Linda E. Graham (1985). *The Origin of the Life Cycle of Land Plants: A simple modification in the life cycle of an extinct green alga is the likely origin of the first land plants. American Scientist, 73(2), 178–186.* doi:10.2307/27853160

land plants originated in ancestors among the green algae.

The life cycle of all land plants, both the bryophytes (such as mosses) and the more numerous and dominant vascular plants, involves the alternation of two distinct multicellular generations, the gametophyte and the sporophyte (see Fig. 1). The gametophyte, or gamete-producing generation, is haploid, meaning that it has a single set of chromosomes in its cells. The sporophyte is diploid, possessing twice the haploid number of chromosomes, and it produces spores by meiosis, a process that divides the diploid number of chromosomes in two; the haploid spores germinate asexually into gametophytes, which produce male gametes (spermatozoids) or female gametes (eggs) that combine sexually and then grow into new sporophytes, completing the cycle.

In vascular plants the sporophyte is the larger, more dominant generation; an oak tree, for instance, is primarily sporophyte, with its gametophytic generations located in the pollen grains and within the microscopic ovaries of the oak flowers. The new sporophyte, or embryo, is located in the acorn of oaks and, more generally, inside the seed of seed plants. In contrast, the sporophyte of bryophytes is often inconspicuous, while the green plant that one observes is the gametophyte. Because the chromosome number of cells in sporophytes is generally diploid, or twice that of haploid gametophytic cells, sporophytes are considered to have an increased potential for genetic variability and evolutionary flexibility as compared to the gametophytic part of the plant life cycle. This may explain the size dominance of the sporophyte over the gametophyte in most land plants.

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This close association between the two alternating generations in embryophytes has great evolutionary significance, as was recognized by Bold (*1*), who suggested that the retention and nurturing of the zygote within the tissue of the gametophyte was probably the stimulus that led to the profound modifications of the sporophyte generation in so many land plants. Recent studies have shown that the young embryo and parental gametophyte actually are involved in a reciprocal developmental relationship that in some ways parallels the relationship between mother and embryo in placental mammals. The plant embryo may induce the development of special placental transfer cells or cause other growth changes in the pregnant gametophyte (*2*). The gametophyte, in turn, may secrete ions, sugars, and other photosynthates such as amino acids that are absorbed and metabolized by the embryo as it begins to grow (*2–5*).

Thus, one of the major issues on which resolution of the mystery of land-plant evolution depends is how this close developmental and nutritional relationship between generations originated. Because green algae and land plants share many important features, most authorities agree that the ancestors of land plants most likely would be classified today among the green algae. Evolutionary theory predicts that phylogenetic pathways are constrained by prior genetic history and that natural selection generally fashions new features from preexistent ones. There is evidence that many biological, physiological, reproductive, and developmental features of higher plant cells were built on genetic foundations inherited from green-algal ancestors.

The problem, however, is that among modern green algae having alternation of generations, eggs and zygotes are not generally retained on parental plants. Rather, green-algal eggs or zygotes are usually released into the water, so that fertilization and zygote development are physically independent of the parent plant. The haploid and diploid components of green-algal life cycles can have no nutritional or developmental interrelationships. Green algae thus lack embryos, a funda-

mental difference from embryophytes that also provides a major distinction between the two kingdoms Plantae, which includes the embryophytes, and Protista (or Protoctista), which includes green algae (*6*). Therefore, the first appearance of the plant embryo was a major step in the evolution of land plants, and is of great concern to paleobotanists and other plant scientists interested in the origins of early plants.

Bower's hypothesis

The nature of the immediate algal ancestors of plants and their role in the origin of the land-plant life cycle has been the substance of much debate for over a century. The continuing controversy centers on two opposing theories, one first proposed in 1874 by Celakovsky (*7*) and the other developed in 1908 by Bower (*8*). Bower was the first to amass evidence in support of the idea that the sporophyte originated as a new component of the life cycle from algae that lacked a sporophyte (see Fig. 2); specifically, embryophytes arose from haploid, haplobiontic algae—algae having a single multicellular generation—resembling the present-day genus *Coleochaete*, which is unusual among green algae in having diploid zygotes that are retained on the haploid parental form (Fig. 3). Bower proposed that a delay in zygotic meiosis could have produced the first multicellular diploid sporophytes that would be, like the embryos of land plants, associated with parental haploid gametophytes.

According to the alternative hypothesis, first suggested as a possibility by Celakovsky and seized upon by later workers who opposed Bower's theories, land plants arose from green algae that were diplobiontic—that already had alternation of two generations. This hypothesis has had considerable support for the past several decades (*9*) despite the major problem of being unable to explain how the sporophytes and gametophytes, which in present-day diplobiontic green algae are completely independent, or free-living, could have developed the intimate nutritional and developmental relationships that are characteristic of embryophytes. In other words, how could a free-living sporophyte become attached to—and parasitic upon—the gametophytic generation?

Resolution of this problem of the origin of the plant

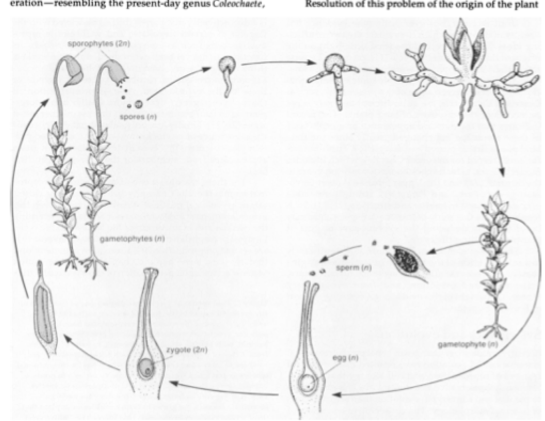

Figure 1. The life cycle of all land plants (shown here for a typical moss) involves the alternation of two multicellular generations. The gametophyte, the generation producing male and female gametes, is haploid; that is, its cells have a single set of chromosomes, *n*. The sporophyte generation is diploid, 2*n* (*shown as gray*), combining the chromosomes of the male and female gametes. Land plants are thought to have evolved from green algae, many of which also have alternation of generations, but land plants are distinguished by the retention of the zygote – the sporophyte embryo – within the nourishing tissue of the parental gametophyte. The understanding of how this relationship first evolved has been considerably advanced recently.

life cycle is now not merely of theoretical significance but will have practical importance in future work on plant biology. For example, understanding as much as possible about the genetic history of plants and the origin of their reproductive processes may be usefully applied to the genetic modification of economically important higher plants by haploid selection and by genetic-engineering techniques. There is special interest in understanding the plant-embryo relationship, for this may lead to development of techniques for the fertilization of isolated plant eggs in vitro, which in turn will facilitate genetic engineering (*10*).

Once identified, modern algae that are most closely related to plants are likely to be useful as simple systems for experimental study of several other poorly understood plant processes believed to be of ancient origin. These include photorespiration, which can decrease crop

number of laboratories for numerous forms of green algae, collectively suggest that the evolutionary line which ultimately led to land plants diverged early from other mainstreams of green-algal diversification (*14–18*).

According to these data, the class Charophyceae (*19*), which includes the Charales and *Coleochaete*, is linked to the ancestry of embryophytes and separated from other algal lineages because, like land plants, advanced charophytes possess a phragmoplast, a distinctive array of microtubules and vesicles that appears during the final stages of cell division in plants. Phragmoplast microtubules are characteristically oriented at right angles to the direction of new cross-wall formation and are thought to be involved somehow in development of new cell walls. Most other green algae accomplish cytoplasmic division rather differently and lack a