Peter
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Physiology and Behaviour of Plants

Wiley

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PHYSIOLOGY AND BEHAVIOUR OF PLANTS

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This book is dedicated to Helen and Edmund Scott, whose love and support through many plant hunts made this work possible.

Preface

We live in an age where we are more dependent upon our understanding of plants than ever before. With the world human population exceeding 6 billion, never has it been more important to be able to feed reliably so many people. Yet, paradoxically, it is an age when interest in plant biology is at an all-time low. The plant biology content of GCSE and A level biology in the UK has become minimal as more and more human biology is added to the curriculum. Funding of plant science research has become minuscule compared to that commanded by the medical sciences. As a consequence, universities employ fewer plant biologists and as a knock-on effect plant biology is scarcely offered as part of a biology degree any longer. Where plant biology is offered, the lecture material can be badly handled and few students are prepared to study it into their final year. But plant biology has to be one of the most interesting subjects in the whole of biology. Plants are central to life and play a crucial role in dictating the diversity of life we currently enjoy on this planet.

  To address this problem, what is not needed is another plant physiology textbook. There are many volumes which do the job of teaching plant form and function very well. But what often comes across in these texts is that plants are stale and irrelevant. Somewhere, the interest, appeal and relevance to the real world has been lost in the detail. If you don't think this is true, then look no further than the most amazing enzyme of plants, RUBISCO. Most books dive into the sub-unit arrangement and its carboxylase/oxygenase properties, but there is nothing to impress the reader that we are discussing the enzyme that supports virtually all of life currently on this planet! RUBISCO is the marvel enzyme of the universe, and yet most students never realize this.

Then consider photo system II, a complex enzyme which splits water to provide an electron donor for a chlorophyll molecule and allows non-cyclical photophosphorylation – but the fact that it generates all of the oxygen we need to breathe and supports the only other known biological autotrophic pathways known in bacteria is lost. So what is, on the face of it, merely a tricky biochemical pathway, suddenly becomes a vital component of our everyday life. Plant biology is amazing in so many ways that this book barely scratches the surface. Having said that, the most interesting and remarkable topics on plant biology have been hand-picked to give students the best chance possible to study plants in all of their glory. The book deliberately steers clear of in-depth discussion of molecular biology and the explosion of knowledge this is providing. This is because much of this knowledge is incomplete and as yet does not give an interesting insight into the mechanisms of plant life. Where molecular mechanisms are discussed, they are always related to the whole plant function, as this is primarily what the text is concerned with – plants.

Peter Scott

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Introducing plants

In this chapter, we look at how plants originated, what floral diversity there is today and the make-up of the plant and its ultrastructure.

The beginning: the evolution of plants and the major divisions

In the beginning, it is most probable that plants evolved from photosynthetic bacteria. From these bacteria the red and green algae evolved; and from freshwater-dwelling green algae the simple lower plants, such as mosses and ferns, evolved; and so on, up to the higher plants. A phylogenetic tree is shown in Figure 1.1 and Table 1.1 to demonstrate the relationship between the members of the plant kingdom and their relative abundance through the history of the planet.

