CellPress

Opinion

Why Plants Were Terrestrial from the Beginning

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The current hypothesis is that land plants originated from a charophycean green alga and that a prominent feature for adaptation to land was their development of alternating life cycles. Our work on cell wall evolution and morphological and physiological observations in the charophycean green algae challenged us to reassess how land plants became terrestrial. Our hypothesis is simple in that the charophycean green algae ancestors were already living on land and had been doing so for some time before the emergence of land plants. The evolution of alternate life cycles merely made the ancestral land plants evolutionary successful and had nothing to do with terrestrialization *per se*.

Trends

Recent phylogenetic analyses have placed the ancestor of land plants close to a common ancestor between Zygnematales and Coleochaetales. Both orders contain species living in, or displaying the capability to live in, terrestrial habitats.

Terrestrialization is not a unique trait for charophytes evolutionarily close to plants. Less advanced classes, such as Klebsormidiophyceae and Chlorokybophyceae, also contain terrestrial species.

Novel analyses of both advanced and basal charophyte biochemistry, transcriptomes, and genomes have revealed a range of terrestrial adaptations that are orthologous to what is observed in land plants.

History behind the Current Hypothesis of Land Plant Terrestrialization

It is proven beyond reasonable doubt that embryophytes originated from **charophytes** (see Glossary), but as to which order of the charophytes is the closest ancestor to embryophytes is the center of some debate. Recent analyses have put either the Coleochaetophyceae or the Zygnematophyceae as closest extant cousins to the embryophytes, followed by Charophyceae, Klebsormidiophyceae, and then Chlorokybophyceae and Mesostigmatophyceae as the ancestral node (Box 1) [1–3].

How the charophytes evolved into embryophytes capable of surviving the terrestrial habitat, on the premise that embryophytes evolved from a freshwater charophyte, has not been discussed. One of the problems in acquiring additional data for this crucial event in the history of the Earth is that the fossil record is generally poor: only single-celled spores remain from that period [4]. There is an abundance of fossils in the records starting from around 400 mya [4], but, at that time, the embryophytes had already conquered Earth.

Box 1. Phylogenetic Relations within Streptophyta

Phylogenetic relations within the Viridiplantae and, more specifically, the streptophytes, have been discussed and updated over the past several decades. The first revolution came with the groundbreaking work of Stewart and Mattox, which identified the phragmoplast as a key trait of more evolved charophytes and embryophytes, uniting them in Streptophyta and separating the charophytes from the chlorophytes [23]. Later, Mesostigmatophyceae and Chlorokybophyceae were transferred from the prasinophytes and the chlorophytes to the charophytes. They are considered the orders closest to the split between chlorophytes and charophytes.

With the streptophytes established as a monophyletic group, several publications appointed different orders of the charophytes as the closest extant ancestor to embryophytes [24–26]. Currently, the consensus is that the either the Zygnematophyceae or Coleochaetophyceae are the closest ancestor [1]. The problem with assigning the ancestor to embryophytes arises from large differences in morphology, physiology, sexual reproduction, and lack of genetic sequence information. Common ancestors, closer to the branch points, are also extinct, creating missing links with crucial information. Additionally, the fossil record is fragmented or completely absent from the interesting time period before the emergence of embryophytes.

Figure I details the phylogeny as presented in [1]. Our finding of rosette-forming CESA in *Chlorokybus* indicates a later location for it, rather than clustering in a clade with Mesostigmatophyceae [11].

