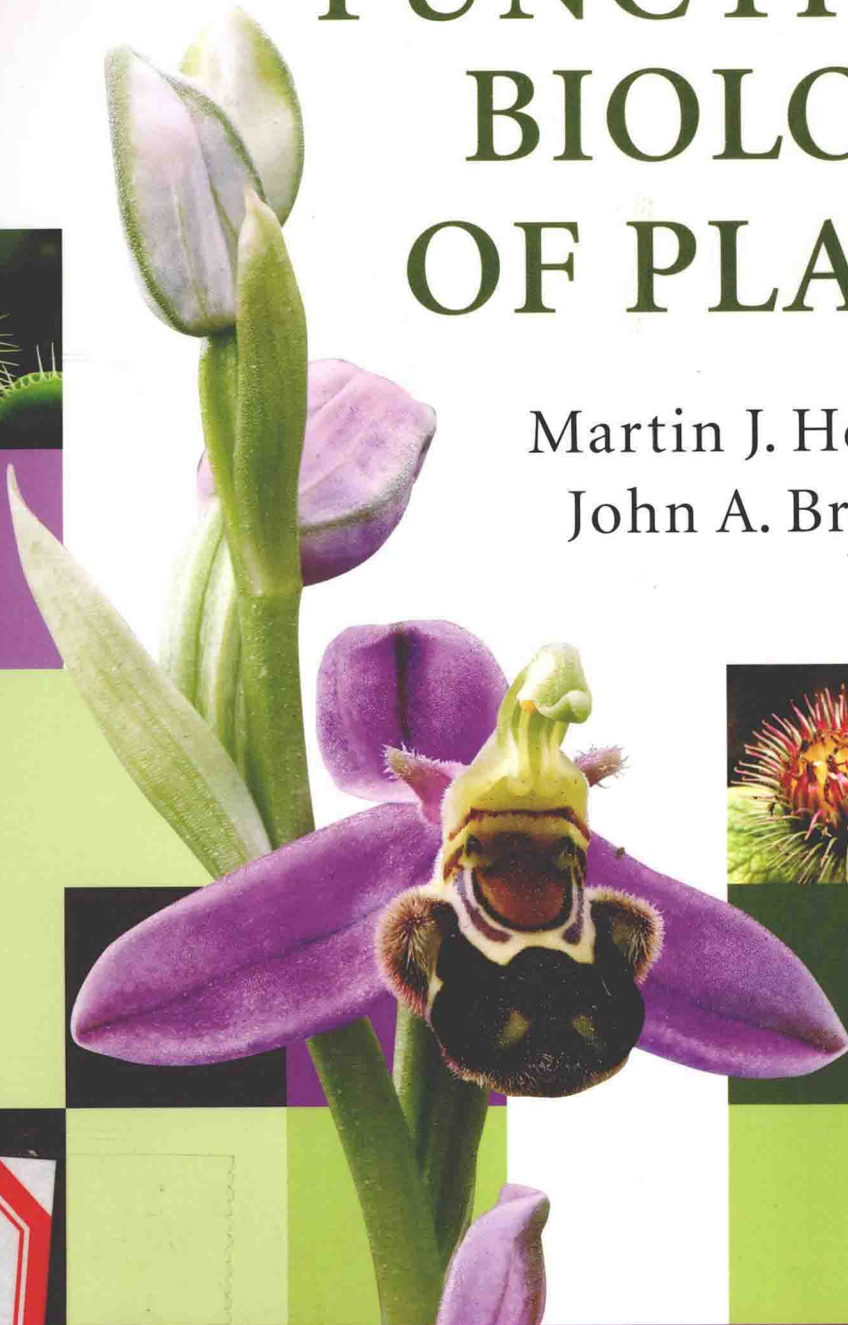


# FUNCTIONAL BIOLOGY OF PLANTS

Martin J. Hodson  
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# Functional Biology of Plants

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MJH would like to dedicate this book to the three plant biologists who have been most influential in his career:

Dr. Helgi Öpik (Swansea University, Wales), who both taught me as an undergraduate and supervised my doctoral studies.

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Prof. Allan Sangster (York University, Toronto, Canada), with whom I had my longest and most successful research collaboration.

