An introduction to the evolutionary significance, ecological roles and diversity of Bryophytes.

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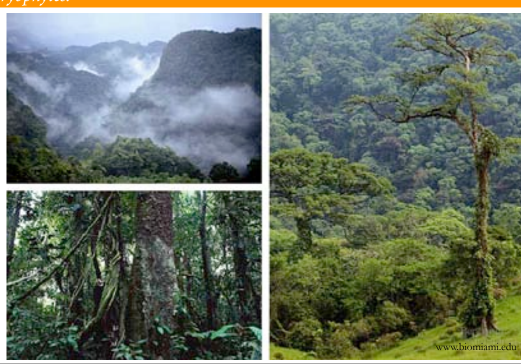
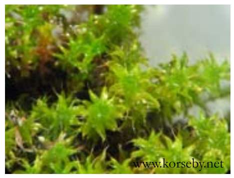


An introduction to the evolutionary significance, ecological roles and diversity of Bryophytes.

1. Bryophytes: my name is *Bryum bicolor*.
2. Evolutionary significance: bryophytes in context of land plant evolution
3. Ecological roles: bryophytes in their ecosystems
4. Diversity: 20,000 species and still counting.
5. Biogeography: time tree of evolution and where they are now!

1. Bryophytes: my name is Bryum bicolor

The term “Bryophyte” is of Greek origin and refers to plants that swell upon hydration.

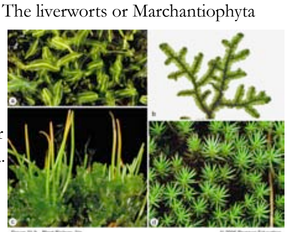


1. Bryophytes: my name is Bryum bicolor

Three distinct evolutionary lineages compose this *strange* group of plants:

The liverworts or Marchantiophyta

The Hornworts or Anthocerotophyta.

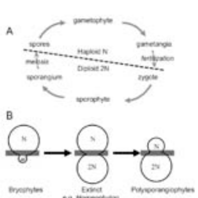


The mosses or Bryophyta

1. Bryophytes: my name is Bryum bicolor

The term “bryophyte” is generally used as a generic word for plants characterized by a life cycle featuring alternating haploid and diploid generations with a dominant gametophyte!

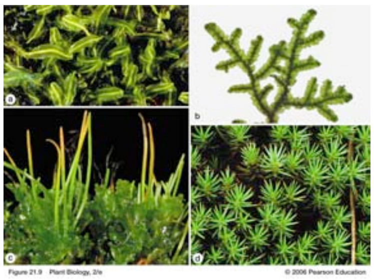
Genome halving:
2N = N+N+N+N
(4 spores)



Sexual reproduction:
N (egg)+N (sperm cell)
=2N (zygote)

1. Bryophytes: my name is Bryum bicolor

Both generations are multicellular, but the gametophyte is only dominant, branched and potentially long-lived, in bryophytes.



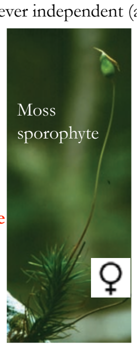
1. Bryophytes: my name is Bryum bicolor

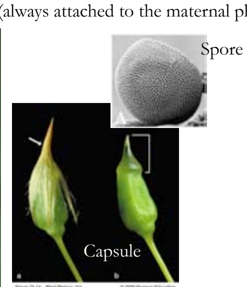
As in all plants, the gametophyte carries the sex organs, multicellular organs that develop either a single egg or many sperm cells.

1. Bryophytes: my name is Bryum bicolor

The sporophyte is also multicellular, but never branched, always short lived, and never independent (always attached to the maternal plant!).

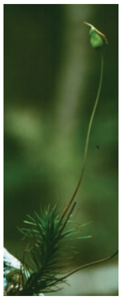
Maternal care





1. Bryophytes: my name is Bryum bicolor

The life cycle of all bryophytes follows a rather simple pattern:



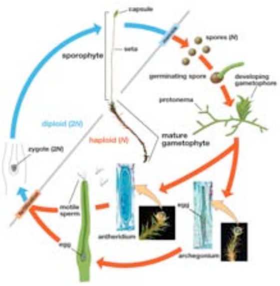


Figure 21.12 Plant Biology, 2/e © 2006 Pearson Education

1. Bryophytes: my name is Bryum bicolor

The life cycle of all bryophytes follows a rather simple pattern:

Dependent and short-lived sporophyte

Free-living and typically perennial gametophyte

> Sexual reproduction **> Spore dispersal and sporophyte dies** **> Sexual reproduction**

1. Bryophytes: my name is Bryum bicolor

Although bryophytes are an evolutionary speaking successful group, their life cycle presents some shortcomings or limitations:

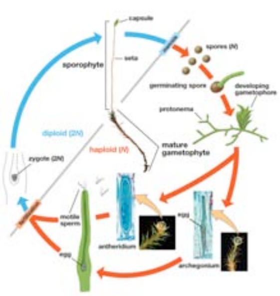


Figure 21.12 Plant Biology, 2/e © 2006 Pearson Education

1. The gametophyte is free living and hence sex organs are exposed and vulnerable.

1. Bryophytes: my name is Bryum bicolor

Although bryophytes are an evolutionary speaking successful group, their life cycle presents some shortcomings or limitations:

2. Sexual reproduction is dependent on water: the sperm cell must swim to fertilize the egg.

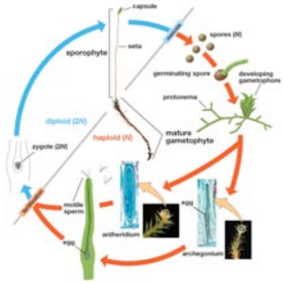


Figure 21.12 Plant Biology, 2/e © 2006 Pearson Education

1. Bryophytes: my name is Bryum bicolor

To overcome dispersal limits of their sperm cells, some species have

acquired splash-cups

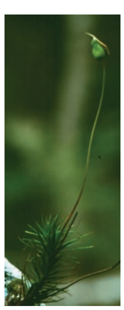
somehow recruited invertebrates

or developed explosive male sex organs

This is linked to a youtube video; search **CONOCEPHALUM** and it should take you to: http://www.youtube.com/watch?v=ALGDLzWcvnU

1. Bryophytes: my name is Bryum bicolor

The life cycle of all bryophytes follows a rather simple pattern:



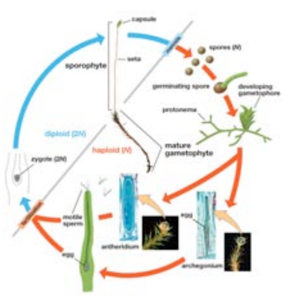
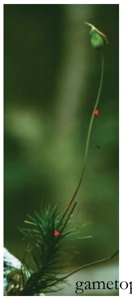


Figure 21.12 Plant Biology, 2/e © 2006 Pearson Education

2. Evolutionary significance of bryophytes

The life cycle of bryophytes is similar to that of other land plants but all other land plants have a dominant sporophyte and reduced gametophyte.

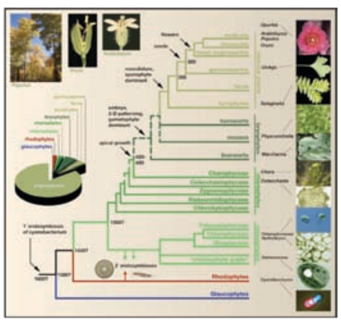


gametophyte

sporophyte

2. Evolutionary significance of bryophytes

They are the same but different: descent by modification!
Bryophytes are evolutionarily connected to other land plants!



Angiosperms/flowering plants

Gymnosperms/conifers

Ferns and their allies

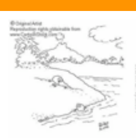
Bryophytes

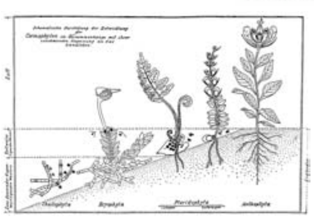
Charophyceae
(aquatic ancestor)

2. Evolutionary significance of bryophytes

Plants emerged from the aquatic habitat maybe some 500 mya.

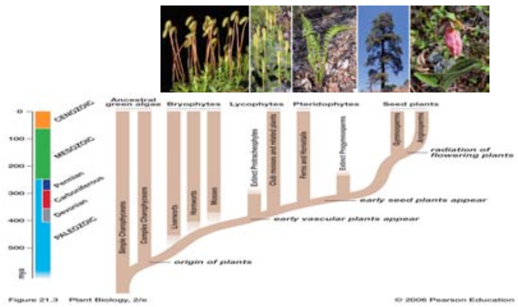
Bryophytes are the direct descendants of the earliest land plants!





2. Evolutionary significance of bryophytes

Bryophytes 1) mark the transition to land and
2) are the first step in the evolution toward flowering plants!



2. Evolutionary significance of bryophytes

In other words: no moss….

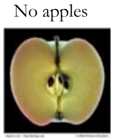
No popcorn

No spices

No beans

No coconut

No apples



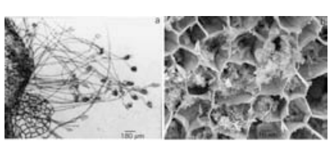
No tubercles

No flower

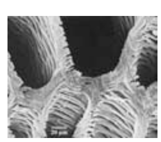
No forests

2. Evolutionary significance of bryophytes

So bryophytes are essential not only for understanding what the earliest land plants may have looked like, but also how they copped on land.



Fungal associations are frequent in bryophytes and may have been essential for understanding the colonization of land.
Mycorrhizae are imperative for plants to succeed on land.

