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The Origin of the Life Cycle of Land Plants

Linda E. Graham

A simple modification in the life cycle of an extinct green alga is the likely origin of the first land plants

The invasion of the land by aquatic plants about 400 million years ago was one of the most significant events in the history of life on earth. Botanists have long been concerned with various aspects of the evolution of land plants, but a particularly difficult problem has been the origin of the plant life cycle. Recently a significant body of evidence has emerged that may help solve this botanical mystery. This article will review the new evidence, which suggests a model of how the life cycle of 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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Probably the most distinctive feature of the land-plant reproductive cycle is that eggs are retained on the parental gametophyte and fertilized there. The resulting young sporophyte, or embryo, then remains associated with the parental gametophyte, and derives nutrition from it for a time during early embryo development. It is for this reason that vascular plants and bryophytes are often referred to as embryophytes, or embryo-producing plants.

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

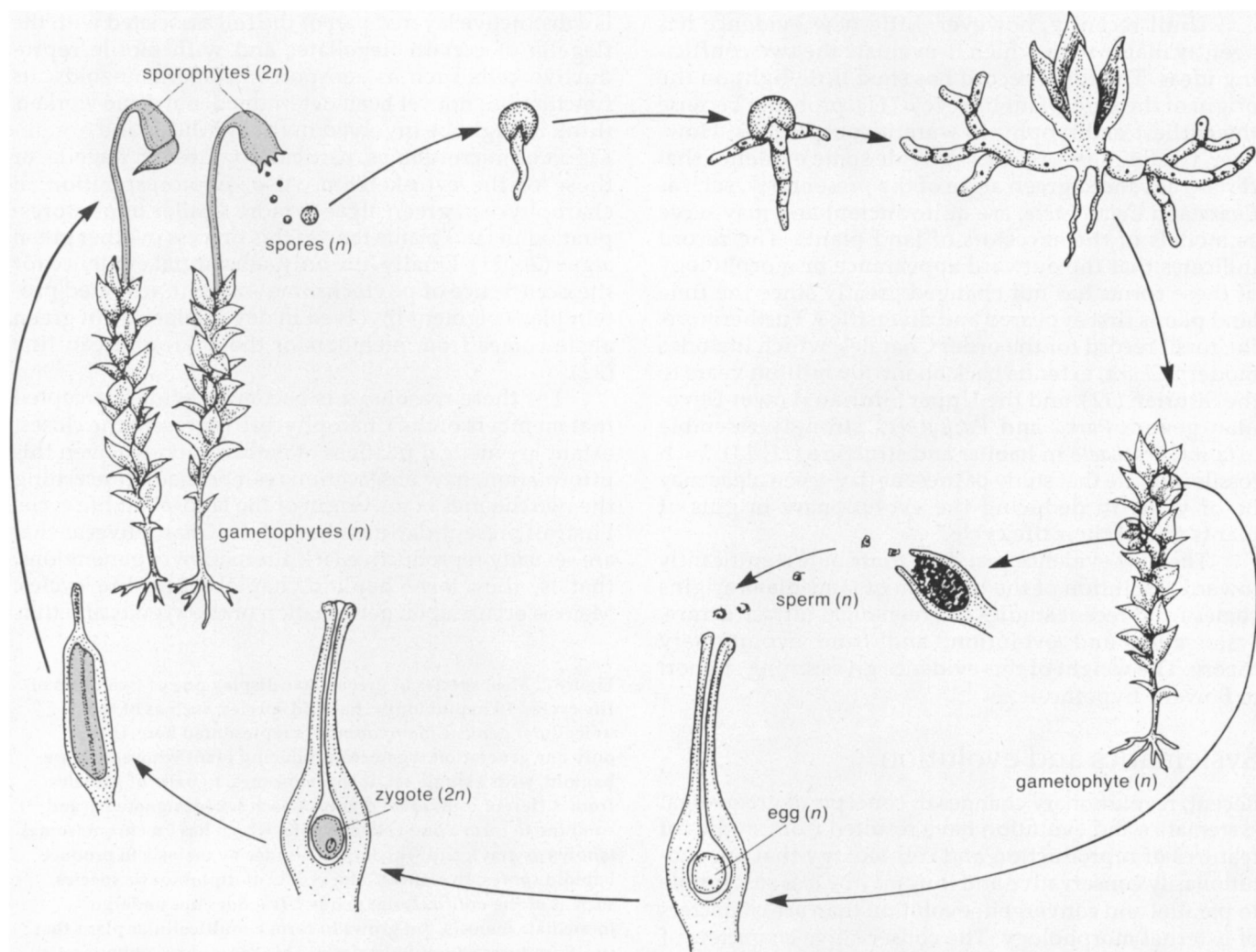


Figure 1. The life cycle of all land plants (shown here for a typical moss) involves the alternation of two multicellular generations. The gametophyte, the generation producing male and female gametes, is haploid; that is, its cells have a single set of chromosomes, n . The sporophyte generation is diploid, $2n$ (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 productivity, and phytochrome-mediated photomorphogenesis, which includes control of flowering and other processes of plant development. Thus, it is important to determine which hypothesis best explains the origin of the embryophytic life cycle and, as a corollary, which extant green algae are most closely related to land plants.

