WHERE WOULD BOTANY BE WITHOUT GREEN ALGAE?

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A review of *Origin of Land Plants* by Linda E. Graham (1993, John Wiley: New York, 287 pp. ISBN 0-471-61527-7), with additional notes.

In the shallow waters close to the shoreline of Lake Sarah in Cass Basin there is a microscopic green alga, *Coleochaete*, barely visible as minute, irregularly shaped discs stuck to the surfaces of stones and aquatic vegetation. However, the importance of this alga is far greater than its apparently minor role in the lake ecosystem would suggest. Evidence has been gathered, particularly during the last two decades, that this is likely to be the closest living descendant of the green alga from which the land plants arose, possibly about 450 to 470 million years ago.

It is easy to forget that the present 300 000 or so species of "land plants", spanning the range from the lowliest liverwort to the most complex of flowering plants, had their origins in the green algae of the division Chlorophyta. This fascinating and detailed volume by Linda Graham of the University of Wisconsin allows us to forget no longer. Not only does it make compelling reading because of our seemingly innate urges to understand origins, whether of ourselves or other organisms in the evolutionary parade, but also it rationalises the quest in topical terms. She emphasises the manner in which such apparently esoteric knowledge could help us increase our ability to manipulate plants to human advantage. The close algal relatives of higher plants can be used as model systems for research which, in Graham's words could "solve some of the most fundamental and perplexing mysteries of plant biology".

The scope of the book is wide-ranging and includes discussion of the many scientific fields which have fed the debate. It takes us from paleobotany and the examination of paleoenvironments, through information gathered by light and electron microscopy, biochemistry, physiology and the application of molecular approaches to studying genetic material.

The evolution of the debate itself is also outlined. Its origins were in the nineteenth century, when two conflicting hypotheses were firmly adhered to by their supporters. The resolution of that conflict came only in the modern era, starting in the early 1970s with the use of transmission electron microscopy.

So what is the present state of play? The Chlorophyta is a large and diverse division of green algae. Most of us will be familiar with examples such as the seaweed "sea-lettuce" (*Ulva*), the green crusts of "*Pleurococcus*" on tree bark, and the slimey skeins of the filamentous freshwater pondweed *Spirogyra*. There is now overwhelming evidence that the members of this great diversity are not so closely related as was once thought. The use of the transmission electron microscope to examine very fine detail of cells suggested that there are at least three major evolutionary lineages

