Bryophytes lecture 1

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Origin of bryophytes?

Fig. 1: Early land plant topologies. (A) A liverwort-sister hypothesis with hornworts sister to vascular plants (e.g. Qiu et al., 2006). In this scenario, the haploid dominant life cycle is plesiomorphic with a derived diploid-dominant life cycle found in vascular plants (in black). The pyrenoid (Py) evolved independently in hornworts and algae (see Villarreal & Renner, 2012). (B) Under the scenario of bryophytes monophyletic and sister to vascular plants (Cox et al., 2014; Wickett et al., 2014) it is impossible to know the state (haploid or diploid dominant) of the ancestor to all land plants. (C) A hornwort-sister hypothesis with mosses sister to vascular plants (e.g. Renzaglia et al., 2000; Wickett et al., 2014). In this scenario, the haploid dominant life cycle is plesiomorphic with a derived diploid-dominant life cycle found in vascular plants (in black). The pyrenoid is a plesiomorphic trait and it seems to be inherited from green algae. (D) A moss-sister hypothesis recovered in some analyses presented by Liu et al. (2014, see section 1).
Origin of Bryophytes? Monophyletic?
Where are in the classification?

Eukaryota
Plantae

Viridiplantae
lineage Streptophytae

Bryophyta - Bryophytes
Marchantiophyta - liverworts
Bryophyta - mosses
Anthocerotophyta - hornworts
Bryophyta

- heterogenous paraphyletic/monophyletic group of plants

- three monophyletic divisions – *Marchantiophyta*, *Anthocerotophyta* and *Bryophyta*

- one of the oldest land plants (Ordovician, early Silurian), first fossils from late Devonian, 390-360 Myr ago
two evolution lineages - *Chlorophytae* and *Streptophytae*
Streptophyta

Preprophase band  Mitotic spindle  Phragmoplast

Preprophase memory

yellow – „Pragmoplastophyta“, Red rings indicate preprophase bands (PPB) and/or the so-called isthmus band (IMB) found in desmid algae. Blue asterisks indicate centrosomes (note that the centrosome-like polar organizers of the liverworts do not contain centrioles). Cytokinesis occurs via phragmoplasts or cleavage (blue and green H-like shapes, respectively; note that some Zygnematophyceae show a combination of both mechanisms, e.g., Mougeotia).

Bryophytes

Characteristics shared with all green plants
("Viridiplantae" e.g. green algae + higher plants):
- combination of photosynthetic pigments, chloroplast structure
- starch as stock substance
- ultrastructure of flagellum (radial basal structure)

Characteristics shared with Streptophytes
(e.g. Charophyta and other Streptophyte algae, Bryophyta, Embryophyta)
- phragmoplast – microtubules of a division spindle across to the new cell wall
- thylakoids has structure of grana (sg. granum) in the chloroplast.
- open mitosis
Evolution of Chlorophytae and Streptophytae

Bryophytes

Fossils of Bryophytes

- first discovery classified without doubts to Bryophytes - *Pallaviciniites devonicus* – New York, dichotomic branching, thallose liverwort (late Devonian, 370-350 Myr ago)

Early Carboniferous

- other discoveries of liverworts

- *Muscites lobatus* – England, first moss discovery
Earth's oldest liverworts — *Metzgeriothallus sharonae* sp. nov. from the Middle Devonian (Givetian) of eastern New York, USA

Carbonized remains of the upper Middle Devonian liverwort *Metzgeriothallus sharonae* sp. nov. are locally common in these lenses. Well-preserved thalli (gametophytes) are only evident by projecting polarized light on the shale and siltstone surfaces. An associated sporophyte capsule is the first evidence of a reproductive structure in a Devonian liverwort. *M. sharonae* is the oldest known liverwort.
Main characteristics with links to higher terrestrial plants (**Embryophyta**)

- development of a multicellular embryo attached to a mother plant for its protection and nourishment
- multi-celled gametangia covered by multi-layer sterile covers
- cuticle (only on capsules)
- sporopollenin in the spore walls (sporopollenin is very durable and tough organic material)
Shared features of Bryophytes, differences from other higher plants

