

FUNCTIONAL BIOLOGY OF PLANTS

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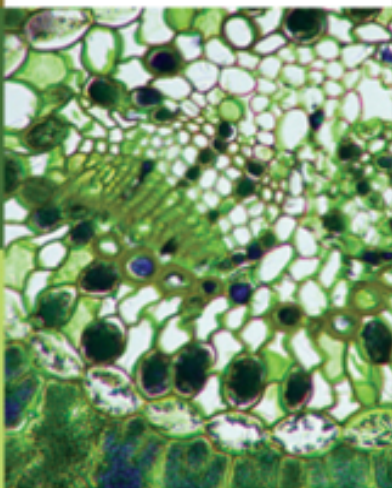
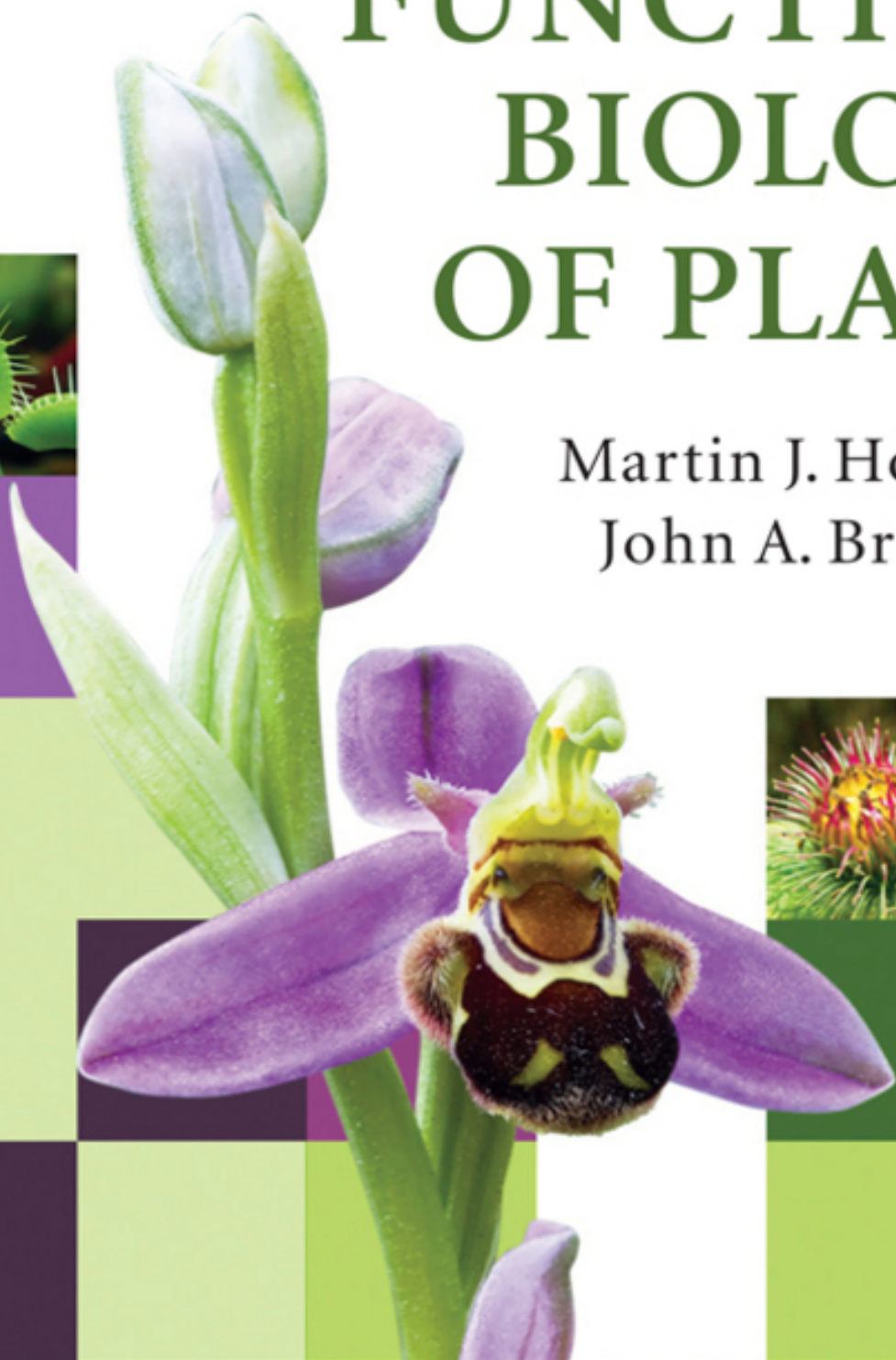