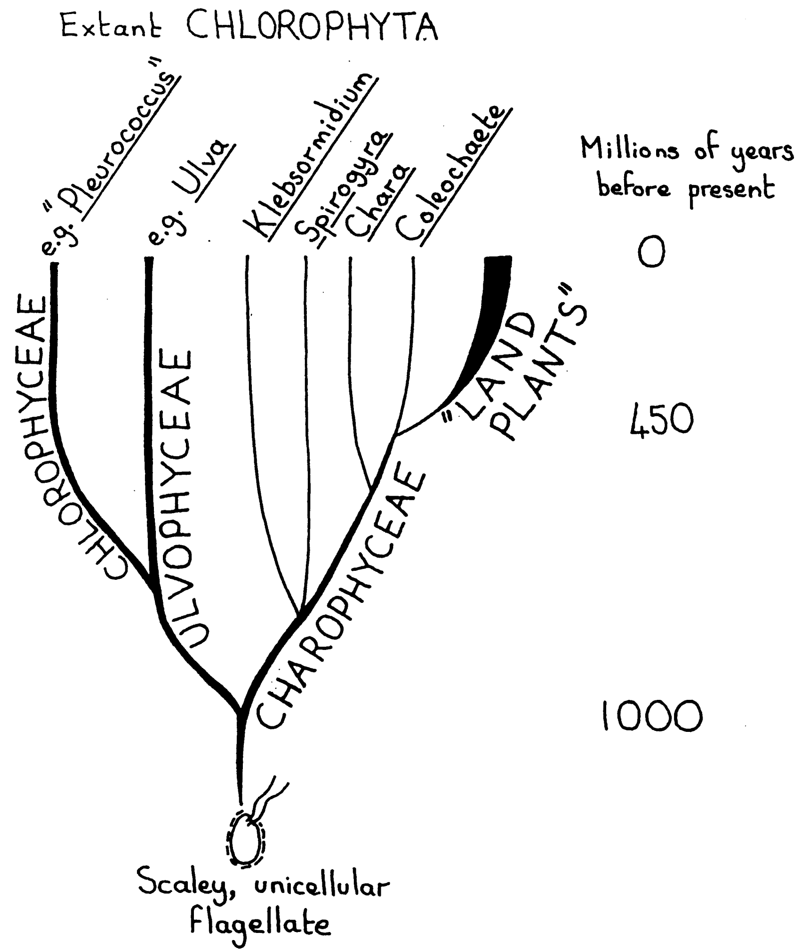


Fig 1. A diagram summarising modern ideas regarding the evolution of the "land plants" and the "green algae" (Chlorophyta). The ancestor of all of these was possibly a microscopic unicellular alga which swam in the ancient oceans.

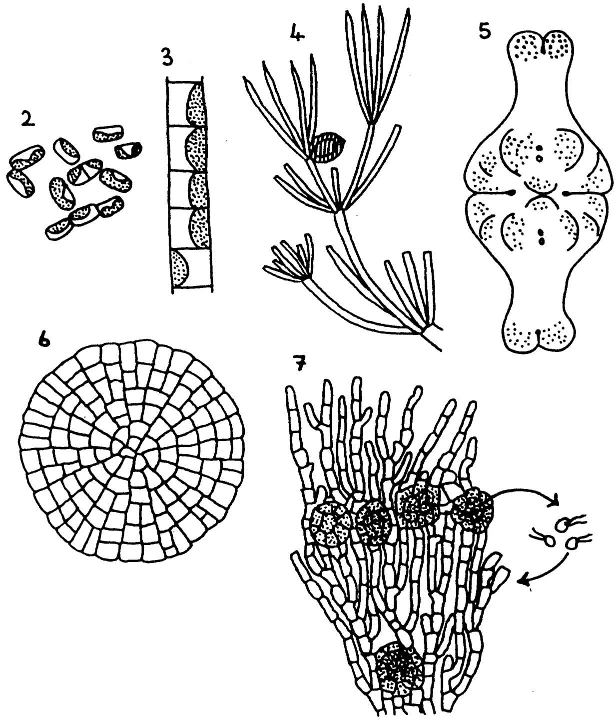
within the division (Fig. 1). This has subsequently been confirmed by biochemical and molecular genetical comparisons of a range of species. In fact, *Ulva*, *"Pleurococcus"* and *Spirogyra* are each members of separate evolutionary lines.

It is the lineage containing *Spirogyra* which is now thought to have produced the "land plants". These algae are placed in the class Charophyceae (Fig. 1). If the internal details of their cells are examined during cell division the pattern is more similar to "land plants" than to other chlorophytes. Also, their microscopic, motile, reproductive cells resemble the motile male sperm cells of the bryophytes, ferns and fern-allies. The hypothesis has been strengthened further by the discovery of similar enzymes in charophycean algae and "land plants" and similar sequences of the building blocks of their genes. Strong evidence from molecular genetics is the recent discovery of an unusual insertion, an "intron", in the DNA that is found in the chloroplasts of both the charophycean algae and "land plants" but which is absent from the other green algae.

Members of the Charophyceae range in structure from the very simple to the most complex of all chlorophytes. Amongst the simplest are the microscopic, readily fragmented, chains of cells found in the genera *Stichococcus* (Fig. 2) and *Klebsormidium* (Fig. 3). Undoubtedly you have recently trampled over millions of these as they are common in garden soils! Another group is abundant in the upland regions of the South Island. This comprises the beautifully symmetrical and ornate "desmids" (Fig. 5), denizens of lakes and bogs and recently brought to our attention by the two Flora of New Zealand volumes by Hannah Croasdale and Elizabeth Flint. *Spirogyra*, which grows densely in the quieter braids of our Canterbury rivers is closely related to the "desmids". However, it is the most complex of this lineage of algae thought to be closest to the "land plants".