Until recently, however, little new evidence has been available with which to evaluate the two conflicting ideas. The fossil record has shed little light on the origin of the land-plant life cycle (11), probably because the earliest embryophytes were inconspicuous. However, the fossil record does provide some evidence that certain advanced green algae of the present day, such as *Chara* and *Coleochaete*, are quite ancient and may serve as models of the ancestors of land plants. The record indicates that the outward appearance or morphology of these forms has not changed greatly since the time land plants first appeared and diversified. Furthermore, the fossil record for the order Charales, which includes modern *Chara*, extends back about 400 million years to the Silurian (12), and the Upper Silurian–Lower Devonian genera *Parka* and *Pachytheca* strongly resemble extant *Coleochaete* in habitat and structure (11, 13). Such fossils indicate that study of present-day green algae may be of value in deducing the evolutionary origins of plants and of their life cycle.

The new evidence that does contribute significantly toward resolution of the problem of land-plant origins comes from recent studies of green-algal ultrastructure, systematics, and evolution, and from evolutionary theory. The weight of this evidence gives strong support to Bower's hypothesis.

Systematics and evolution

Recent, revolutionary changes in concepts of green-algal systematics and evolution have resulted from studies of features of reproduction and cell biology that are evolutionarily conservative and thus may be less susceptible to parallel and convergent evolution than are characters of external morphology. The conservative characters of greatest significance include certain biochemical features, the organization of the cell-division process, and the fine structure of reproductive cells, especially the flagellar apparatus and cytoskeleton (i.e., the protein-fiber structural framework) in motile reproductive cells (gametes and zoospores). Such data, accumulated by a