Figure 1.1 Schematic diagram of the phylogeny of plants. The diagram shows the evolutionary relationship between the different species and the relative abundance in terms of species numbers (shown by the width of the dark red lineage tree). On the *y* axis the different time periods of the evolutionary history of plants are shown. The diagram is based on that presented by Ridge 2002.
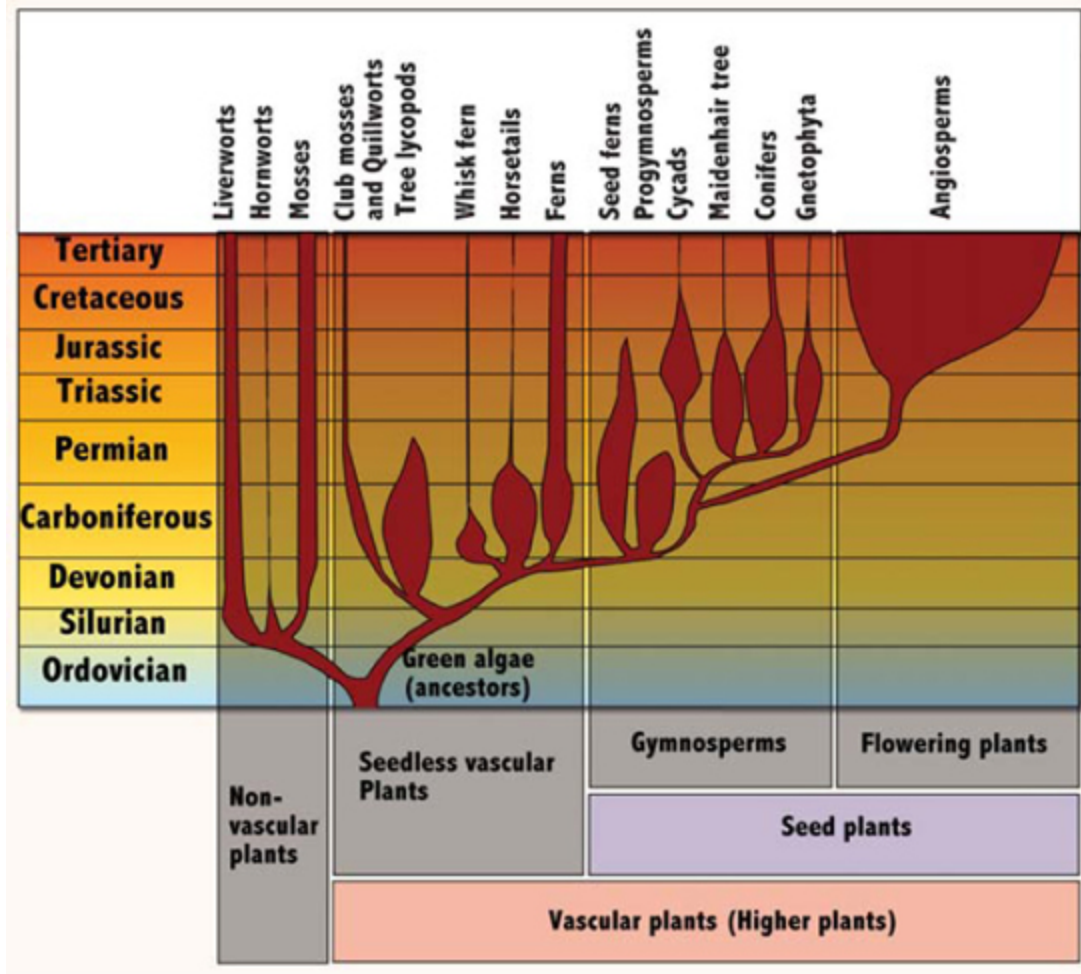
Table 1.1 Estimates of numbers of species occurring in plant divisions.

Plant division	Common name	Approximate number of species
Hepatophyta	Liverworts	6000
Anthocerophyta	Hornworts	100
Bryophyta	Mosses	10 000
Lycophyta	Club mosses and quillworts	1000
Tree lycopods		Extinct
Psilotum	Whisk fern	3
Equisetum	Horsetail	15
Pterophyta	Ferns	11 000
Peltasperms	Seed ferns	Extinct
Progymnosperms		Extinct

Cycadophyta	Cycads	140
Ginkophyta	Maidenhair tree	1
Coniferophyta	Confers	550
Gnetophyta	Vessel-bearing gymnosperms	70
Angiosperms	Flowering plants	23 5000

These estimates are based on there being around 260 000 different species of plant in the world. Species of plants based on data from Ridge 2002.

Conquering the land

The origin of plants was in water, where both photosynthetic bacteria and then algae originated. Light penetration of water reduces with depth, and on average only 1% of incident light reaches to a depth of over 15 m. As a consequence, there is a body of water at the surface known as the photic zone, where all of the photosynthetic activity in oceans occurs. A great deal of this photosynthetic activity still occurs at the shores of the oceans, where more complex algae have evolved; as a group these are commonly referred to as seaweeds. Algae are restricted to the oceans and freshwater bodies since, as part of the life cycle of algae, gametes (sex cells) that swim through water are required for sexual reproduction. This is thought to have been a major hindrance to plants attempting to colonize the land surface of the Earth and to overcome this, new reproductive systems needed to evolve.

   For the colonization of the land, methods of gamete transfer that were independent of water needed to evolve. Bryophytes (the mosses and liverworts), the first land-dwelling plants, still depend on moisture to complete their reproductive cycle (Figure 1.2). Sperm is released from haploid male gametophytes (a gamete-producing individual involved in the life cycle of bryophytes) which must swim to fuse with the egg cell of the haploid female gametophyte.

This fusion yields a diploid zygote that divides to form a stalked cup-like structure, which releases haploid spores. These spores then form haploid male and female gametophytes. As a direct consequence of this life cycle and its requirement for water, mosses and liverworts are restricted to growing in moist habitats. In addition, these plants have no waterproof cuticle or vascular tissue, and are therefore very limited in their ability to transport water and carbohydrate made during photosynthesis to the rest of the plant. This makes it necessary for these plants to have a prostrate growth habit (rarely exceeding 2 cm in height), colonizing banks near to areas of water. Bryophytes do possess root-like structures known as rhizoids, but these are thought to have a function of anchorage rather than for transporting water to the aerial tissues. As a result of their inability to regulate water in the plant, bryophytes are poikilohydric; therefore, if the moisture declines in their habitat it also begins to decrease in their tissues. Some mosses can survive drying out but others need to be kept wet to survive. However, the ability to tolerate temporary drying of a habitat is a first step to colonizing dry land.

