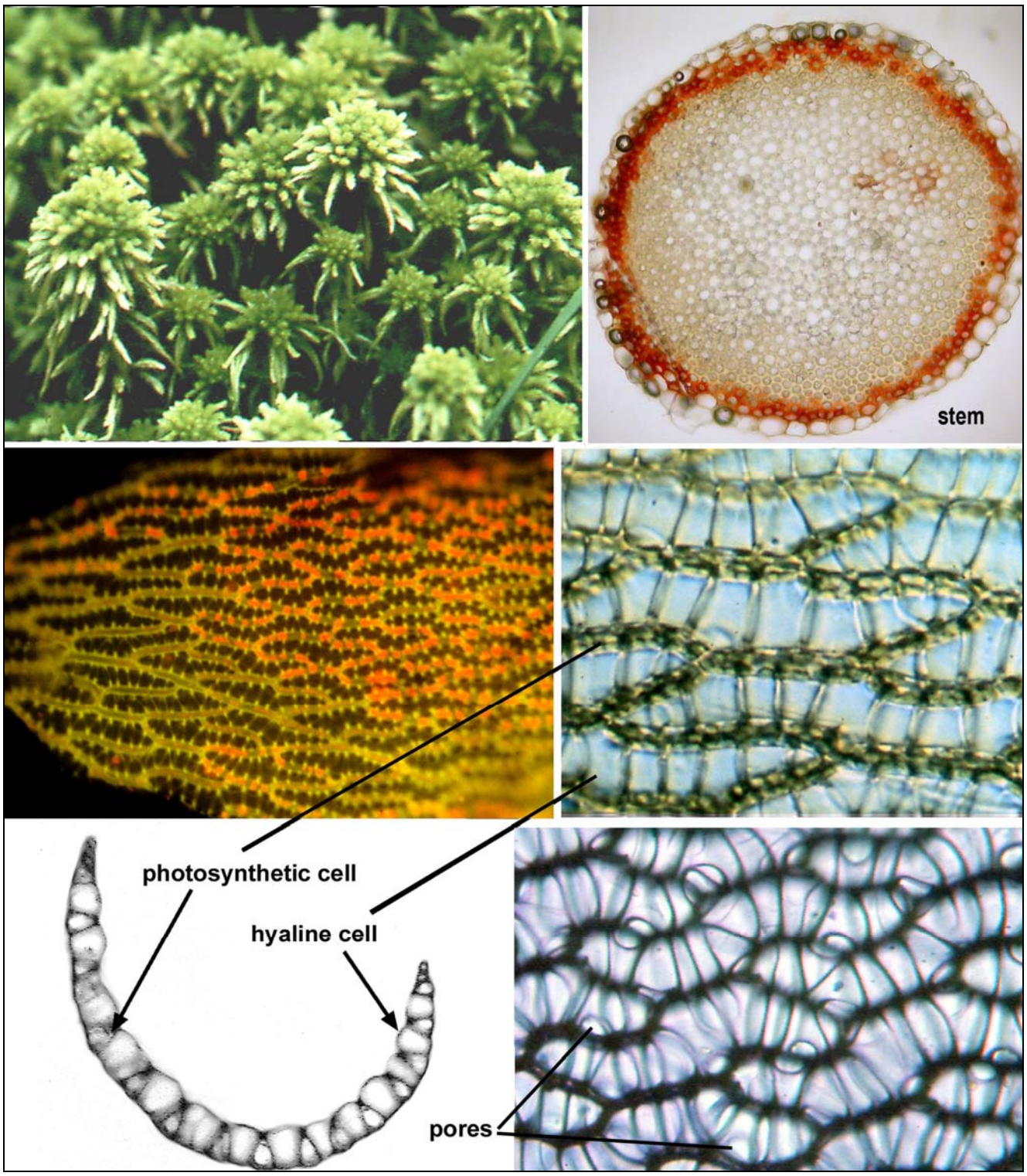

Figure 44. Vegetative characters of ***Sphagnum***, Class Sphagnopsida. **upper left:** ***Sphagnum wulfianum*** capitula; **upper right:** cross section of stem showing hyaline cells of interior and outer layer (photo by David Tng, with permission); **middle left:** leaf showing pattern of hyaline and photosynthetic cells illuminated by UV light; red areas indicate chlorophyll fluorescence; **middle right:** portion of leaf showing photosynthetic and hyaline cells (note fibrillae on hyaline cells); **lower left:** cross section of leaf showing hyaline cells that nearly enclose the photosynthetic cells; **lower right:** methylene-blue-stained portion of leaf showing pores in hyaline cells. Photos by Janice Glime, except as noted.

