
Hornworts
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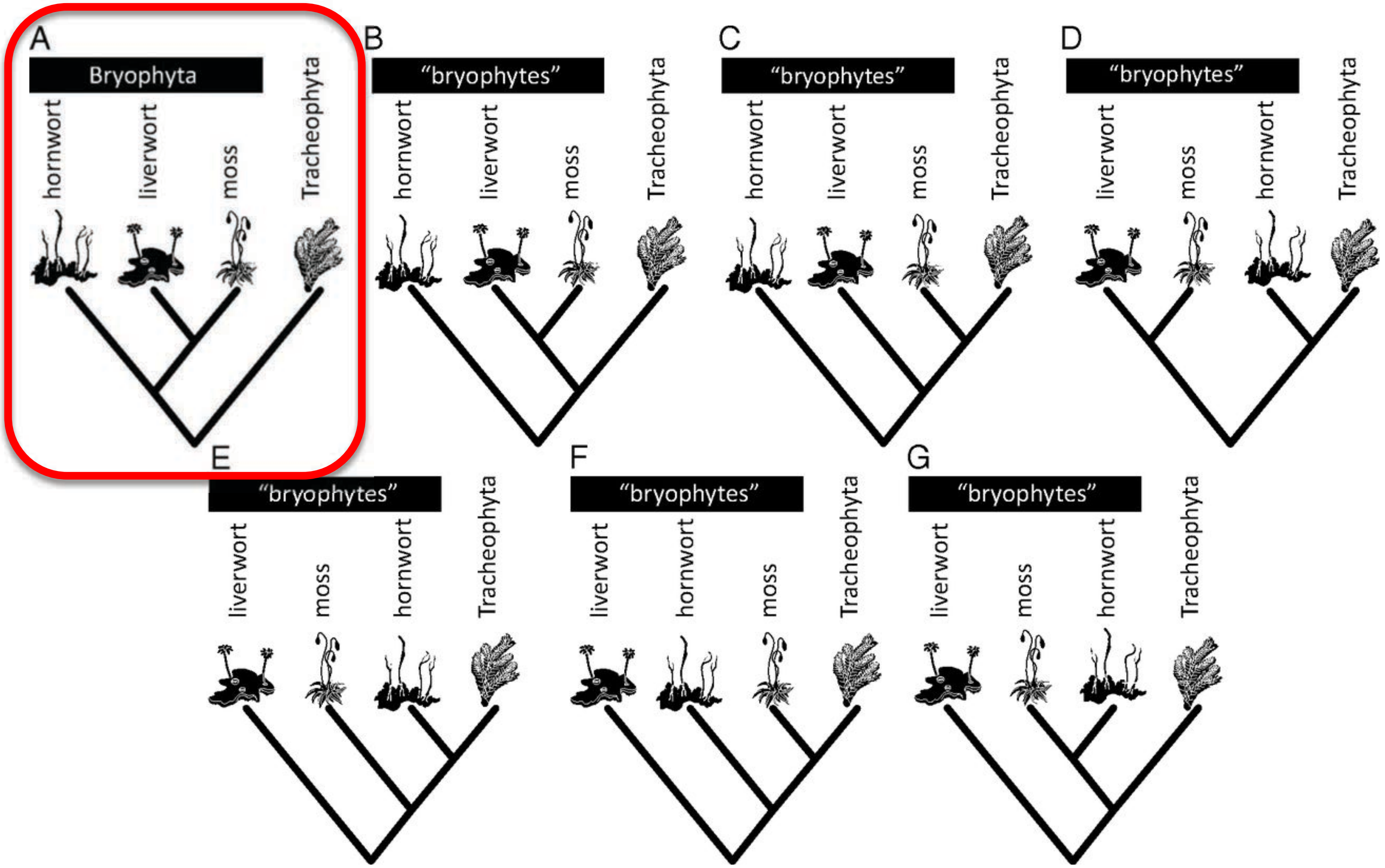
Introduction

The origin of hornworts dates back to 450-500 Mya (but extant diversity <100 my). This rather ancient origin suggests that hornworts had a long time for evolutionary diversification and hence great morphological and perhaps taxic diversity. **This did not happen**, or at least the extant diversity is low ± 200 species.

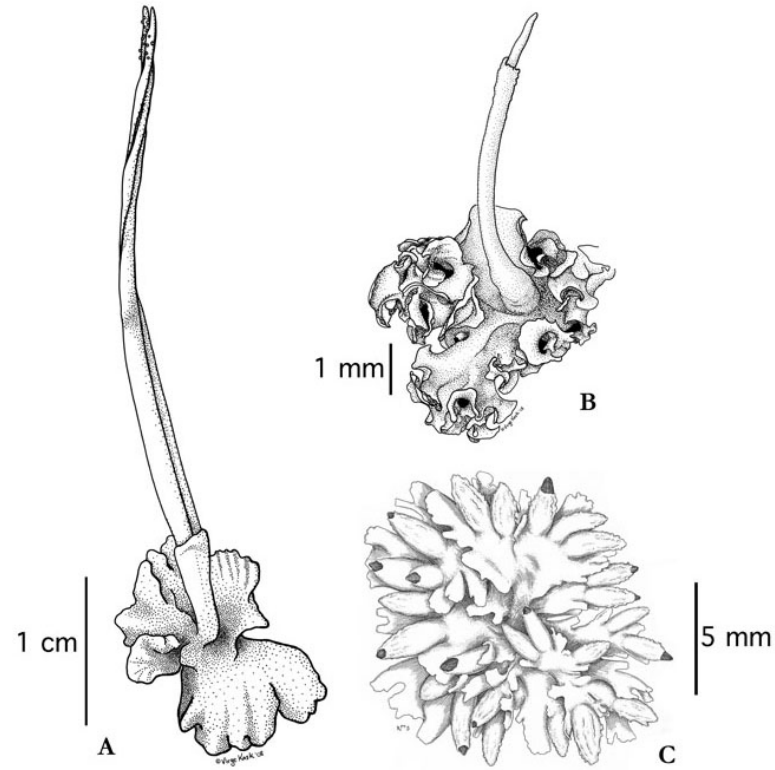


Intro & Gametophyte

Hornworts: least diverse lineage of bryophytes

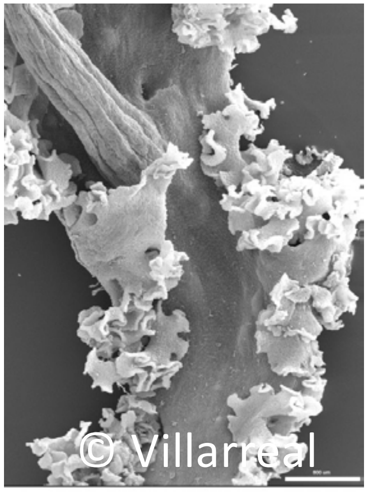
Etymology: horn-like sporophyte!

Vegetative body (gametophyte):
- always thalloid/ribbon-like like some liverworts
- bilaterally symmetric
- lateral appendages lacking but margin can be incised (*function?*) or perforated.



Vanderpoorten & Goffinet 2009

Nothoceros sp.



Dendroceros

Gametophyte

The growth of the thallus is accounted for by the activity of single apical cell, as in all bryophytes.

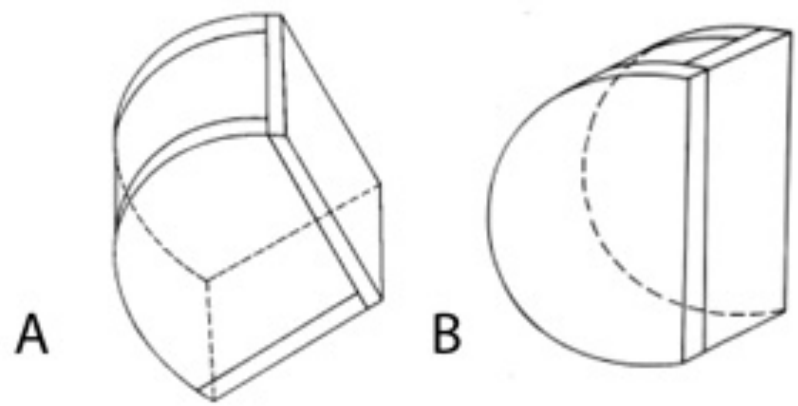
Apical cell (AC) is in a notch and covered by mucilage (M).

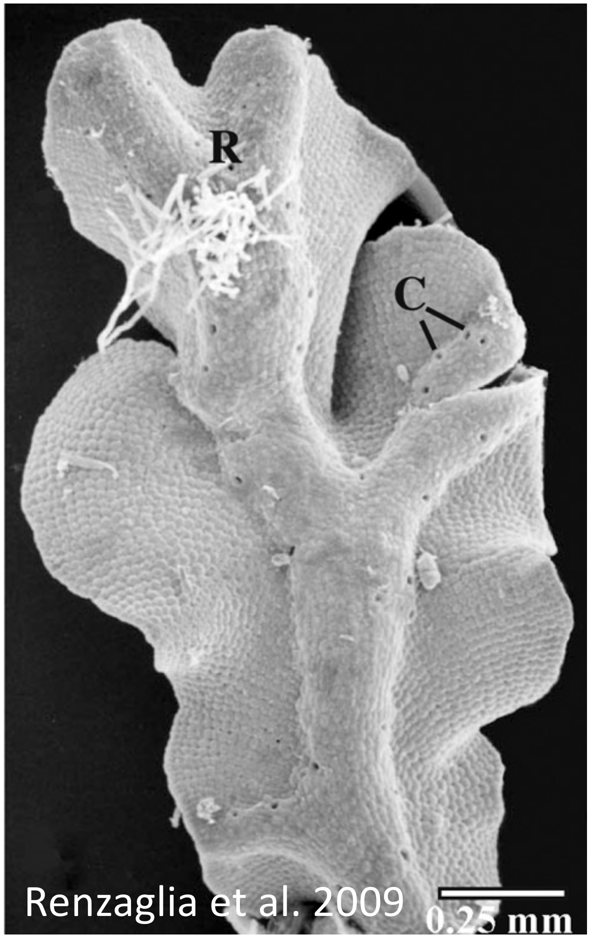
Gametophyte

The shape of the apical cell is wedge-shaped [A] or hemidiscoid [B].

The wedge shaped cell has with 4 cutting faces (2 lateral, 1 dorsal and 1 ventral) and resulting in an orbicular growth form (rosettes).

The hemidiscoid cell has 3 faces (2 lateral and 1 basal) results in a ribbon-shaped thallus.

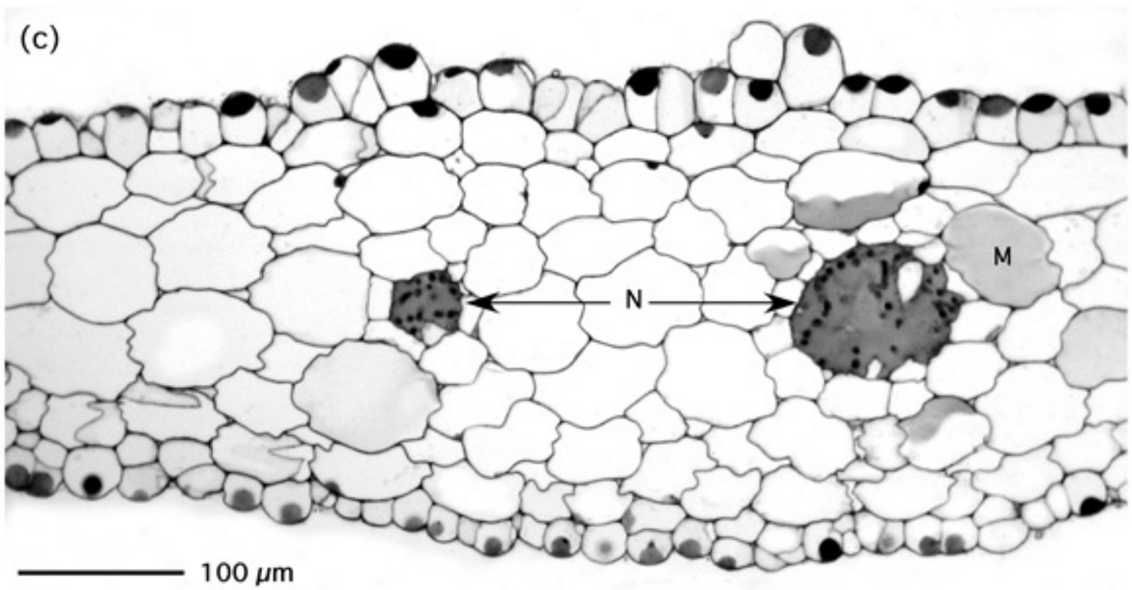




Gametophyte

The thallus lack conspicuous internal differentiation except for schizogenous cavities ultimately housing cyanobacteria. (≠ *schizogeny* and *lyzogeny*?)

Some cells are specialized in synthesizing, storing and secreting mucilage (a carbohydrate potentially essential for water retention).



Renzaglia & Villarreal 2006

Vanderpoorten & Goffinet 2009

Upper surface bears sex organs, rarely some outgrowth.
Rhizoids on the lower surface are always unicellular (like in __________).