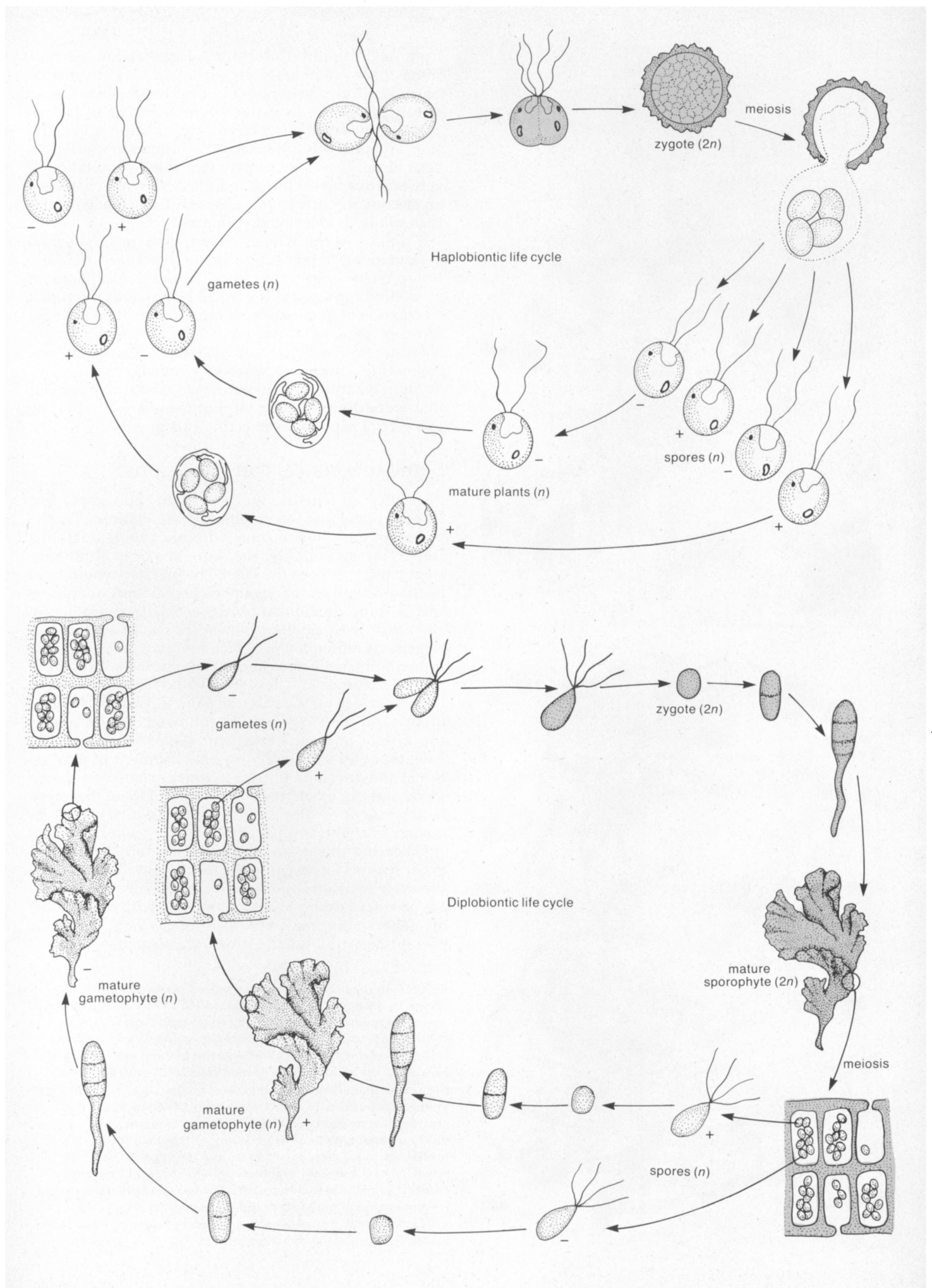
number of laboratories for numerous forms of green algae, collectively suggest that the evolutionary line which ultimately led to land plants diverged early from other mainstreams of green-algal diversification (14–18).