Figure 1.2 The life cycle of a bryophyte (mosses). There are around 10 000 different bryophyte species. The life cycle of bryophytes occurs in two phases, the sporophytic phase and the gametophytic phase. In the sporophytic phase the plant is diploid and develops as sporophyte. This releases spores which form gametophytes that are haploid. These form into separate sex gametophytes. The male gametophyte releases sperm, which is motile and swims towards the archegonium on the female gametophytes that bears the egg cells. These fuse to yield a zygote that then forms the sporophyte.
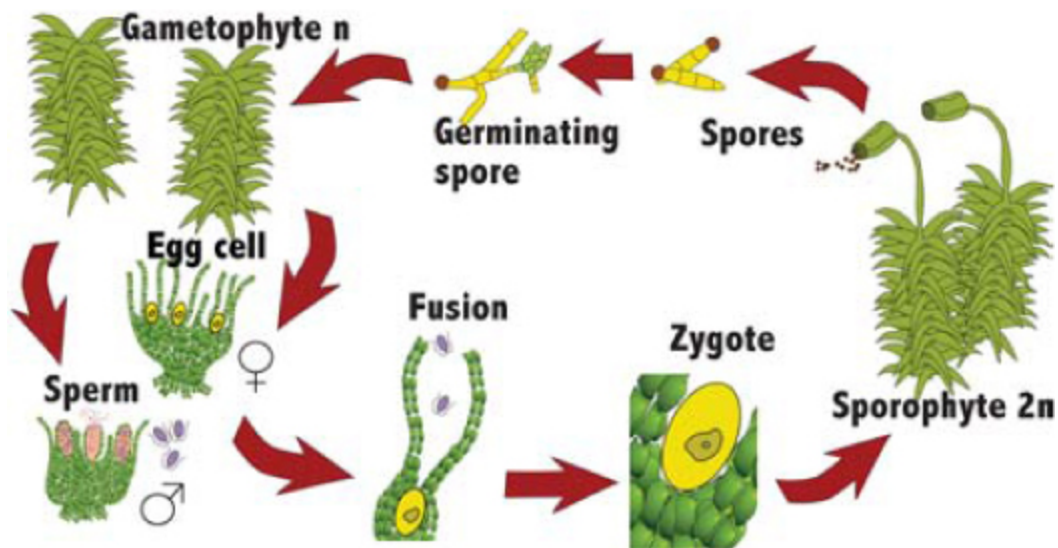
The mosses exhibit little ability to control water loss and if plants were ever to colonize a greater area of the land, the non-vascular plants needed to evolve solutions to this problem by developing a water transport system and a means of regulating water loss from the plant surface. The hornworts possess stomata on their leaf surfaces and therefore took the first steps to regulating water loss while maintaining gaseous exchange, which is essential for photosynthesis. These structures are absent in the mosses but present in more advanced plants. The prostrate growth of the mosses does not use light effectively and makes the damp habitat very competitive. As a consequence, there must have been a great selective pressure for structures to evolve in plants which raised the plants off the ground, which will have led to the evolution of a limited upright shoot in the bryophytes.

The evolution of the pteridophtyes (ferns) marked the development of a simple vascular tissue, allowing long-distance transport of water and carbohydrate around the plant. It also permitted the evolution of the upright shoot, thereby making taller plants possible. Ferns use a method for sexual reproduction similar to that of mosses (Figure 1.3). The adult fern plant is diploid and releases haploid spores, which divide and form male and female

gametophytes. The male releases haploid mobile gametes, which swim and fuse with the female gametes to form diploid zygotes, which then divide to form the adult ferns. Pteridophytes possess distinct leaves, which enhance their ability to photosynthesize. Although the pteridophytes possess a water-resistant cuticle, they exhibit poor control of water loss from their leaves and in most instances are still restricted to moist habitats. The spores released by the adult ferns are tolerant of desiccation but movement of the male gamete still requires water. The ferns were the first plants to evolve lignin as a defence and support structure (see later). Plants that contain vascular tissue are frequently referred to as 'higher plants'.

Figure 1.3 The life cycle of a pteridophyte (ferns). The adult fern, or sporophyte, is diploid and on maturity releases spores from sori on the underside of leaves. These spores fall to the soil and germinate and from a gametophyte, also known as a thallus. This matures and forms an archegonium (where egg cells form) and an antheridium (where the sperm develops). The sperm are released and swim to the egg cells, with which they fuse to form diploid zygotes. The zygote then develops into an adult fern.