Without their guidance and friendship, I would never have got as far as writing this book.

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Dr Cecil Prime (1909–1979) at Whitgift School, Croydon: a firm but caring school teacher whose love and knowledge of plants was infectious. This led me to study plants at university and I was grateful, as a ‘first-generation’ university student, for his continued interest and support during my undergraduate years.

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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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We are also grateful to the institutions and farms that have graciously allowed us to use photographs taken

on their grounds: Westonbirt Arboretum, UK; the University of Oxford Botanic Garden, UK; the University of Leeds, UK; Boyce Thompson Arboretum, Superior, Arizona, USA; the National Botanic Gardens, Glasnevin, Dublin, Ireland; Manor Farm, Haddenham, Buckinghamshire, UK (farmer Tom Bucknell); and Manor Farm, Warmington, nr. Banbury, UK (farmer John Neal). Many thanks also to those relatives, friends and colleagues who have supplied photographs or who have granted permission to use their previously published pictures.

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# Contents

- Preface, ix
- Acknowledgements, x
- 1 Origins, 1
- 1.1 Plants – what are they?, 1
  - 1.2 Back to the beginning, 1
  - 1.3 Eukaryotes emerge, 2
  - 1.4 Photosynthetic eukaryotes – the first ‘plants’, 3
  - 1.5 The greening of Earth – plants invade the land, 4
  - 1.6 Embracing the terrestrial lifestyle, 6
  - 1.7 Arrival of the angiosperms, 8
  - 1.8 Sex and the alternation of generations, 11
- 2 Introduction to Plant Cells, 14
- 2.1 Plant cells, 14
  - 2.2 Cell walls, 15
  - 2.3 The plasma membrane, 21
  - 2.4 Cell compartmentation, 23
  - 2.5 Chloroplasts, 24
  - 2.6 Mitochondria, 27
  - 2.7 The nucleus, 29
  - 2.8 The vacuole, 31
  - 2.9 Endomembrane systems, 31
  - 2.10 Microbodies/peroxisomes, 32
  - 2.11 Ribosomes, 34
  - 2.12 The cytoskeleton, 34
  - 2.13 The mitotic cell cycle, 36
  - 2.14 Metabolism, 42
- 3 Genes, Gene Expression and Development, 56
- 3.1 Genes, 56
  - 3.2 Gene expression, 59
  - 3.3 Chloroplasts and mitochondria, 65
  - 3.4 Control of gene expression – switching genes on and off, 69
  - 3.5 Molecular aspects of development, 75
  - 3.6 Plant hormones, 75
  - 3.7 Light receptors, 86
  - 3.8 Concluding comments, 92
- 4 From Embryo to Establishment, 94
- 4.1 Introduction, 94
  - 4.2 Embryogenesis, 94
  - 4.3 Endosperm, 99
  - 4.4 Perisperm, 100
  - 4.5 Late embryo growth, storage deposition and desiccation, 100
  - 4.6 Seed coat, 109
  - 4.7 ‘Recalcitrant’ seeds, 109
  - 4.8 Apomixis, 109
  - 4.9 Seeds and fruit, 110
  - 4.10 Fruit development and ripening, 112
  - 4.11 Dormancy and quiescence, 114
  - 4.12 Germination, 115
  - 4.13 Establishment, 120
- 5 Roots, 124
- 5.1 External morphology of roots, 124
  - 5.2 Root anatomy, 124
  - 5.3 Root growth, 126
  - 5.4 Soil chemistry and water relations, 130
  - 5.5 Plant mineral nutrition, 132
  - 5.6 Movement of nutrients to the root surface, 133
  - 5.7 Absorption of water and nutrients, 133
  - 5.8 Mycorrhizae, 139
  - 5.9 Root nodules and nitrogen fixation, 139
  - 5.10 Tropisms, 142
  - 5.11 Gravitropism in roots, 143
- 6 Stems, 145
- 6.1 Structure of the stem, 145
  - 6.2 The young stem, 145
  - 6.3 The shoot apical meristem, 146
  - 6.4 Shoot organizational forms, 148
  - 6.5 The mature stem, 148
  - 6.6 The tallest, largest and oldest plants, 151
  - 6.7 Ageing and senescence, 152
  - 6.8 Long-distance xylem transport, 154