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Functional Biology of Plants

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Preface

As we complete the manuscript of *Functional Biology of Plants*, many thousands of refugees, driven by drought and famine from the Horn of Africa, have found their way to camps in Kenya. Nowhere is it more obvious that people need feeding, yet it is also true to say that, with appropriate land use, the continent of Africa could become self-sufficient in food production.

This is not the place to discuss the political and economic challenges that will need to be faced; rather, we state that plant growth has never been so important. It may be true in some developed countries that students seem relatively uninterested in botany or plant biology, but it is equally true that we need to know more about plants and how they work, at least partly in order to harness and, indeed, to increase their potential in human nutrition. Thus we hope that this book will engender interest in the functioning plant.

We have not set out here to write a book about plant biochemistry or cell biology or molecular biology or genetics. Instead, after an introduction to plant function at those levels, we have attempted to show how activities at molecular and cellular levels are integrated and coordinated in the functioning of whole organs and of whole organisms—the plants themselves. In the later parts of the book, we place plants into their natural environments as they deal with abiotic and biotic stresses before considering, in the final chapter, the importance of plants in relation to some of the pressing problems facing humankind in the 21st century.

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Chapter 1

Origins

1.1 Plants—What are They?

We might simply define plants as photosynthetic eukaryotes—a description that would certainly include all the types of organisms that find their way into courses in botany or plant biology. However, as will become clear later in this chapter, such a definition brings together some very diverse groups whose common ancestor existed possibly as long ago as 1.6 billion years before the present time. These include glaucophytes (very simple unicellular aquatic organisms), all the different groups loosely known as algae and also the land plants, including the most advanced of these, the angiosperms (flowering plants), on which this book is mainly focused.

Charles Darwin, in a letter to Joseph Hooker, the Director of the Royal Botanic Gardens at Kew, described the origin of flowering plants as an ‘abominable mystery’. They seemed at that time to appear in the fossil record without any obvious immediate precursors. Our understanding today, although somewhat more extensive than it was in Darwin's time, is still far from complete; the mystery is not yet completely solved. To appreciate this, it is necessary to go right back to the origin of cellular life and then of eukaryotes. It is a fascinating story.

1.2 Back to the Beginning

For much of the 20th century, our knowledge of the history of life on Earth went no further back than the dawn of the Cambrian period—‘only’ 550 million years ago. Fossils of quite sophisticated marine eukaryotes have been dated to that time and, during the Cambrian period itself, a very wide range of new lifeforms appeared. This flourishing of diversity in this period is known as the *Cambrian explosion*. However fascinating this is, it does not actually tell us of the earliest lifeforms.

Intense searches in pre-Cambrian rocks were conducted from the mid-1960s onward, but for many years failed to yield any fossils. However, one of those pivotal moments in science came when the American paleobiologist William Schopf identified fossil micro-organisms dating back 3.5 billion (i.e. 3.5×10^9) years. Whether or not these represent the oldest living things on Earth is still not clear. Some paleochemists have suggested that there is chemical evidence of life processes in rocks dating back 3.8 billion years, while others are of the opinion that the chemicals that supposedly indicate some form of metabolism at that time could equally have arisen by non-biogenic processes. Nevertheless, Schopf's discovery unlocked the ‘log-jam’ and, since then, many more fossils have been found in pre-Cambrian rocks. Furthermore, paleochemical analyses have given us a good idea of what conditions on Earth were like during this period. To this we can add detailed knowledge of the molecular biology and genetics of organisms living today. All this has enabled scientists to build up a picture of the main features of the evolution of living organisms during the pre-Cambrian.

So, life originated around 3.5 billion years ago (and possibly slightly earlier). The predominant, indeed probably the only, organisms then were similar to modern

prokaryotes. Earth's atmosphere contained no free oxygen at that time, so these early bacteria were inevitably all anaerobic. Indeed, study of the properties of amino acids in modern anaerobic and aerobic organisms indicates strongly that the genetic code evolved under anaerobic conditions.