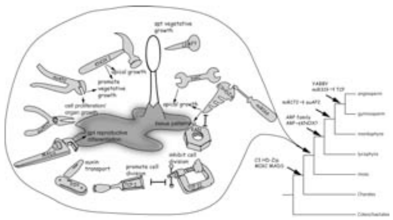


Some bryophytes have water conducting cells that may be the precursors of true tracheids in vascular plants.

2. Evolutionary significance of bryophytes

So bryophytes are essential not only for understanding what the earliest land plants may have looked like, but also how they copped on land, but also for understanding the origin of all structures that make up a "higher" plant.

Bryophyte hold the fundamental tool box to make a plant!



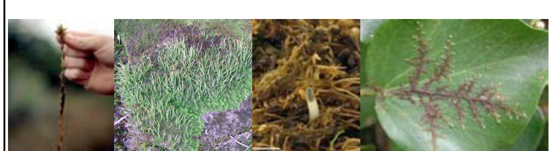
Floyd & Bowman, 207, Int. J. Pl. Sciences

3. Ecological roles of bryophytes

3. Ecological roles of bryophytes

Bryophytes are everywhere, except in the ocean.

They grow on trees, leaves, rocks, wood, dung, beetles and underground!



3. Ecological roles of bryophytes

Bryophytes are autotrophic organisms (fix C)

intercept atmospheric moisture and nutrients

establish associations with "mining" partners (fungi or cyanobacteria)

are spatially and temporally widespread

are often abundant and maybe even dominating,…

We can thus predict that they could play critical ecological roles and hence contribute important ecological services.

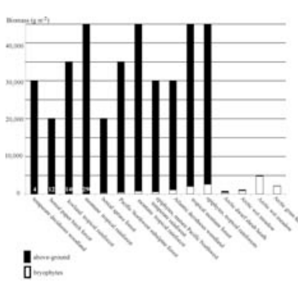
3. Ecological roles of bryophytes

Because they get water and nutrients in part from precipitation, they do not rely on organic soil, and hence can live on bare mineral soil. Some bryophytes are pioneer species critical for the development of a soil layer.

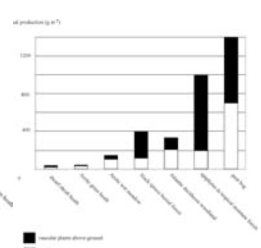
Australian bryophyte soil crusts. Photomicrograph (in a plane polarized light) of a thin section of the bryophyte crust, showing the importance of acrocarpous mosses in the formation of the crust (based on Eldridge 1998). From Vanderpoorten & Goffinet (2009). Introduction to Bryophytes.

3. Ecological roles of bryophytes

Bryophyte contribute *significantly* to the ecosystem biomass and production.



Bryophyte biomass in a range of terrestrial ecosystems in proportion to the above-ground biomass.



Annual production (gm^{-2}) in a range of terrestrial ecosystems in proportion to the above-ground production of vascular plants.

3. Ecological roles of bryophytes

Bryophytes absorb water and dissolved nutrients through their entire surface (first served when it rains!): important entry point and reservoir in ecosystems.

Mineral inputs and accumulation in two forests with luxuriant bryophyte ground covers. From Bates (2009) in Goffinet & Shaw (Bryophyte Biology 2nd edition).

(a) Coed Cymerau oakwood, Wales (after Rieley *et al.*, 1979)

	kg ha^{-1} yr^{-1}			
	Ca	Mg	K	Na
Throughfall	10.0	13.9	19.0	103.8
Litterfall	21.0	4.2	10.2	3.1
Total input (T + L)	31.0	18.1	29.2	106.9
Bryophyte accumulation	4.1	3.9	14.3	1.6

(b) Washington Creek black spruce forest, Alaska (after Oechel & Van Cleve, 1986)

	mEq m^{-2} per season				
	N	P	Ca	Mg	K
Combined throughfall and litterfall	24.0	0.6	29.0	5.0	4.0
Bryophyte accumulation	92.0	5.0	14.0	12.0	16.0

3. Ecological roles of bryophytes

Bryophytes absorb water and dissolved nutrients: important input into ecosystems.

From an ecosystem perspective: more nutrients retained overall (in epiphytes, then recycled via decomposition, and not lost to runoff).

3. Ecological roles of bryophytes

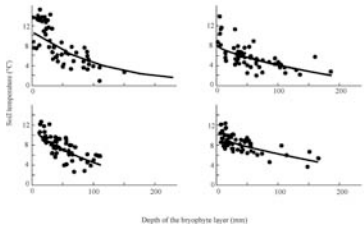
Bryophytes absorb water and dissolved nutrients: important input into ecosystems.

From an ecosystem perspective this is great: more nutrients retained overall (not lost to runoff).

For the shrub and tree layer, well, these nutrients are not immediately available, and their growth may be hence be limited.