Adult fern Sporophyte (2n) — Egg cell — Spores (n) — Zygote (2n) — Sperm — Gametophyte
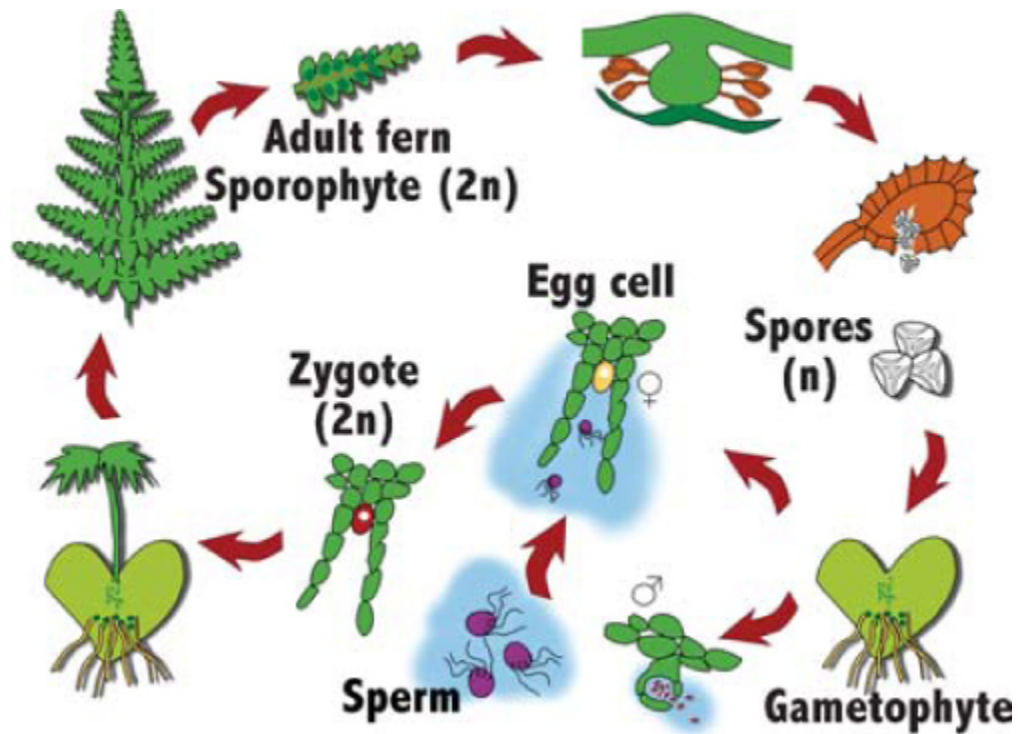
A small number of ferns and lycophytes exhibit heterospory (separate sex spores). In bryophytes and pteridophytes discussed so far, the spores are all identical. However, with heterosporous species the male sperm are formed from a microgametophyte and the female gamete from a macrogametophyte (Figure 1.4). The formation of separate sex gametophytes is considered to be one of the major steps towards the formation of plants that bear seeds.

