CHAPTER 2-5

BRYOPHYTA - SPHAGNOPSIDA

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 the 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**. We will leave such arguments to the systematists, but certainly its morphological differences play a major role in its unusual ecology. Until recently it was composed of 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 novo-caledoniae*, an **epiphyte** (Iwatsuki 1986; plants that grow on another plant without deriving nutrients from it).

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 2). 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 2) 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 3), 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.

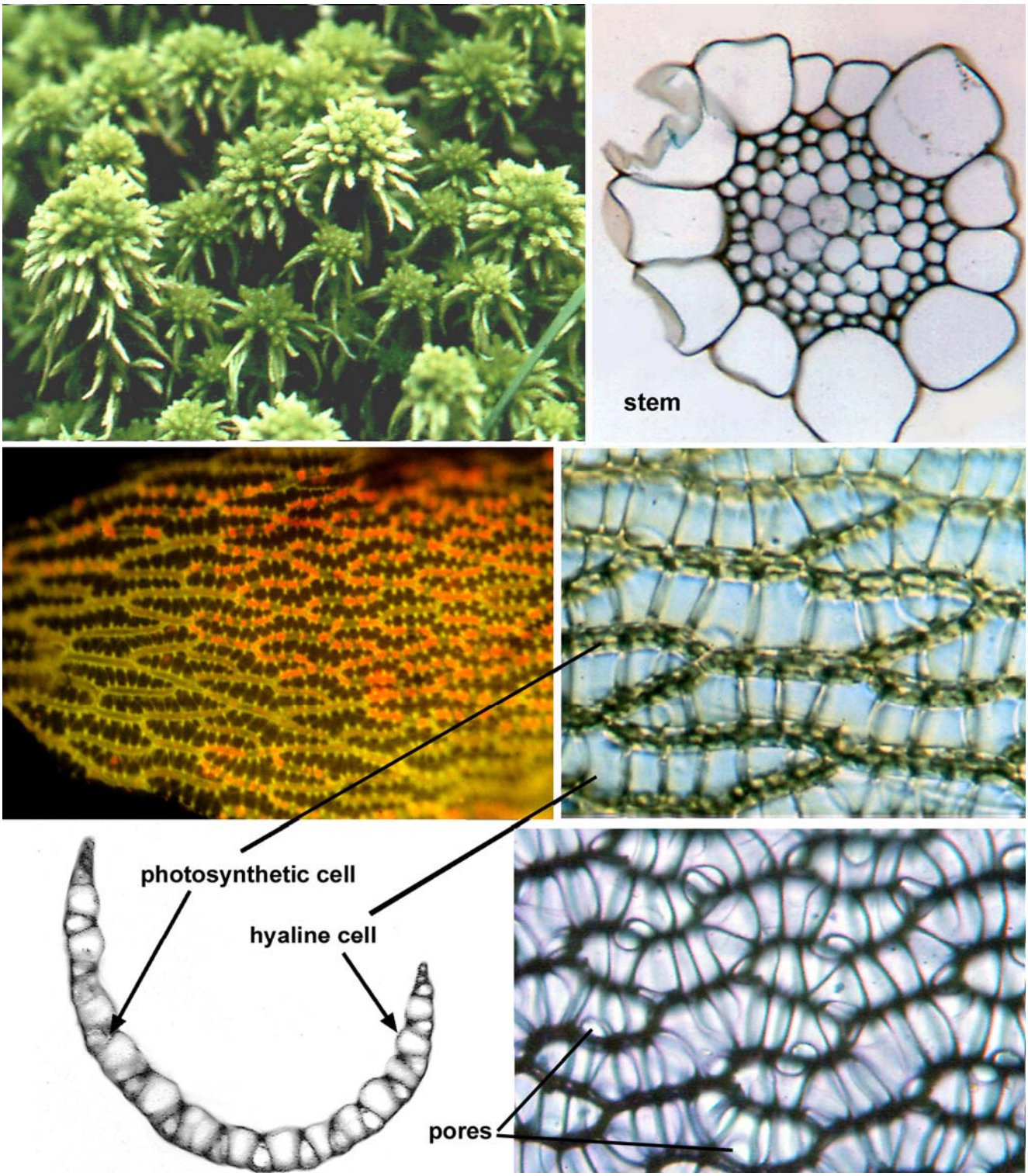

Figure 2. Vegetative characters of *Sphagnum*, Class Sphagnopsida. **upper left:** *Sphagnum wulfianum* capitula; **upper right:** cross section of stem showing hyaline cells and "woody strand;" **middle left:** leaf showing pattern of hyaline and photosynthetic cells illuminated by UV light; red areas 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.