Figure 45. ***Sphagnum fimbriatum*** showing capitulum where archegonia will arise. Photo by Janice Glime.

The **antheridia** are nearly globose (Figure 46) and are nestled among the leaves near the tips of the capitulum branches, usually endowing those tips with a reddish color (Figure 47). The **archegonia** are terminal on short branches near the center of the capitulum.

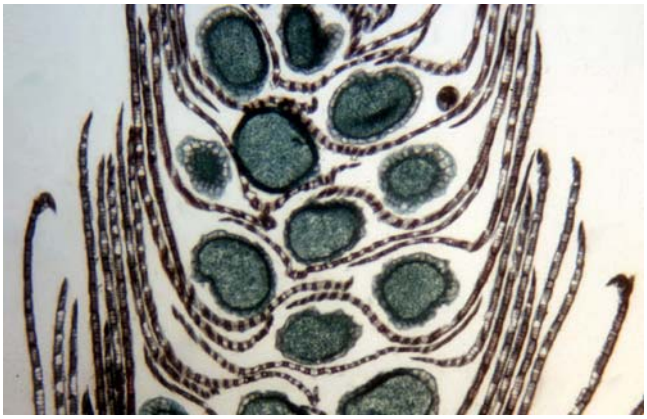

Figure 46. Globose ***Sphagnum*** antheridia nestled among the leaves of a capitulum branch. Photos by Janice Glime (**top**) and Yenhung Li (**bottom**), with permission.

Jennings (1915) and Bryan (1915 in Jennings 1915) recognized the unique character of ***Sphagnum***. They described a globose antheridial head that began development in August, before the September initiation of the archegonia. They discovered that some of the oldest archegonia matured by 25 October, whereas others did not mature until spring. But the uniqueness was the structures. The archegonia have a stalk, thick venter, and a narrow, twisted neck, all characteristic of mosses. But their inactive cover cell, intercalary growth of the archegonia, and the small number of canal cells (8-9) are characteristic of liverworts.

Figure 47. Antheridial branches in the capitulum of ***Sphagnum***. Red coloration is from the antheridia. Photo by Janice Glime.

Sphagnum* capsules** (Figure 48), or sporangia, are rarely seen in many of the species, but some fruit abundantly. Nevertheless, one must be lucky to see them because they, like the liverwort sporophytes, are **short-lived**. They develop from fertilized eggs (**zygotes**) in the capitulum (Figure 45). As these develop embryos, they likewise form a **foot**, **stalk**, and **capsule** (Figure 48), but the stalk does not elongate. Instead, it remains with its foot, embedded in gametophyte tissue. ***Sphagnum is much like the liverworts in that its stalk matures after the capsule is mature, but in ***Sphagnum***, this watery stalk (**pseudopodium**, pl. **pseudopodia**) is part of the gametophyte generation, not the sporophyte (Figure 48). It soon disintegrates, as do the liverwort stalks.

The capsule does not split as in liverworts and the **Takakiopsida**, **Andreaeopsida**, and **Andreaeobryopsida** in the **Bryophyta**, but instead possesses an **operculum** (lid; top part of capsule of mosses that comes off for spore dispersal) that is shed prior to spore dispersal (Figure 48), as in the **Bryophyta** classes **Bryopsida** and **Polytrichopsida**. However, unlike most members of the latter two classes, it lacks a **peristome** (set of teeth-like appendages around the opening of capsule; Figure 48). The **columella** (Figure 48), that central mass of sterile tissue that is like a column in **Bryopsida** and **Polytrichopsida**, is globose in ***Sphagnum***, protruding like a knob into the center of the capsule without reaching its top. **Elaters are lacking**, a characteristic shared with all other **Bryophyta** (*sensu stricto*).

