



# Plant phylogenetics: The never-ending cycle of evolutionary gains and losses

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Title: The never-ending cycle of evolutionary gains and losses

One sentence summary:

The Zygnematophyceae is the sister clade to the land plants, but their biology remains mysterious. In a new study, Hess *et al.* propose a resolved phylogeny and a scenario for the evolution of multicellularity in that clade.

Text: (~1300 words)

Evolution of organisms is driven by the continuous gains and losses of functional traits. Such events occur in all kingdoms and can have a massive impact on life on Earth. Understanding trait evolution opens a door to a global comprehension of the history of life. Among the numerous traits that shaped life on Earth, the colonization of land by plants, 450 MYA, had been a crucial step in the evolution of extant terrestrial life. Terrestrialization occurred before the radiation of the embryophytes, the lineage encompassing all extant land-plants such as flowering plants, ferns and non-vascular plants. Plant diversity, however, is not limited to embryophytes but also includes thousands of algae of which the Zygnematophyceae lineage, a clade of freshwater algae, represents the sister lineage to embryophytes. The comparisons between Zygnematophyceae and embryophytes holds the potential to discover the innovations responsible for the sustainable colonization of land by plants. In that context, better describing the biology and evolutionary history of the Zygnematophyceae is essential.

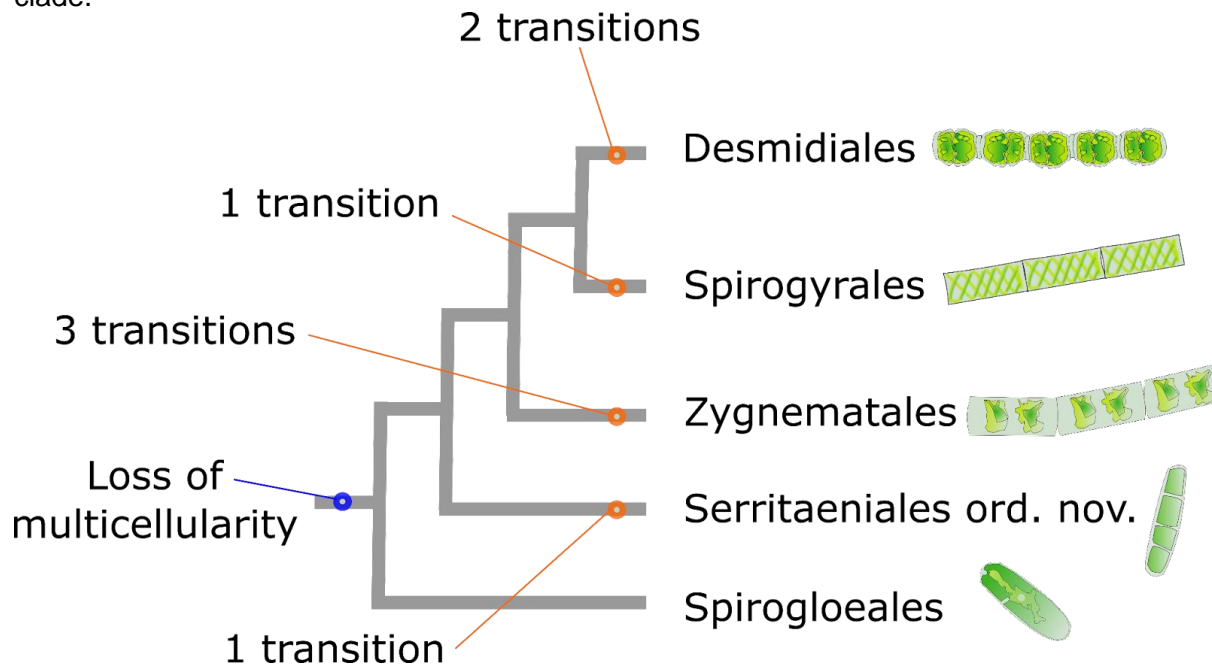
### **The complex history of the Zygnematophyceae**

In their work published in this issue of *Current Biology*, Hess *et al.* had two ambitious goals. First, proposing a solid phylogeny of the Zygnematophyceae and then defining the evolution of an iconic trait, multicellularity, in that clade.

The authors gathered a large dataset of more than 326 protein sequences from 84 species, including the re-discovered *Mougeotopsis calospora* strain MZCH580 which displays atypical features such as the lack of pyrenoids. The phylogeny built on this dataset offers a well-resolved distribution of the Zygnematophyceae in five orders (Figure 1), with the currently sequenced genomes covering three of them.