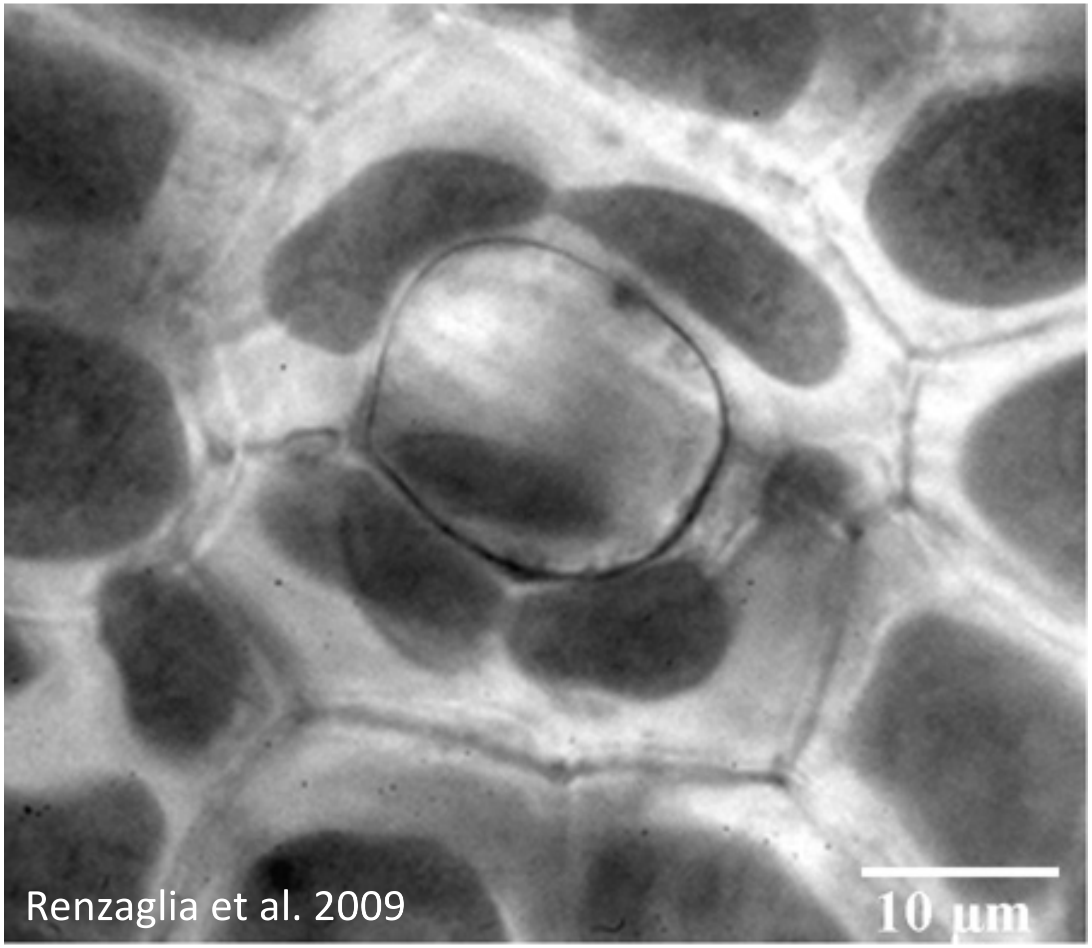
Gametophyte

The lower epidermis includes some specialized cells that are kidney-shaped like stomatal guard cells.

Hornworts lack stomata on the gametophyte!

These cells define a pore, that remains open.

The pore leads to a chamber that houses cyanobacteria embedded in mucilage (hence the name **mucilage clefts**).

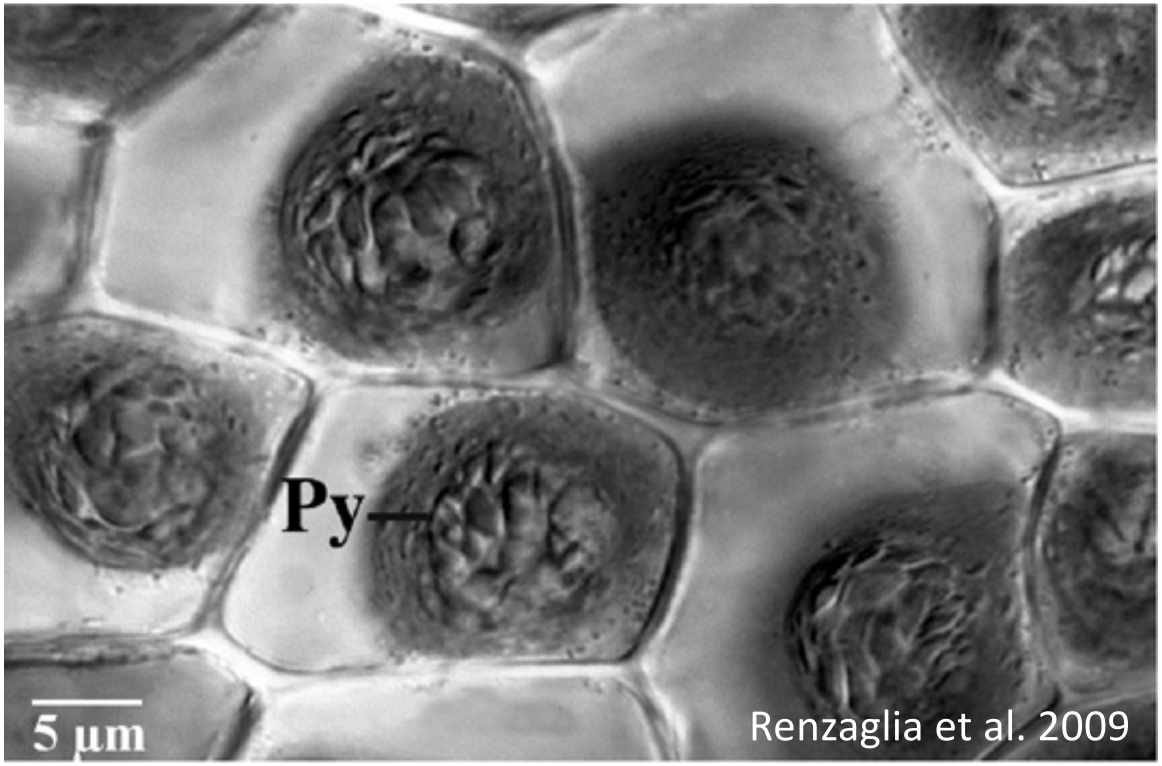


Gametophyte

The photosynthetic cells of most taxa include a single chloroplast. Only in *Megaceros* are chloroplasts small and numerous.

But as in all bryophytes and perhaps land plants, meiosis is monoplastidic, meaning there is always only one chloroplast during meiosis!

When the chloroplast is large and single, it shows a region called the pyrenoid, which corresponds to the concentration of RUBISCO.



What is RUBISCO?

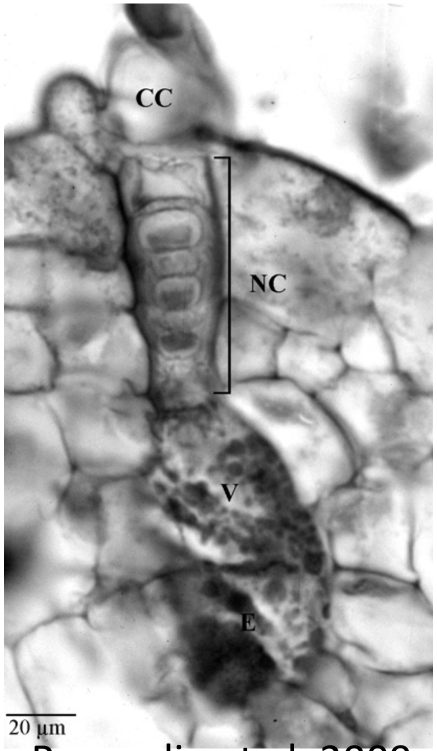
Pyrenoids also known from algae!

Gametophyte: sex organs

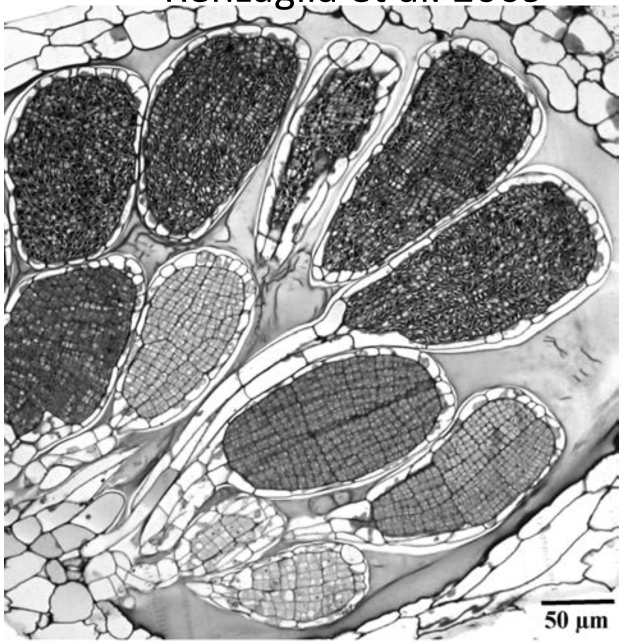
Gametangia are produced along the midrib/midline.

Archegonia are sunken with the neck protruding above the surface (cc = cover cells).

Antheridia are stalked and always clustered inside a chamber within a schizogenous cavity in the thallus!



Renzaglia et al. 2009



Gametophyte: sex organs

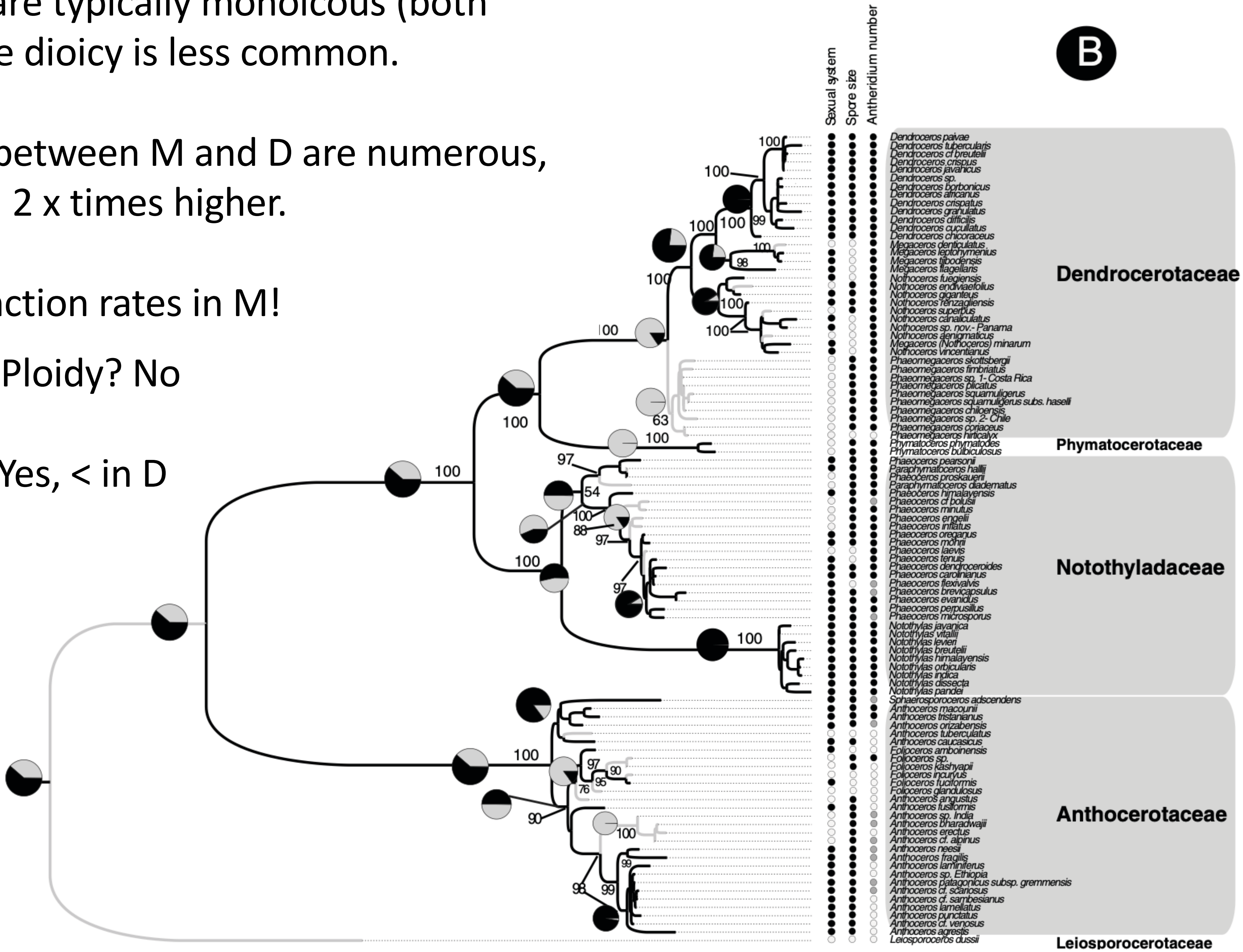
Hornworts are typically monoicous (both sexes) hence dioicy is less common.