Within the capsule, meiosis occurs, producing the spores. When the spores are mature, the **operculum** (Figure 48) is shed explosively when the capsule shrinks and compresses the gases, dispersing nearly all the spores in one blast of 4-6 atmospheres of pressure (Crum 2004; see Chapter 4-9). In fact, bryological folklore claims that one can hear the explosions when the sun and moisture are just right to cause the capsules to explode. No extant sphagnologist seems to have actually heard this, but following a ***Sphagnum*** field trip at an international meeting in Great Britain, one of the bryologists was startled

to hear ping...ping-ping...ping-ping-ping while he was sitting in bed reading. He had put his ***Sphagnum*** with capsules under the bed lamp to dry, and so it had, with capsules shrinking and exploding. The pings were opercula hitting the metal shade on the lamp!

It appears that ***Sphagnum*** is prolific in its spore production, with mean number per capsule ranging from 18,500 in ***Sphagnum tenellum*** to 243,000 in ***S. squarrosum*** (Sundberg & Rydin 1998) and **source strength** (estimated original number of spores in capsules that dehisced during experiment) ranging 8-90 million spores (Sundberg 2005). And these spores seem to disperse quite well, with only 2-14% of those dispersed remaining within the parent colony. Being large helps. The larger capsules dispersed a greater percentage of spores, had a smaller percentage trapped within the parent colony, and thus dispersed more spores to greater distances.

In the presence of moisture and light, and at least some nutrients, particularly phosphates (see Sundberg & Rydin 2002; Claeys 2017), the spores germinate to form a short thread. This thread soon, however, divides in more than one direction to form a **thalloid protonema** (Figure 48), as in most liverworts. A similar thalloid protonema is present also in other bryophytes such as ***Andreaea*** (Bryophyta class Andreaeopsida) and would be more appropriately called a **sporeling**. Like the liverworts, and unlike the other mosses, each protonema produces **only one bud**, thus only one mature gametophyte.