Figure 3. *Sphagnum fimbriatum* showing capitulum where archegonia will arise. Photo by Janice Glime.

The **antheridia** are nearly globose (Figure 4) and are nestled among the leaves near the tips of the capitulum branches, usually endowing those tips with a reddish color (Figure 5). The **archegonia** are terminal on short branches near the center of the capitulum.

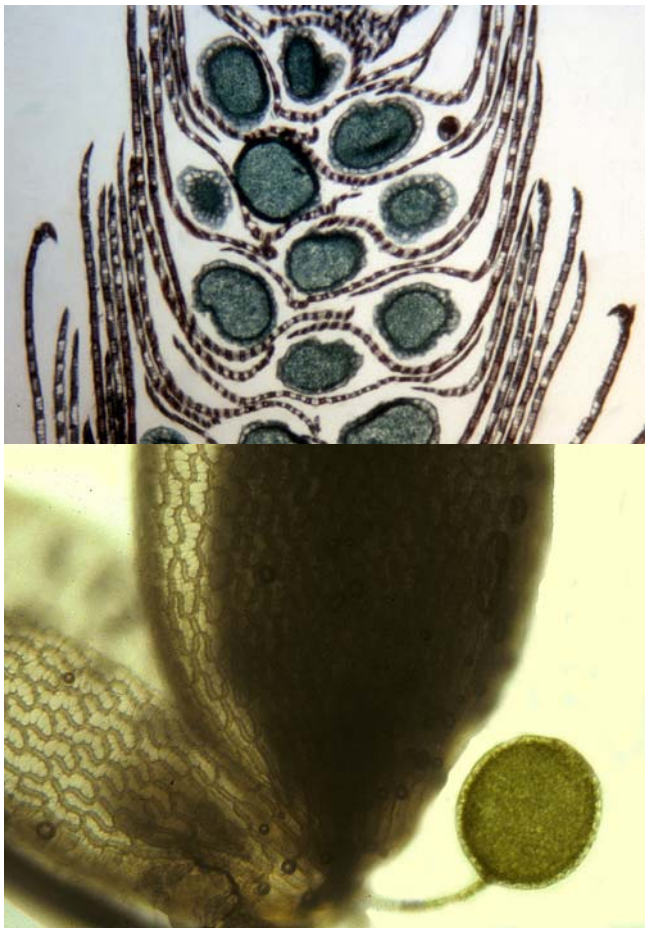

Figure 4. Globose *Sphagnum* antheridia nestled among the leaves of a capitulum branch. Photos by Janice Glime (top) and Yenhung Li (bottom).

Figure 5. Antheridial branches in the capitulum of *Sphagnum*. Red coloration is from the antheridia. Photo by Janice Glime.

Sphagnum **capsules**, 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 3). As these develop embryos, they likewise form a **foot**, **stalk**, and **capsule**, 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 6). 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 6), 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). The **columella**, 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 6) 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). 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, ranging 8-90 million among six species examined by Sundberg (2005). And these spores seem to disperse quite well, with only 2-14% of those dispersed remaining within the parent colony. And being large helps. The larger capsules dispersed a greater percentage of their spores, had a smaller percentage trapped within the parent colony, and consequently dispersed more spores to greater distances.

In the presence of moisture and light, the spores germinate to form a short thread. This thread soon, however, divides in more than one direction to form a **thalloid protonema** (Figure 6), 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.