- 6.9 Translocation in the phloem, 155
- 6.10 Biological clocks in plants, 157
- 6.11 Phototropism – how do stems curve towards the light?, 160
- 6.12 Gravitropism in stems, 160
- 6.13 Thigmotropism, 161
- 6.14 Nastic movements, 161
- 6.15 Bud dormancy, 163
- 7 Leaves, 166
  - 7.1 External morphology of leaves, 166
  - 7.2 The anatomy of the leaf, 166
  - 7.3 Control of leaf growth and development, 167
  - 7.4 Photosynthesis, 168
  - 7.5 Photorespiration, 174
  - 7.6 The photosynthesis/transpiration dilemma, 177
  - 7.7 C<sub>4</sub> photosynthesis, 178
  - 7.8 Crassulacean acid metabolism (CAM), 181
  - 7.9 Sources and sinks, 182
  - 7.10 Stomata, 184
  - 7.11 Leaf senescence and abscission, 186
- 8 Flowers, 189
  - 8.1 Introduction, 189
  - 8.2 What is a flower?, 189
  - 8.3 Organization of flowers and flowering – inflorescences and life-styles, 191
  - 8.4 Formation of flowers, 192
  - 8.5 Gametogenesis, 198
  - 8.6 Pollination and fertilization, 204
  - 8.7 Evolution, 214
- 9 Environmental Stresses, 216
  - 9.1 Responses to stress, 216
  - 9.2 Temperature, 217
  - 9.3 Waterlogging, 221
  - 9.4 Drought, 223
  - 9.5 Salinity, 226
  - 9.6 Chemical stress, 228
  - 9.7 Light and radiation, 232
- 10 Acclimation and Adaptation to Environmental Stresses, 235
  - 10.1 Adaptation and acclimation responses, 235
  - 10.2 Temperature, 236
  - 10.3 Resistance and adaptation to waterlogging, 240
  - 10.4 Resistance and adaptation to drought, 243
  - 10.5 Resistance and adaptation to salinity, 247
  - 10.6 Tolerance and adaptation to toxic metals, 252
  - 10.7 Adaptations to light and radiation, 256
- 11 Biotic Stresses, 260
  - 11.1 Plant/plant competition, 260
  - 11.2 Plant/animal interactions, 265
  - 11.3 Plant pathology, 271
- 12 Plants and the Future, 284
  - 12.1 Climate change, 284
  - 12.2 Loss of plant biodiversity, 288
  - 12.3 Biomass and biofuels derived from plants, 291
  - 12.4 Genetically modified crops, 297
  - 12.5 Conclusion, 300
- Glossary, 302
- Index, 309



## 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 microorganisms dating back 3.5 billion (i.e.  $3.5 \times 10^9$ ) 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.

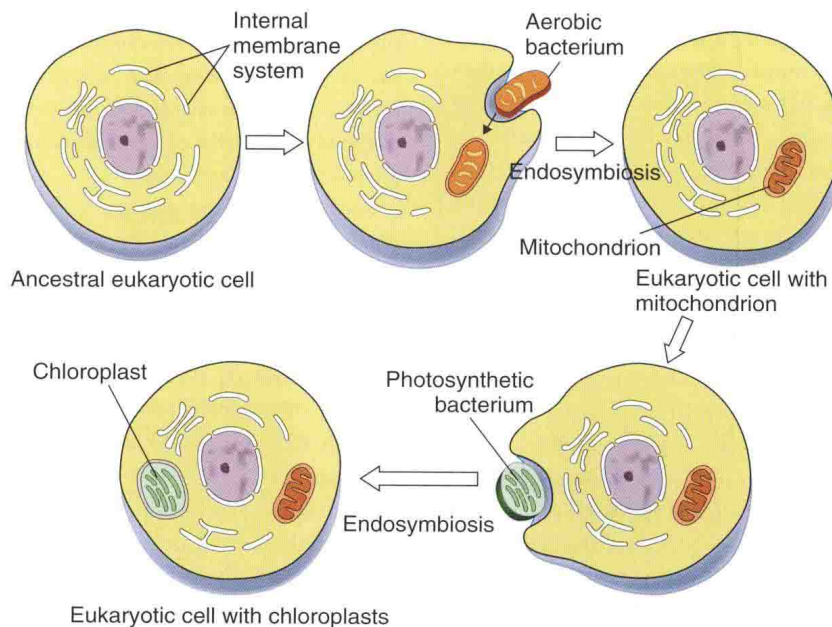
### 1.3 Eukaryotes emerge

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.

