
Plant Life

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Preface

Photosynthetic organisms are vital and fascinating. They are the factories which trap the energy which drives almost all ecosystems. But plants are also extremely diverse in both their size and their shape, ranging in form from tiny cyanobacteria a matter of micrometres in diameter to 100 metre high trees. Despite this we felt that they always seemed to draw the short straw in biology courses. In many school curricula the concentration is almost entirely on the process of photosynthesis, and the delightful variety of the forms and lifestyles of plants is swept under the carpet. At the other extreme, plant diversity courses at universities tend to plough remorselessly through all the different taxonomic groups of plants. They emphasize a bewildering variety of morphological and reproductive characteristics, but fail to treat plants as living organisms. Consequently courses tend to become exercises in rote learning rather than in understanding plant life.

We felt that it was high time to redress the balance by writing a book with a strong evolutionary theme, and fortunately in many ways the timing is ideal for such an enterprise. Recent advances in cladistics and molecular systematics have given us a far better idea of how plants are related to each other and how they evolved. At the same time popular books, and television series such as *The Private Life of Plants* have shown that treating plants as animals are treated—as competing and struggling organisms—pays dividends. They come to life and even seem to exhibit individual personalities. This book takes this approach, and, using some of the excellent zoology texts as a model, investigates plants from an evolutionary perspective to tell what we feel is the fascinating story of plant life.

Of course one cannot understand the pattern of plant evolution without knowing something about how evolution works or how it can be studied. The

first section of the book therefore outlines evolutionary and phylogenetic theory. This theory is then used to enlighten the story, told in the second section of the book, of how the major taxonomic groups of plants live and how and why they evolved. But plants from different taxonomic groups are by no means evenly distributed around the globe. The final section examines the varied vegetation types found in the different parts of the globe, and investigates how and why plant diversity varies. It seeks to explain why certain groups of plants are more successful and examines the many ingenious means all sorts of plants use to survive.

The book has taken too long to produce! We would like to thank the succession of commissioning editors from Blackwell Science, Simon Rallison, Susan Sternberg and Ian Sherman, for their interest and encouragement throughout the process. We would also like to thank the reviewers John Dodge, Karl Niklas, Thomas Speck and Barry Thomas for their helpful comments and suggestions on early drafts of the manuscript. Any remaining errors are ours. Much of the merit of a book of this sort must be due to the quality of the illustrative material. In our case we have been enormously fortunate to have been supplied with this by our knowledgeable and helpful colleagues: Fred Rumsey, who produced the excellent set of line drawings; Sean Edwards, who supplied most of the photographs; Elizabeth Cutter, Sally Huxham and Bill Chaloner. We thank all of them for supplying us with illustrations, some of which we did not even know we wanted! Finally we would like to thank our families: Yvonne, Russ and Max for all their encouragement and forbearance throughout the long gestation period of this book.

Roland Ennos and Liz Sheffield

Part 1

Evolution and plant diversity

1.1 INTRODUCTION—THE DIVERSITY OF PLANT LIFE

There are two overriding impressions you receive if you survey the world of plants. The first is one of bewildering diversity, despite the fact that most plants produce food by the same mechanism—photosynthesis. This is true most obviously in numerical terms, because there are probably over half a million species of photosynthetic organisms. But there is also a vast diversity of forms, since photosynthetic organisms range from tiny unicellular algae under a micrometre in diameter to huge multicellular trees over 100 m tall and 100 tonnes in weight.

The second impression, which you get when you look more closely at each species, is the perfection of its adaptations to its own particular lifestyle. Each photosynthetic organism seems to be well suited, and apparently well designed, to live in its own particular habitat. Cacti, for instance, are adapted to the dry desert habitat by having thick, barrel-like stems which are well suited for storing water; and spines, which help protect the water from being stolen by animals. They make a striking contrast with kelps which have adapted to the subtidal environment in which mechanical forces dominate. Their flexible fronds are ideally suited to resist the battering of waves and they are securely cemented to the sea bed by a holdfast.

It is the aim of this book not only to *catalogue* the diversity of photosynthetic organisms and *describe* their adaptations, but also to explain *how* this has been achieved. The key to understanding both diversity and adaptation is Darwin's theory of **evolution by natural selection**, and therefore this book will have a strong evolutionary slant. Modern plants are not just a random collection of organisms which may

be conveniently placed by taxonomists into arbitrary groups, but are the results of millions of years of struggle for life. As we shall see, this has resulted not only in the evolution of large numbers of species, but has also driven evolution in directions which are, with the benefit of hindsight, readily explicable. Once plants invaded land, for instance, selection for taller and taller plants would have made the evolution of trees almost inevitable.