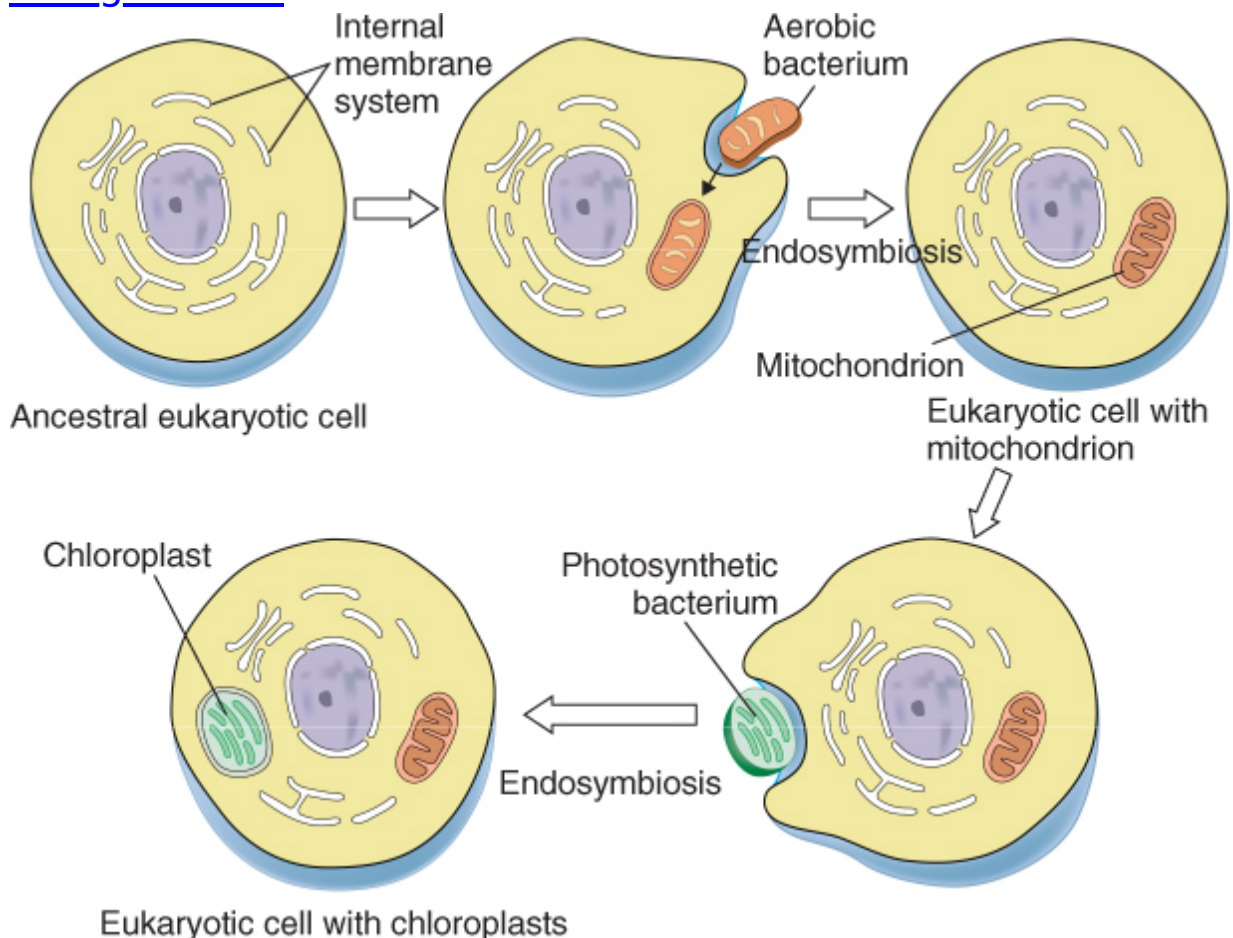
A good case has been made that the earliest cells were similar to today's Gram-positive bacteria and gave rise to two further lineages—the Gram-negative bacteria and the Archaea (or archaeobacteria). The origin of the Archaea has thus been dated as occurring very early in the history of life. Fossil evidence indicates that photosynthetic bacteria (like modern cyanobacteria) first appeared about 2.8 billion years ago. The presence of photosynthetic organisms led to the '**great oxidation event**' (between 2.2 and 2.45 billion years ago), which was bad news for anaerobic organisms because it generated free oxygen, which was (and still is to an extent) toxic to them. This selective pressure led to the evolution of aerobic organisms, capable of using oxygen in energy generation, probably at least two billion years ago.