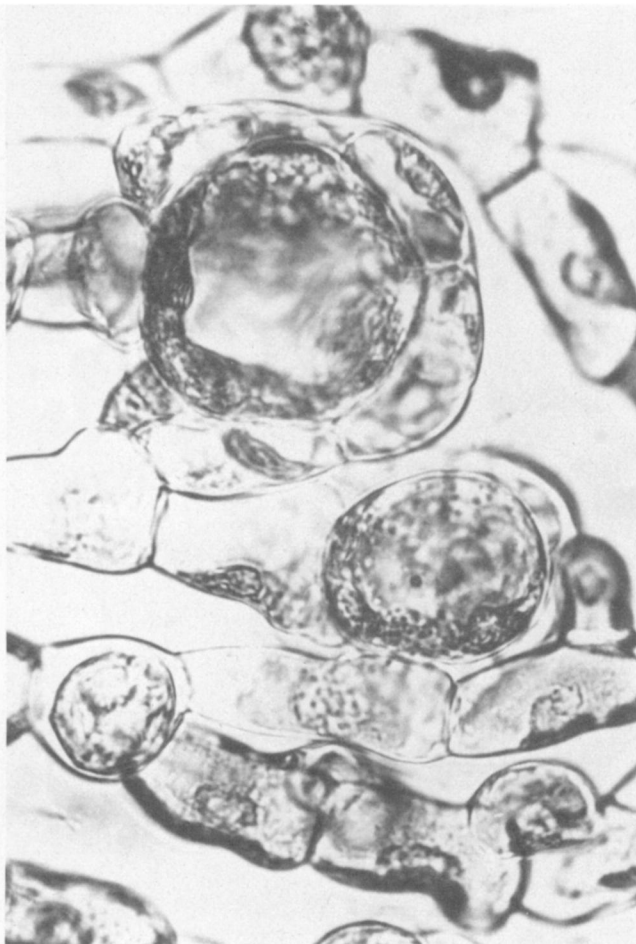
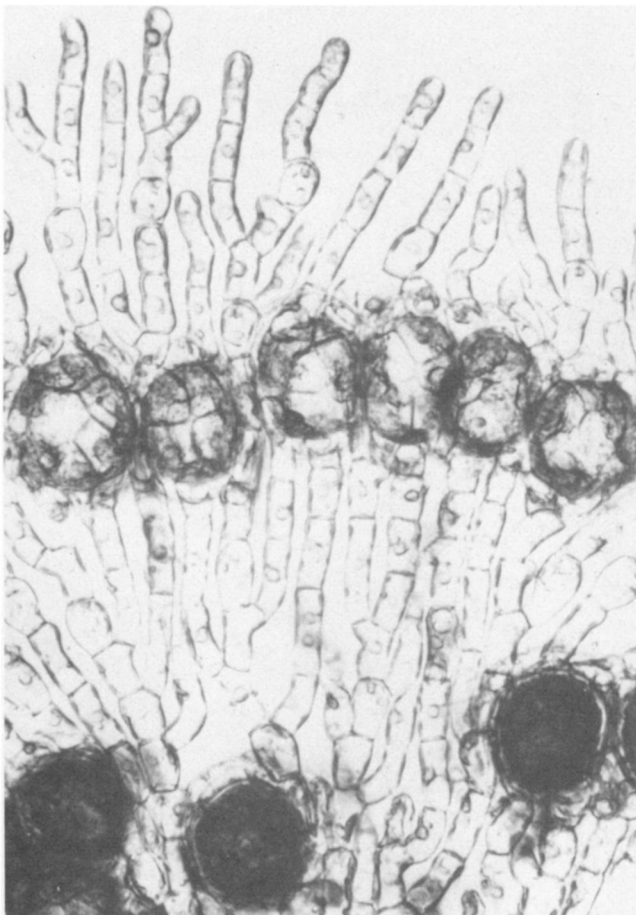
According to these data, the class Charophyceae (19), which includes the Charales and *Coleochaete*, is linked to the ancestry of embryophytes and separated from other algal lineages because, like land plants, advanced charophytes possess a phragmoplast, a distinctive array of microtubules and vesicles 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 phragmoplast.

Charophytes are further distinguished by their flagellated reproductive cells, which contain a multilayered structure and microtubular cytoskeleton similar to those of all the land plants that produce flagellated spermatozoids, including bryophytes, fern allies, ferns, and certain gymnosperms. The multilayered structure is a distinctive layered part of the cell associated with the flagella of certain flagellates and with motile reproductive cells such as zoospores or spermatozoids. Its function has not yet been determined, but some workers think it might be involved in the synthesis and organization of microtubules, particularly those in flagella, or those of the cytoskeleton. Also, photorespiration in charophycean green algae is more similar to photorespiration in land plants than to this process in other green algae (20, 21). Finally, the only substantial evidence for the occurrence of phytochrome—a light-activated protein plant pigment involved in development—in green algae comes from members of the charophycean line (22).

For these reasons, it is becoming widely accepted that members of the Charophyceae represent the closest extant green-algal relatives of embryophytes. Given this information, new observations can be made concerning the two theories of the origin of the land-plant life cycle. First, all present-day members of the Charophyceae that are sexually reproductive lack alternation of generations; that is, they have haploid, haplobiontic life cycles. Meiosis occurs upon germination of the zygote, and thus

Figure 2. Most species of green algae display one of two types of life cycles. In haplobiontic, haploid species, such as of the unicellular genus *Chlamydomonas* represented here, there is only one generation, a gamete-producing plant whose cells are haploid, with a single set of chromosomes, n ; pairs of gametes from different individual plants of each sex (designated + and –) combine to form a one-celled zygote, which has $2n$ chromosomes (shown as gray), and which then divides by meiosis to produce haploid spores. In contrast, the zygote of diplobiontic species, such as of the multicellular genus *Ulva*, does not undergo immediate meiosis, but grows to form a multicellular plant that itself produces spores by meiosis. This sporophyte, whose cells have the same diploid number of chromosomes as the zygote ($2n$), can produce a far greater number of spores than the meiotically dividing zygote of the haplobiontic life cycle, which is limited by the size of the zygote. The diplobiontic life cycle of algae – and of the land plants – is thought to have evolved from the haplobiontic by a delay in meiosis.





there is no multicellular diploid generation. Second, none of the extant green algae that do have alternation of multicellular generations have the combination of advanced, plantlike characteristics, such as phragmoplasts, multilayered structures, plantlike photorespiration, and phytochrome that are exhibited by charophycean algae. It seems unlikely that this constellation of conservative biochemical and ultrastructural characters arose convergently in some other lineage that gave rise to land plants and then became extinct.