Figure 1.4 The life cycle of a heterosporous pteridophyte. In a small number of instances species of ferns are heterosporous and this is thought to be a crucial evolutionary step in the formation of the flowering plants. In Figure 1.3 the egg cell and the sperm are the same size, but in heterosporous pteridophytes, the female gamete (macrogametophyte) is much larger than the male gamete (microgametophyte).
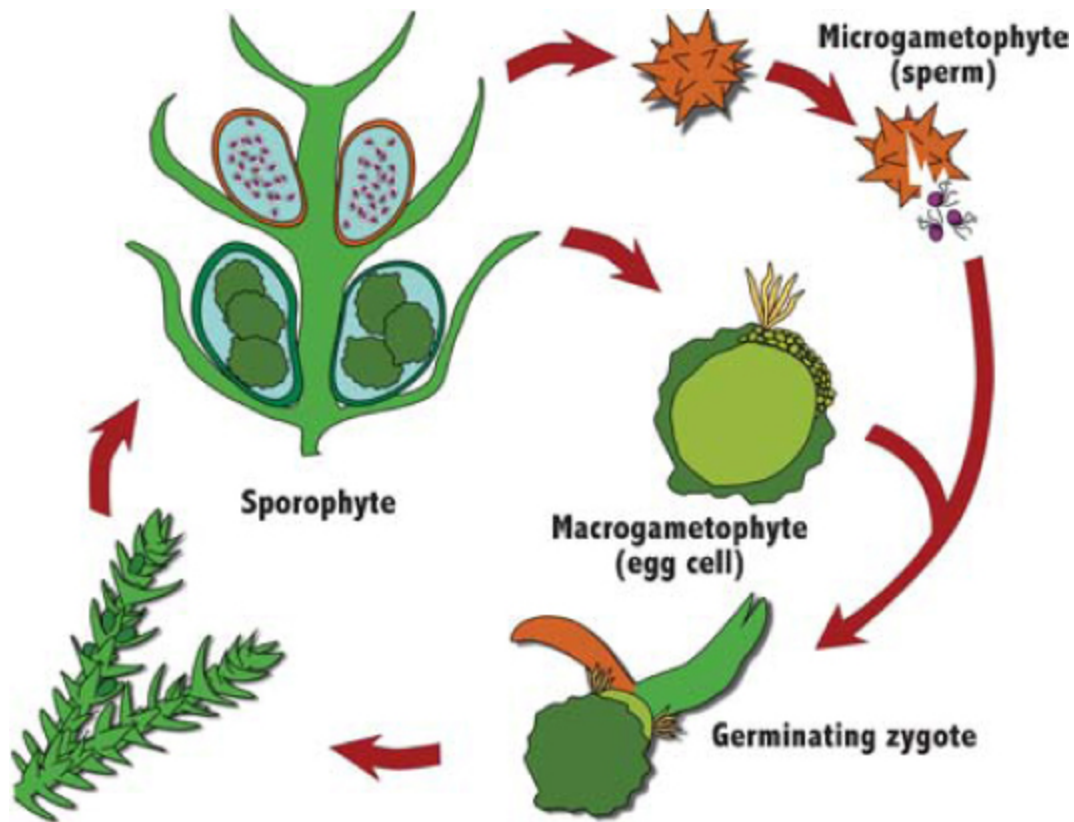
The habitat range of plants on land was widened considerably with the evolution of plants that produce seeds. The transition from being wholly aquatic to wholly terrestrial is considered complete in such plants. The seed-bearing plants are divided into two divisions, the gymnosperms (Pinophyta) and the angiosperms (flowering plants, Magnoliophyta). The angiosperms form the largest and most diverse plant division. Angiosperms produce reproductive structures in specialized organs called flowers, where the ovary and the ovule are enclosed in other tissues. The gymnosperms do not form a flower and the reproductive structures are in the form of cones, in which the ovule is not enclosed at pollination. On formation of a seed, the embryo is covered by a specialized scale leaf rather than the ovary and this gives rise to the name 'gymnosperm', which means 'naked seed'. Gymnosperms were widespread in the Jurassic and Cretaceous periods of the Earth's history but there are now fewer than 800

different species. They occupy a range of different habitats from temperate forests to more arid habitats. Most of the species are trees and shrubs, which are adapted very well to temperate areas of the world, where water availability is limited over extensive periods of the year (due to ground frosts). Species such as pines are well adapted to cold climates through features such as small needle-shaped leaves (which hold little snow and are resistant to weather damage), sunken stomata (which reduce water loss) and a thick waxy cuticle. There are a few examples of gymnosperms which live in desert habitats, such as *Welwitschia*, and in tropical habitats, such as the cycads, but these species are limited in number.

The gymnosperms were once the dominant division of plants on Earth, but in the Cretaceous period there was a huge expansion in the number of angiosperms, which led to the steady decline of gymnosperms. The failure of gymnosperms to maintain the dominant position appears to be the result of improvements in reproductive biology in the angiosperms. Gymnosperms use wind as a means of transferring pollen from the male cones to the female cones (Figures 1.5 and 1.6). The use of air currents for pollination will be discussed in greater detail in Chapter 9, but suffice it to say here that this process is inefficient and wasteful of resources. Moreover, gymnosperms rely mainly on the scale leaf around the seed to disperse it, with a few species such as yews using primitive fruits to attract animals. Angiosperms, however, evolved a huge range of different methods for attracting insects and animals for flower pollination and for the subsequent seed dispersal. The evolution of broader leaves may have been a disadvantage in colder climates, but everywhere else this allowed increases in efficiency of photosynthesis and hence growth rates.