3. Ecological roles of bryophytes

Bryophytes also indirectly affect vascular plant growth by lowering the soil temperature, which may lead to permafrost or simply reduce microbial activity (and hence reduce decomposition).



Effect of depth of the bryophyte layer on the temperature of the top soil layer at four different sites in Spitzbergen (Based on van der Wal & Brooker 2004).
From Vanderpoorten & Goffinet (2009). Introduction to Bryophytes.

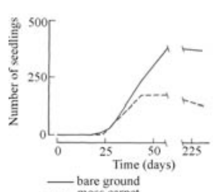
3. Ecological roles of bryophytes

In some cases an extensive bryophyte layer threatens successful germination of vascular plant seeds, this is particular alarming in case of invasive mosses.

Campylopus introflexus
a primarily austral species has been introduced to the N Hemisphere

3. Ecological roles of bryophytes

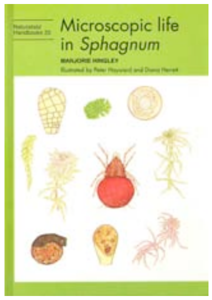
In some cases an extensive bryophyte layer threatens successful germination of vascular plant seeds, this is particular alarming in case of invasive mosses.



Effect of the invasive moss *Campylopus introflexus* on the germination and survival of seedlings of heath (*Calluna vulgaris*).
(Based on Equihua & Usher 1993) From Vanderpoorten & Goffinet(2009) Introduction to bryophytes

3. Ecological roles of bryophytes

Bryophytes may also compose the primary food source for invertebrates, or simply offer these organisms shelter, breeding grounds, …



3. Ecological roles of bryophytes

The perhaps most important ecological and global impact by bryophytes is their dominance in peatlands.

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The perhaps most important ecological and global impact by bryophytes is their dominance in peatlands.

Region	Max. Area (10^6 ha)	% of Total	Region	Max. Area (10^6 ha)	% of Total
Eurasia	180.2	44.1	Africa	4.9	1.1
N. America	171.1	41.9	C. America	2.6	0.6
S. Asia	43.6	10.7	Pacific	0.3	0.1
S. America	6.2	1.5			

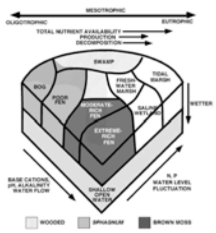
From O'Neil 2000. Bryophyte Biology.

3. Ecological roles of bryophytes

Peatlands are particular wetlands were peat accumulates.

Peat accumulates when production exceeds decomposition.

Peat accumulates when microbes can decompose organic matter fast enough or not at all, for example, when the soil is frozen, water logged and thus anaerobic, the water is highly acidic.

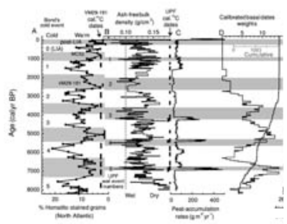


Vitt & Wieder 2008

3. Ecological roles of bryophytes

Peat accumulates as long as the conditions are right, i. e., in some cases for the last 8000 years!

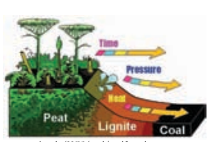
From: www.imcg.net



Since peat is *fossilized* plant material we can study past vegetations, climate,…

3. Ecological roles of bryophytes

Peat accumulates as long as the conditions are right, i. e., in some cases for the last 8000 years!

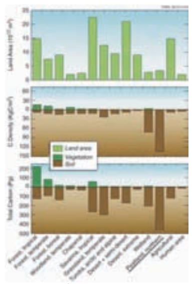


www.uky.edu/KGS/coal/coalform.htm

Since peat is *fossilized* plant material we can also use it as fuel. This is done in Europe and in Chile.

3. Ecological roles of bryophytes

Since peat is *fossilized* plant material it is in fact stored C, and hence E. Peatlands have the largest C sink on the planet, and hence the largest source of potential green house gases.



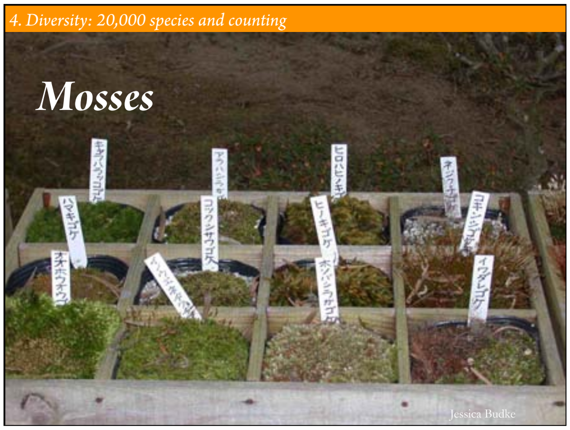
From: www.imcg.net

If climate change results in an increase of atmospheric T°, peatlands may see their water table be lowered, creating aerobic conditions suitable for microbial activity, thus decomposition, hence C release, and thus accentuation of the green house effect.