1.2 FACTORS AFFECTING PLANT EVOLUTION

1.2.1 The physical environment

There is no doubt that the physical environment in which a plant grows strongly constrains its evolution. All plants require water, nutrients and light, and to obtain them their body form has to change with the habitat.

Because marine organisms are surrounded by water they do not have the problem of desiccation and have no need to develop special water-conducting tissues. However, because water rapidly attenuates light and because dissolved gases diffuse only slowly, they need adaptations to obtain adequate light and nutrients. Consequently many marine forms are unicellular and motile, using flagella to stay up in the upper illuminated regions and to move to nutrient-rich areas.

In contrast, although the air that surrounds land plants rapidly supplies the gases they require, it allows them to desiccate rapidly. Most land plants have therefore had to develop special root systems for absorbing water from the soil, and vascular

systems to conduct it to their leaves. As a consequence they are by necessity immobile.

Some habitats are also so extreme that only a few particularly well-adapted organisms can survive in them. For example, encrusting algae are the only forms that can survive on severely wave-swept shores. Similarly rocks in deserts are colonized only by the few species of lichens that can tolerate the near-permanent desiccation.

1.2.2 The limitations of physical explanations

Adaptation to the physical environment can explain much, but by no means all, about the diversity of plants. First, there are far more species of plants than there are physical habitats. Second, many plants are not found in parts of the world where they are perfectly capable of growing. Cacti, for instance, will also thrive in much wetter places than the deserts in which they are found and they are even absent from the deserts of the Old World. Finally, and most crucially, many of the most important attributes of plants cannot be explained by physical factors alone. There is no physical reason, for instance, why trees should have trunks and branches; because they do not photosynthesize, they will be merely a drain on a tree's resources. If a physicist were to design an ideal 'efficient' land plant it would resemble the simple liverwort *Pellia*, being a simple layer of photosynthetic cells lying on the soil surface.

1.2.3 Biological interactions

Because physical factors cannot alone explain the diversity of plant form it is clear that other factors must be involved. It is generally accepted that the evolution of plants has also been greatly driven by their struggle for life with other organisms. The great diversity and adaptive perfection of plants is therefore due more to their biological interactions (Fig. 1.1) rather than just to their adaptations to their physical environment.

Competition

The most obvious of the selection pressures that have driven (and continue to drive) the evolution of plants

is **competition** with other plants. Our ideal low-lying land plant would be rapidly outcompeted by any plants that managed to grow above; they could shade it out by producing multicellular stems to hold up the leaves. As well as competition for light, plant evolution also has been driven by competition for the other essentials of life: water, nutrients and even space itself. Some plants can even discourage growth of competitors near them by secreting growth-inhibiting substances, a process called **allelopathy**.

Defence

Other important selection pressures are driven by attempts by other organisms to exploit the photosynthesis of a plant. Plants have evolved defences which prevent this happening, but there are many ways in which plants can be exploited. Most obviously, plants can be eaten by animals, a process known as **herbivory**. Considering the huge number of herbivores and the inability of most plants to move, it is surprising that any plants survive at all! But plants can also be exploited by smaller organisms which penetrate their tissues and exploit them from the inside. When this invasion is practised by tiny organisms such as viruses, bacteria and fungi this results in **disease**. When it is carried out by small animals, in contrast, it is usually described as **endophagy**, and when another plant carries out the process it is known as **parasitism**. Many of the evolutionary novelties devised by plants are defensive mechanisms which reduce their losses by these processes.

Exploitation

Yet other selection pressures are driven by the attempts of plants themselves to exploit other life forms. These include **parasitism** of other plants; the consumption of animals to obtain energy and nutrients, a process known as **carnivory**; and associations with other organisms to exchange benefits, a process known as **mutualism**. Mutualistic partnerships are widespread and have been extremely important in the evolution of plants. They can occur between two species of plants; between plants and bacteria, as in the root nodules of legumes; between plants and fungi, as in lichens or mycorrhizas; and between

organisms, even those that live together in a mutually beneficial relationship, is an **evolutionary arms race**, in which each organism struggles to gain the maximum possible advantage. A meadow is not just a peaceful collection of pretty flowers but a battlefield of warring organisms, each fighting for its life and its chance to pass on its genes to future generations. Botany is the study of the ingenious solutions plants have come up with to survive in this battlefield.