Figure 1.5 The life cycle of a gymnosperm. Mature gymnosperms such as conifers form two types of cones; the female cone is called the ovulate cone and the male cone is called the pollen cone. The female egg cell forms from a macrospore mother cell, which undergoes meiosis to form a tetrad of macrospores. Only a single one of these survives and undergoes many mitotic divisions to form ultimately the female gametophyte. An egg cell forms which can be up to 3 mm in diameter, making it the largest egg cell in the plant kingdom. The male gametes are released and are carried by air currents to the ovulate cones. The pollen germinates and fertilizes an egg cell. This goes on to develop into a zygote and ultimately a seed. This seed is not enclosed by an ovary, which gives the gymnosperms ('naked seeds') their name. There are four distinct divisions of the gymnosperms: Coniferophyta, Cycadophyta, Ginkgophyta and Gnetophyta. These are split into less than 800 different species recognized currently.
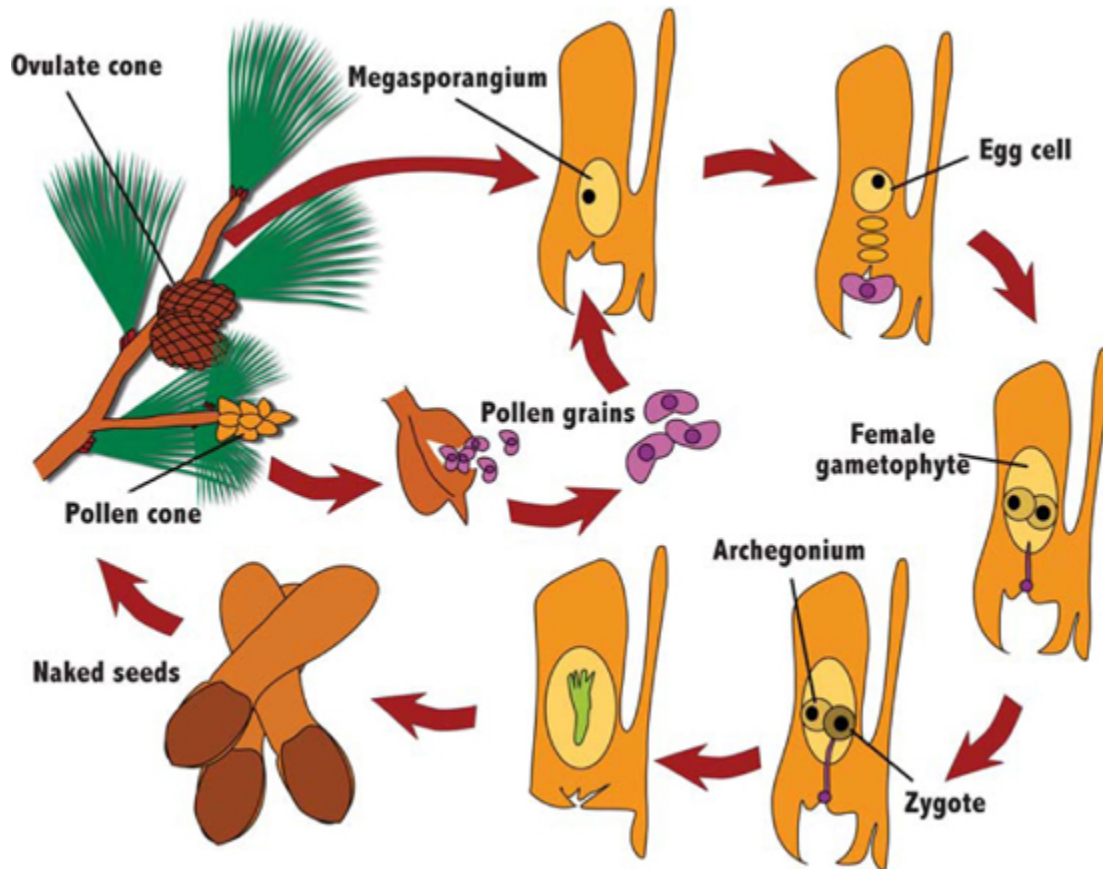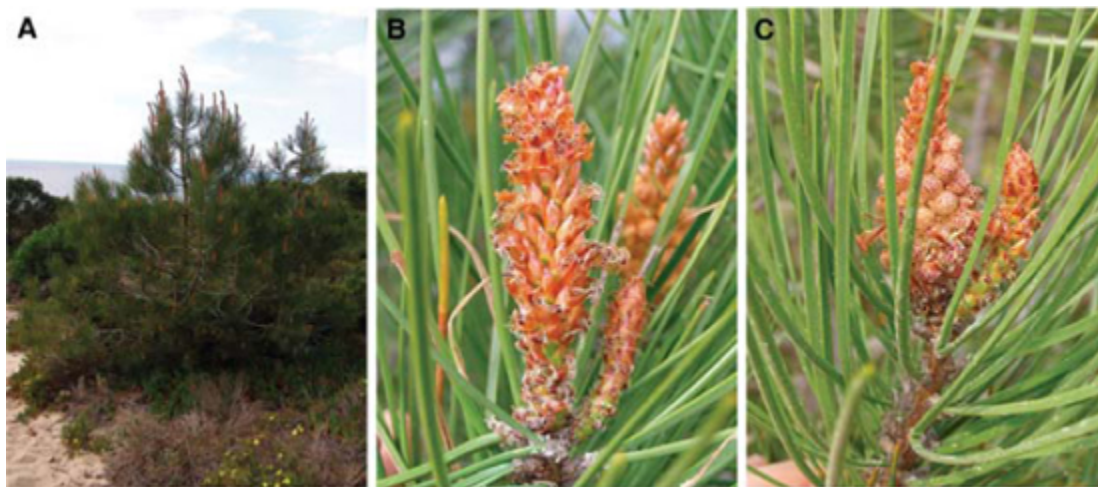
Figure 1.6 Gymnosperm cones. Here the male (B) and female cones (C) of the stone pine (*Pinus pinea*) are shown.