3. Ecological roles of bryophytes

But let's not forget the obvious: bryophytes add esthetics to the forests!

4. Diversity: 20,000 species and counting



A small break?

4. Diversity: 20,000 species and counting

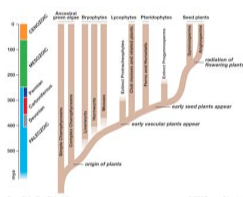
Bryophytes comprise approximately 20,000 species.

They are organized into three lineages:

Liverworts

Mosses

Hornworts



They tend to differ in the architecture of the gametophyte and sporophyte,

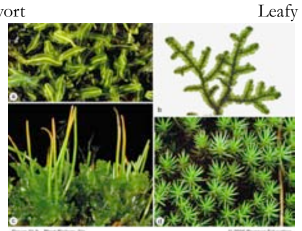
but none of these lineages is characterized by a single unique trait!

4. Diversity: 20,000 species and counting

Their vegetative (photosynthetic) body is either composed of a stem with leaves or a flattened leafless ribbon (i.e., a thallus).

Thalloid liverwort

Leafy liverwort



Hornworts (always thalloid)

Mosses (always leafy)

4. Diversity: 20,000 species and counting

Their sporophyte is always composed of a single axis with a terminal spore producing tissue.

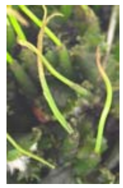
Capsule "exploding"
Spore release sudden
Seta short-lived

Capsule opening by a lid
Spore release gradual
Seta long-lived

"Capsule" long, unzipping
Spore release gradual
Seta absent

Liverwort

Moss



Hornwort

4. Diversity: 20,000 species and counting

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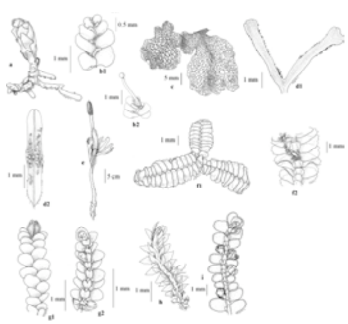
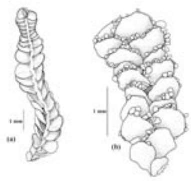
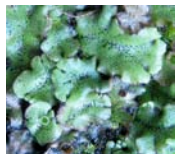
Liverworts: broad morphological amplitude (leafy to thalloid)



4. Diversity: 20,000 species and counting

Liverworts: broad morphological amplitude (leafy to thalloid)

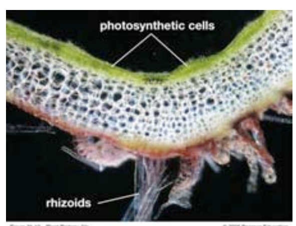




Major differences pertain to orientation of the leaves or anatomical complexity of thallus.

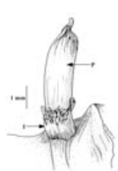
4. Diversity: 20,000 species and counting

Complex thalloids may be the most conspicuous liverworts.
Their name refers to the "complex" anatomy.



Rhizoids are unicellular root-like structures that may serve as entry point for mycorrhyzal fungi!

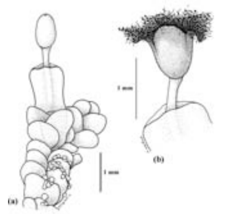
4. Diversity: 20,000 species and counting



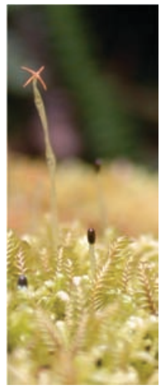
Protective gametophytic structures around the archegonia and, later, the young sporophyte, in the simple thalloid liverwort *Pallavicinia lyellii*, comprised of an involucre I and a pseudoperianth P

Perianth of *Leptoscyphus australis* with a laciniate mouth margin (photo B. Malcolm).

4. Diversity: 20,000 species and counting

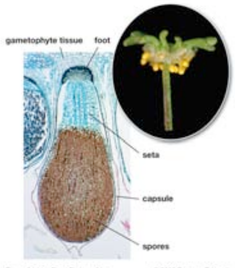


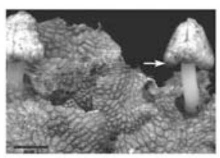
Capsule matures while protected; then a seta grow overnight, and the capsule opens along four lines.



The epiphytic *Radula complanata* reproduces by both vegetative, discoidal gemmae on the leaves and spores (a). Note the short seta that merely insures that the capsule dehisces beyond the perianth. The capsule exhibits a typical four-valved dehiscence, liberating the spore mass and elaters (b).

