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CHAPTER 2-8

ANTHOCEROTOPHYTA

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Figure 1. ***Notothylas orbicularis*** thallus with involucres. Photo by Michael Lüth, with permission.

Anthocerotophyta

These plants, once placed among the bryophytes in the Anthocerotae, now generally placed in the phylum **Anthocerotophyta** (hornworts, Figure 1), seem more distantly related, and genetic evidence may even present them as more like ferns as we understand them better (Hori *et al*. 1985; Sherman *et al*. 1991; Nickrent *et al*. 2000; Knoop 2004; Groth-Malonek 2005). Yet other chemical evidence places them close to the liverworts (Hanson *et al*. 1999); they lack isoprene emission, as do liverworts, whereas mosses and ferns possess it. However, such characters may prove to be retained or lost adaptively and contribute little to phylum level relationships.

The hornworts are divided into two classes (Stotler & Crandall-Stotler 2005), a concept supported by molecular data (Frey & Stech 2005). **Anthocerotopsida** is the largest and best known of these, with two orders and three families. The second class is **Leiosporocerotopsida**, a class with one order, one family, and one genus. The genus ***Leiosporoceros*** differs from members of the class **Anthocerotopsida** by having the Cyanobacterium ***Nostoc*** in longitudinal canals. In the other hornworts, the ***Nostoc*** colonies are scattered in discrete globose colonies (Villarreal A. & Renzaglia 2006).

As in other Bryobiotina, the gametophyte in the Anthocerotophyta is the dominant generation, but then, there are a few ferns in which the gametophyte might also be considered dominant. Hornworts differ from Marchantiophyta in having typically only **one chloroplast per cell** in the thallus, **lacking oil bodies**, and possessing a **pyrenoid** (a proteinaceous body serving as a nucleus for starch storage and common in green algae) (Figure 2).

Figure 2. Hornwort cells showing single chloroplast, doughnut-shaped pyrenoid in center, and absence of oil bodies. Photo by Chris Lobban, with permission.

Some **Anthocerotophyta** have interesting adaptations to help them get the most from their environmental resources. The **pyrenoid**, present in many taxa, has a concentration of Rubisco, and this permits it to concentrate CO_2 (Hanson *et al*. 2002). Furthermore, the thallus typically has colonies of ***Nostoc*** (Figure 3-Figure 5), a member of the Cyanobacteria, embedded within the tissues and providing a conversion of atmospheric nitrogen into a form the hornwort can use. This fixed nitrogen is transferred from the gametophyte thallus to the sporophyte. Furthermore, if the gametophyte happens to be grown in the dark, and the sporophyte is illuminated, it can transfer the photosynthate to the gametophyte (Bold *et al*. 1987). And that sporophyte can have twice the photosynthetic carbon fixation of the gametophyte (Thomas *et al*. 1978)!

Figure 3. Probably ***Megaceros*** with ***Nostoc*** colonies. Photo by Chris Lobban, with permission.

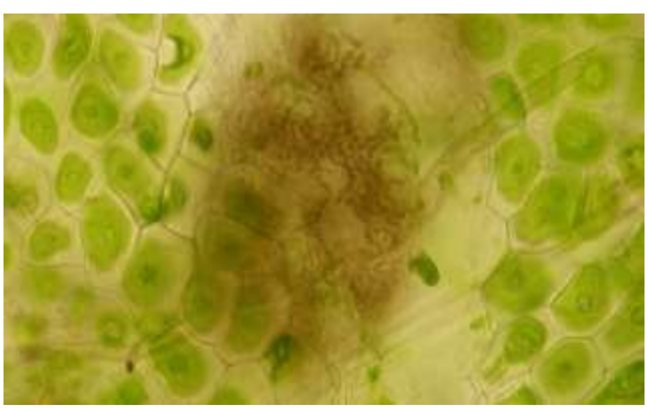

Figure 4. ***Nostoc*** (brown cells) in hornwort. Photo by Chris Lobban, with permission.