Transitions between M and D are numerous, with D—>M 2 x times higher.

Higher extinction rates in M!

Correlates? Ploidy? No

Spore size? Yes, < in D



Villarreal & Renner 2013 BMC Evol. Biol. 13:239

Sporophyte

The first division of the zygote is longitudinal versus transverse in other bryophytes.

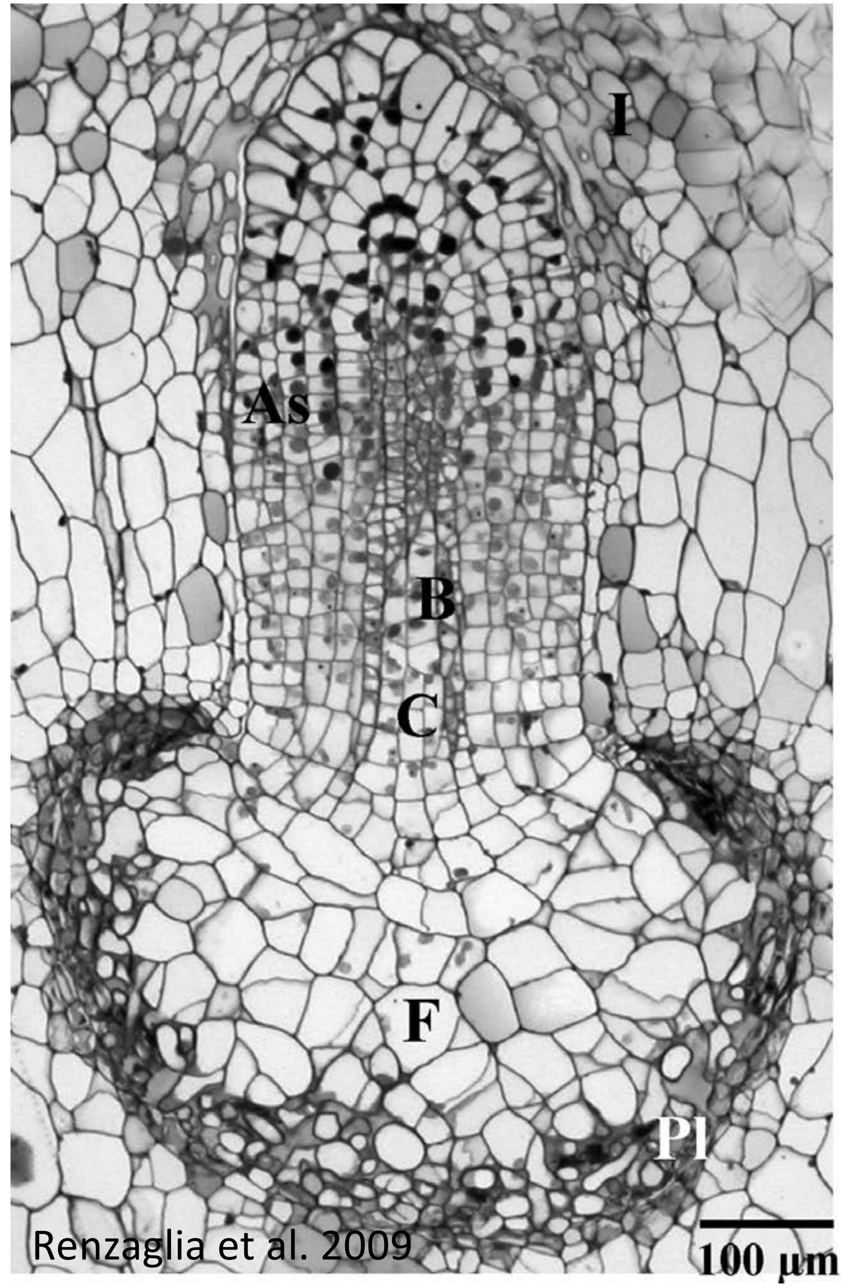
Embryo forms an enlarged foot and upper region => “capsule” or sporangium.

How does the sporophyte grow? Options are: apical cell, intercalary meristem or…..

Hornworts are characterized by the presence of a intercalary meristem.

Hence the sporophyte grows acropetally!

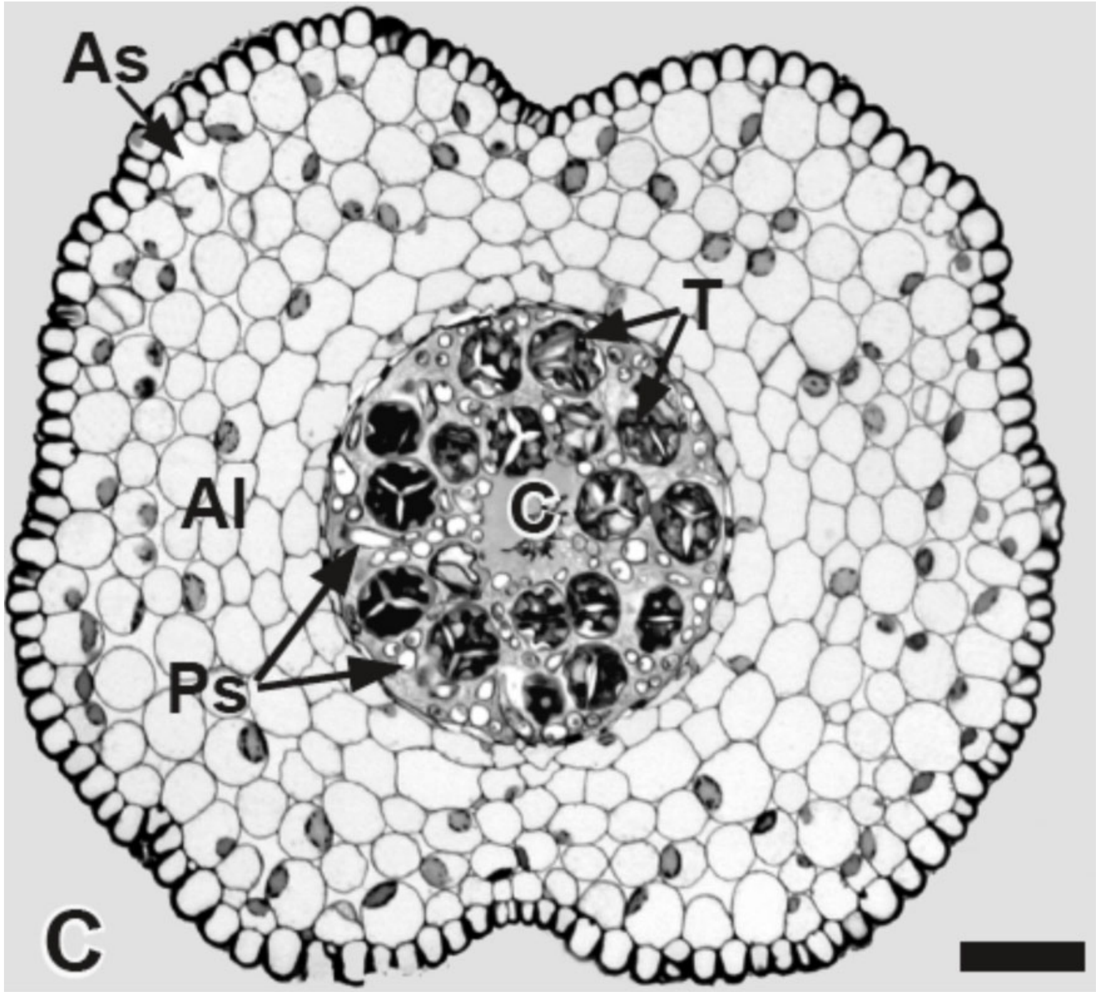
A seta is always lacking!



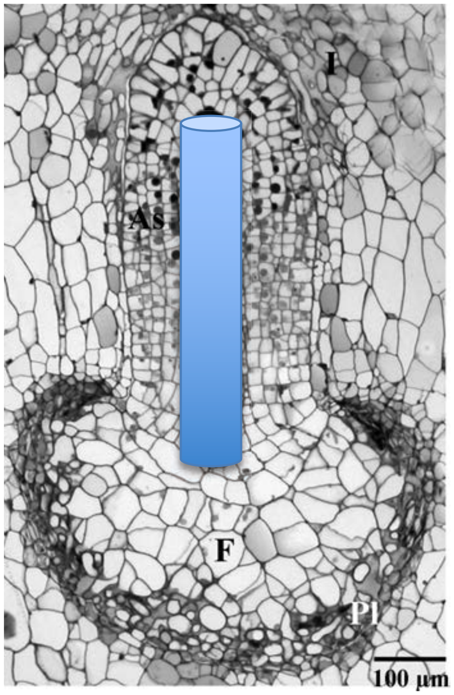
Sporophyte

Derivatives from meristematic cells follow two distinct trajectories.

The innermost one compose the endothecium, which will form the **columella**.



Villarreal & Renzaglia 2006

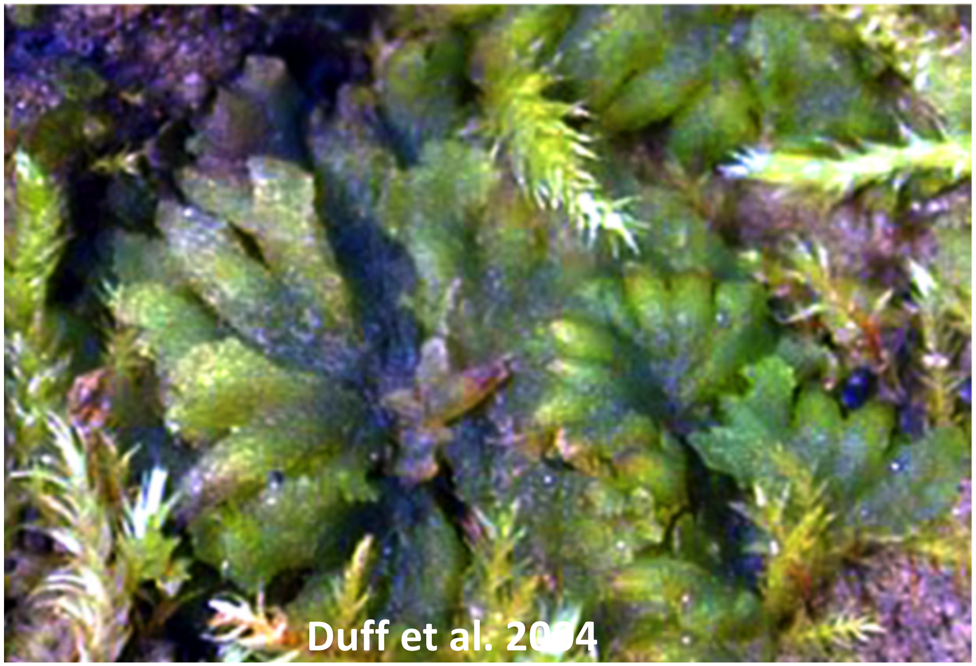


Renzaglia et al. 2009

The outer layer or amphithecium forms of course the epidermis, and assimilative tissues but also the sporogenous cells (≠ from other bryophytes except ______)

Sporophyte

The basal meristem is typically ± "continuously" active, some sporophytes are 7 or more cm long/tall!



In *Nothotylas*, it soon stops dividing, and the sporophytes are basically immersed, or enclosed in the involucre!

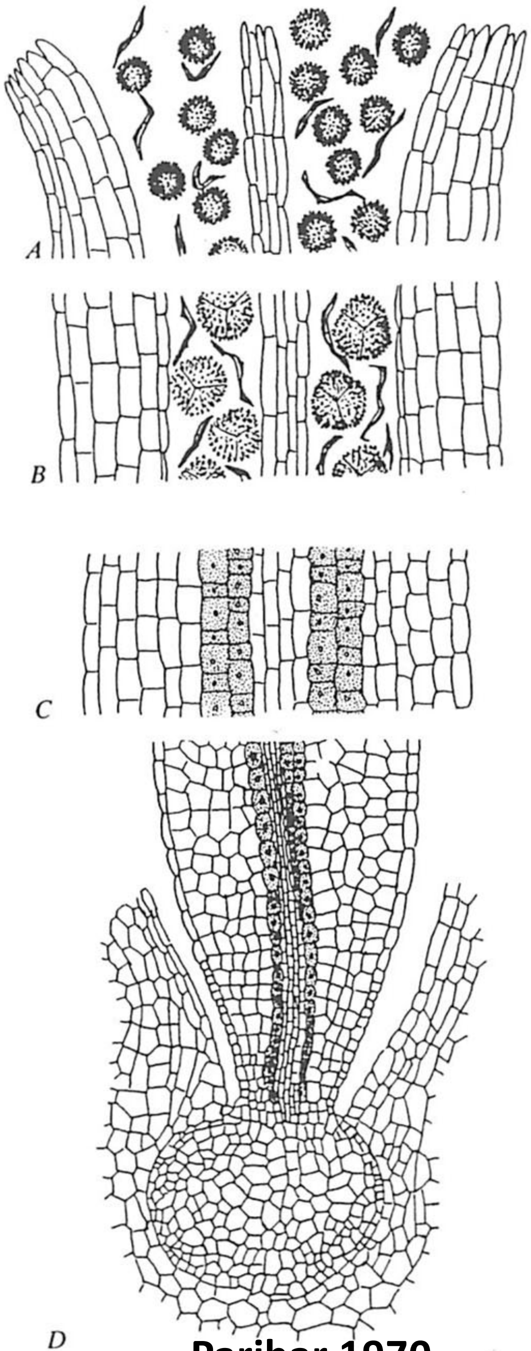
Sporophyte

A consequence of the basal meristem is that cells, including sporogenous cells (and hence spore mother cells) are continuously been produced from the bottom.