Thus, on the whole, recent work in green-algal systematics strongly supports the hypothesis that embryophytes originated from haplobiontic, haploid charophycean algae as described by Bower (8), and that alternation of generations in other green-algal lineages arose in parallel. However, while the charophycean algae are now widely accepted as close relatives of embryophytes, there are workers who suggest that embryophytes arose from hypothetical extinct charophytes that were diplobiontic (23). But there are compelling theoretical reasons for rejecting this possibility.

Some theoretical considerations

Regardless of whether the land-plant sporophyte and its nutritional and developmental association with the gametophyte evolved from a diploid zygote or from a free-living sporophyte, the sequence of evolutionary steps must have been the same. The first step would have been development of oogamous sexual reproduction—that is, reproduction in which specialized, immobile eggs fuse with smaller, motile sperm, as opposed to isogamous reproduction, which involves unspecialized, indistinguishable male and female gametes, as in more primitive forms. The next step would have been retention of the egg on the parental gametophyte at the time of fertilization. This would be followed by retention of the zygote and its subsequent development on the gametophyte, and finally by establishment of a nutritional and developmental relationship between sporophyte and gametophyte. Because each of these four steps is dependent on the previous one, an alternative sequence of events is unlikely.

Bearing this sequence in mind, there are several major reasons for rejecting the hypothesis that the plant life cycle evolved from a diplobiontic one. First, there are no extant examples of green algae with alternation of generations that are also oogamous. Also, in present-day diplobiontic green algae, gametes are re-

Figure 3. In the highly branched species *Coleochaete pulvinata*, shown in the upper photograph magnified 280 times, eggs and sperm are produced at the growing edge (top). Following fertilization, the resulting zygotes enlarge greatly and acquire a cellular covering (center); older zygotes (bottom) appear darker because of the accumulation of food reserves. As can be seen at the greater magnification of the lower photograph ($\times 1,100$), very young zygotes seem to attract neighboring filaments; as they enlarge, developing zygotes may actually stimulate unidirectional growth of neighboring cells, which then proliferate into a close covering around the zygotes. This retention of the diploid zygotes within the haploid tissue of the parental gametophyte, a characteristic of all land plants, occurs in no other genus of green algae and is the primary reason why *Coleochaete* may be considered as a model of an ancestor of land plants. (Lower photograph after ref. 41.)

leased from gametophytes, so that fertilization and subsequent zygote and sporophyte development are independent of the parental gametophyte.

In contrast, Bower's hypothesis that the land plants evolved from haplobiontic green algae similar to present-day *Coleochaete* has the great advantage that most of the evolutionary steps—oogamy, retention of the egg on the parental gametophyte, and retention of the zygote—would already have been accomplished in the green-algal ancestor. Of course, it is possible that diplobiontic, oogamous forms that retained eggs and zygotes became extinct after giving rise to land plants. However, the following theoretical consideration suggests that this is unlikely.

Haploid, haplobiontic life cycles are widespread among protists—one of the five kingdoms of organisms that includes algae, slime molds, and protozoa (6)—and therefore are probably primitive life cycles. A major disadvantage of such a life cycle is that relatively few products, generally only four, result from each zygotic meiosis. A number of different types of protists have solved this problem by a delay in meiosis long enough for the zygote to develop into a multicellular diploid structure that is capable of producing more than four meiotic products; in other words, these protists have developed a diplobiontic life cycle. The new diploid generation, or sporophyte, serves to protect the genome from the effects of deleterious mutations, as well as to increase the number and diversity of recombinant progeny (24).

If, in a diplobiontic green alga, the free-living, photosynthetic sporophyte were to abandon independent existence and assume an embryophyte-like association with the gametophyte, the size of the attached sporophyte, and consequently the number of meiotic products that could be produced, is likely to be reduced. In comparison to diplobiontic forms, such an alga is likely to be at a competitive disadvantage in environments that favor production of more spores for each fertilization event, or production of separate generations that can exploit seasonal or habitat variations. Indeed, it is difficult to conceive of any selective advantage for the multistep evolutionary pathway required to generate a land-plant life cycle from a diplobiontic one.