1.3 Eukaryotes Emerge

The idea that chloroplasts and mitochondria may have been derived from bacteria was first mooted in the 19th century, but it was not until the 1960s that the idea received wider attention. Based on her studies in cell biology, Lynn Margulis proposed specifically that mitochondria were derived in evolution from aerobic bacteria that had been engulfed by anaerobic bacteria, establishing the lineage that led to modern eukaryotes. According to this view, the inner membrane of the mitochondrion represents the original plasma membrane of the engulfed bacterium and the outer mitochondrial membrane represents the plasma membrane of the original host cell (see [Figure 1.1](#)). A second engulfment, this time of a photosynthetic (cyano)bacterium,

led to the lineage(s) of photosynthetic eukaryotes and eventually to plants.

Figure 1.1 Diagram of 'engulfment' events leading to the formation of eukaryotic cells and then of photosynthetic eukaryotic cells. The original engulfing cell ('ancestral eukaryote') was almost certainly descended from an archaebacterium. It must have already possessed some features of eukaryotic cells, including a membrane system and possibly a nucleus (see text). Reproduced, with permission, from <http://scienceisntfiction.blogspot.com/2011/04/endosymbiotic-origins.html>



It is fair to say that, although some scientists embraced it enthusiastically, the **endosymbiotic theory** was not widely accepted when Margulis originally proposed it.

Nevertheless, there was interest in what was called the 'autonomy' of chloroplasts and mitochondria. DNA from these organelles was unequivocally identified, as was the whole range of protein synthesis 'machinery'. To all intents and purposes, these organelles appeared to be organisms within organisms—except that they had only a fraction of the number of genes needed to support independent life. If the endosymbiont hypothesis was correct, then transfer of genes from the endosymbiont to the host genome must have occurred during subsequent evolution.

Further analysis showed that a wide range of molecular biological features—including gene promoters, ribosome structure, sizes of particular types of RNA and the initiation of protein synthesis in plastids and mitochondria—resembled much more the equivalent features in bacteria than those of the major genetic system in the eukaryotic cells that contain the organelles. Further, the plastids of glaucophytes have a peptidoglycan wall, similar to the cell walls of cyanobacteria. All this is, of course, consistent with the endosymbiotic hypothesis and, by the time Margulis published her book *Symbiosis in Cell Evolution* in 1981, the hypothesis was accepted by the majority of biologists.

Further research during the past three decades has further confirmed the validity of the hypothesis, and it is now firmly stated that eukaryotes arose by the engulfment of an aerobic α -proteobacterium. Whether the 'host' cell was an archaean or a eubacterium is a matter for discussion. However, comparisons of biochemical mechanisms involved in DNA, RNA and protein synthesis, and of the sequences of genes and proteins, suggest a close relationship between the eukaryotic and archaeobacterial clades. The authors of this book thus favour an archaeobacterial origin for the eukaryotes, as shown in [Figure 1.1](#), but there are some who believe that eukaryotes and archaeobacteria are sister clades, having diverged from a common ancestor.

Whichever of these two views one holds, there are still further problems to consider, of which we highlight three:

- First, there are some 60 clear differences between the organization, activity and structure of eukaryotic and prokaryotic cells. One of these differences is that prokaryotes are incapable of phagocytosis. However, the engulfment of a proteobacterial cell by an archaeobacterial cell, a key part of the endosymbiont theory, would have been achieved by phagocytosis. So, either we envisage that a sub-group of ancient archaeobacteria had already acquired some eukaryote-like features, such as phagocytosis, or that merger of two cells occurred by an unknown process.
- The second problem concerns another of these major differences, namely the sequestration of the main genome inside a complex organelle—the nucleus. With this came specific mechanisms for the division and segregation of the genome in the processes of mitosis and meiosis (the latter arising as part of the evolution of sexual reproduction). There has been much speculation on the evolution of the nucleus, but to date no really convincing hypothesis has emerged. The origin of this major feature of all eukaryotic cells remains totally mysterious.
- The third problem is that of the age of the eukaryotic lineage. The ‘molecular clock’ approach uses comparisons of sequences of genes and proteins in diverging lineages. Assumptions about rates of mutation, based on rates in living organisms, give an estimate of when lineages diverged from each other. This method places the origin of the eukaryotes at between 1.9 and 2.0 billion years ago, and there is some support for this dating from the fossil record. Most paleobiologists accept this dating, but there is a small group who contest it vigorously, suggesting that the

eukaryotic lineage is much younger, dating back ‘only’ 800–900 million years. The authors of this book accept the majority view.