These cells begin their maturation immediately, and those of the amphithecium may enter meiosis.

Hence **meiosis is asynchronous** in hornworts!

Thus, along a single sporophyte, one can see all stages of the development of spores!



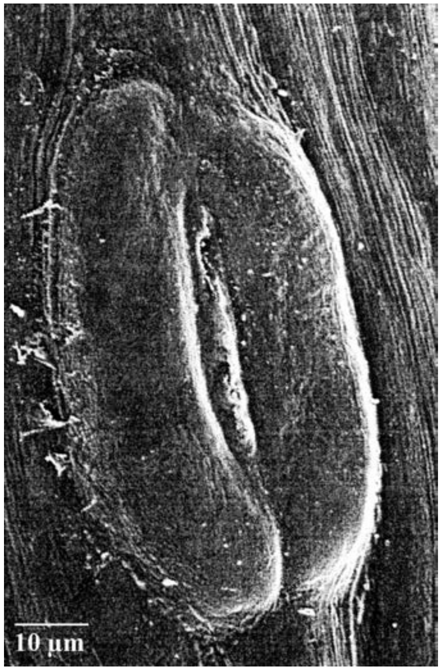
Parihar 1970

Sporophyte

The capsule walls bears specialized cells defining a pore, the stoma.

Stomatal guard cells are similar to those in mosses and vascular plants, but are non-functional and likely did not serve in gas exchange.

Other function?



Renzaglia et al. 2009

Sporophyte

Early in the development of the sporophyte, before sporogenesis, the cells undergo a division yielding a spore mother cell and and a (pseudo)elaterocyte.

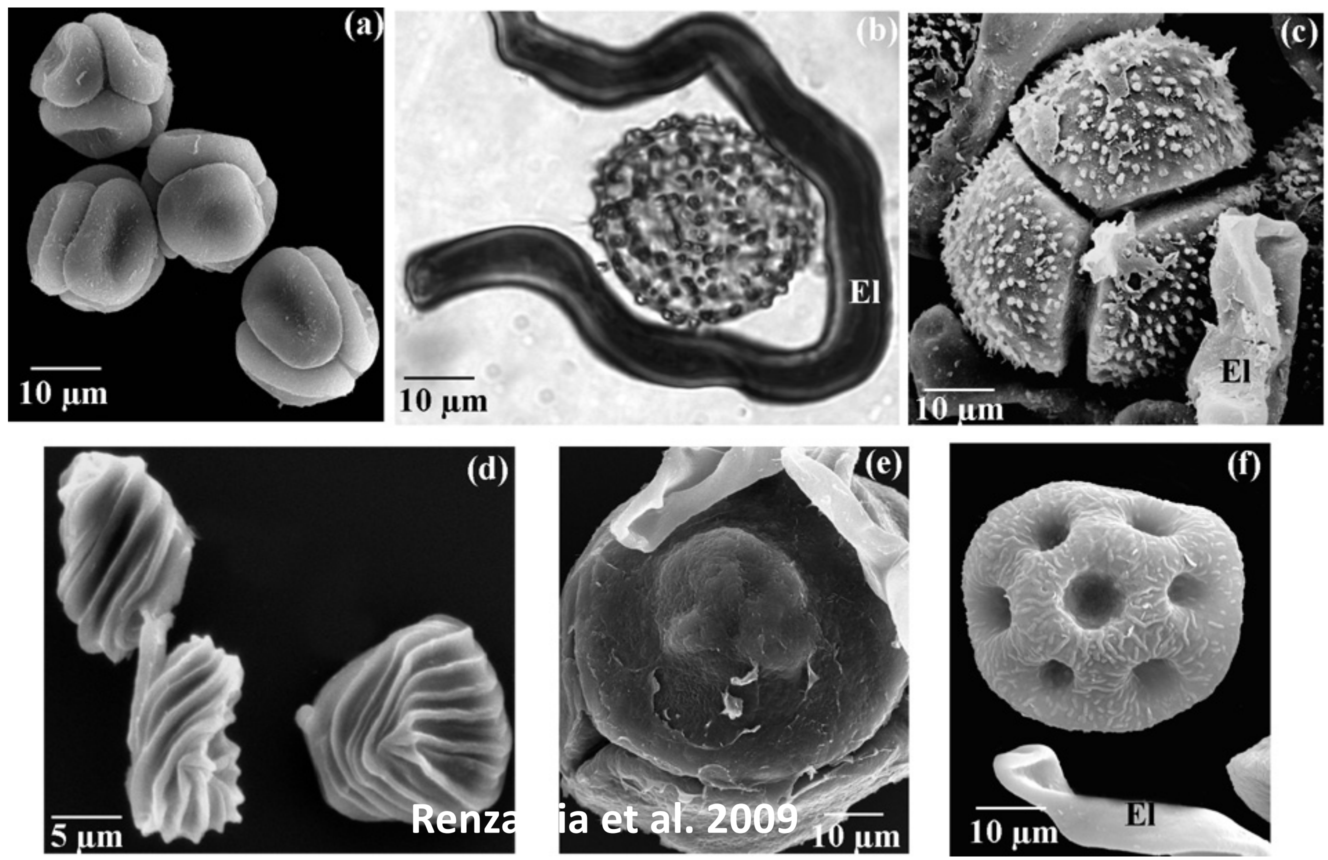
Why pseudo-elaters?

(Pseudo)elaters consist of 1 or > diploid cells arranged in layers alternating with spores.

SMC immediately undergo meiosis.

PMC undergo repeated mitotic Divisions.

Hence the # of pseudoelaters is much > than that of spores!



Renza ia et al. 2009

Sporophyte

At maturity the sporophyte dehisces from the apex down, along predetermined axial lines, or groves.

Asexual reproduction

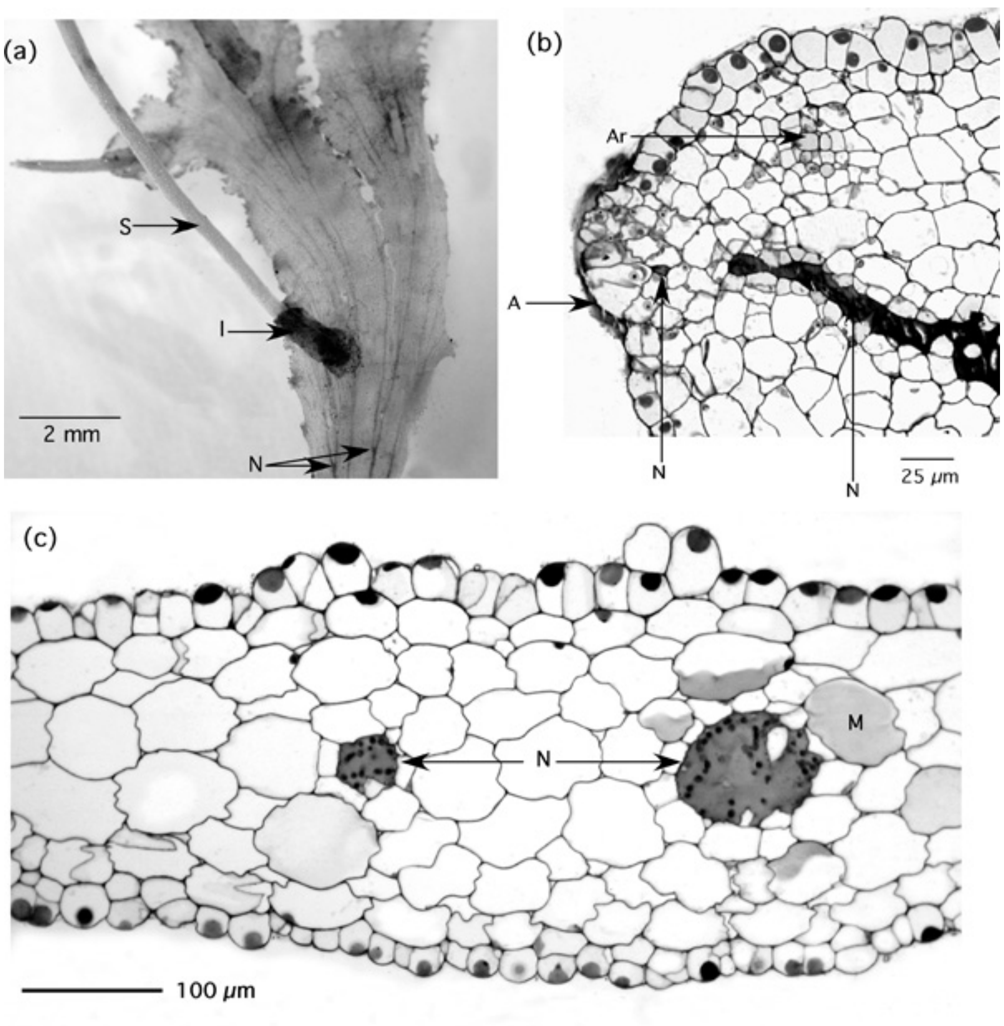
Like liverworts and mosses, hornworts may develop specialized asexual reproductive structures, mostly along the thallus margin or in the form of rhizoidal tubers, but these are uncommon.

In *Nothoceros aenigmaticus*, a species formally considered endemic to SE USA, male and female populations are allopatric and persist solely through propagation by thallus fragmentation in the SE!

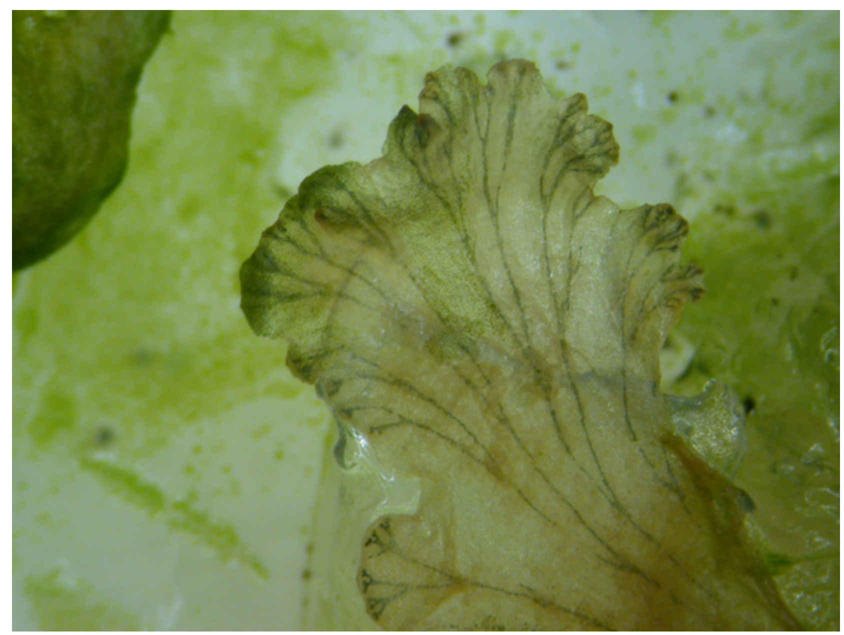

Nothoceros fuegianus (Cape Horn)