Interestingly, the origin of the life cycle of advanced red algae seems to offer a parallel to the origin of the sporophyte generation in plants. Advanced red algae have an alternation of three generations; two of these are usually free-living, and the third, called the carposporophyte, is attached to the female gametophyte and is probably partially parasitic on it (25). This carposporophyte may also stimulate development of a protective layer of gametophytic filaments called a pericarp. Thus, the red algae may exhibit an intimate developmental and nutritive interaction between generations that parallels that of embryophytes. Since male gametes of red algae lack flagella that would make them motile, fertilization rates may be low. The carposporophyte is thought to compensate by producing many copies of the products of any successful fertilization (26). Searles (26) has suggested that the evolutionary development of the land-plant sporophyte is related to reduced fertilization rates in drier terrestrial habitats, favoring production of greater numbers of spores for each fertilization. Thus, the selective pressures and evolutionary responses

leading to the origin of the red-algal carposporophyte and to the land-plant sporophyte may have been analogous.

It is also interesting to note that in developing the carposporophyte phase, red algae have not given up their original diploid generation (the tetrasporophyte), which is generally free-living. If diplobiontic green algae had acquired an attached sporophyte, one might expect to find some forms having three alternating generations such as occur among advanced red algae, but these do not exist. Collectively, such observations support the hypothesis that land plants arose from advanced charophycean algae by a single evolutionary step, a delay in meiosis.

Advanced charophycean algae

The evidence suggests that the present-day genus most closely resembling the now-extinct immediate ancestors of embryophytic land plants is *Coleochaete*. It is likely that some other present-day charophytes are more specialized than these ancestors (24). *Chara* and *Nitella*, for instance, have the most complex specialized plant bodies, gametangia (structures in which gametes are produced), and male gametes known among green algae. In spermatozoids, the thin plates of the multilayered structure are either highly modified, as in *Nitella* (27), or missing altogether, as in *Chara* (28, 29). These facts suggest that Charales (*Chara*, *Nitella*, and close relatives) have diverged substantially from the main evolutionary line leading directly to embryophytes.

The less-specialized bodies, gametangia, gametes, and multilayered structures of *Coleochaete* suggest a closer relationship to the direct ancestry of plants. *Coleochaete* has certain features—the photorespiratory enzyme glycolate oxidase (20), photorespiratory organelles or peroxisomes, a phragmoplast at cytokinesis (21), and multilayered structures in male gametes (30)—in common with other charophytes (19) and land plants. Since embryophytes lack zoospores (motile, flagellated spores), the widespread occurrence of zoospores in *Coleochaete* and in some other charophycean genera demonstrates the aquatic affinities of these green algae, and argues against a suggestion that charophycean algae originated and diversified on land and then became secondarily aquatic (23).

Certain advanced characters are shared by *Coleochaete* species and were probably also features of charophytes ancestral to the genus. These include ovoid spermatozoids resembling those of *Lycopodium* (30–31), which are thought to be the primitive type among lower land plants (32), production of a layer of cells covering zygotes (33), and production of more than four meiospores (i.e., spores resulting from meiosis) per zygote. In at least one species, this last feature is based on the occurrence of more than one round of DNA replication prior to meiosis (34). Some or all of these attributes probably characterized the ancestors of the Charales and land plants as well.

A number of embryophyte-like features occur in some, but not all, the species of *Coleochaete*: localized growth (a peripheral meristem) (35), parenchyma (36), putative placental transfer cells with localized wall ingrowths (37), and multicellular, internal antheridia (30, 38). Most likely, *Coleochaete* evolved these features in

parallel with the charophytes that gave rise directly to plants in response to selective pressures operating in similar habitats.

A model for the origin of land plants

In regard to the origin of the embryophyte life cycle, the most significant feature of *Coleochaete*—retention and subsequent development of the zygote on the haploid parental body (Fig. 3)—makes it a model for the green-algal ancestor of embryophytic land plants. The parent-embryo relationship is likely to have first evolved as a result of particular selective pressures of the aquatic environment.