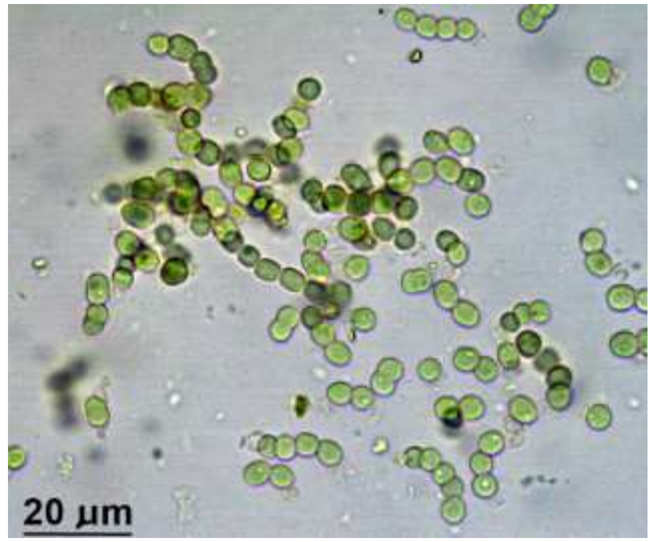

Figure 5. ***Nostoc*** from ***Anthoceros agrestis***. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

At least some members have associated fungi. Ligrone (1988) reported fungi in association with ***Phaeoceros laevis***. The fungus colonized the parenchyma cells except at the growing tips of the thallus and epidermal cells. The infected cells increased their cytoplasmic contents, but the chloroplast lost starch and the pyrenoids disappeared. The chloroplast became branched and these branches intermingled with the arbuscular fungal hyphae.

The sporophyte is like that of ***Sphagnum*** in **lacking a sporophyte stalk** (seta) on the capsule (Figure 6) and like the Bryophyta in having a **columella** (Figure 7-Figure 8) that is not in liverworts. The capsule also has **stomata** surrounded by two kidney-shaped **guard cells** (Figure 9), characters shared with Bryophyta. Instead of elaters, they have **pseudoelaters** (arising from division of a pseudoelater mother cell and outnumbering spores; Figure 10) of one, two, or four cells, usually with **no spiral thickenings** [except ***Megaceros*** and ***Dendroceros*** (Renzaglia 1978)] (Figure 11). The pseudoelaters probably provide nutrition, at least initially, but at maturity they twist, contributing to dehiscence and dispersal (Renzaglia 1978).

Figure 6. ***Phaeoceros*** showing gametophyte thalli at base and horn-like sporophytes. Photo by Janice Glime.

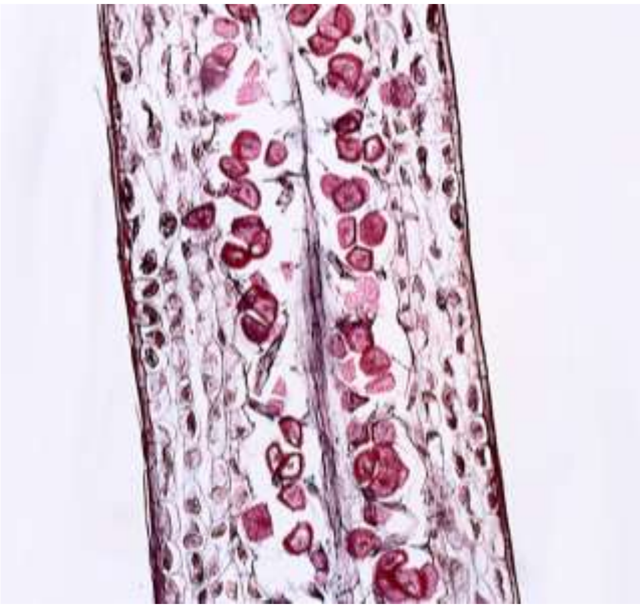

Figure 7. ***Anthoceros*** sporophyte longitudinal section showing spores and spore tetrads. Note central columella. Photo by George Shepherd, through Creative Commons.