Symbiosis

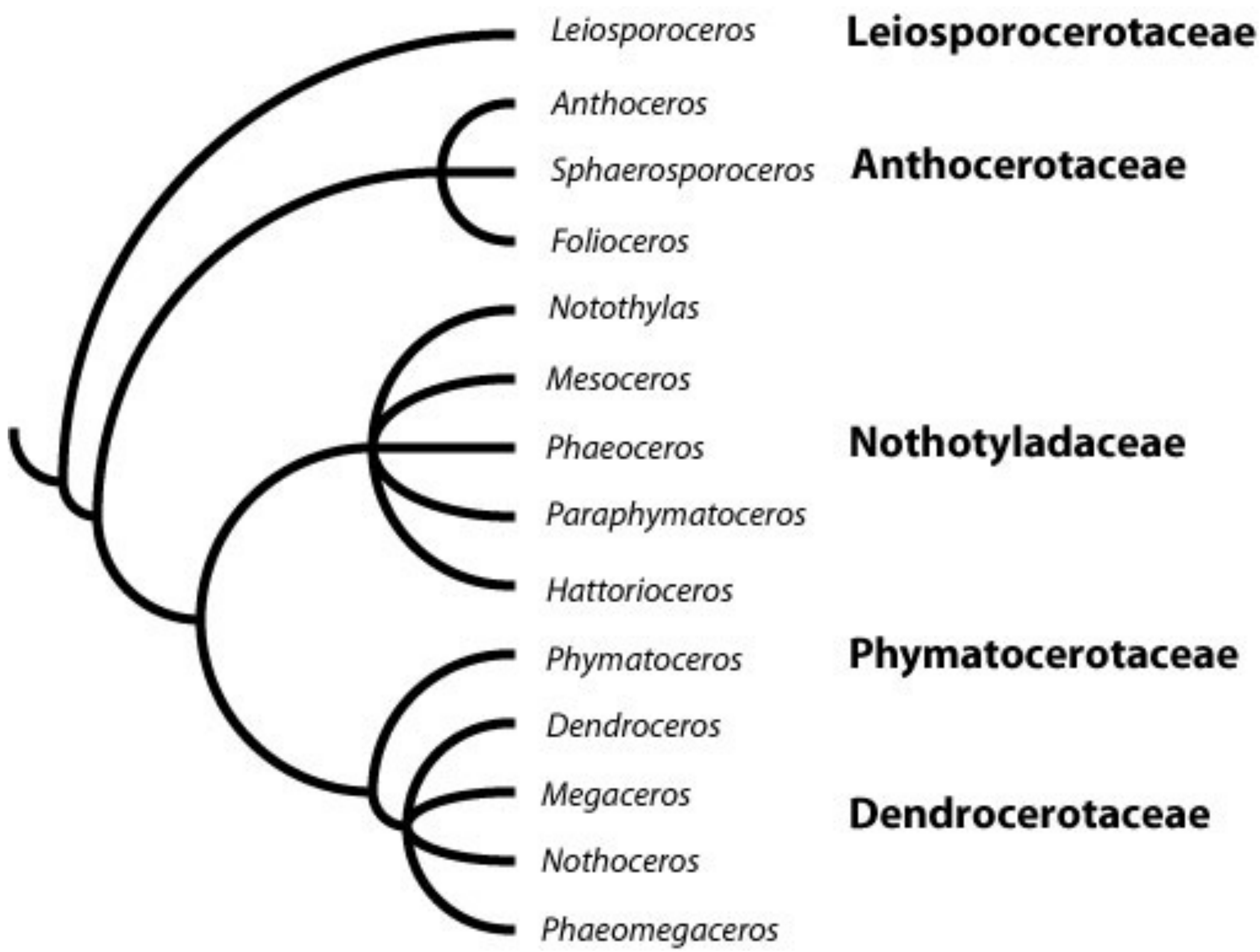
Among bryophytes, hornworts are best "known" for their association with endophytic cyanobacteria. The *Nostoc* colonies are sought after partners because of their ability of ____________________ which takes place in __________________.



Nostoc colonies are typically globose except in *Leiosporoceros*, where they grow along with the thallus, forming like a veination.



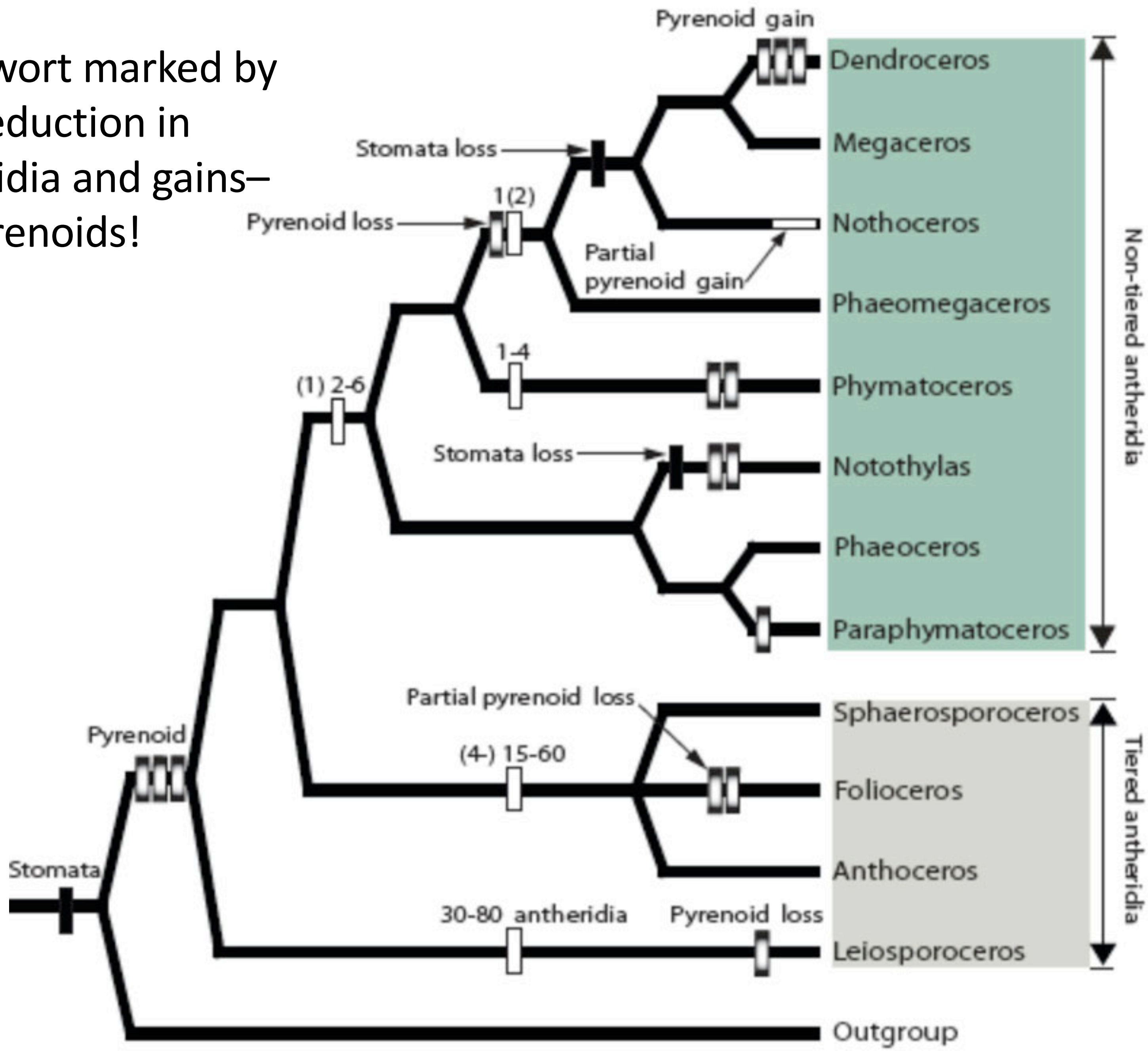
Phylogeny



Leiosporoceros
Leiosporocerotaceae
Anthoceros
Sphaerosporoceros
Anthocerotaceae
Folioceros
Notothylas
Mesoceros
Phaeoceros
Nothotyladaceae
Paraphymatoceros
Hattorioceros
Phymatoceros
Phymatocerotaceae
Dendroceros
Megaceros
Dendrocerotaceae
Nothoceros
Phaeomegaceros

Evolution

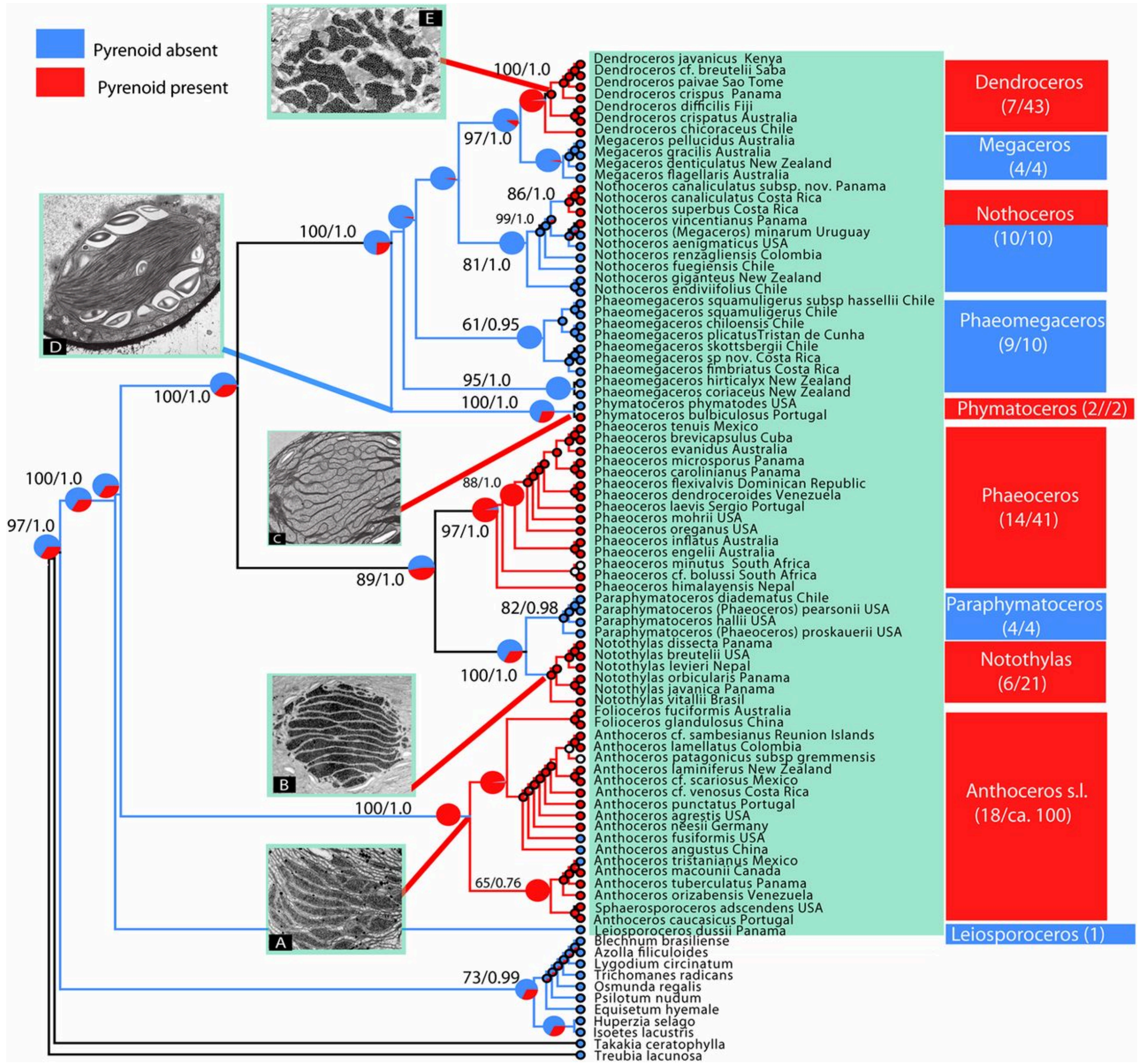
Evolution of hornwort marked by loss of stomata, reduction in number of antheridia and gains–losses-gains of pyrenoids!



Evolution

Homoplasy of the pyrenoid.

If multiple "aquisitionS", what may this tell us about the trait itself?



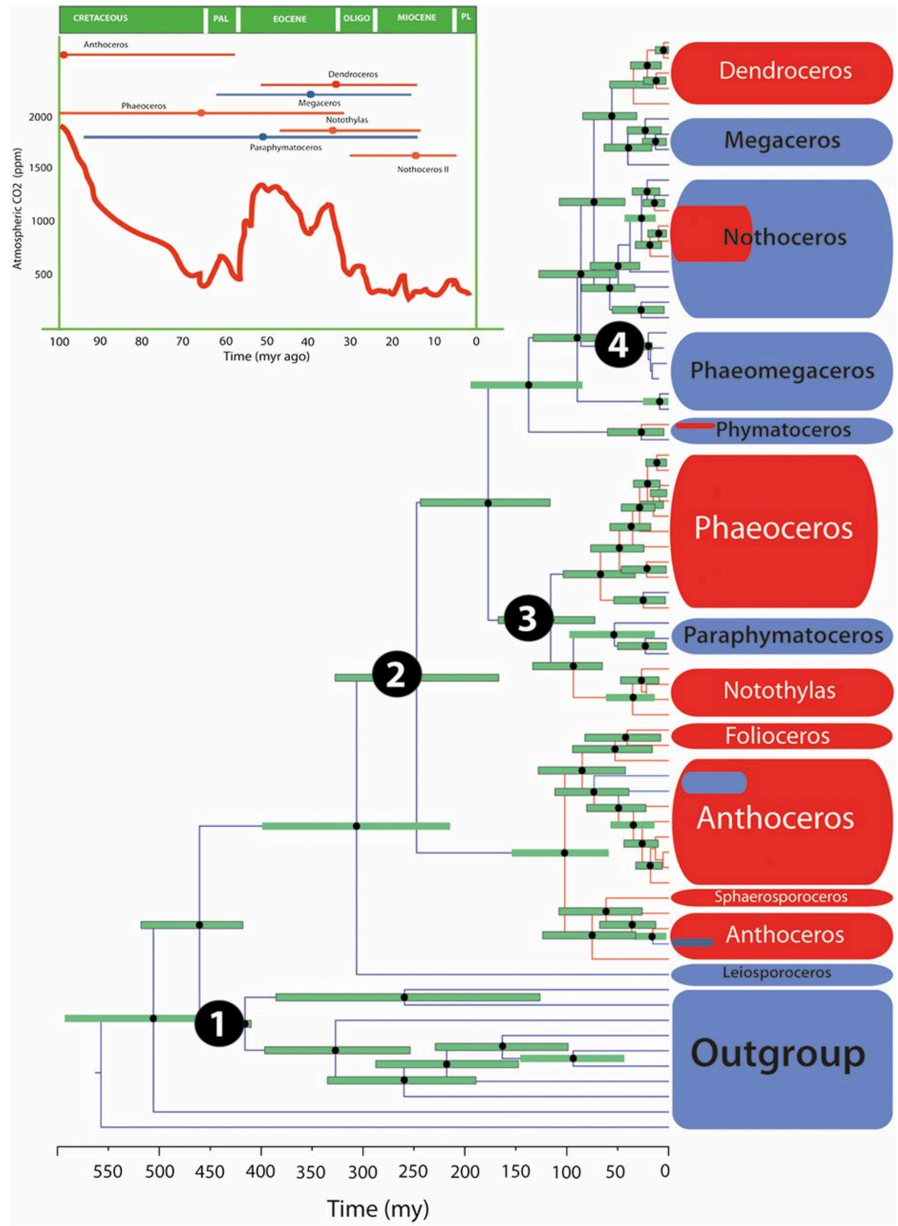
Villarreal & Renner PNAS 2012;109:18873-18878

SumEvoluitonmary

Environmental trigger for the independent evolution of pyrenoid.