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



**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 archaeobacterium. 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>

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  $\alpha$ -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 flagellum<sup>i</sup>), 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’.*

<sup>i</sup>The Greek word *kontos* actually means ‘barge-pole’ or ‘punt-pole’ and gave rise to the English word *quant*.

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 CO<sub>2</sub> 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.

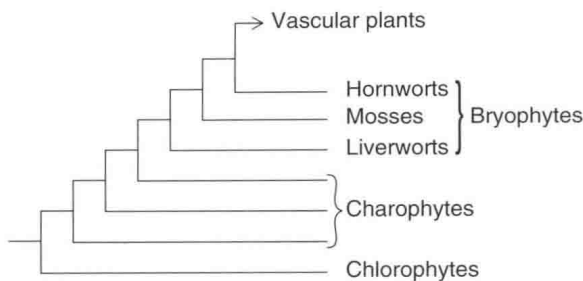
In the simplest examples, this occurs in the zygote, straight after fertilization, but in many protists there is an alternation of generations in which a lifeform that produces gametes alternates with a lifeform that produces spores.

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



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

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).

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.

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

**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

earliest land plants, studies of genome structure, of gene sequences and of particular biochemical mechanisms in extant plants, point to the liverworts.

For example, in common with charophytes, the immediate progenitors of land plants, the mitochondrial DNA of liverworts lacks a particular type of intron<sup>ii</sup>, the type II intron (see Chapter 3, section 3.2.1). All other bryophytes and all vascular plant groups possess three mitochondrial type II introns, although there have been subsequent losses in some lineages within these plant groups. Indeed, those who use molecular data in constructing phylogenies suggest that such data settle the question beyond doubt, so that is the position we take here: the earliest land plants were liverworts, from which mosses and hornworts diverged. The latter eventually gave rise to vascular plants (see next section).

## 1.6 Embracing the terrestrial lifestyle

While terrestrial habitats may indeed provide a good light environment, they also pose some strong challenges for living organisms. The lifestyle of modern bryophytes almost certainly typifies the way in which the earliest multicellular land plants dealt with those challenges. Such a lifestyle is successful in its own way, in its own ecological niches, but it can hardly be said to have conquered the land. Invasion is different from conquest.

<sup>ii</sup>An intron is a sequence of DNA that interrupts the coding sequence of a gene (see Chapter 3, section 3.2.1).

Nevertheless, the popular view of early land plants is one of conquest. We are very accustomed to reconstructions and artistic presentations showing a rich flora of vascular plants. The dominant forms differ according to which geological period is being portrayed, but the common feature is that it is *vascular plants* which make up these fossil forests. Conquest, rather than just invasion of the land, required a number of adaptations, including mechanisms or structures for prevention of water loss and for movement of water within the plant. Furthermore, the selective pressure to seek the light also led to the need for support as many plants evolved an upright stance.

In modern floras, symbiosis between green plants and soil-dwelling fungi features very strongly, as seen in different types of **mycorrhizae** (see Chapter 5, section 5.8). It now seems likely that mycorrhizae, and possibly other forms of symbiosis, were important in helping green plants to invade the land. Mycorrhizae identical in form to modern vesicular-arbuscular mycorrhizae have been discovered in association with *Aglaophyton major*, a very early Devonian land plant, suggesting that nutrient transfer mutualism (symbiosis) may have been in existence when plants invaded the land. This would have aided green plants in exploiting nutrient-poor substrates.