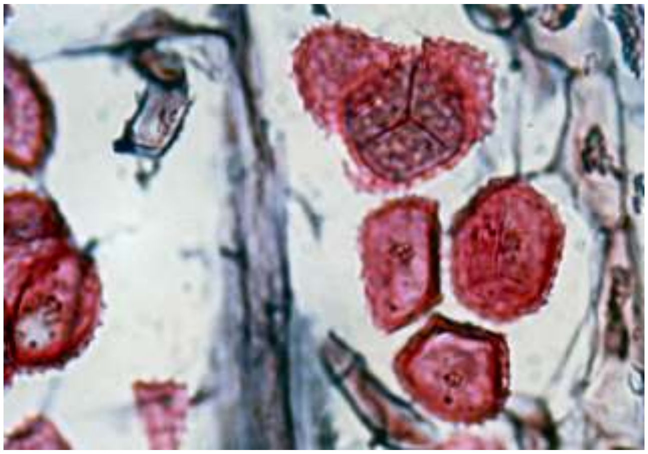

Figure 8. ***Anthoceros*** sporophyte longitudinal section showing spores and spore tetrads. Note central columella. Photo by George Shepherd, through Creative Commons.

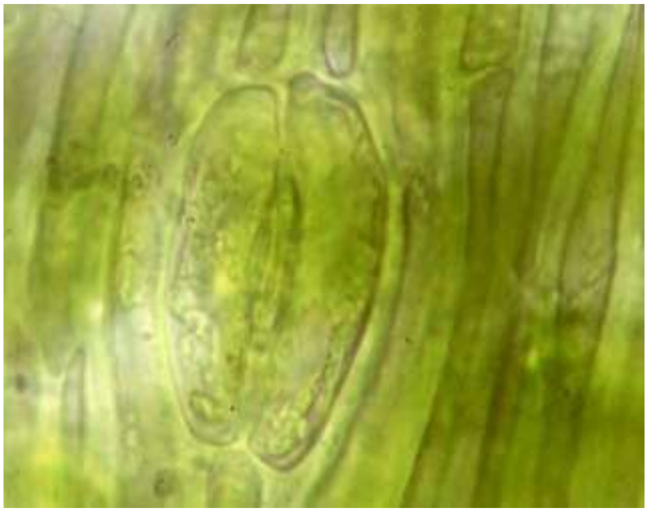

Figure 9. Stoma and guard cells on sporophyte of ***Anthoceros angustata***. Photo by Hironori Deguchi from <www.digital-museum.hiroshima-u.ac.jp>, with permission.

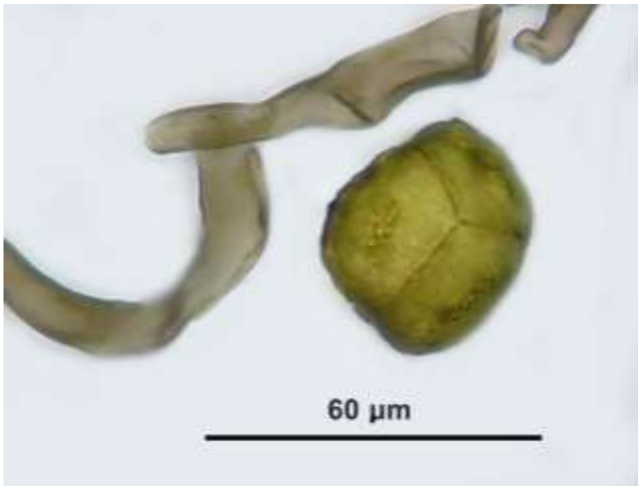

Figure 10. ***Phaeoceros*** spore and pseudoelater. Photo by David H. Wagner, with permission; scale modified by Janice Glime.