4. Diversity: 20,000 species and counting

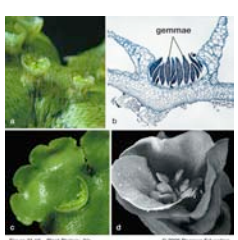


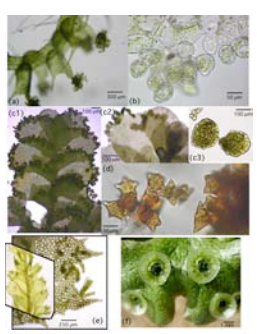


The complex thalloid *Conocephalum conicum*, dorsal view, with a conical carpocephalum. A tubular involucre (arrow) encloses the nearly mature sporophyte

4. Diversity: 20,000 species and counting

Vegetative reproduction is common, not surprisingly since sexual reproduction is dependent on water!





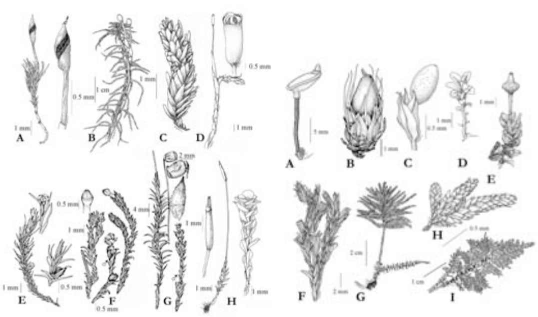
4. Diversity: 20,000 species and counting

Mosses


Graham et al.

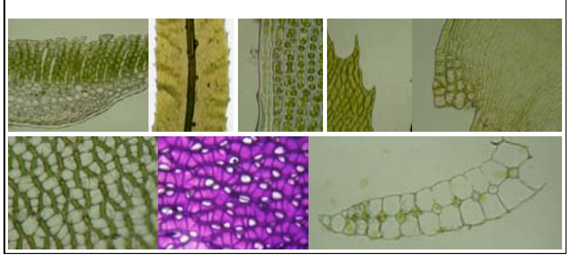
4. Diversity: 20,000 species and counting

Major architectural differences in both capsule and vegetative plants.

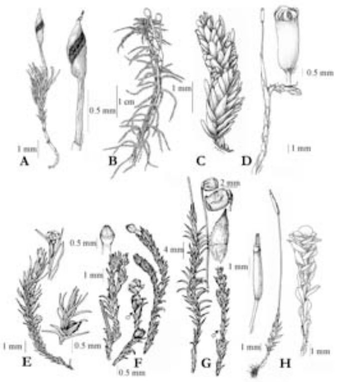


4. Diversity: 20,000 species and counting

Vegetative plants show putative adaptation retaining, moving, acquiring and quickly loosing water.



4. Diversity: 20,000 species and counting

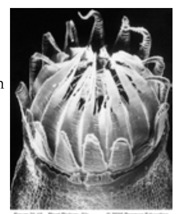


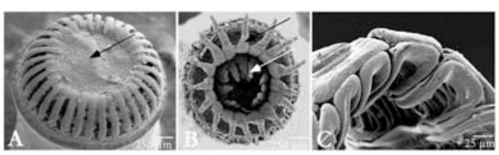
Major moss lineages are best defined by the mode of dehiscence of spore release:

1 or 4 slits or lid?

4. Diversity: 20,000 species and counting

The loss of a lid typically reveals a complex set of teeth that may move and control spore release!

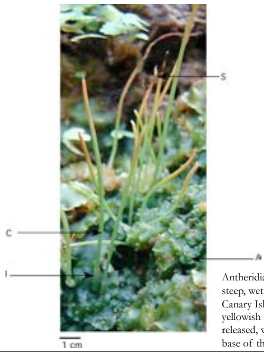




4. Diversity: 20,000 species and counting

4. Diversity: 20,000 species and counting

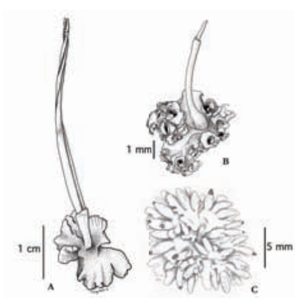
Hornworts: thalloid gametophyte and horn-like sporophyte!



Antheridia and mature sporophyte in *Phaeoceros laevis* thriving on steep, wet rocky slopes of humid laurel forests in La Palma, Canary Isl. A: antheridia; C: capsule; I: involucre. Note the yellowish apex of the capsule from which yellow spores S are released, while new spores are still being produced at the green base of the capsule (photo A. Vanderpoorten).

4. Diversity: 20,000 species and counting

Hornworts: 100-200 species



Variation of thallus morphology in hornworts. (a) Typical thallus in rosette in *Phaeoceros*. Note the horn-like sporophyte that dehisces along one or two vertical lines. (b) deeply incised thallus margins in *Dendroceros*, giving the appearance of irregular leaves emanating from a thickened midrib. (c) *Notothylas orbicularis*, vigorous plant with mature and immature sporophytes, which are reduced in size owing to the terminate development of the basal meristem (reproduced from Schuster 1992).