Evidence for the early evolution of vascular plants comes from fossils, from new, less destructive techniques for investigating fossil structure, from comparative anatomy and physiology of extant plants and from molecular phylogenetic studies. These studies provide strong evidence that the hornworts were the immediate ancestors of vascular plants. It is interesting that hornworts can exert some degree of control over water loss and gas uptake because they possess stomata, an important adaptation to life on land and a feature found in all vascular plants (see Chapter 9, section 9.4).

The evidence for a single origin ('monophyly') of the vascular plants comes both from comparative morphology and from an increasing array of DNA sequence data. What is not so clear is the position in the evolutionary tree of some fossil plants found in a remarkable assemblage in the Rhynie chert in Scotland. These fossils, which include *Aglaophyton*, *Horneophyton* and *Rhynia*, possess some features of vascular plants but also retain several bryophyte-like characteristics.

The earliest true vascular plants were the lycopsids or lycophytes. These first appeared in the late Silurian period. Modern members of the group include quillworts



**Figure 1.3** *Lycopodium thyoides*.

Photograph by Dr Gordon Beakes © University of Newcastle upon Tyne. Image from Centre for Bioscience (Higher Education Academy) ImageBank.

(*Isoëtes*), *Selaginella* and club mosses (*Lycopodium*; see Figure 1.3). Today they are relatively scarce, but in the Carboniferous period they were a dominant group, with tree lycopods forming extensive forests. The ability to grow as trees reflects the dual function of vascular tissue, both as a means of conducting water and nutrients throughout the plant and as a means of support of large aerial structures (see Chapters 5 and 6). Tree lycopods eventually became extinct in the Permian period, but they left a legacy, providing the bulk of the material from which coal was formed.

Molecular phylogenetic evidence indicates strongly that lycopods gave rise to a lineage which then diversified into several groups, including the ferns and other fern-like plants, horsetails and eventually the various seed-plant groups. The horsetails, still represented in today's biosphere, are particularly interesting. Like lycopods, they produced dominant forests of tall plants. The ability to grow tall was related to the role of silica in supporting the stems, in contrast to today's tall plants, which are

supported by lignin (see Chapter 2, section 2.2.4 and Chapter 6, section 6.5).

In summary then, the invasion of the land that started with bryophytes became a conquest as vascular plants appeared and then diversified. Indeed, the diversification of plant life on land (and its knock-on effects on the evolution of other organisms) known as *the Siluro-Devonian primary radiation*, is regarded as the terrestrial equivalent of the Cambrian explosion of marine life (as discussed in section 1.2).

Examination of fossil assemblages in strata of different ages reveals a succession of plant groups appearing, some of which became abundant for at least several million years. Many of these groups survive today, but there are some notable exceptions. We have already seen that tree lycophytes, dominant in Carboniferous forests, became extinct in the Permian. The fossil record also contains a major phylum, the progymnosperms, that arose in the late Devonian and early Carboniferous and flourished for a time. The name is somewhat misleading, because they produced spores rather than seeds<sup>iii</sup> and did not give rise to modern gymnosperms. Nevertheless, the late Carboniferous/early Permian periods saw the emergence of gymnosperm groups which are still represented in extant floras. Indeed, gymnosperms were one of the dominant groups in late Triassic and early Jurassic forests – an indication of the selective advantages of the seed-based mode of reproduction (see Box 1.2).

### Box 1.2 Advantages of seeds

Reproduction via seeds provides distinct advantages for life on land. Fertilization does not require water because the sperm does not have to swim to the egg. The one exception to this amongst seed plants is *Ginkgo biloba*,\* in which the sperm are motile. The seed that develops following fertilization is effectively an embryo held in a state of quiescence or dormancy, usually provided with a food store and surrounded by a protective coat.

\*Maidenhair tree: the sole extant member of a group of gymnosperms that arose in the Permian and were abundant through to the end of the Triassic. *Ginkgo* is illustrated in Figure 7.1, Chapter 7.

<sup>iii</sup>The name *gymnosperm* means ‘naked seed’, in contrast to *angiosperms*, in which seeds are enclosed in a structure called the carpel.