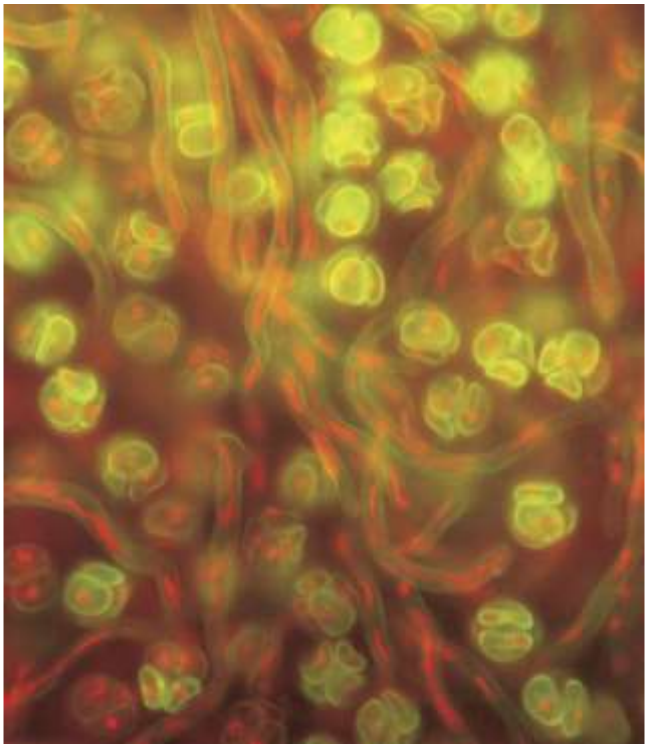

Figure 11. ***Leiosporoceros dussii*** spores and pseudoelaters using fluorescence microscopy. Note the absence of spiral thickenings in the elaters. Photo by Andrew Blackwell, and Juan Carlos Villarreal A., Southern Illinois University, with permission.

Meiosis is **continuous**, occurring at the base of the capsule, causing the tip of the sporophyte to have more mature spores than the base (Figure 12-Figure 14), a feature unique to the Anthocerotophyta. Dispersal results as the **capsule splits** into valves from the top down (Figure 25), and consistent with its development, this peeling back of the capsule occurs slowly over time, retaining the lower spores while dispersing the upper ones. The valves twist in response to moisture changes, perhaps aiding in dispersal. The **spores mature progressively** from top to bottom of the capsule (Figure 13) as the capsule splits and **continues**

to grow at its base, unlike any other Bryobiotina (Figure 26).

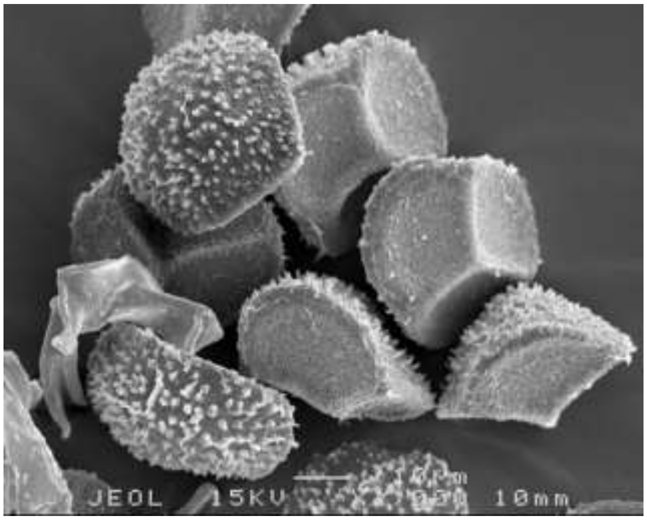

Figure 12. SEM of ***Phaeoceros carolinianus*** meiospores. Photo by Christine Cargill at Trin Wiki.

Figure 13. Hornwort sporophyte foot in gametophyte tissue. Note that basal portion of the sporophyte contains sporogenous tissue; those above have undergone meiosis. Oval area at the base of the sporophyte is the foot, imbedded in the gametophyte. Photo by Michael W. Clayton. Permission pending

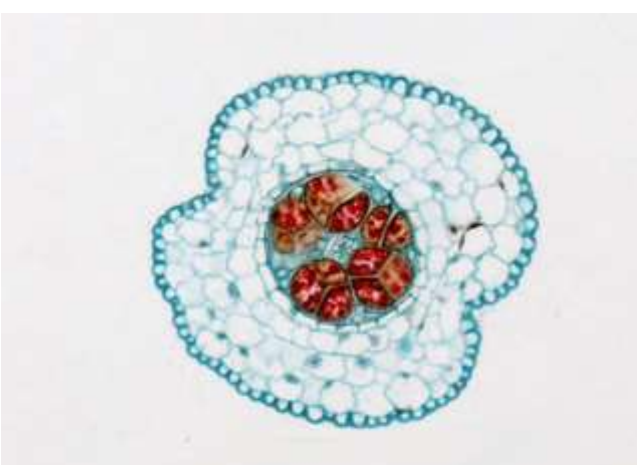

Figure 14. ***Anthoceros*** sporophyte cross section, showing meiospores and columella. Photo from Botany 321 website at University of British Columbia, with permission.