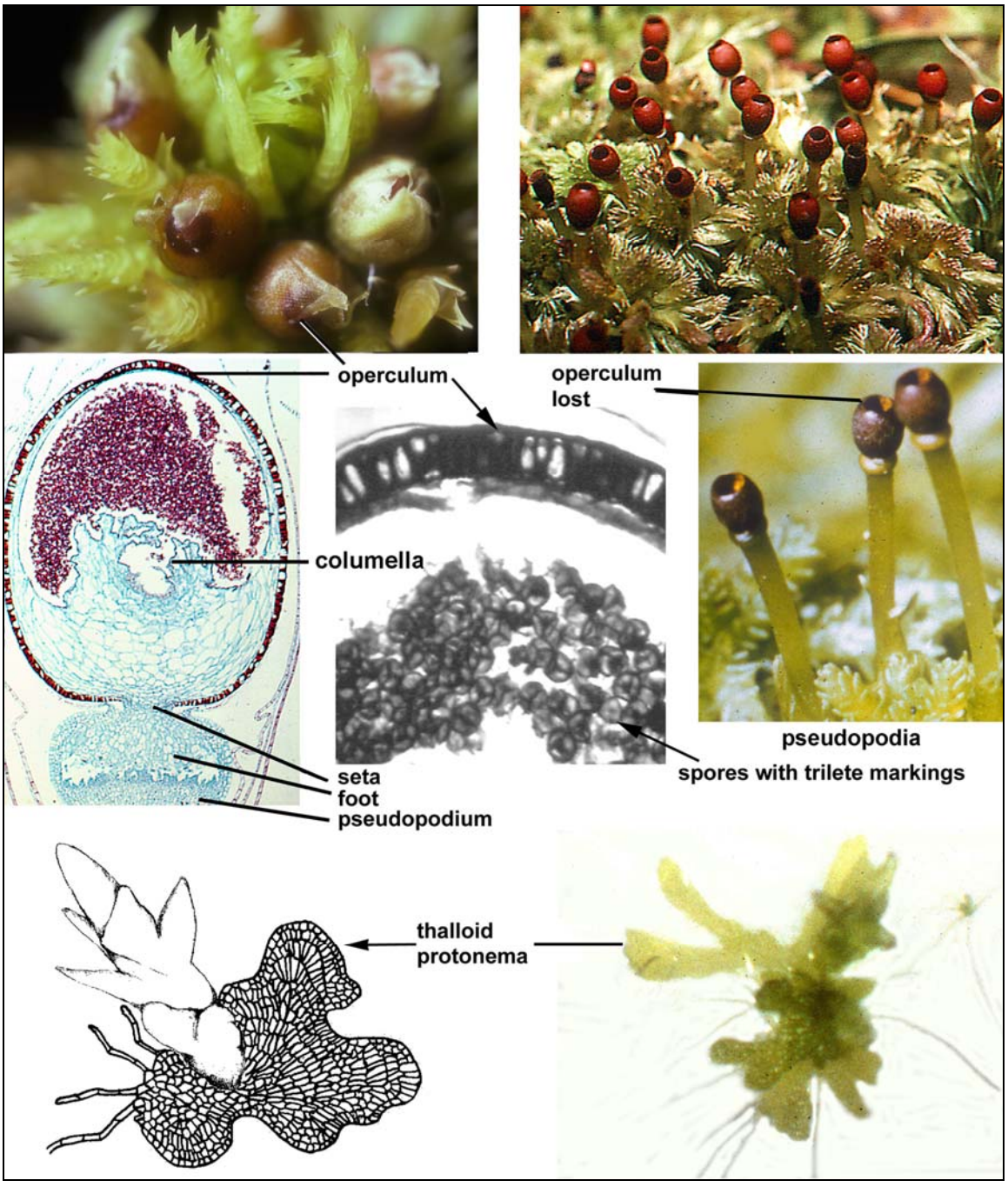

Figure 48. ***Sphagnum*** life cycle stages. Upper left photo by Zen Iwatsuki; others by Janice Glime. Protonema drawing by Margaret Minahan and Noris Salazar Allen, with permission.

Flatbergiaceae (= Sphagnaceae?)

Shaw (in Shaw *et al*. 2010) separated this family morphologically from **Sphagnaceae** by its efibrillose leaves. It is currently monotypic, with only the species ***Flatbergium sericeum***. Currently, however, both Tropicos and The Plant List (Kew) consider this genus to belong in the **Sphagnaceae**. A second species is implicated for the family (Devos *et al*. 2016), based on molecular data. This would transfer ***Sphagnum novo-caledoniae*** to ***Flatbergium novo-caledoniae*** (Figure 49).

Figure 49. ***Flatbergium novo-caledoniae***. Photo courtesy of Kjell Flatberg.

Ambuchananiaceae

Not many of us get to describe a new order. And certainly no one was expecting one in the **Sphagnopsida**! (Shaw 2000; Buchanan 2008). But this organism, this moss, was certainly something new! – ***Ambuchanania leucobryoides*** (Figure 50).

Figure 50. ***Ambuchanania leucobryoides*** showing similarity to some species of ***Sphagnum***. Photo by Lynette Cave, with permission.

Excerpts from correspondence with Rod Seppelt

"We knew it from two localities in south western Tasmania. Alex Buchanan found it in acid gravelly sand outwash near the coast. Heathy vegetation, very low nutrient status soils. The plants were mostly buried in the sand, only the top few mm showing."

"When I first saw the material I kept trying to put it in **Leucobryaceae**. Same habit, hence the epithet. Initially I thought I saw a peristome. The leaves did not fit anything in **Leucobryaceae**. Then the penny dropped – it had no peristome. The position of the archegonia also started to ring bells."...

"So, no protonema is, as yet, known. We have a second locality, inland, from acid, low nutrient, peat amongst button grass moorland (*Gymnoschoenus*, which is a tussock sedge, not a grass). Alex spotted it amongst the base of some *Isolepis* material (pressed) that had been brought into the Tasmanian Herbarium for incorporation."

"Leaf morphology. Yes, it does have chlorophyllose cells and hyaline cells. The thickenings on the walls of the hyaline cells are a bit weird... Norton Miller first asked me if I thought of describing it as a second genus in Sphagnaceae."

"Ultimately, Howard Crum wrote to say that he was so convinced that it was so different from ***Sphagnum***, but within the **Sphagnales**, that it required a separate genus ***Ambuchanania***, new family **Ambuchananiaceae**. Incidentally, Jon Shaw has managed to get some DNA sequencing (incomplete) but he concurs that it is not ***Sphagnum***, although (I believe) happy to see it remain in the Sphagnales."

