CHAPTER 2-8
ANTHOCEROTOPHYTA

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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 CO₂ (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)!

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 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

*Anthoceros* 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 tuberculatis* 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 Bryobiota. Amplified from Crandall-Stotler (1996) and Gradstein et al. (2001).

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