- life cycle – dominance of a gametophyte
- sporophyte +- ephemerous, totally dependent on gametophyte
- absence of lignine (conductive tissue, e.g. in timber)
- gametophyte: protonema and gametophore
- gametophore growth by an apical cell, not by meristematic tissue
How many bryophytes?

worldwide 16-20 000 of species
   (120-150 hornworts, 6-8 000 liverworts, 10-12 000 mosses)

Europe ca 1750 species
   (8 hornworts, 450 liverworts, 1300 mosses)

Czech Republic  859 species
   (4 hornworts, 207 liverworts, 648 mosses)

year 2012
Bryophyte life cycle

- heteromorphic alteration of generations
- **gametophyte** – haploid, fotoautotrophic;
  - meiospore → protonema → gametophore → gametangia (♀ archegonia, ♂ antheridia) → egg cell (oosphera), spermatozoide
- **sporophyte** – diploid, G- dependent
  - zygote → foot, seta, capsule (sporogenic structures)
- **fertilization** only through water
http://www.tutorvista.com/content/biology/biology-iii/kingdoms-living-world/bryophytes.php
Bryophytes:

Mosses

Liverworts

Hornworts

Pohlia sp.
**Anthocerotophyta - hornworts**

**Figure 12-17** Diagrammatic rendering of structures of *Anthoceros*, the hornwort. 

*Phaeoceros carolinianus*

*Dendroceros*
Gametophyte

- **spores** incorporated into tetrads, pseudoelaters
- **thallus** thallose, rosette-forming, lower surface cavities with *Nostoc*
- **rhizoids** smooth
- **cells** parenchymatic, the only chloroplast with pyrenoid per cell
- **gametangia** embedded in the thallus, and in contact with surrounding vegetative cells
- **spermatozoids** symmetrical, clockwise arranged flagellums
- **asexual reproduction** – not common

*Photo by K. S. Renzaglia, Duff, Nickrent & Renzaglia, hornwort pages*
Fig. 3. Transmission electron micrographs of chloroplasts in hornworts. A. *Leiosporoceros dussii* (Steph.) Hässel. Chloroplast in the assimilative layer of the sporophytes showing peripheral starch and centralized grana. B. *Folioceros fuciformis* Baradw. Central pyrenoid with lens-shaped subunits separated by narrow grana and surrounded by starch grains. Bar = 0.5 µm. Shaw & Renzaglia 2004

*Phaeoceros laevis*; A.M.F. Tomascu, Ohio Univ.
Fig. 2. Diversity in growth forms among hornworts. 

A. Photograph of *Anthoceros punctatus* L. Small orbicular gametophyte with both immature and almost ripe sporophytes, growing on soil. Image provided by Christine Cargill. 

B and C Scanning electron micrographs (SEM) of gametophyte of *Dendroceros crispatus* (Hook.) Nees. B. Ventral surface showing monostromatic wings and thickened midrib with bulging *Nostoc* colonies (arrow). Note the numerous small pores (mucilage clefts) along either side of the midrib. C. Dorsal surface showing sunken archegonia (arrow) on the midrib and developing sporophytes enclosed within gametophytic involucre.

D. SEM of *Notothylas orbicularis* (Schwein.) Sull. Small orbicular gametophytes growing on bare soil; note the numerous small, horizontally oriented sporophytes enclosed in involucre. Bar = 0.2 mm, except in A, bar = 3 mm. Shaw & Renzaglia 2004
Sporophyte

- **foot** - haustoria
- **capsule** – cylindrical, horn-shaped, indeterminate growths, gradual maturation of spores, breaking in two parts
- capsule wall with stomata, columella
Hornworts spores

Phaeoceros carolinianus, proximální a distální povrch spor mírka = 10 µm.; tetrády s pseudoelatery; http://www.science.siu.edu/landplants/anthocerophyta.html

Leiosporoceros dussii, tetrády spor s pseudoelatery
tetrády. Christine Cargill
division: Anthocerotophyta

(class: Leiosporocerotopsida: one species, round spores, not in tetrads)

class: Anthocerotopsida

(Leiosporoceros dussii)
Anthoceros agrestis – hlevík polní, field hornwort

annual plant, growing on bare soil on fields, fallow lands, sporophytes are produced in autumn
*Anthoceros agrestis* – field hornwort
Dendroceros - epiphytic species
Dendroceros (foto J. Fehrer)
Phaeoceros carolinianus (Australia)