Correlation between acquisition and low CO_2 ambiguous.

In fact pattern does not fit the hypothesis that pyrenoid evolution relates to times of low CO_2 concentration



Villarreal & Renner PNAS 2012;109:18873-18878

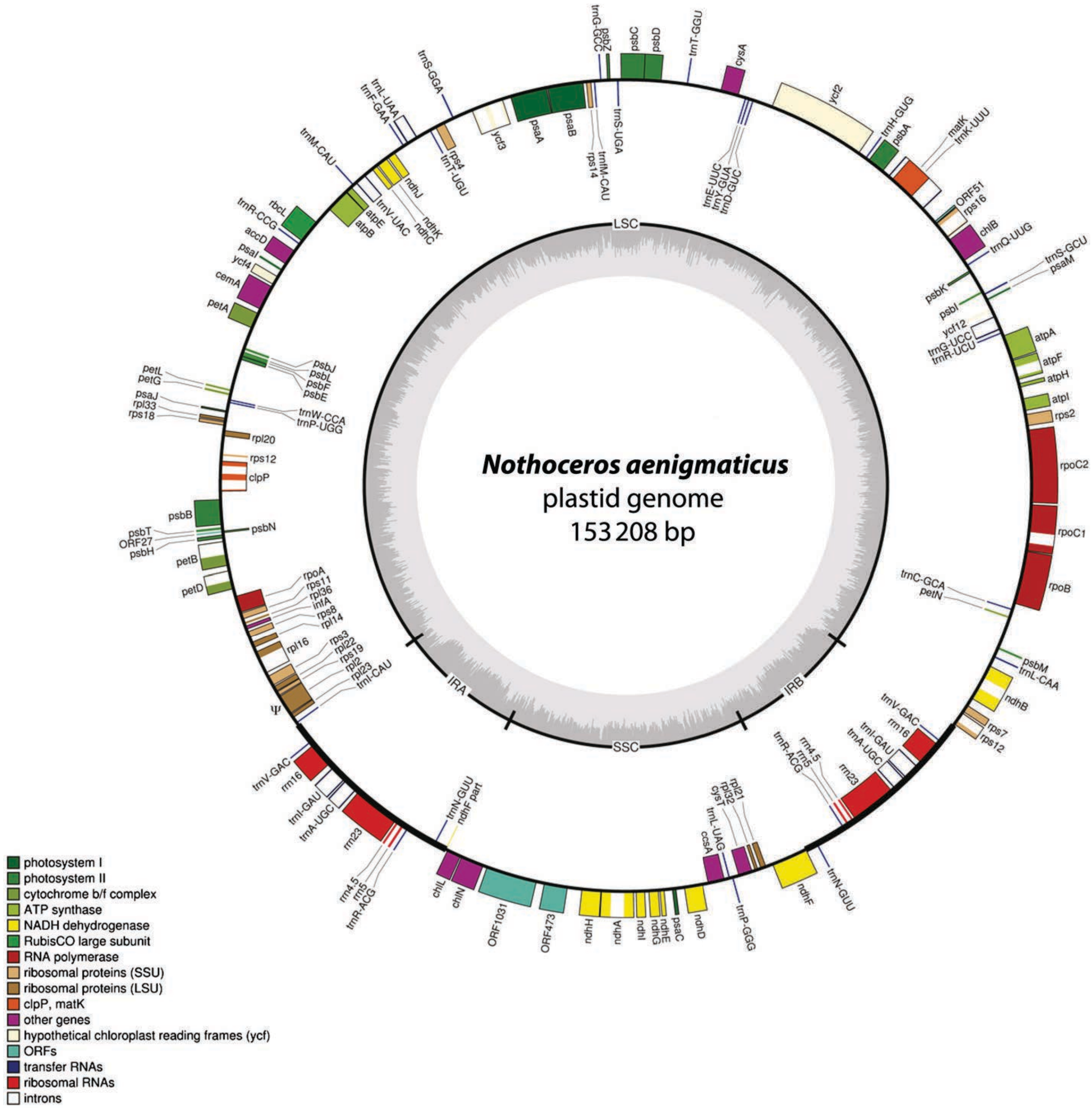
Hornwort plastid genome

124 unique genes:

- 88 protein-coding genes
- 4 ribosomal RNAs
- 32 transfer RNAs

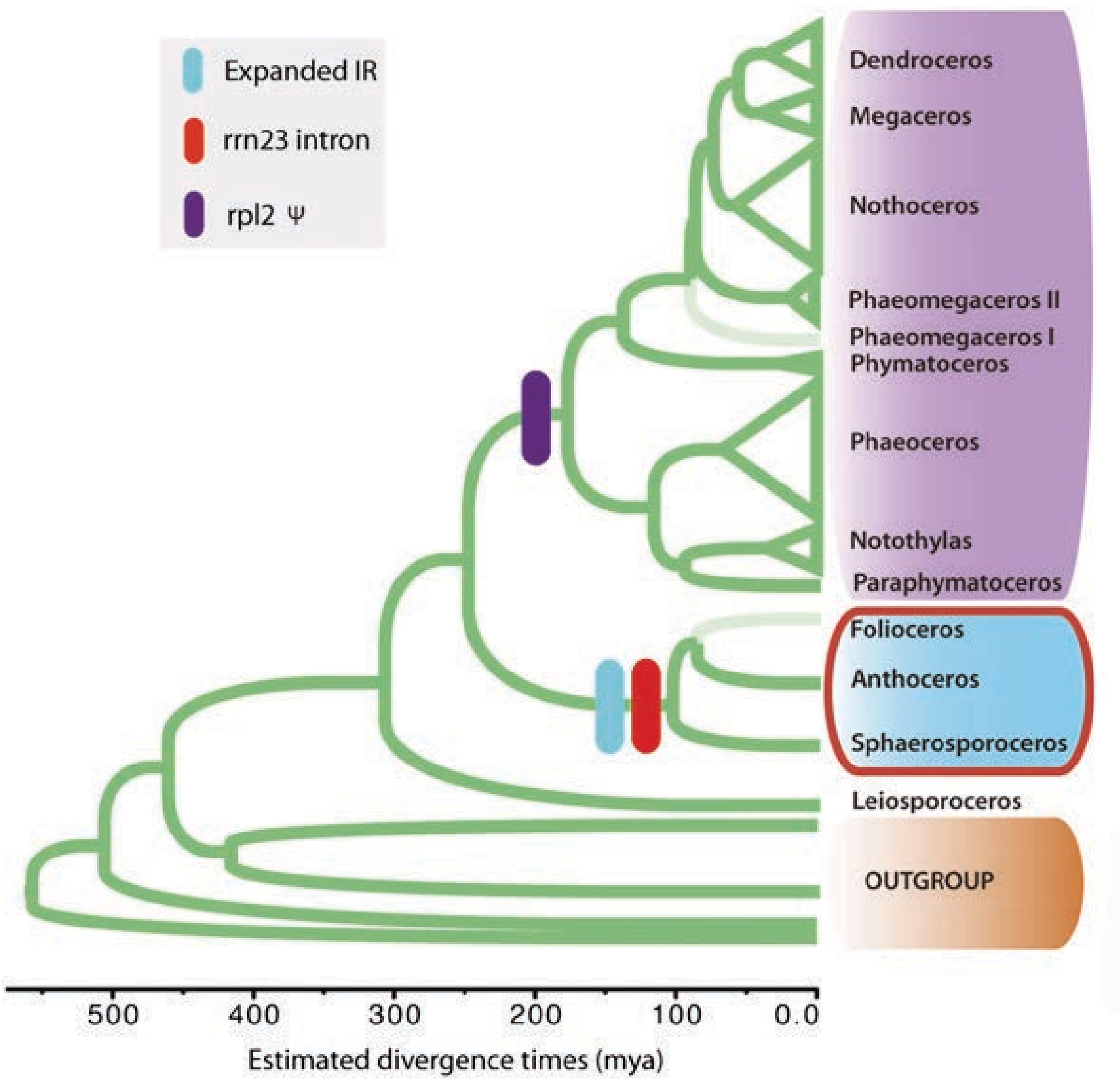
High levels of RNA editing

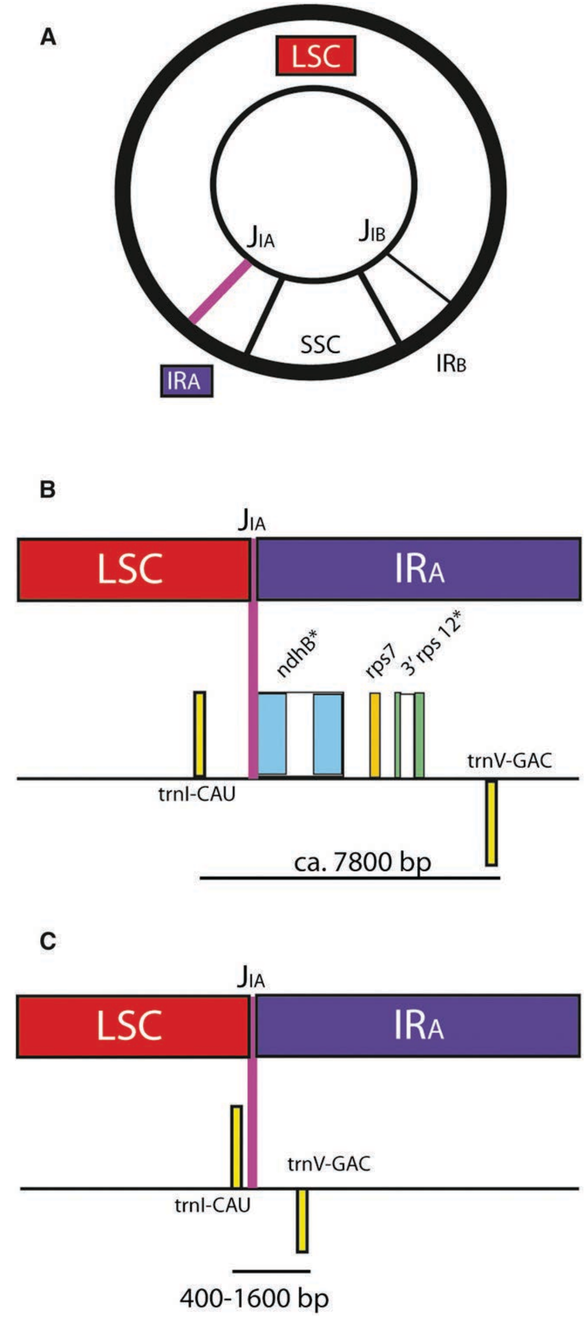
A. agrestis: 1549 sites of chloroplast RNA editing (636 C-to-U and 913 U-to-C edits)