Although gymnosperms are not as successful as angiosperms, they still have an important place in the ancestry of the flowering plants. Most of the structures thought of as typical in flowering plants can be found in

individuals of the gymnosperms, but no species contains them all. The closest relative to the gymnosperms is thought to be the phylum Gnetophyta, which contains species such as *Welwitschia mirabilis* and *Ephedra viridis* (see Chapter 19). Angiosperms first appear in fossil records in the early Cretaceous period, around 140 million years ago, but despite their late appearance they have been spectacularly successful (Willis and McElwain, 2002). The features that identify angiosperms are:

1. The presence of an enclosed ovary (covered by carpels and two layers of integument).

2. The formation of flowers.

3. The presence of specialized vascular tissues for nutrient and water movement.

4. The presence of double fertilization for the formation of the embryo and endosperm.

There are around 350 different families of flowering plant and 260 000 different species. The life cycle of a typical angiosperm is shown in Chapter 9. The angiosperm division is subdivided into two classes of plants, the Magnoliopsida (dicotyledons, around 180 000 species) and the Liliopsida (monocotyledons, around 80 000 species, about 33% of these belonging to the famly Orchidaceae). The principal characteristics that allow easy identification of these classes are shown in Table 1.2. Monocotyledons produce pollen with a single pore or furrow, which is the place where the pollen tube will emerge on the stigmatic surface upon germination. This means that if the pollen grain lands with this furrow facing away from the stigma, fertilization is more difficult to achieve. In dicotyledons there are three such furrows and this is thought to result in a furrow always being in contact with the surface of the stigma, therefore making fertilization easier (Endress, 1987). However, both classes are very successful in terms of land area covered and number of different species. From the earliest fossil records there is

compelling evidence that the dicotyledons were the first angiosperms to evolve, with very few monocotyledon tissues being preserved as fossils at this time. However, many of the monocotyledon species known today are thought to have evolved from species originating in the early Cretaceous period. It is thought that the absence of monocotyledons from the fossil record may be a result of there being fewer monocotyledon species and the fact that they are generally herbaceous and do not possess woody tissues, which would make them less likely to be preserved as fossils.

Table 1.2 The usual distinguishing characteristics between monocotyledons and dicotyledons.

Feature	Monocotyledons	Dicotyledons
Flower structure	Petals and sepals in groups of three	Petals and sepals in groups of four or five
Pollen	Monocolpate (one pore or furrow)	Tricolpate (three pores or furrows)
Cotyledons	One	Two
Vascular tissue arrangement in leaves	Parallel	Net-like
Vascular bundles through stem	No apparent order in arrangement	Encircling the stem just under the epidermis of the stem
Secondary growth	Absent	Present

Redrawn from Raven *et al*. (1992) and Magallon *et al*. (1992). There are exceptions to these characteristics, but those listed are the common features that allow easy identification.

The most recent evolutionary change to have occurred, judging from the plant fossil record, is the appearance of plants possessing modifications to the usual C3 pathway for photosynthesis, i.e. C4 and Crassulacean acid metabolism (CAM) plants. These plants are discussed in greater detail in Chapter 12.

The evolution of lignin

Lignin is a complex polymer of phenylpropane units, containing very variable bonding, bound to cellulose to make the cell wall of plants ([Figure 1.7](#)). The structure is very rigid and forms a strong support or defence structure in various plant tissues. The evolution of lignin synthesis in plants was essential for the transition from prostrate plants to upright plants. In order to move water through tissues, osmosis can be relied on for short distances, but if the plant is to become upright, reinforced transport vessels are needed in the form of the xylem (see Chapter 4). It has been proposed that plants could not grow taller than a few centimetres in height without the evolution of lignin (Niklas, 1997). Lignin is thought to have evolved around 430 million years ago and the key to its appearance has been proposed to be the high oxygen levels present in the atmosphere at that time (Willis and McElwain, 2002). Lignin played a central role in the evolution of plants because it permits the support of upright plants, which optimized the use of light levels. It allowed the evolution of the upright ferns and ultimately the first trees. The evolution of upright plants also permitted the movement of plants into a wider range of habitats and hence allowed plants to conquer the land. In addition, lignin is not easily broken down by other organisms; it was therefore an excellent defence compound. As a consequence of this, large amounts of plant material could not be degraded and gradually became buried in the earth, yielding what we now know as oil and coal. These reserves provided a huge sink for taking CO_2 out of the atmosphere and storing it in an organic form. This supported a fall in global CO_2 levels, which in turn influenced evolution of all the other organisms on the planet. It is only in the present day that this stored CO_2 is being re-released into the atmosphere through the actions

of humankind, with the knock-on effect of potential global warming.