4. Diversity: 20,000 species and counting

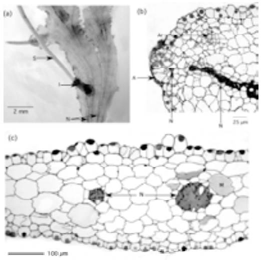
Hornworts: spore dispersal

The sporophyte matures from the base upward, and contains spores nearly throughout.

At maturity the sporophyte dehisces along two vertical lines (like two zippers), and spores are released gradually.

4. Diversity: 20,000 species and counting

Hornworts: typically associated with cyanobacteria.



The N-fixing symbiosis between cyanobacteria and hornworts. Example of the *Nostoc-Leiosporoceros* association (reproduced from Villareal & Renzaglia 2006). (a) Dorsal view of the thallus showing bifurcating strands of *Nostoc* parallel to the main axis of the thallus (arrows). Note the mature sporophyte S with a basal involucre I. (b) and (c): Longitudinal (b) and transverse (c) section of the thallus with *Nostoc* canals (arrows) originating behind the apical cell A and scattered mucilage cells (mc).

5. Time tree of evolution and where they are now.

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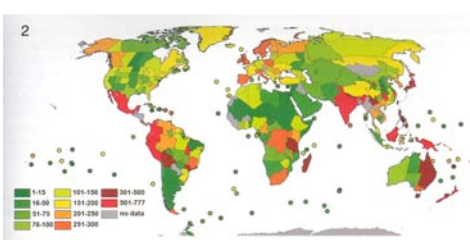
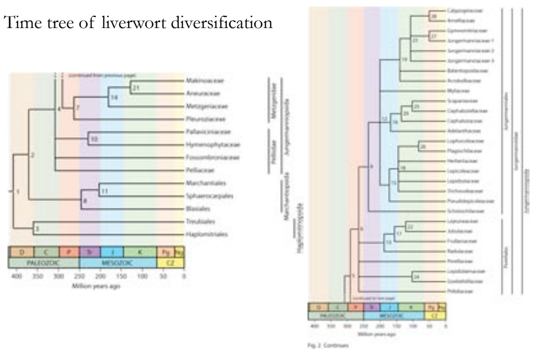
Bryophytes are old lineages but are all species old and thus likely widespread?



Distribution of global liverwort species diversity.
Von Konrat et al. 2008.

5. Time tree of evolution and where they are now.

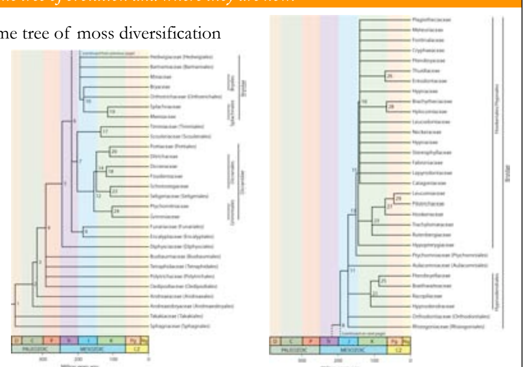
Time tree of liverwort diversification



N. Wikström, X. He-Nygrén, and A. J. Shaw. Liverworts (*Marchantiophyta*). Pp. 146–152 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

5. Time tree of evolution and where they are now.

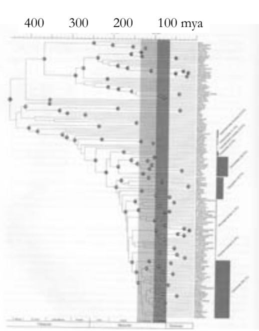
Time tree of moss diversification



A. E. Newton, N. Wikstrom, and A. J. Shaw. Mosses (Bryophyta). Pp. 138–145 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

5. Time tree of evolution and where they are now.

Time tree of moss diversification



Chronogram of the embryophyte lineages. From Newton et al. (2006) Pleurocarpous mosses. Systematics and Evolution

Bryophytes compose an ancient lineage but maybe genera are of "recent" origin, and even when genera originated in the Cretaceous, species may be "young".

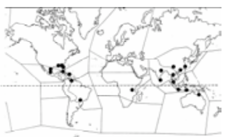
5. Time tree of evolution and where they are now.

Patterns of distributions

Holartic

Subantarctic

Endemic

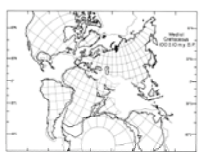


Pantropical

5. Time tree of evolution and where they are now.

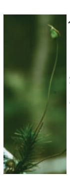
Patterns of distributions: long-distance dispersal or vicariance?