Chara and related genera (Fig. 4) are easily mistaken for aquatic angiosperms. They will have been seen by anyone who has peered into our local ditches, rivers and lakes at the plants attached to the sediments. Superficially they are almost identical to the angiosperm waterweed *Ceratophyllum*. However, in structure and reproduction they are completely different. These algae mostly consist of giant cells which can be up to several centimetres in length, each containing thousands of chloroplasts and nuclei. Reproduction is typically algal, although rather advanced compared with most. A large egg cell contained in a specialised female structure (Fig. 4) is fertilised by a small motile sperm. The single cell zygospore which is the product of fertilisation germinates directly into a new adult alga after it has fallen from the parent. Two notable similarities to land plants are the possession of microscopic connections joining the cytoplasm of adjacent cells and the restriction of cell division to certain regions, especially the apices of the filaments. However, the link between these algae and the land plants is only via an ancient ancestor shared by both and from which both now differ considerably. *Chara* and its relatives are very well-adapted for their aquatic existence. However, the much smaller *Coleochaete* (Figs 6 and 7) appears to have had an ancestor with characteristics which provided pre-adaptation for life on land.

It is thought that the immediate algal ancestors of plants were similar to modern filamentous species of *Coleochaete* and were highly adapted to life in shallow water. In particular, *Coleochaete* prefers the higher availability of carbon dioxide, needed for



Figs. 2-7. 2. *Stichococcus* (1000x). 3. *Klebsormidium* (400x). 4. *Nitella* (10x), a relative of *Chara*. 5. *Euastrum* (800x), a "desmid". 6 and 7. *Coleochaete*. 6. A species in which the radiating filaments are closely packed together (150x). 7. Detail of a portion of a species in which the filaments are more loosely arranged (500x). The shaded, spherical structures are the zygotes with surrounding filaments of the parental plant. The zygotes are shown to produce motile spores which on settling develop into filaments.

photosynthesis, which is present in the relatively turbulent water around the edges of lakes. This gas is even more readily available in the atmosphere where it diffuses at a rate 10 000 times faster than in water. Perhaps the transition to land by the ancestral form was aided by this enhanced supply of carbon dioxide. A reproductive feature shared by *Coleochaete* and all "land plants" is the retention of the fertilised egg cell, the zygote, by the parental organism (Fig. 7). In "land plants" this leads to the production of a multicellular life-stage formed by multiple divisions of the zygote, for instance the stalk and capsule of mosses and the embryo in the seed of an angiosperm. In *Coleochaete,* however, although the zygote stays attached to its parent over winter it then simply germinates to produce up to 32 motile spores, each driven by two whip-like flagella (Fig. 7). The spores swim away, settle, and grow into new adult filaments. However, an intriguing similarity is that, as in all "land plants", the parent provides nourishment for the development of the zygote. In *Coleochaete* the zygote enlarges greatly as organic nutrients are passed to it from the adjacent parental cells which are specialised for this purpose. The suggestion is, as first propounded by Bower in 1908, that in the lineage leading to the "land plants", the zygote, instead of simply releasing spores, first underwent cell divisions to form a multicellular life stage. This was similar to that found in modern thalloid liverworts, remaining attached to the parent which provided its nourishment. Eventually it matured to produce the spores which, following dispersal, grew into the stage which commenced the life-cycle once again with the production of eggs and sperm.

Although the pieces of the jigsaw seem to fit conveniently together all is by no means explained and Graham points to some major gaps in our understanding of "land plant" origins. Why did charophycean algae or their early descendants invade the land? Was the availability of unoccupied habitats the main stimulus? Was it due to the development of a protective ozone screen shielding the land surface from excessive ultra-violet radiation? Did the green alga become associated with a fungal partner which allowed both to survive the desiccation and nutrient stresses of life on land? Or was there a decrease in the atmospheric carbon dioxide which made absorbing enough of this gas whilst underwater even more difficult, and made the land a more attractive proposition? The lack of a fossil record of the transition is also frustrating. The very earliest fragmentary fossils, thought by some to be of plants at the same level of organisation as modern liverworts, are from about 455 million years ago. Fossils that can be unambiguously attributed to *Coleochaete*-like algae are unknown.

This potted summary does not do justice to Graham's detailed and enthusiastic exposition. Although parts of the book require previous background knowledge to ease understanding, others are fully comprehensible to the interested layperson. It is richly and expertly illustrated and the important messages are accompanied by cartoons provided by the author's husband. Not many scientific texts go to those lengths although I wish they did. If I have whetted your appetite the book is in the library at the University of Canterbury, or failing that you are welcome to borrow my copy. And please at least spare a kind thought for the green algae when you are next enraptured by a rare alpine plant clinging to the loftiest of ridge tops.