

CHAPTER 2-8

ANTHOCEROTOPHYTA



Figure 1. *Notothylas orbicularis* thallus with involucre. Photo by Michael Lüth.

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.

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).

The thallus typically has colonies of *Nostoc*, 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)!

The sporophyte is like that of *Sphagnum* in **lacking a stalk** (seta) on the capsule (Figure 2) and like the Bryophyta in having a **columella** that is not in liverworts. The capsule also has **stomata** surrounded by two kidney-

shaped **guard cells** (Figure 3), characters shared with Bryopsida. Instead of elaters, they have **pseudoelaters** (arising from division of a pseudoelater mother cell and outnumbering spores) of one, two, or four cells, usually with **no spiral thickenings** [except *Megaceros* and *Dendroceros* (Renzaglia 1978)]. The elaters probably provide nutrition, at least initially, but at maturity they twist, contributing to dehiscence and dispersal (Renzaglia 1978)

Meiosis is **continuous**, causing the tip of the sporophyte to have more mature spores than the base, a feature unique to the Anthocerotophyta. Dispersal results as the **capsule splits** into valves from the top down (Figure 4), 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 as the capsule splits and **continues to grow at its base**, unlike any other Bryobiotina (Figure 6).

Spores germinate to form a short protonema that does not remain threadlike, but gets areas that are more three-dimensional, much like a fern protonema.

The mature gametophyte thallus resembles that of a club moss (Lycopodiophyta) in that the antheridia may occur in groups within a chamber. The archegonia are likewise embedded within the thallus, again like those of the club mosses.



Figure 2. *Phaeoceros* showing gametophyte thalli at base and horn-like sporophytes. Photo by Janice Glime.

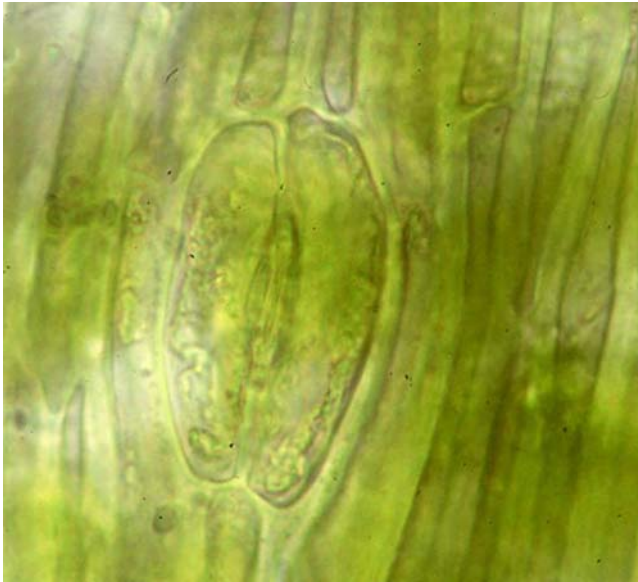


Figure 3. Stoma on sporophyte of *Anthoceros angustata*. Photo by Hironori Deguchi from www.digital-museum.hiroshima-u.ac.jp.



Figure 4. *Phaeoceros oreganus* sporophytes showing the splitting tip. Photo by Li Zhang.



Figure 5. *Phaeoceros oreganus* sporophytes. Photo by Zhang Li modified in Photoshop.



Figure 6. 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
Stomates	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, & Andreaebryopsida; 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.

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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.

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