Most species of *Coleochaete* are littoral epiphytes—that is, they grow in waters near the shore, firmly attached to larger plants (macrophytes) or to inorganic substrates such as rocks or discarded bottles and cans. The adaptive advantage of zygote retention may be that zygotes are more likely to remain in the shallow water near the shore through winter and into spring, when they germinate and produce meiospores that swim a

short distance before settling. Thus, upon their release, spores are close to suitable substrates for attachment and growth in a well-lighted environment. This may confer an advantage for spring colonization over other littoral epiphytes whose zygotes are released from the parental bodies and are thus more likely to overwinter in deeper water or in the sediments.

In *Coleochaete*, the attachment of the zygote occurs because a layer of vegetative cells belonging to the parental generation covers exposed surfaces of mature zygotes. Observations of the growth of this cellular cover suggest that zygotes probably induce its development. This phenomenon is best observed in the filamentous species *C. pulvinata* shown in Figure 3, where filaments in the vicinity of young zygotes grow toward the zygotes, eventually covering them (39). Such interaction during growth between cells of differing chromosome levels occurs in no other green-algal genus; it is comparable to developmental changes observed in gametophytic cells adjacent to zygotes in embryophytes, and to the growth of filaments around gametangia of Charales.

As Figure 3 shows, zygotes in *Coleochaete* are much larger than the parental vegetative cells. *Coleochaete* is unusual among haplobiontic, haploid green algae in that 8 to 32 spores are produced per zygote, rather than 4 or fewer as is usual. The large number of meiotic products in this genus may well be an adaptation allowing rapid colonization of substrate space at the beginning of the growing season (34).

Parka, *Coleochaete*'s presumed fossil relative, indicates that selective pressures in shoreline habitats during the Silurian (or earlier, when the first land plants are believed to have appeared) favored production of large zygotes and, consequently, of greater numbers of spores (13). *Parka*, probably also a littoral epiphyte associated with the macrophyte *Zosterophyllum*, produced very large sporangia (spore-producing structures), covered by a cellular layer, which contained numerous spores (13). Thus, production of large numbers of spores as an adaptation for rapid colonization (40) may have been common among charophycean epiphytes in the Silurian. In *Coleochaete* an additional cycle of premeiotic DNA replication apparently occurs, so that zygote nuclei may have DNA levels two (and perhaps even more) times higher than expected (34), an increase that probably represents extra copies of chromatids (the paired strands resulting from recent replication of chromosomes), which may then undergo genetic exchange and assort in various ways. This may confer the potential for an increased number of recombinant progeny, thus yielding greater genetic diversity as compared to organisms producing four or fewer meiotic products per zygote.

Production of more than four, and of more diverse, meiospores as an adaptation to littoral life may have served as a preadaptation (41) that led to the evolution of increasingly larger diploid phases of the life cycle by increasingly longer delays in meiosis. Indeed, the extra premeiotic DNA replication that occurs in *Coleochaete* might be viewed as a first step toward delay in meiosis. After shoreline habitats became accessible for colonization—perhaps because of reductions in ultraviolet levels resulting from increased levels of atmospheric oxygen and ozone (42)—an alga or early plant that could produce greater numbers of more diverse spores for