Villarreal et al. 2013. Ame. J. Bot. 100

Hornwort plastid genome



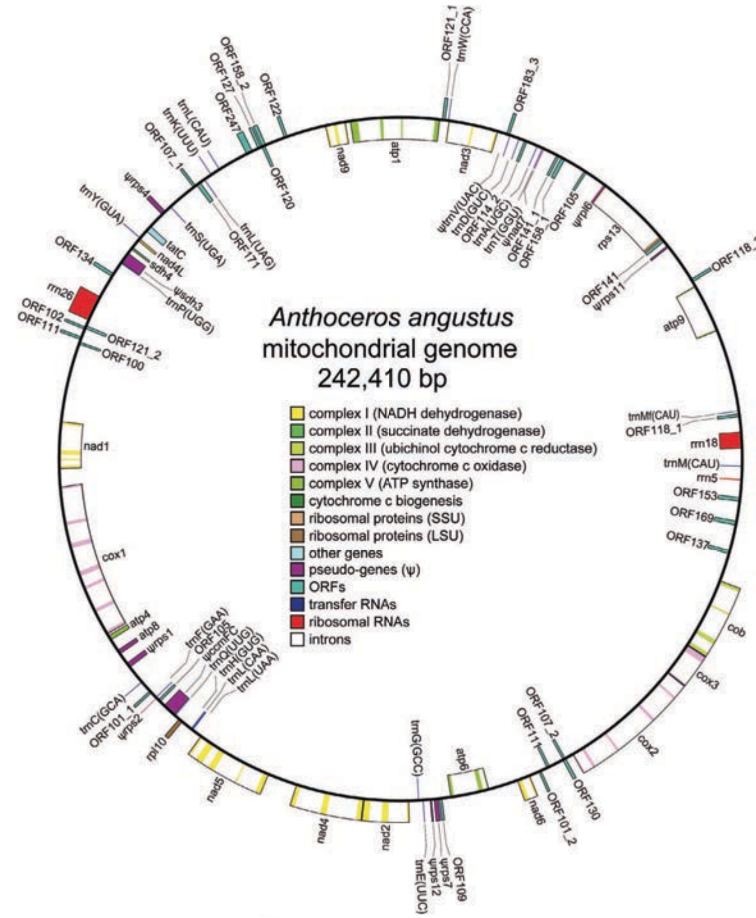


Villarreal et al. 2013. Ame. J. Bot. 100

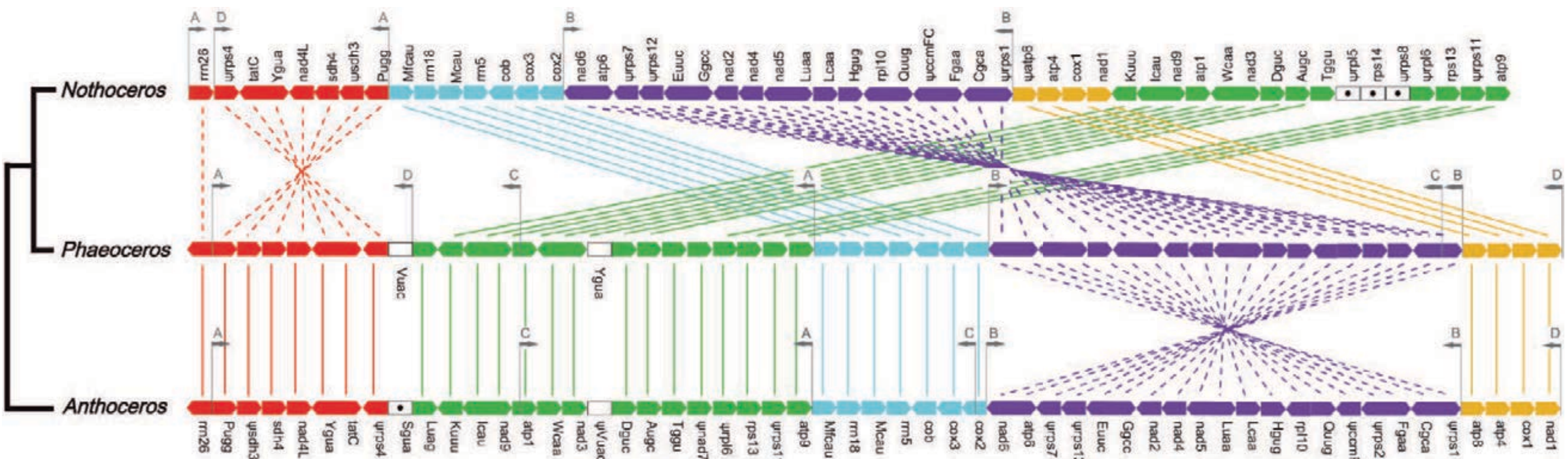
Hornwort mitochondrial genome

Mitogenome: 242,410 B

- 21 protein coding genes
- 3 rRNA genes
- 20 tRNA genes,
  - 38 introns in 16 protein-coding genes, most intron-rich plant mt genome
- 10 putatively pseudogenized PCG



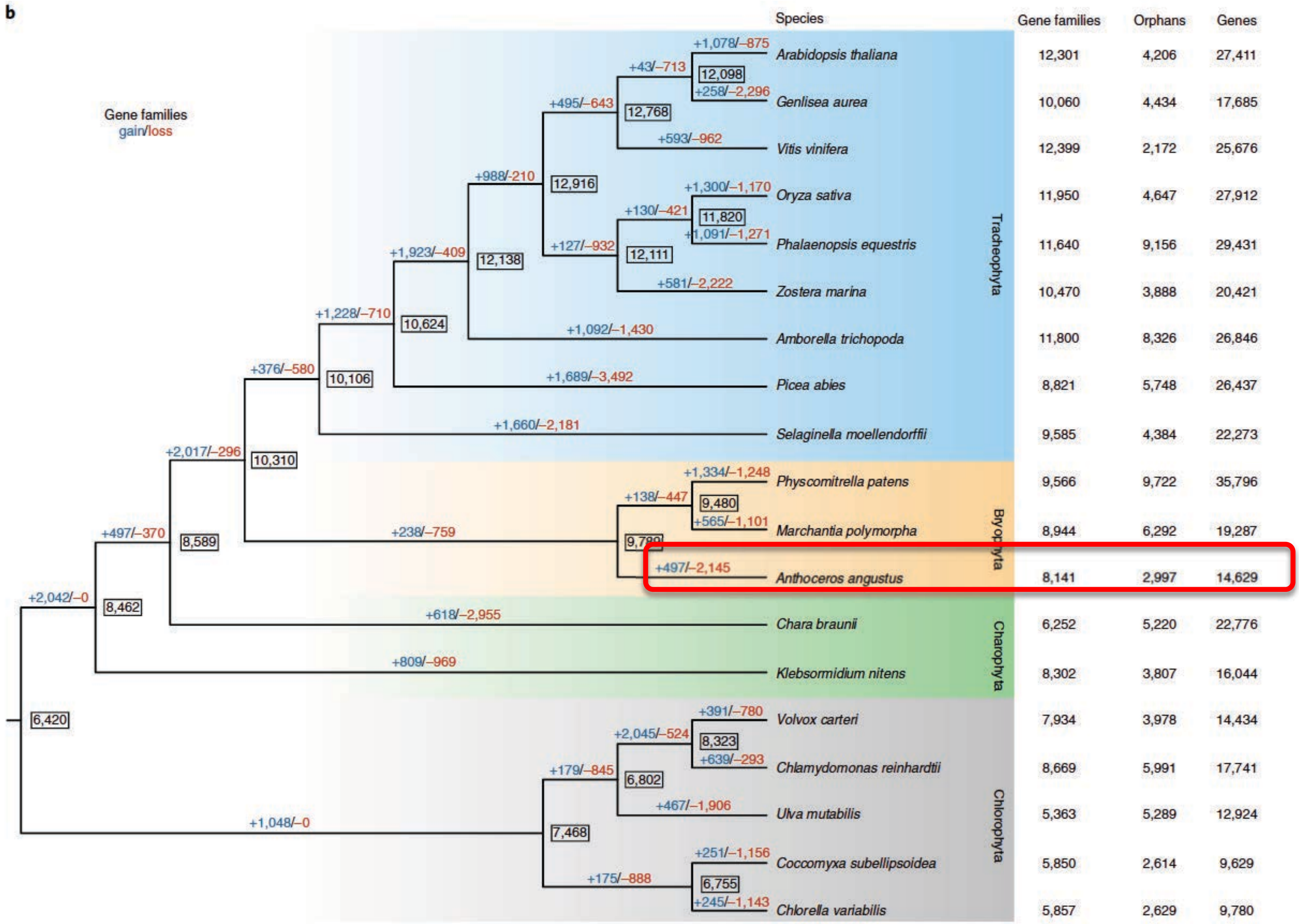
In *A. agrestis* : 496 events of C-to-U and 403 sites of U-to-C editing



Dong et al. 2018. Bryologist 121.

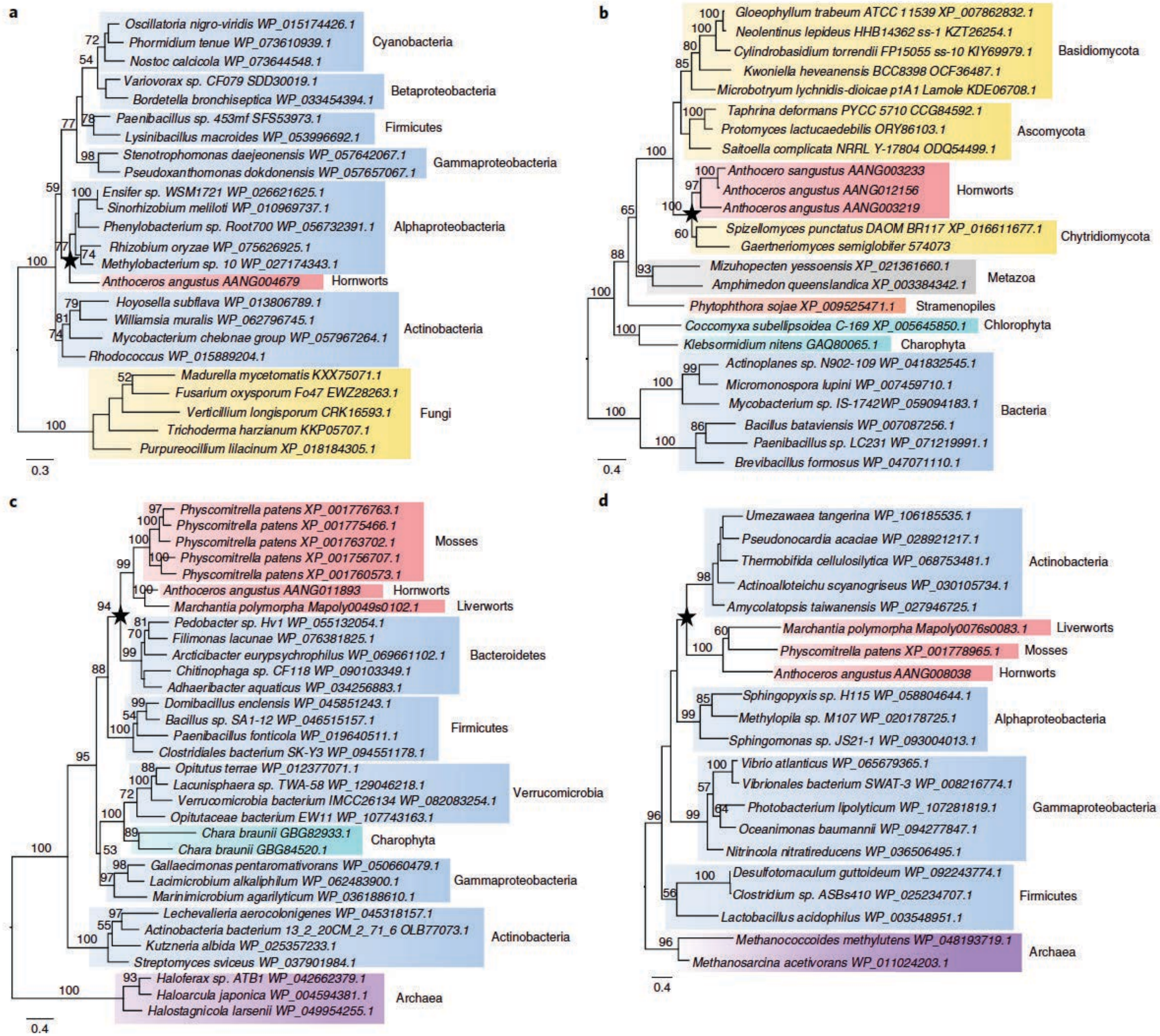
Hornwort genome

Genome small (±119 MB; 14,629 PC genes; TE%: 60) with minimal redundancy. Expansions in gene families —> RNA editing, UV protection and desiccation tolerance.



Evolutionary significance of hornworts

HGT from bacteria and fungi <— stress-response, metabolic pathways (some shared with other bryophytes)



Evolutionary significance of hornworts

"Ferns are well known for their shade-dwelling habits. Their ability to thrive under low-light conditions has been linked to the evolution of a novel chimeric photoreceptor—neochrome—that fuses red-sensing phytochrome and blue-sensing phototropin modules into a single gene, thereby optimizing phototropic responses."