Figure 1.7 The structure of lignin. The group of compounds known as lignin are among the most abundant organic chemicals on earth. Lignin makes around one-third of the dry weight of wood and is especially used by plants to reinforce the xylem for support. It is also a very effective defensive compound, being very difficult to break down and metabolize. It is a biopolymer made up of several different monomers, two of which are shown, coniferyl and sinapyl alcohol (A). These monomers are polymerized to make the complex structure of lignin, an example of which is shown in (B).
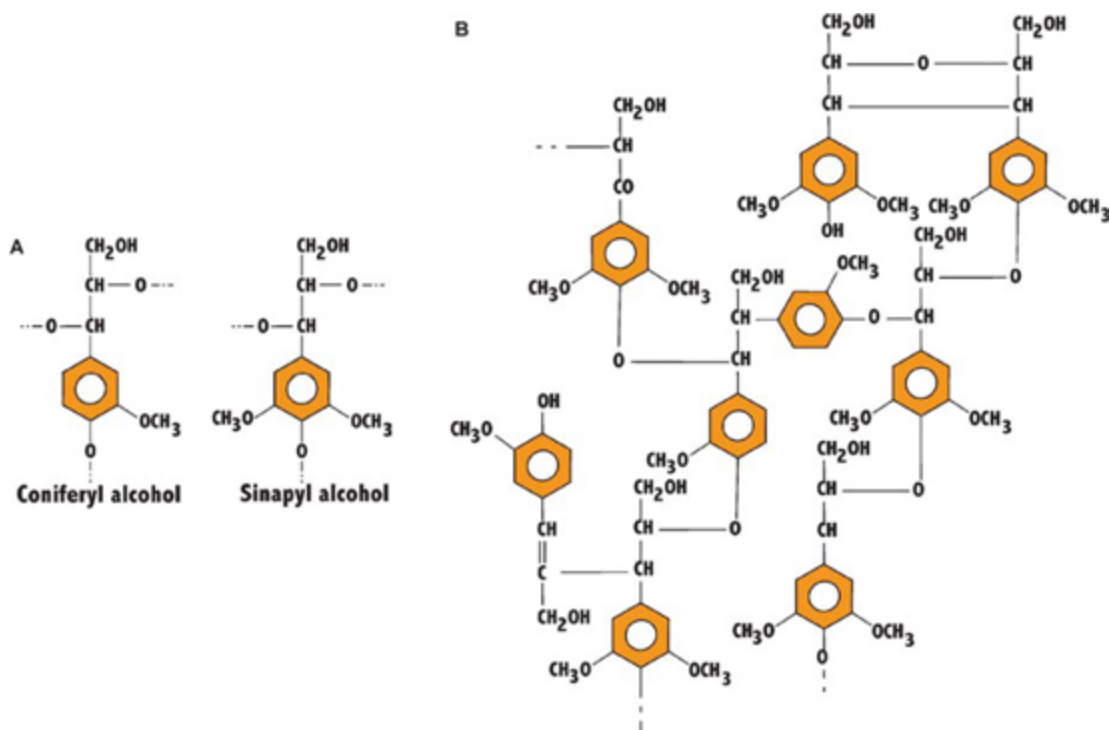
Plants and mass extinction

Over the course of the Earth's history, there are five recognized periods of mass extinction in the marine fauna records. These are times when 20–85% of all living marine

fauna species are recorded to have disappeared in the fossil record. The most well-known of these events is at the boundary between the Cretaceous and Tertiary periods, when all the dinosaurs are thought to have become extinct. At this point, around 80% of all animal species became extinct. How did plants fare at this time? There is a marked reduction in the abundance and range of species represented in the fossil record at this point in time (Saito *et al.*, 1986). There was then a striking, but temporary, rise in the abundance of fern spores, which was followed by a major reduction in the diversity of fossil plants compared with that prior to the boundary event. It is thought that this may represent major destruction of much of the vegetation, followed by a rapid process of revegetation. However, different areas of the world seem to have been affected in different ways, such that in some regions the vegetation cover appears scarcely to have changed. The extinction rate of plants at this time has been estimated as 5–10% (Halstead, 1990). This period was therefore one in which a great deal of the Earth's biomass was lost, but there were no mass extinctions, as observed with the fauna species. Similar observations were made at the other points of mass extinction noted in the fauna fossil records.

Why did mass extinctions not occur in the plant kingdom? The answer to this question reveals something about the versatility of plants and why they are so successful. Most animal species are very mobile and if their habitat becomes less amenable to survival, they can simply move to a new region. However, if the changes are far-reaching, it may not be within the organism's capacity to move beyond the stressed habitat and death or extinction is likely. These major extinction events are all likely to have been global catastrophes resulting in major changes in the world's climate, therefore escape would have been impossible. Plants, however, have always had to tolerate the