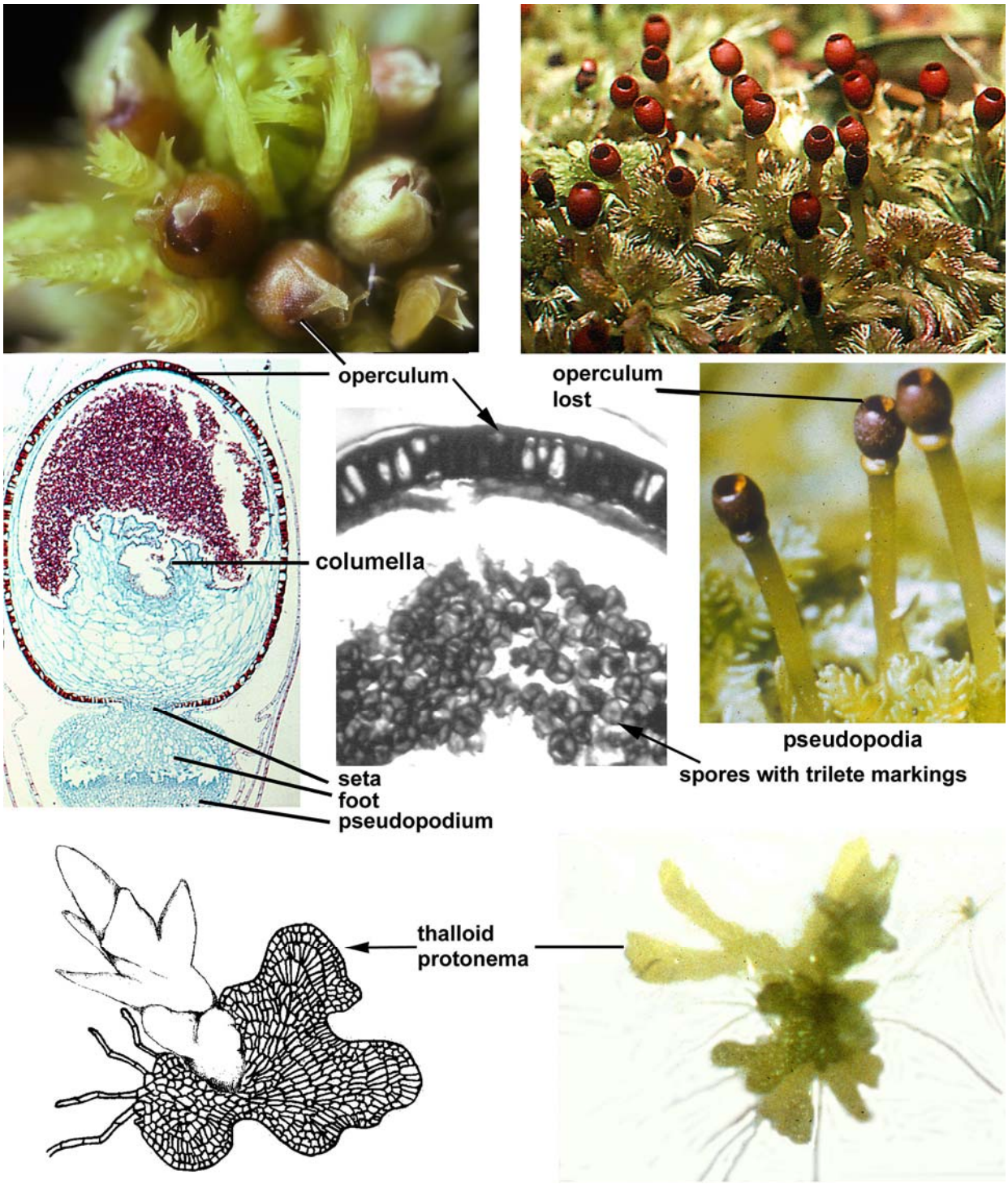

Figure 6. *Sphagnum* life cycle stages. Upper left photo by Zen Iwatsuki; others by Janice Glime. Protonema drawing by Margaret Minahan and Noris Salazar Allen.

Ambuchananiaceae

Not many of us get to describe a new order. And certainly no one was expecting one in the Sphagnopsida! But this organism, this moss, was certainly something new! – *Ambuchanania leucobryoides*.

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."

Now, this strange, yet somewhat familiar genus resides not just in a new family, but a new order, the Ambuchananiales. 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**. 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**.

Summary

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

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.

Literature Cited

Crum, H. 2004. Mosses of the Great Lakes Forest. 4th ed. The University of Michigan Herbarium, Ann Arbor. 592 pp.

Iwatsuki, Z. 1986. A peculiar New Caledonian *Sphagnum* with rhizoids. Bryologist 89: 20-22.

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