1.4 Photosynthetic Eukaryotes—The First ‘Plants’

The emergence of photosynthetic organisms and the resulting ‘great oxidation event’ provided the selective pressure for the emergence of aerobic organisms and the establishment of the eukaryotic lineage. However, we can say with some justification that the arrival of photosynthetic eukaryotes was even more significant. This large and now diverse array of autotrophic organisms, ranging from simple single-celled organisms to huge forest trees, has had a greater effect on the world's ecosystems than any other, and thus the engulfment of a photosynthetic cyanobacterium by an early aerobic eukaryote was a key step in the development of life on Earth.

Eukaryotes had split relatively rapidly into two groups: the unikonts (with one flagellumⁱ), which gave rise to animals and fungi; and the bikonts (with two flagella). It was among the latter that photosynthetic ability was acquired, approximately 1.6 billion years ago. The Australian cell biologists Geoffrey McFadden and Giel van Dooren leave us in no doubt about the significance of this event:

‘This fusion of two cell lineages ... brought the power of autotrophy to eukaryotes and descendants of this partnership have populated the oceans with algae and the land with plants, providing the world with most of its biomass’.

From this foundational step, there arose several of the groups that we included in our earlier loose definition of plants, including the green plants (see Box 1.1).

Box 1.1 : Abundance of green plants

The role of plants in contributing to biomass is clearly seen by considering *cellulose* (Chapter 2, section 2.2.1). This polysaccharide component of the cell walls of nearly all photosynthetic eukaryotes is the most abundant organic compound on Earth.

Furthermore, the most abundant protein in the world and the most abundant naturally occurring polar lipid in the world are both associated with photosynthesis. The protein is the primary carboxylating enzyme, *ribulose biphosphate carboxylase oxygenase* (also known as Rubisco; see Chapter 7, section 7.4.5), while the lipid, *monogalactosyl diglyceride* (MGDG), is an essential component of the chloroplast thylakoid membrane (see Chapter 2, section 2.5.2). It is ironic that many biologists are unfamiliar with these two important molecules.

However, the story does not end there. There are many photosynthetic eukaryotes, some of them loosely classified in the past as algae, in which the plastids do not have the 'classical' double membrane but instead have four (or in some groups, three) membranes round them. Where did these complex plastids come from? Detailed sequence analysis of their genes and the genes of 'conventional' plastids indicate strongly that *all* plastids arose from a single ancestral source—the originally engulfed cyanobacterial cell. Study of the extra membranes round these complex plastids shows that they originated when a non-photosynthetic eukaryote engulfed a photosynthetic eukaryote.

The extra membranes round these plastids thus represent the plasma membranes of the engulfed cell and of the host. The major event of this type was the engulfment of a red algal cell, which led to lineages that include cryptophytes (which still carry a relic of the nuclear genome of the engulfed cell, the nucleomorph, with approximately 500

genes in a much reduced genome), the dinoflagellates (which have lost the host-derived outer plastid membrane), the brown algae and the diatoms.

In some of the lineages arising from this secondary symbiosis, the plastid has been lost or is much reduced. The Apicomplexa, a phylum that includes the malaria parasites (*Plasmodium* species) provide examples of this. Until the evolutionary origin of this group was understood, the possession of plastids by these organisms seemed very bizarre. The organisms are, of course, non-photosynthetic; over the course of evolution, their plastids (known as apicoplasts) have lost all the components of the photosynthetic machinery. However, they still have an important role in fatty acid metabolism and are essential to the life of the organism.

Finally in this section, it is noted that there have certainly been more than one of these secondary symbioses. The current view is that three such events took place in total, the other two involving engulfment not of red but of green algal cells. One of these events gave rise to the euglenoids (e.g. *Euglena gracilis*), which, like the dinoflagellates, have lost the outermost of the four chloroplast membranes. The other event led to the emergence of the chlorarachniophytes, which, like the cryptophyte lineage arising from the 'main' secondary symbiosis, have retained the vestiges of the engulfed cell's genome in the form of a nucleomorph.