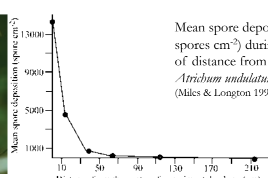
Is this distribution resulting from transatlantic dispersal of spores or the breakup of broad past range along with the former continent?



5. Time tree of evolution and where they are now.

Patterns of distributions: long-distance dispersal or vicariance?



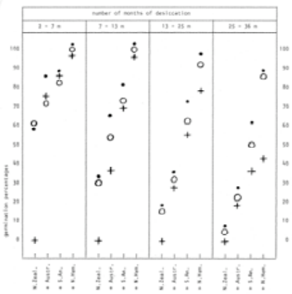


Mean spore deposition (number of spores cm^{-2}) during 30 days as a function of distance from experimental colony in *Atrichum undulatum*
(Miles & Longton 1992, Journal of Bryology).

Most spores fall close to the maternal plant.

5. Time tree of evolution and where they are now.

Patterns of distributions: long-distance dispersal or vicariance?

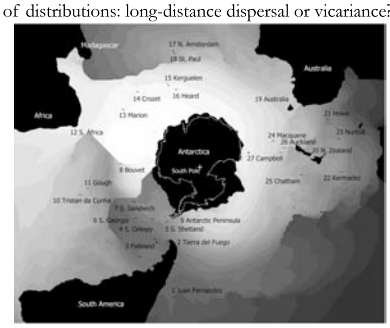


Percentages of germination of spores exposed to desiccation at ambient room relative humidity during 2-36 months (●) followed by subsequent wet freezing during four days at –30–C (O) or followed by subsequent dry freezing during four days at –30–C (+) in 139 moss species with contrasting geographic ranges, including endemics to (i) New Zealand; (ii) New Zealand+Australia/Tasmania; (iii) New Zealand+Australia/Tasmania+southern America/Sub-Antarctic islands; (iv) New Zealand and northern hemisphere (reproduced from van Zanten 1978 with permission of the Hattori Botanical Laboratory)

Some spores certainly would withstand the harsh conditions of LDD

5. Time tree of evolution and where they are now.

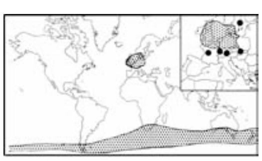
Patterns of distributions: long-distance dispersal or vicariance?



And broad disjunction may be bext explained by LDD!

5. Time tree of evolution and where they are now.

Patterns of distributions: long-distance dispersal or vicariance?

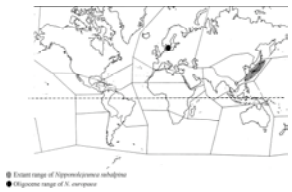


World distribution of the moss *Orthodontium lineare*, exhibiting a primary sub-Antarctic range.
(redrawn from Söderström 1992)

In some cases the dispersal agent is human and broad disjunctions result from recent introductions.

5. Time tree of evolution and where they are now.

Patterns of distributions: neo- versus paleoendemic?

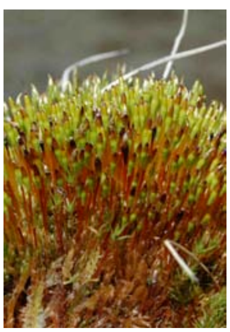


Extant range of *Nipponolejeunea subalpina* and Oligocene range of *N. europaea* (redrawn from Schuster 1893).

Paleoendemism is impossible to document unambiguously without fossils.

5. Time tree of evolution and where they are now.

Patterns of distributions: one or more species?



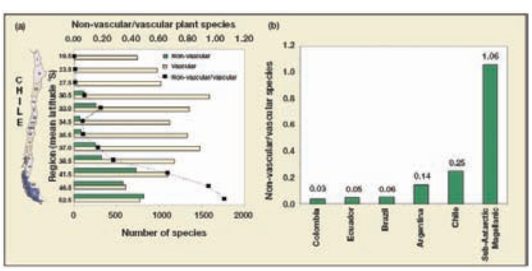
Species are defined by a genetic cohesiveness resulting from random interbreeding.

Are disjunct populations genetically isolated and hence representing two or more evolutionary lineages?

So called cryptic species are increasingly demonstrated using DNA evidence.

3. Ecological roles of bryophytes

Bryophyte contribute significantly to the ecosystem plant biomass.



Latitudinal and geographic patterns in plant species richness.
From Rozzi et al. Frontiers in Ecology and the Environment

Conclusions

Conclusions

1. Bryophytes are defined by a simple life cycle with a free living sex-bearing generation
2. Bryophytes mark the conquest of land by plants and are the precursors of higher plants, and are hence essential to understand the early evolution of plants and the origin of complex traits
3. Bryophytes occur in all terrestrial ecosystems, and play critical roles in nutrient and water flow.
4. Bryophytes are morphologically diverse, with multiple and elaborate features.
5. Bryophytes are old lineages undergoing active speciation.