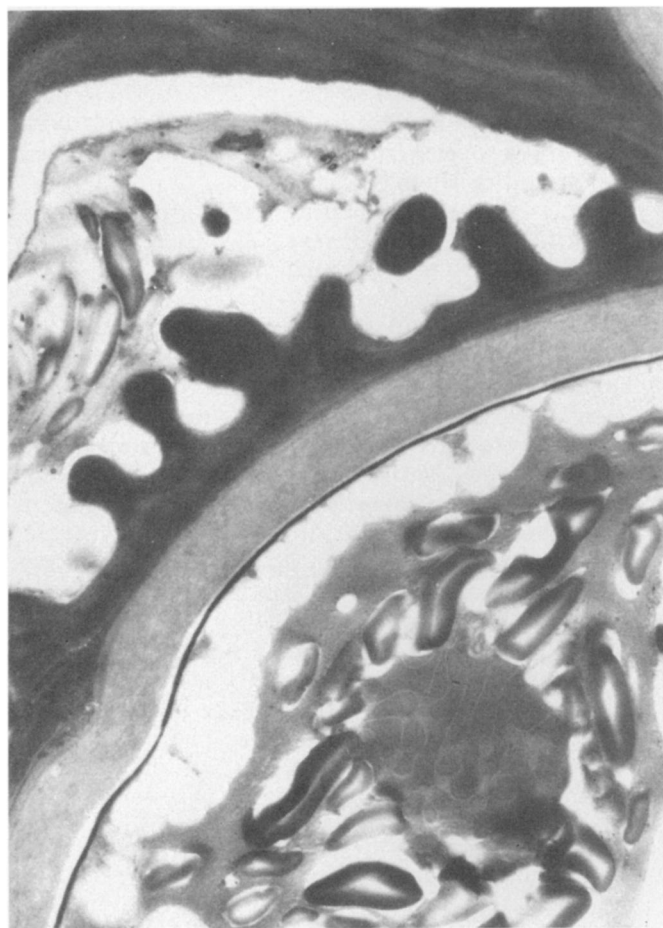


Figure 4. A high-voltage electron micrograph of *Coleochaete orbicularis* ($\times 6,700$) shows the boundary between a zygote (lower right) and its neighboring cover cell (upper left), which has localized ingrowths from its outer wall into the cell. These ingrowths, similar to those of placental transfer cells in embryophytic land plants, are believed to function as do intestinal villi in humans; that is, they increase the surface area of membranes across which nutrients are transported. The structures within the zygote are starch grains and lipid droplets.

every zygote (i.e., for every instance of successful fertilization) would presumably have an evolutionary advantage over similar organisms producing fewer, genetically less diverse meiotic products (43). In fact, green algae from lines of descent other than the Charophyceae have colonized the land. Examples include numerous genera of unicellular and colonial soil algae (44) and *Fritschiella*, a morphologically complex form once thought to be a land-plant progenitor. The highly specialized Trentepohliales may have originated on land from unicellular soil algae (18). But there is no evidence that any of these forms gave rise to any embryophyte group.

The close association between zygote and cover cells in *Coleochaete* also provides an opportunity for the haploid and diploid phases of the life cycle to develop a nutritional relationship similar to that occurring in embryophytes. Zygotes of *Coleochaete* contain chloroplasts (37), and thus can presumably photosynthesize. However, the zygotes become much larger than vegetative cells and accumulate large amounts of starch and lipid storage materials as they mature. There is circumstantial evidence that zygote photosynthesis may be supplemented by photosynthates secreted from covering cells during the time that reserves are stored. In at least one species, *C. orbicularis*, conspicuous, localized wall ingrowths occur in covering cells, as shown in Figure 4. These cover cells resemble gametophytic placental transfer cells of embryophytes in structure, location, and time of development. Among embryophytes, placental transfer cells facilitate movement of photosynthate across cell membranes and cell walls at the junction between sporophyte and gametophyte, where connecting strands of cytoplasm are lacking (2–4). Wall ingrowths of transfer cells function to increase the surface area of the wall-membrane complex (2–4), where transport enzymes are located (45).

In the aquatic environment, extensive transfer of solutes between zygotes and adjacent cells of most algae is unlikely, because cytoplasmic connections are disrupted by thickening of the zygote wall, and because photosynthates moving through cell walls and intercellular spaces can readily dissolve into the surrounding medium. Only in a tightly associated complex of zygote and parental cells, such as in *Coleochaete*, can short-distance transport across membranes and walls of adjacent cells occur to any great extent (41). The advantage of photosynthate importation by zygotes is that more resources are available for the production of spores at zygote germination.

Probably a major factor in the success of charophytes on land was the ability to maximize the result of sexual reproduction by virtue of a nutritional and developmental relationship between life-cycle phases. Phragmoplasts, multilayered structures, and other features of charophycean algae may have contributed to their ability to colonize the land. However, some of these characters may simply have been inherited by plants as components of a genome successful for other reasons. *Coleochaete* provides a model for the way in which similar charophycean algae could have acquired a variety of adaptations to littoral life, which later proved useful in the conquest of land.

Coleochaete also illustrates how charophycean algae could—and probably did—give rise to the first em-

bryophytes by a simple, one-step process, delay in meiosis. Such a step is apparently an easy one, as it must have occurred each time alternation of generations arose in protists. The *Coleochaete* model also explains the origin of the nutritional and developmental relationship between generations that was apparently so influential in subsequent plant evolution. The evidence currently available suggests that continued study of *Coleochaete* is likely to result in further progress toward understanding the origins of plants and may also influence the direction of evolutionary studies in various groups of plants (9).

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"There's the strong force, the weak force, gravity, electromagnetism, and then there's that certain something I feel when I see you."