1.5 The Greening of Earth —Plants Invade the Land

The evolutionary 'journey' from the first living organisms to the emergence and initial diversification of photosynthetic eukaryotes, discussed here in the space of a few

paragraphs, covered a period of well over two billion years (the secondary symbioses described above are dated by different authorities at some time between 1.2 and 0.55 billion years ago). All the events described took place in water and, even today, 40-70 per cent of the world's primary production (based on photosynthesis) occurs in marine environments (despite the fact that the total 'photosynthetic biomass' of marine photosynthetic organisms is only about 0.33 per cent of the total). Admittedly, photosynthetic prokaryotes—cyanobacteria—are responsible for a large proportion of the CO₂ of that fixed in marine environments, but marine algae of various lineages, and especially diatoms, are also very important.

As a habitat, water has one major disadvantage for photosynthetic organisms: the deeper the water, the less light there is. Light may be reflected off the water surface, it may be scattered by particles in the water and it is absorbed by the water. The speed at which the latter happens depends on the wavelength of the light; light at the red end of the spectrum is absorbed before light at the blue end of the spectrum. Thus, in clear water, red light penetrates only to about 15 metres, whereas blue light may reach 100 m. There is therefore a zone—the **euphotic zone**—in which light penetration is adequate to support photosynthesis. In general, shallow water occurs on the margins of land masses and, in this primal history of photosynthetic eukaryotes, the land represented a major niche (actually, of course, a wide array of niches), endowed with a much better light environment.

Although better access to light was an obvious advantage, there were also obvious disadvantages. The need for water in order to maintain life meant that the possibility of desiccation was a serious problem. Water is also the medium into which algae release their gametes. Sexual reproduction on land would be more difficult. Furthermore,

immersion in water made for easy uptake of nutrients and also provided support for the larger organisms.

Successful conquest of the land needed solutions to these problems and, based on fossil evidence, this did not occur until between 450 and 490 million years ago. It was another defining event in the history of planet Earth, albeit an event that unfolded slowly. There are now at least 370,000 species of land plants. Their evolution and diversification led to dramatic changes in Earth's environment, including a reduction in the concentration of carbon dioxide in the atmosphere, which resulted in a lowering of the planet's surface temperature. Linda Graham refers to all this as a '*quiet but relentless transformation of terrestrial landscapes*' which initiated the development of new ecosystems and the provision of niches for the evolution of other organisms.

In the transition from water to land, we see a major change in the predominant lifestyle. The aquatic ancestors of the land plants, in common with the majority of modern aquatic photosynthetic eukaryotes, were protists. Most protists are single-celled; the relatively few multicellular forms have little in the way of cellular differentiation, even though some (such as kelps) are very large. Some more complex protists, including the kelps and other brown algae, possess a region of dividing cells, equivalent to the meristems of land plants. The organization of these protist meristem-like regions is simpler than it is in land plants, with fewer possible planes of division.

Simpler protists are capable of, and in many circumstances do undergo, asexual reproduction. In those forms that also reproduce sexually (i.e. by the fusion of gametes), a meiotic division is necessary somewhere in the life cycle. In the simplest examples, this occurs in the zygote, straight after fertilization, but in many protists there is an alternation of generations in which a lifeform that

produces gametes alternates with a lifeform that produces spores.

In contrast to the protist life style, we see in land plants the **embryophyte** lifestyle. Embryophytes are multicellular, with clear cellular and tissue specialization. Dividing cells are organized in regions known as **meristems**; meristematic cells possess more than two cutting planes and can thus generate three-dimensional structures. All embryophytes exhibit alternation of generations and possess antheridia (male gametophyte organs) and archegonia (female gametophyte organs) or the equivalent of these structures. Above all, their embryos are **matrotrophic**, meaning that for all or part of their period of existence they are closely associated with maternal tissues, from which they draw nutrients and signalling molecules.