Using this resolved Zygnematophyceae phylogeny, Hess *et al.* inferred the evolution of multicellularity based on ancestral state reconstruction method. Multicellularity in Zygnematophyceae is not a binary trait but rather takes different forms. Ancestral trait reconstructions with various coding of the multicellularity state, from simple two to more complex four states, suggested an unicellular ancestor of all Zygnematophyceae followed by at least five independent gains. This unicellular ancestor would thus have evolved from the multicellular most recent common ancestor (MRCA) of the Zygnematophyceae and embryophytes through reductive evolution. However, as pointed out by the authors, ancestral state reconstruction is highly dependent on the sampling and the future addition of new species could rewrite the evolutionary history of this complex trait. Multicellularity is not the only trait lost in Zygnematophyceae. *M. calospora* has lost pyrenoids, a sub-cellular compartment involved in carbon concentration mechanisms, which is found in green algae. Additionally, the MRCA of the Zygnematophyceae had likely lost plasmodesmata, the connection between plant cells. Altogether, the work by Hesse *et al.* perfectly illustrates that trait losses play an essential role in the diversification of life <sup>1</sup>.

The loss of multiple traits in the Zygnematophyceae will have a profound impact on defining the innovations linked to the colonization of land by plants. This stresses the need for considering the diversity of the paraphyletic streptophyte algae to determine what was gained in embryophytes. This comparative work goes beyond traits into genomic comparisons. For instance, genes involved in the perception of microbe-derived signals are absent from the sequenced Zygnematophyceae genomes, but present in the *Chara braunii* genome and in embryophytes<sup>2</sup>. A direct, pairwise, comparison between Zygnematophyceae and embryophytes would have led to the conclusion that these genes evolved in the MRCA of the embryophytes. Using comparative phylogenomics on a similar dataset, one can envision identifying genes associated with multicellularity and plasmodesmata across the streptophytes that were lost in the MRCA of the Zygnematophyceae. The trait diversity observed in Zygnematophyceae, resulting from ancient and recent gains and losses emphasize the need for multiple model species in that clade.



**Figure 1. Phylogeny of the Zygnematophyceae proposed by Hess *et al.*** The loss of multicellularity is indicated as well as the maximal number of transitions to a multicellular state across the phylogeny.

### Reversal or convergent evolution: does multicellularity in Zygnematophyceae reject Dollo's law?

Besides structuring the comparative work to study the colonization of land by plants, the hypothesis proposed by Hess *et al.* that both multicellularity and plasmodesmata were absent from the MRCA of the Zygnematophyceae provides an interesting framework to study a case of successive gain - loss - gain. In the 19th century, Louis Dollo proposed that such a reversal was impossible<sup>3</sup>. However, there is growing evidence in animal systems, based on ancestral trait reconstruction, that such a reversal has actually occurred in multiple times (see<sup>4-6</sup>). Determining the underlying genetic pathway in diverse lineages is the only way to firmly demonstrate that a trait is indeed *the same* and to validate the re-gain of a lost trait. Such a demonstration has been conducted for a rather simple trait, the flower pigmentation in the genus *Petunia*, which was regained via a 2-bp deletion in a transcription factor, mitigating the mutation that led to color loss<sup>7</sup>. Phenotypic diversity for flower color is distributed in the genus *Petunia*, spanning ~3 MY of

evolution. The scenario proposed by Hess *et al.* of multiple gains of multicellularity in the Zygnematophyceae could represent a much deeper case of rejection of Dollo's law of impossible reversal. In the future, comparative phylogenomics of unicellular and multicellular Zygnematophyceae and other streptophytes holds the potential to identify genes linked with multicellularity. Such a genomic approach would strongly benefit from the sequencing of a Coleochaete genome, the last class of streptophyte algae without sequenced members. In the longer term, forward genetics conducted in diverse Zygnematophyceae will provide the final answer.

Beyond testing an old concept of evolutionary biology, the comparative framework provided by Hess *et al.* demonstrates how reduction can be favored during evolution. The fact that unicellularity has been maintained in some of the Zygnematophyceae lineages, while multicellularity seems very stable once re-gained in other lineages indicates that selection must have acted on both traits in past and extant ecosystems. Comparing these lineages *in naturae* may reveal the ecological drivers that have shaped the gain, loss and re-gain of multicellularity in plants. Zygnematophyceae diversification occurred at a time where the first embryophytes were expanding on land. Many Zygnematophyceae are epiphytic, including on the bark, shoots and leaves of embryophytes. One provocative hypothesis could be that reduction of Zygnematophyceae allowed them to co-evolved with embryophytes.

The complex biology of the Zygnematophyceae is slowly being unraveled. The sequencing of additional genomes, the development of efficient genetic transformation methods and the emerging scientific community studying them will reveal the mystery this understudied clade still hides. The robust phylogeny provided by Hess *et al.* is an important stepping stone in that direction.

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