Dendroceros is a tropical genus that is unusual among the Anthocerotophyta by growing on tree bark and leaves. Furthermore, it produces multicellular green spores (Figure 15) (Schuette & Renzaglia 2010). Schuette and Renzaglia suggest that the precocious development of the spore, resulting in **endospory**, permits it the time and resources necessary to survive the desiccating habitat where it lives.

Figure 15. ***Dendroceros tubercularis*** endospores. Photo by Karen Renzaglia, with permission.

Spores in **Anthocerotophyta** germinate to form a short **protonema** that does not remain threadlike, but gets areas that are more three-dimensional, resembling a tuber (Figure 16).

Figure 16. ***Anthoceros dichotomus*** protonema. Photo from Plant Actions through Eugenia Ron Alvarez, with permission.

The mature gametophyte thallus resembles that of a club moss (Lycopodiophyta) in that the **antheridia** may occur in groups within a chamber (Figure 17-Figure 23). The archegonia are likewise embedded within the thallus, again like those of the club mosses. The structure of the archegonium is illustrated in Figure 24.

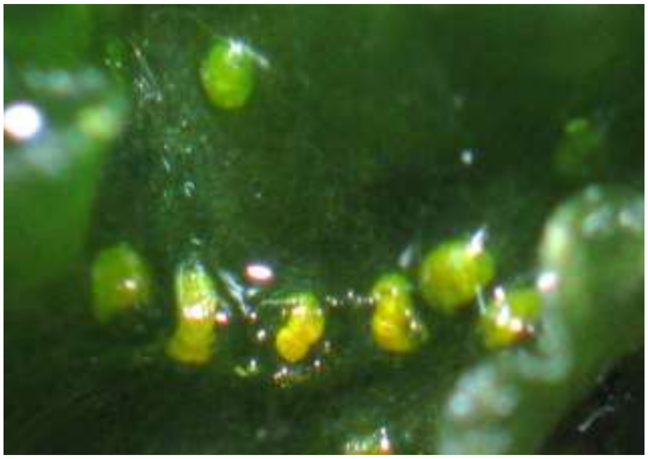

Figure 17. Hornwort **antheridia**, illustrating the clustering. Photo by Tom Thekathyil, with permission.

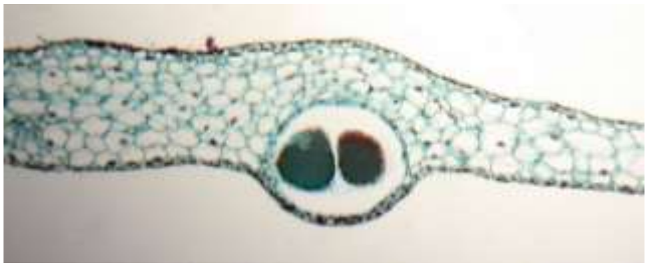

Figure 18. **Antheridia** in thallus of hornwort. Photo from Botany 321 website at University of British Columbia, with permission.

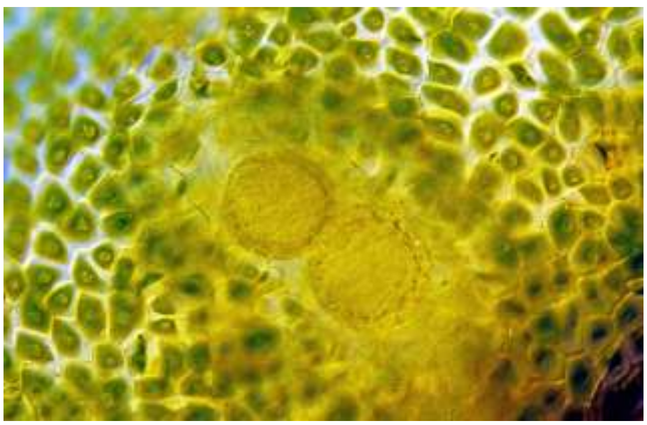

Figure 19. ***Phaeoceros*** gametophyte with **antheridia**. Photo by George Shepherd, through Creative Commons.