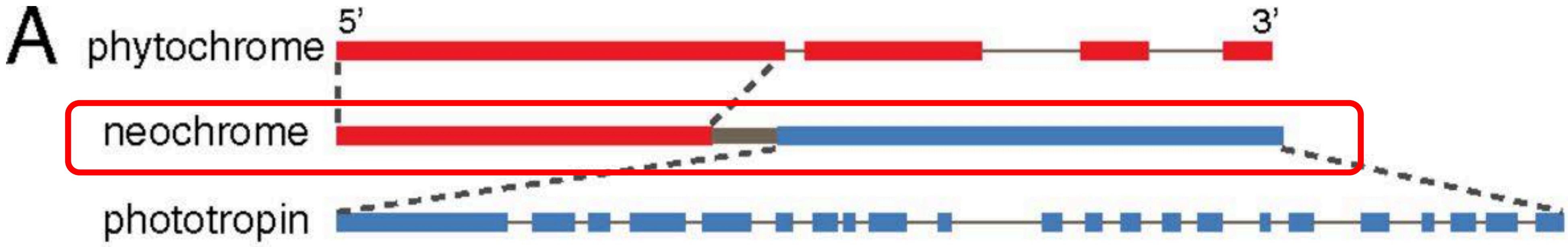
PNAS

Horizontal transfer of an adaptive chimeric photoreceptor from bryophytes to ferns

Fay-Wei Li[a,1], Juan Carlos Villarreal[b], Steven Kelly[c], Carl J. Rothfels[d], Michael Melkonian[e], Eftychios Frangedakis[c], Markus Ruhsam[f], Erin M. Sigel[a], Joshua P. Der[g,h], Jarmila Pittermann[i], Dylan O. Burge[j], Lisa Pokorny[k], Anders Larsson[l], Tao Chen[m], Stina Weststrand[l], Philip Thomas[f], Eric Carpenter[n], Yong Zhang[o], Zhijian Tian[o], Li Chen[o], Zhixiang Yan[o], Ying Zhu[o], Xiao Sun[o], Jun Wang[o], Dennis W. Stevenson[p], Barbara J. Crandall-Stotler[q], A. Jonathan Shaw[a], Michael K. Deyholos[n], Douglas E. Soltis[r,s,t], Sean W. Graham[u], Michael D. Windham[a], Jane A. Langdale[c], Gane Ka-Shu Wong[n,o,v,1], Sarah Mathews[w], and Kathleen M. Pryer[a]

Evolutionary significance of hornworts

Plants rely on various “receptors” to assess changes in their environment, particularly light!



Neochrome: chimeric molecule:
phytochrome (**red** sensing) + phototropin (**blue** sensing).

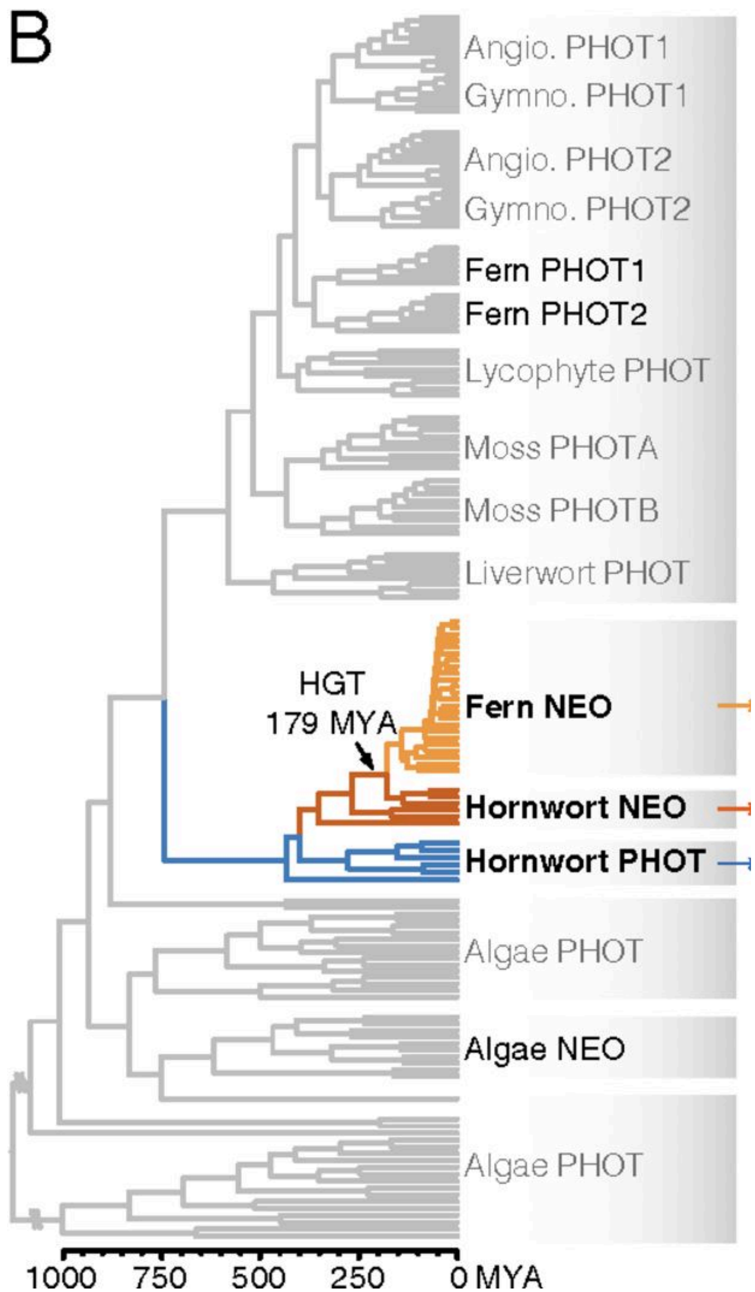
Where do they occur? So far: **Green algae and ferns!**

How can we explain such phylogenetic distribution?

And it only occurs in ferns that arose AFTER the rise of angiosperms!

Actual legend to figure:
Neochrome is a chimeric photoreceptor in which the N terminus consists of a phytochrome sensory module fused to an almost complete phototropin sequence at the C terminus.

Evolutionary significance of hornworts



Phototropin (and neochrome) phylogeny

First: neochromes discovered in hornworts.

Analyses of the DNA sequences yielded this tree.

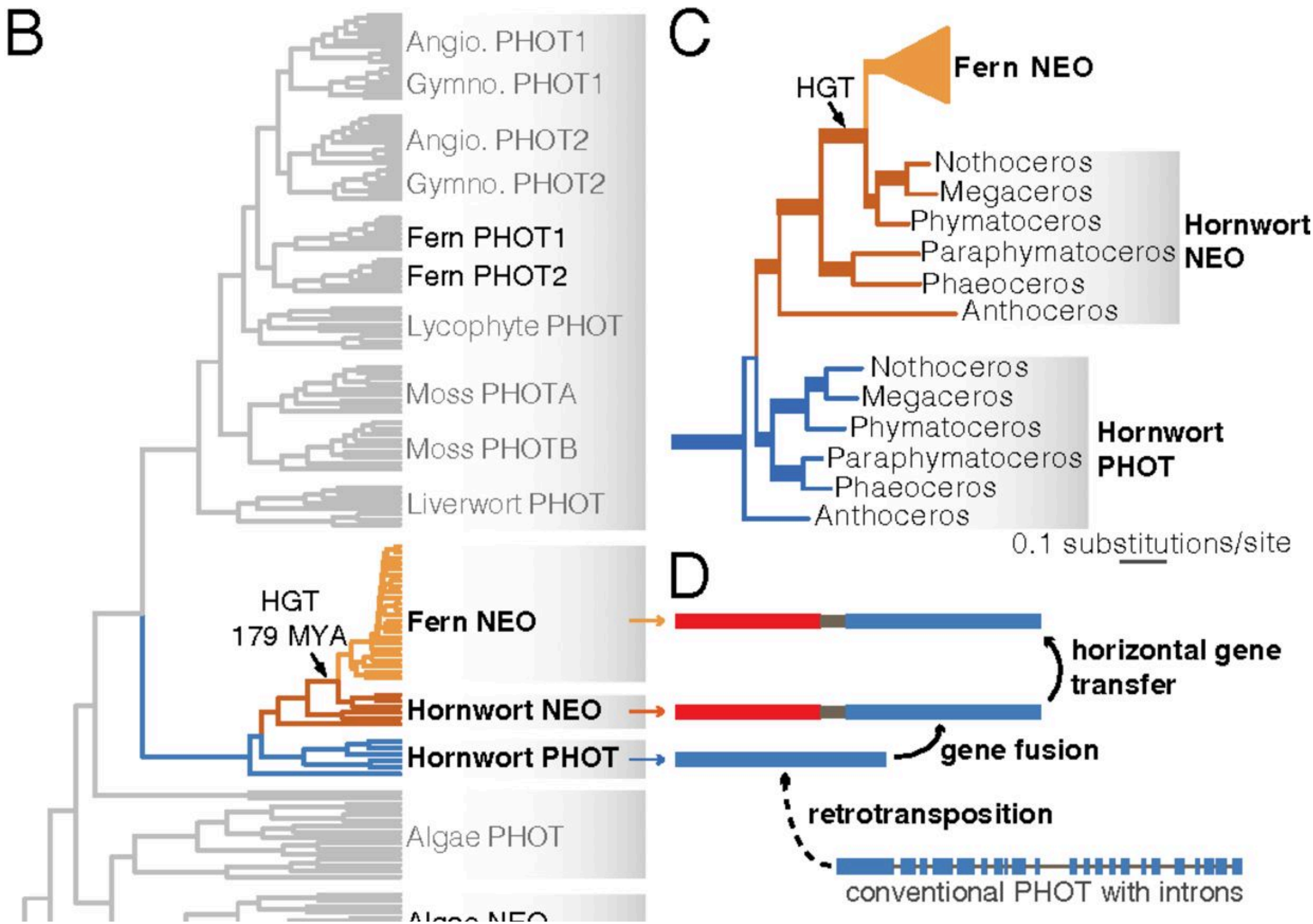
What is happening in the upper portion of the tree?

Gene tree = species tree? Yes, with one duplication in seed plants.

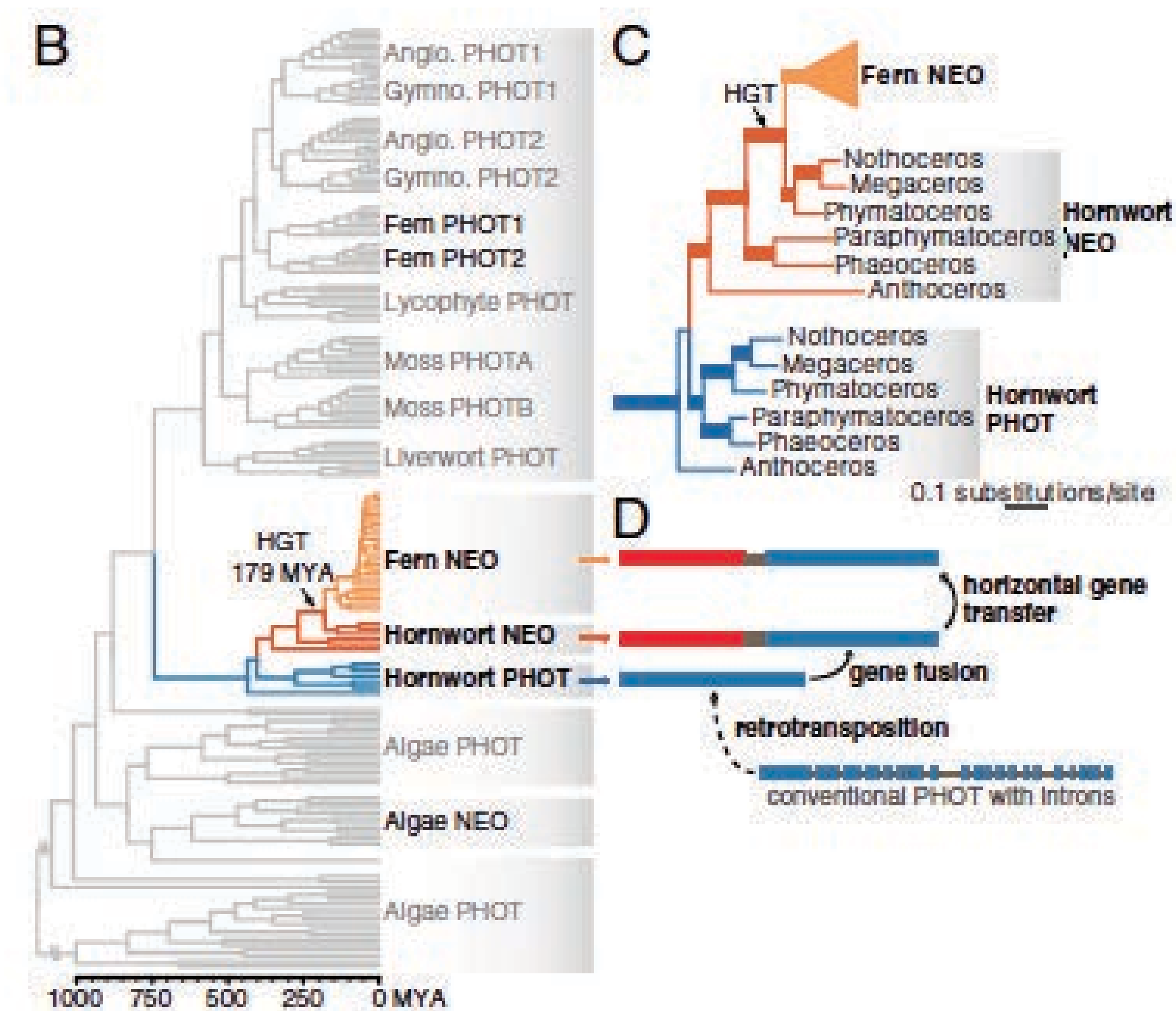
What about the median (colored) portion?

1. Position of hornwort?
2. Position of fern NEO!

Evolutionary significance of hornworts



Evolutionary significance of hornworts



1. Neochrome evolved in green algae and in hornworts (not in ferns as previously thought!)

2. Neochrome "gene" was transferred from hornwort to ferns via HGT.
   How? Not clear
   When? ± 180 mya

3. Also recurrent HGT among ferns!