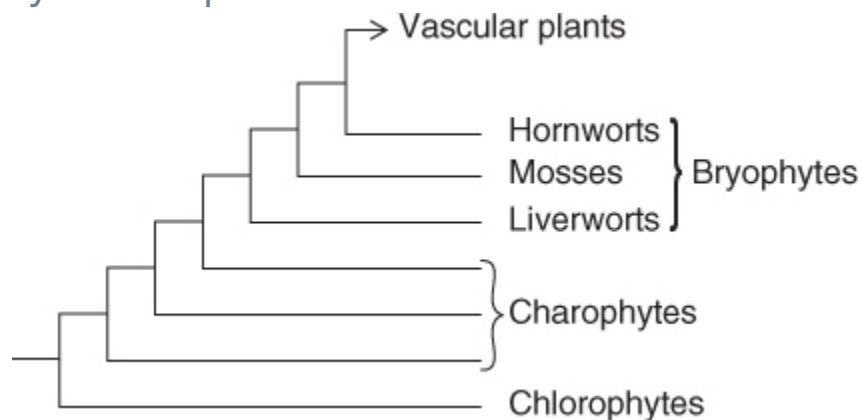
The simplest, and probably the most primitive, embryophytes, the mosses and liverworts (Bryophyta) are still extensively reliant on water. They have no obvious means of restricting water loss and there are no specialized water-conducting cells. The plants also require water to enable the male gametes to swim to the female gametes within the archegonia in order to bring about fertilization. Modern bryophytes are desiccation-tolerant (i.e. they can recover from severe dehydration) and it is likely that this was also true of the earliest members of this group.

So how and when did these early land plants arise? Study of the cell biology and ultrastructure of modern green algae and bryophytes shows that the bryophytes resemble more the charophyte algae than the chlorophyte algae. For example, in both charophytes and bryophytes (and indeed in all embryophytes), the mitotic spindle is persistent and mitosis is open. The cell wall between daughter cells is laid down via a structure called the **phragmoplast** (see Chapter 2, section 2.12.2), involving a cleavage furrow with a

microtubule array oriented at 90° to the plane of cell division.

There are also clear biochemical similarities between charophytes and embryophytes, while molecular phylogenetic analysis, based on gene sequences in nuclear, plastid and mitochondrial genomes, places the charophytes as a sister group to all embryophytes. Furthermore, extant charophytes have rudiments of the matrotrophic embryo, in that there are cellular interactions between haploid maternal cells and diploid zygotes that are thought to be involved in nutrient transfer. They also possess cell wall polymers that inhibit fungal degradation. In particular, a polymer laid down in charophyte zygotes resembles strongly the sporopollenin present in the cell walls of seed-plant pollen. All these data suggest that embryophytes and charophytes are descended from a common ancestor which itself had arisen by divergence from the chlorophytes ([Figure 1.2](#)).

Figure 1.2 Diagram illustrating the positions of the chlorophytes and charophytes in the ancestry of embryophyte land plants.



Although the family tree for the earliest embryophytes appears clear enough from the data based on extant species, the fossil record is much less helpful. The main problem is that the earliest fossil evidence (consisting of tetrads of spores) for embryophyte land plants dates back

about 450–490 million years, to the mid-Ordovician period (see [Table 1.1](#)) whereas the earliest known fossil charophytes occur in rocks from upper Silurian strata, dating back about 414 million years. Thus we have no clear picture of the immediate ancestor of the embryophytes. We do not know whether the embryophyte lifestyle evolved in an aquatic environment, or whether charophytes invaded the land before the origin of embryophytes. The existence today of many species of both chlorophyte and charophyte algae that live in terrestrial habitats (albeit still needing water for sexual reproduction) certainly shows that the latter was possible. Nevertheless, from our point of view as we follow the journey from the earliest living organisms to flowering plants, the main point is clear: the land was invaded.

Table 1.1 The geological periods

Period	Years before present
Quaternary	1.8 million to present day
Tertiary	66.4 million to 1.8 million
Cretaceous	144 million to 66.4 million
Jurassic	208 million to 144 million
Triassic	245 million to 208 million
Permian	286 million to 245 million
Carboniferous	360 million to 286 million
Devonian	408 million to 360 million
Silurian	438 million to 408 million
Ordovician	505 million to 438 million
Cambrian	570 million to 505 million
Pre-Cambrian	4.5 billion to 570 million

There is still some discussion about which of the three bryophyte lineages—hornworts, mosses or liverworts—represent the earliest land plants. Although there is some support (mainly from comparative anatomy and morphology) for the view that hornworts were the earliest land plants, studies of genome structure, of gene sequences