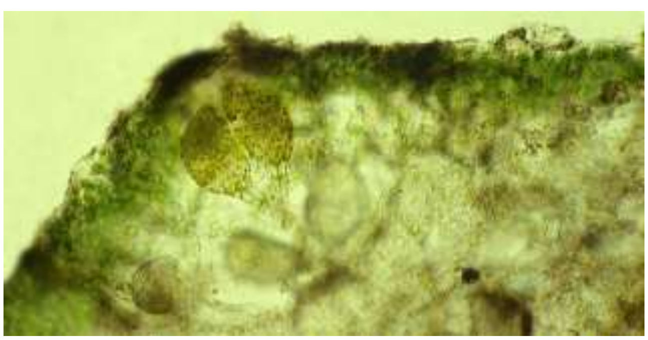

Figure 20. ***Anthoceros punctatus*** **antheridia**. Photo from Plant Actions website through Eugenia Ron Alvarez, with permission.

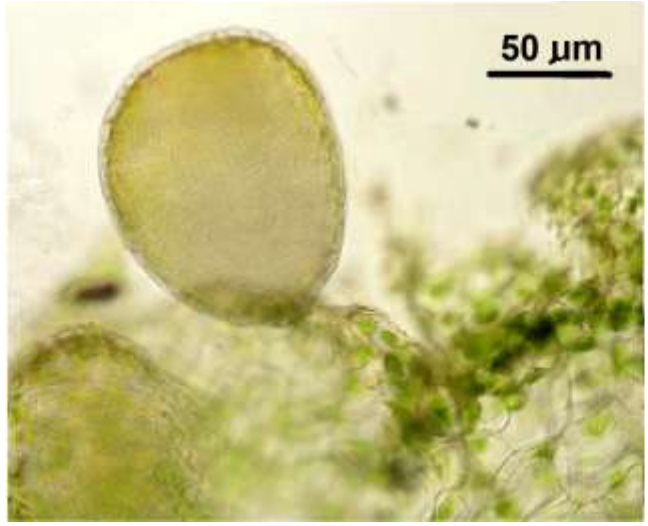

Figure 21. **Antheridium** of a hornwort. Photo by Hatice Ozenoglu Kiremit, with permission.

Figure 22. **Antheridia** of a hornwort dispersing its sperm. Photo by Hatice Ozenoglu Kiremit, with permission.

Figure 23. Antheridium of hornwort (probably ***Phaeoceros carolinianus***) expelling sperm. Tom Thekathyil (pers. comm. 17 September 2009) reported that sperm were still alive several hours later. Photo by Tom Thekathyil, with permission.

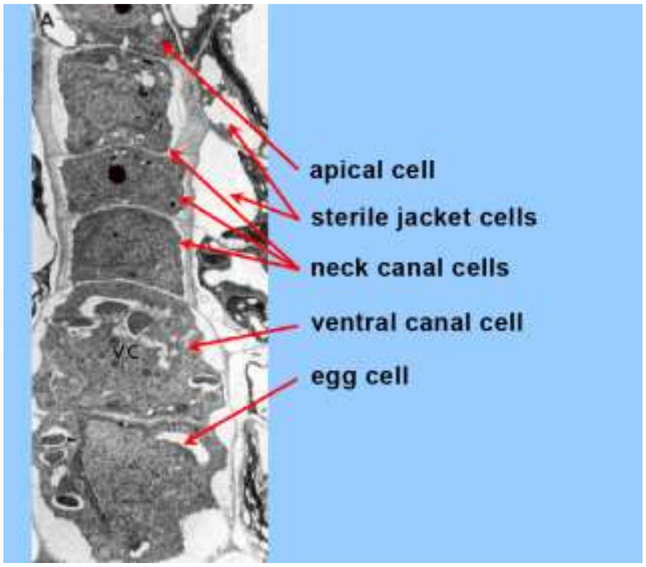

Figure 24. Hornwort archegonium. Photo from Science Land Plant website at Southern Illinois University, with permission.

Figure 25. ***Phaeoceros oreganus*** sporophytes showing the splitting tips of mature capsules. Photo by Li Zhang modified in Photoshop.