Today, the gymnosperms are represented by just four groups – the Gnetophyta or Gnetales (see below), the Coniferae, *Ginkgo* and the cycads (Cycadophyta; Figure 1.4). Except for the conifers, these groups are just relicts in terms of their former abundance and dominance. For example, there are only a few species of cycads, while *Ginkgo biloba* is the sole living representative of a once more diverse group.

## 1.7 Arrival of the angiosperms

Modern angiosperms share with each other many features that are not represented at all in other groups (see Box 1.3) and on that basis they have been regarded as a single discrete group arising from one ancestral lineage – i.e. they are monophyletic. This view has been extensively confirmed by modern molecular phylogenetic analysis.

### Box 1.3 Essential features of angiosperms

The term ‘angiosperm’ derives from two Greek words: *angeion*, meaning ‘vessel’ and *sperma*, meaning ‘seed’. The angiosperms are those plants whose seeds develop within a surrounding layer of plant tissue, called the carpel, with seeds attached around the margins. This arrangement is easily seen by slicing into a tomato, for example.

Collectively, carpels, together with the style and stigma, are termed the ovary, and these plus associated structures develop into the mature fruit. The enclosed seeds and the presence of carpels distinguish angiosperms from their closest living relatives, the gymnosperms, in which the seed is not enclosed within a fruit but, rather, sits exposed to the environment.

Some defining characteristics of angiosperms include flowers, carpels and the presence of endosperm, a nutritive substance found in seeds, produced via a second fertilisation event. Angiosperms thus exhibit the phenomenon of **double fertilisation** (see Chapter 8, section 8.6.3).

But from where did the angiosperm lineage arise? What is the sister group to the angiosperms? If these questions could be answered, we would be making progress towards solving Darwin’s abominable mystery. Prior to the availability of molecular techniques, morphological comparisons had led to the angiosperms being regarded as sister group to the Gnetales, a varied group of gymnosperms represented today by just three families. The most bizarre of these is the family Welwitschioideae, type genus *Welwitschia*, which produce flowers that rest on the ground (see Figure 10.9, Chapter 10).





**Figure 1.4** The cycad *Encephalartos ferox*, native to coastal habitats in Mozambique. Photo: MJH. Used with the permission of Oxford Botanic Gardens.

Angiosperms and Gnetales were together known as the anthophytes, but it is now clear from molecular phylogenetic analyses that the anthophyte hypothesis is untenable. However, that is not to say such analyses have solved the problem. When molecular phylogenetic analysis first became available, it was widely thought that its careful application to seed plants would sooner or later lead to an understanding of angiosperm origins. However, this has not proved to be the case. Indeed, some plant scientists believe that the mystery is as deep now as it was in Darwin's day. The problem is that different analyses tell different stories, depending on which genes are used in the analysis and whether DNA or protein sequences form the basis for comparison. Thus, the distinguished evolutionary botanist, James Doyle, at Davis, California, wrote in 2008: '*Much of what we thought we knew 10 years ago about seed plant phylogeny... has been thrown into doubt by molecular analyses.*'

Doyle also wrote that: '*Resolution of these problems requires integration of molecular, morphological and fossil data in a phylogenetic framework.*'

The data from fossils include analyses of flowers and flower-like structures in presumed angiosperms such as

*Archaeofructus* from the early Cretaceous (currently the earliest known fossils of angiosperm-like flowers date from this period) and in seed ferns. The molecular data include molecular clock estimates that put the origins of angiosperms no earlier than the Jurassic period. This integration of approaches suggests that the divergence from the gymnosperms (and more specifically from the cycads) of the lineage that led to angiosperms happened probably as early as the Carboniferous. In other words, the last common ancestor between the two groups of extant seed plants – gymnosperms and angiosperms – was alive in the Carboniferous period. This divergence established the lineage known variously as the angiosperms or the pan-angiosperms. However, as pointed out by Doyle in a personal communication to JAB, the early members of this lineage: '*... need not have looked any more like modern angiosperms than pelycosaurs (in an early Permian branch from the mammalian stem lineage) look like mammals.*'

So, although the gymnosperms (and in particular the cycads) are the nearest living relatives to modern angiosperms, the actual sister-group to angiosperms is to be found among extinct groups within the pan-angiosperms, namely the seed ferns (Figure 1.5). Current