An endemic of Tasmania, ***Ambuchanania leucobryoides*** occurs in sandy washes known as "daisy pans" derived from Precambrian quartzite (Johnson *et al*. 2008). ***Ambuchanania*** has been collected at two relatively inaccessible, high elevation localities in western Tasmania (Yamaguchi *et al*. 1990).

Now, this strange, yet somewhat familiar genus resides not just in a new family, but a new order, the **Ambuchananiales** (Shaw 2000; Shaw *et al.* 2003). It differs from ***Sphagnum*** in **lacking fascicles**, being **sparsely branched**, and **lacking the "wood" cylinder** of the stem. Its **leaves** are **partially bistratose** but have those telltale **hyaline** and **photosynthetic cells** (Figure 51-Figure 52). It is anchored by **rhizoids**, a character found in ***Sphagnum*** only in one epiphytic species. Its **archegonia** are located **terminally** on stems and its **capsules** are **cylindrical**, and likewise perched on an elevated **pseudopodium**.

Figure 51. ***Ambuchanania leucobryoides*** leaf showing hyaline and photosynthetic cells. Photo by Lynette Cave, with permission.

Figure 52. ***Ambuchanania leucobryoides*** leaf cross section showing hyaline and photosynthetic cells. Photo by Lynette Cave, with permission.

In addition, the genus ***Eosphagnum*** has been added to the **Ambucananiaceae**, an older species that has been reclassified (Shaw *et al*. 2010). This genus has the single species ***E. rigescens*** (an older name for ***E. inretortum***; Figure 53) (Shaw *et al*. 2016).

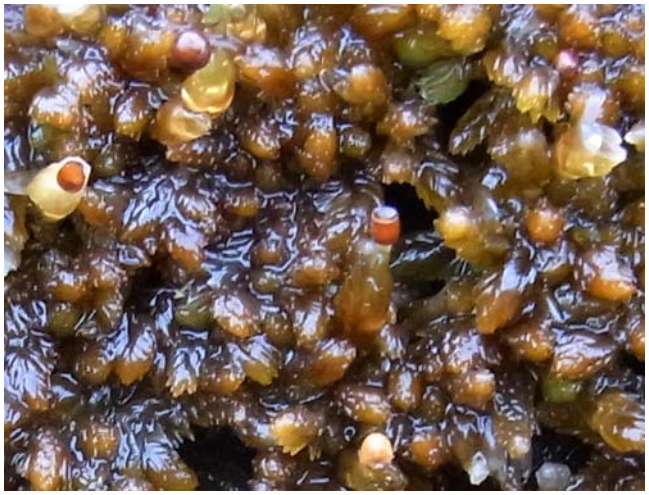

Figure 53. ***Eosphagnum rigescens*** with capsules. Photo courtesy of Blanka Aguero.

Summary

The **Sphagnopsida** are in the **Bryophyta**, although some researchers put them in a separate phylum, the **Sphagnophyta**. Only four genera are known, a large genus – ***Sphagnum***, ***Ambuchanania*** and ***Eosphagnum*** – monotypic genera in a separate order, and ***Flatbergium***.

Sphagnopsida have a **dominant gametophyte** generation with leaves that have a network of **hyaline** and **photosynthetic cells**. Gametophores produce **archegonia** and/or **antheridia** in the **capitulum** and the **embryo** develops within the archegonium.

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis**. The stalk supporting the ***Sphagnum*** sporophyte is a deliquescent extension of the gametophyte (**pseudopodium**) and it develops after the **capsule** is mature. **Sphagnopsida** lack teeth in the capsule but have an **operculum**, which the capsule sheds explosively.

The life cycle involves a **protonema** that develops from the germinating spore, becoming **thalloid** in ***Sphagnum***, whereas it becomes a branched thread in true mosses. The protonema produces one **bud** that develops into a leafy **gametophore**.

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. I appreciate Rod Seppelt's correspondence that added human interest to this story. Louis Thouvenot took pictures of ***Flatbergium*** (=***Sphagnum***) ***novo-caledoniae*** for me so I could illustrate rhizoids. Lynette Cave answered my call for pictures of ***Ambuchanania*** and notified me of an error in the text. Jon Shaw helped me update the nomenclature and classification for the **Sphagnopsida**. Blanka Aguero provided me with images of ***Eosphagnum***. Llo Stark provided a valuable review of the chapter.

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