Figure 26. Anthocerotophyta – hornworts. **Upper left:** ***Anthoceros bulbicosus*** thallus and undehisced sporophyte. **Upper right:** cleared section of gametophyte thallus, collar, and hornlike sporophyte. **Lower left:** Cross section of ***Anthoceros*** thallus. Although the sporophyte is complex, the gametophyte is quite simple, perhaps indicating reduction. Note the lack of specialized tissues and absence of air chambers. **Lower right:** Older sporophyte of ***Phaeoceros carolinianus*** showing yellow color near tips of sporophyte due to mature spores. Upper left and lower right photos by Michael Lüth; upper right and lower left photos by Janice Glime.

Table 1. Comparison of the phyla of Bryobiotina. Amplified from Crandall-Stotler (1996) and Gradstein *et al.* (2001).

Character	Marchantiophyta	Bryophyta	Anthocerotophyta
Protonema	Mostly globose or thalloid, forming one bud; no gemmae	Filamentous, forming many buds; may produce gemmae	Globose, forming one bud; no gemmae
Gametophyte form	Leafy shoot or thallus; thallus simple or with air chambers; dorsi-ventral	Leafy shoot	Simple thallus; dorsi-ventral
Branches	Developing from leaf initial cells or inner stem cells, rarely stem epidermis	Developing from stem epidermis	
Leaf origin	2 initial cells (1 in Calobryales & Metzgeriales)	1 initial cell	
Leaf arrangement	Leaves in two or three rows, ventral row usually of different size	Leaves usually in spirals	Not applicable
Leaf form	Leaves unistratose, divided into 2+ lobes, no costa	Leaves unistratose in most, undivided, costa present in some	Thallose
Leaf/thallus cells	Usually isodiametric, have trigones; numerous chloroplasts	Often elongate, rarely possess trigones; numerous chloroplasts	No trigones; 1-4 large chloroplasts
Special organelles	Complex oil bodies often present	Simple, small oil bodies or none	Single plastids with pyrenoids
Gemmae	Common on leaves	Common on leaves, stems, rhizoids, or protonemata	Absent
Water conducting cells	Present only in a few simple thalloid forms	Present in both gametophytes and sporophytes of many	Absent
Rhizoids	Hyaline, one-celled	Brown, multicellular	Hyaline, one-celled
Gametangial position	Apical clusters (leafy forms) or on upper surface of thallus	Apical clusters	Sunken in thallus, scattered
Paraphyses	Usually lacking; often have mucilage filaments	Usually associated with antheridia & archegonia	Lacking
Growth of sporophyte	Apical	Apical	Grows continuously from basal meristem
Stomata	Absent in both generations, but pores present on some gametophyte thalli	Present on sporophyte capsule	Present in both sporophyte and gametophyte
Seta	Hyaline, elongating just prior to spore release, rigid when turgid, deliquescent	Photosynthetic, emergent from gametophyte early in development in Bryopsida & Polytrichopsida, rigid due to cell structure, persistent; not elongating in Sphagnopsida – pseudopodium present	Absent
Calyptra	Ruptures & remains at base of seta, lacks influence on capsule shape	Ruptures & persists at apex of seta & capsule, influences capsule shape	Lacking
Capsule	Undifferentiated, spherical or elongate; jacket uni- or multistratose; often with transverse or nodular thickenings	Complex with operculum, theca and neck; jacket multistratose; lack transverse or nodular thickenings	Undifferentiated, horn-shaped; jacket multistratose
Sterile cells in capsule	Spirally thickened elaters	Columella	Columella and pseudoelaters
Capsule dehiscence	Into 4 valves; spores shed simultaneously	At operculum & peristome teeth in Bryopsida & Polytrichopsida, spores shed over extended period; valvate in Takakiopsida, Andreaeopsida, & Andreaeobryopsida; lacking peristome in Sphagnopsida	Into 2 valves; spores mature & shed over extended period
Chemistry	Monoterpenes, sesquiterpenes, & diterpenes; lunularic acid	Triterpenes; ABA	Terpenoids(?)