Phaeoceros laevis  (Spain)
**Marchantiophyta** - liverworts

frondose (thallose) and foliose (leafy)
liverworts - Marchantiophyta

- heterogeneous group
- thallose x leafy (frondose x foliose)
- fossils Paleogene – late Devonian (370-350 Myr ago) thalloid *Pallaviciniites devonicus*, early Carboniferous (350-320 Myr. ago)
- diverse biotopes, tropical areas

*Moerckia blyttii*

*Lophozia lycopodioides*
Conocephalum

Metzgeria

Riccia

Riccia fluitans (zvětšeno)
**Bazzania stolonifera**

**Chiloscyphus coadunatus**

**Plagiochila asplenioides**

**Trichocolea tomentella**
Gametophyte – leafy liverworts

- **stem** – branched or unbranched, erect or decumbent, circular or oblong in section, different cell types, sometimes covered by cuticle (in parts)

- **leaves** – 1 layer of one type cells, variable shape, divided, different marginal structures, two rows of lateral leaves + 1 row of ventral leaves (amphigastria)

*Plagiochila asplenioides*
leaves of liverworts
- **cells** – differens shape, hexangular, with oil bodies
- **oil bodies** – products of metabolism (terpenoids, from ER) taxonomical feature, ephemeral, dissappearing in herbarium very quickly!
- **rhizoids** – simple, unicellular, attach to substrate
- **spores** – unicellular, rounded
- **protonema** – small (only several cells), ephemeral
Cells and oil bodies of liverworts

Jungermannia

Nardia lescurii

Jubulopsis novae-zelandiae

Frullania squarrosula

Rectolejeunea maxonii

Lophocolea bicuspidata
Gametophyte - thallose liverworts

- **thallus** (whole) from the same type of cells or different layers, cavities with *Nostoc*
- **rhizoids** smooth or with tubercles
- **air chambres** – covered by simple or barrel-like pores
- **oil bodies** – not so often

*Pellia neesiana*

*Conocephalum conicum*
Gametangia - leafy liverworts

- **antheridia** ♂, **archegonia** ♀ – formed on short side-branches

- **calyptra** – protection of young sporophyte

- **perianth** – protected structure of archegonium
Gametangia – thallose liverworts

- on the thallus surface

or

- on discoidal receptaculum elevated by archegonio-/antheridiophores

Marchantia polymorpha

Symphyogyna brasiliensis
Marchantia polymorpha
Sporophyte

- ephemeral
- capsule, mature capsule, then it undergoes elevation up at maturity
- foot
- stalk (seta) – different length, hyaline
- capsule – spherical, breaks to four valves, no collumela
- spores, elaters – sterile cells with helix-shaped walls
Pellia epiphylla, NPR Zemská brána, Orlické hory
Asexual reproduction

- gemmae
- outgrowths (branches)
- fragmentation

*Marchantia polymorpha*

*Metzgeria furcata*

*Mylia anomala*
Marchantia - gemmae

www.anbg.gov.au

www.biology.iastate.edu
**Water regime**

- poikilohydric organisms
- no „pure“ vascular bundles → water reception by whole thallus

**Radula complanata** – lower part of phylloids holds water

**Frullania dilatata** – can-shaped lower part

**Trichocolea tomentella** – phylloids divided to hairs, paraphyllia on stems
liverwort stands

terricolous – *Marchantia*, cf. *Mannia* →
liverwort stands

epiphytic - *Frullania*
liverwort stands

epilithic - *Scapania*
liverwort stands

epiphytic – *Lophozia, Lepidozia*
liverwort stands

aquatic - Riccia
liverwort stands

epiphylic – Frullania, Ephemeropsis
liverwort stands

cave entrances - *Jubula*
Uses of liverworts

**Medicine, antibiotics** – *Marchantia polymorpha* - liver inflammations (China)
- *Riccia* sp. – skin diseases (Himalayas)
- *Conocephalum, Marchantia* – in vegetable oil to bits, burns, open wounds (China)
- *Herbertus* – instead of a cigarette filter (Himalayas) (Himálaj)
- *liverworts* (in general) = substances which slow down bacteria growts (antibiotical effects)
Herbertus aduncus