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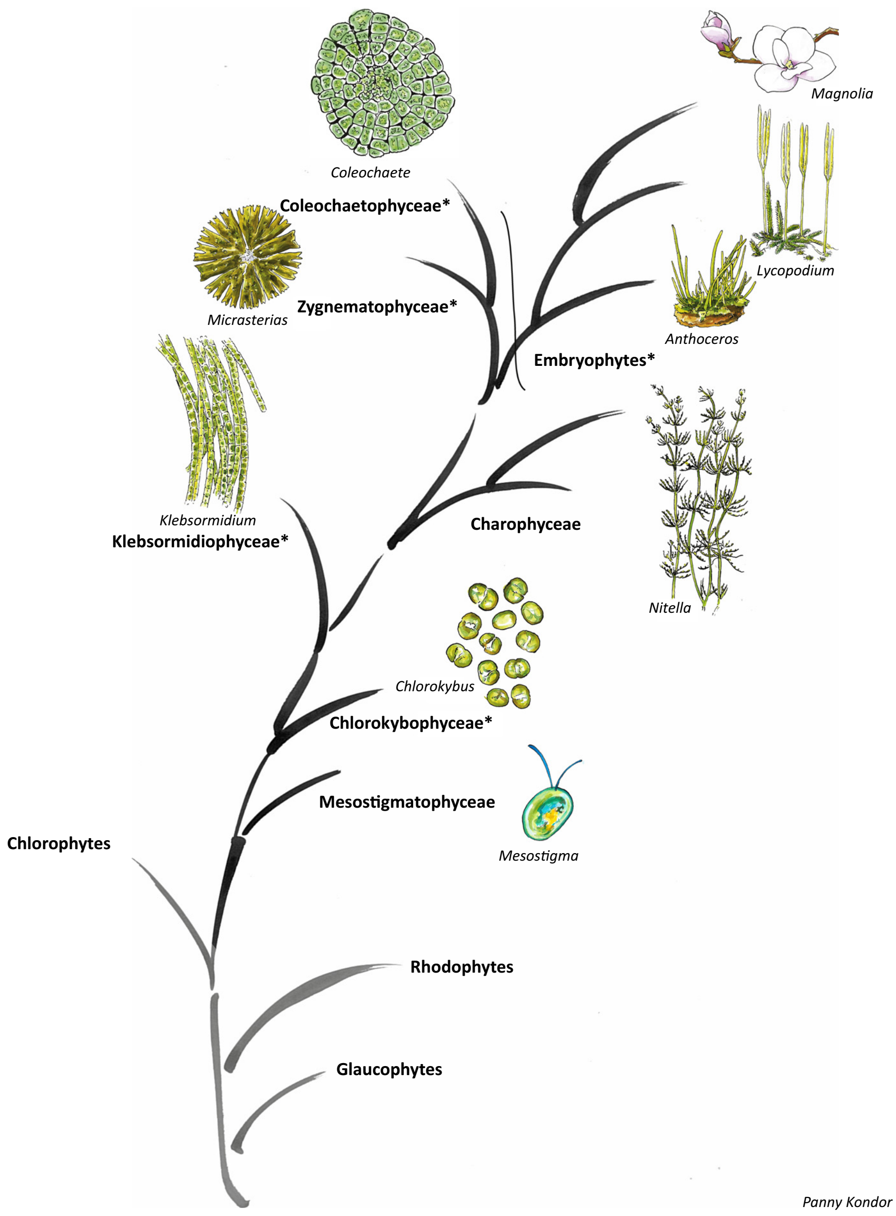

Figure I. Evolution of the Green Plant Lineage. Classes with terrestrial or facultative terrestrial species are indicated with an asterisk [21]. Modified from [1].

Glossary

Alternating life cycle: life cycle involving two different stages, usually a haploid and a diploid stage. Alternating life cycles can either be homologous or antithetic, with homologous life cycles showing similar growth characteristics and antithetic life cycles showing different growth characteristics in the alternating life stages. 'Haplontic' indicates that the organism is single celled in the diploid state, as seen in Charophytes, while 'haplodiplontic' means that the diploid state is multicellular, as in vascular plants, for example.

Charophytes: a paraphyletic group of green algae that, together with the embryophytes, form the clade of Streptophyta. The ancestor of all land plants is found among the charophytes.

Conjugation: fusion of the contents of two cells that do not differ from ordinary vegetative cells until the beginning of the mating process.

Lignin: comprises aromatic alcohols known as monolignols, which in plant cell walls are polymerized by enzymatically driven radical-radical coupling into a complex biopolymer.

Mixed-linkage glucan: a polymer comprising alternating β- (1-3) and β-D(1-4)-linked glucosyl residues in a somewhat regular pattern.

Rhamnogalacturonan xylosyltransferase (*RGXT*): encodes a protein with UDP-xylose-dependent xylosyltransferase activity, which transfers xylose onto L-fucose in rhamnogalacturonan-II.

The hypothesis by Bower, that the evolution of antithetic **alternating life cycles** was instrumental in adapting to the terrestrial habitat, has as its key observation the fact that the sporophyte of, for example, a fern, whose gametophyte is essentially amphibious, provided the organism with a platform for evolving water transport systems and other adaptations to life in air [5]. This spurred the radiation and diversification of land plant orders and families to inhabit almost every terrestrial habitat on Earth. This is widely accepted [6] and not questioned by us. It is not altogether certain that Bower intended his hypothesis to also account for the primordial terrestrialization event, but if it was meant to, it is open to critique and was challenged in 1980 by Stebbins and Hill [7]. They suggested that unicellular charophytes invaded land and that