Summary

The traditional bryophytes are classified into three phyla (Marchantiophyta, Bryophyta, Anthocerotophyta) that can be placed in the subkingdom Bryobiotina. **Anthocerotophyta** (hornworts) differ in having a sporophyte that is shaped like horn and continues to grow at the base as spores mature and are dispersed at the apex.

Anthocerotophyta have a **dominant gametophyte** generation. Gametophytes produce **archegonia** and/or **antheridia** and the **embryo** develops within the archegonium.

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis** over a prolonged period of time, with the youngest spores at the base. **Pseudoelaters** are produced along with the spores, but are formed by mitosis and remain $2n$. **Capsules** split longitudinally and peel backward from the tip.

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. Eugenia Ron Alvarez and Tom Sobota offered use of images at the PlantActions web site and provided me with high resolution images.

Literature Cited

Bold, H. C., Alexopoulos, C. J., and Delevoryas, T. 1987. Morphology of Plants and Fungi. Harper & Row, Publishers, Inc., New York, NY, 912 pp.

Crandall-Stotler, B. 1996. Bryophytes. Mosses, Liverworts and Hornworts. Accessed 28 December 2004 at http://bryophytes.plant.siu.edu/bryophytes.html.

Frey, W. and Stech, M. 2005. A morpho-molecular classification of the Anthocerotophyta (hornworts). Nova Hedw. 80: 541-546.

Gradstein, S. R., Churchill, S. P., Salazar Allen, N. 2001. Guide to the Bryophytes of Tropical America. Memoirs of the New York Botanical Garden Vol. 86: 577 pp.

Groth-Malonek, M., Pruchner, D., Grewe, F., and Knoop, V. 2005. Ancestors of trans-splicing mitochondrial introns support serial sister group relationships of hornworts and mosses with vascular plants. Molec. Biol. Evol. 22: 117-125.

Hanson, D., Andrews, T. J., and Badger, M. R. 2002. Variability of the pyrenoid-based CO2 concentrating mechanism in hornworts (Anthocerotophyta). Funct. Plant Biol. 29: 407-416.

Hanson, D. T., Swanson, S., Graham, L. E., and Sharkey, T. D. 1999. Evolutionary significance of isoprene emission from mosses. Amer. J. Bot. 86: 634-639.

Hori, H., Lim, B.-L., and Osawa, S. 1985. Evolution of green plants as deduced from 5s RRNA sequences. Proc. Natl. Acad. Sci. USA 82: 820-823.

Knoop, V. 2004. The mitochondrial DNA of plants: Peculiarities in phylogenetic perspective. Current Genetics 46: 123-139.

Ligrone, R. 1988. Ultrastructure of a fungal endophyte in *Phaeoceros laevis* (L.) Prosk. (Anthocerotophyta). Bot. Gaz. 149: 92-100.

Nickrent, D. L., Parkinson, C. L., Palmer, J. D., and Duff, R. J. 2000. Multigene phylogeny of land plants with special reference to bryophytes and the earliest land plants. Molec. Biol. Evol. 17: 1885-1895.

Renzaglia, K. S. 1978. A comparative morphology and developmental anatomy of the Anthocerotophyta. J. Hattori Bot. Lab. 44: 31-90.

Schuette, S. and Renzaglia, K. S. 2010. Development of multicellular spores in the hornwort genus *Dendroceros* (Dendrocerotaceae, Anthocerotophyta) and the occurrence of endospory in Bryophytes. Nova Hedw. 91: 301-316.

Sherman, T. D., Vaughn, K. C., and Duke, S. O. 1991. A limited survey of the phylogenetic distribution of polyphenol oxidase. Phytochemistry 30: 2499-2506.

Stotler, R. E. and Crandall-Stotler, B. 2005. A revised classification of the Anthocerotophyta and a checklist of the hornworts of North America, north of Mexico. Bryologist 108: 16-26.Thomas, R. J., Stanton, D. S., Longendorfer, D. H., and Farr, M. E. 1978. Physiological evaluation of the nutritional autonomy of a hornwort sporophyte. Bot. Gaz. 139: 306-311.

Villarreal A., J. C. and Renzaglia, K. S. 2006. Structure and development of *Nostoc* strands in *Leiosporoceros dussii* (Anthocerotophyta): A novel symbiosis in land plants. Amer. J. Bot. 93: 693-705.