1.3 THE PROCESS OF EVOLUTION

1.3.1 The theory of evolution by natural selection

Before we can make sense of the diversity of plant life it is essential to understand the process of evolution by natural selection, which was first described by Darwin and outlined in his book *On the Origin of Species* (1859). Darwin's theory can be summarized logically in a simple four-stage argument.

- 1 More individuals are produced than can survive.
- 2 There is a struggle for existence.
- 3 Individuals show variation. Those with favourable characteristics are more likely to survive and reproduce.
- 4 Because selected varieties produce similar offspring to themselves, these varieties will become more abundant.

Therefore, given competition, variation and inheritance, evolutionary change over time is *inevitable*. It was Darwin's genius to recognize the central role of variation, which is often a destructive phenomenon, in producing progressive change. There is no doubt that his ideas were strongly influenced by his knowledge of domestic animals and of the breeding of pigeons. In these animals, new breeds can be produced by selecting for breeding only those individuals which possess the desired traits. In a similar way, Darwin argued, nature would select organisms with better characteristics for survival, by killing off their competitors. His use of the term **natural selection** was chosen deliberately to contrast with the **artificial selection** imposed by breeders on their stock.

1.3.2 Inheritance, genes and microevolution

Darwin had one major problem: his ignorance of a convincing mechanism for inheritance. The findings of Mendel, which were rediscovered only after Darwin's death, remedied this defect and showed that the inherited material was particulate in nature: something which is essential if natural selection is to work. Mendel found that the form and behaviour (or **phenotype**) of an organism is controlled by large numbers of particles called **genes** which are passed, apart from a few mutations, unaltered through the generations. Together, these genes make up an organism's **genotype**.

Discrete characters

Studies of the small-scale **microevolution** have shown that natural selection can alter a population of organisms in two ways. The first involves **discrete characters** which are influenced by a single gene: characters like the colour and texture of Mendel's peas or the tolerance of certain grasses to metal pollution. If one of two possible forms is favoured by the environment the frequency of the favoured genes will increase. Eventually it may even sweep through the entire population to **fixation**. For instance when grasses were grown on copper-mine waste (Fig. 1.2a), plants with a gene for tolerance to copper grew better and left more descendants. Consequently the frequency of the tolerance gene increased over time.

Continuous characters

The second way in which selection can result in evolution involves **continuous characters**, such as the height, diameter and seed size of plants, which are influenced by a large number of genes, each of which has a small effect. Without selection there will be some variation in these characters because the sum of the effect of the genes will often be higher or lower than the mean, just by chance. Usually the numbers of organisms at particular values will follow a normal distribution. If selection pressure is applied to these characters, the relative numbers of genes in the population will be altered and the population will

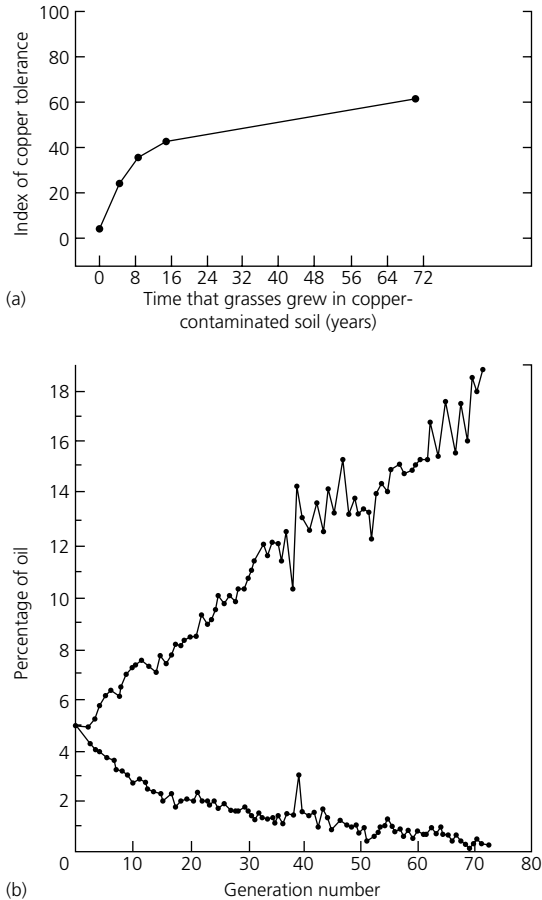


Fig. 1.2 Examples of evolution. (a) Response of creeping bent grass *Agrostis stolonifera* to copper contamination. The index of copper tolerance was higher in populations of plants that had been living longer in areas contaminated with copper. This shows that natural selection had resulted in evolution which improved the chance of survival of the population. (Redrawn from Berg, 1997.) (b) Response of maize *Zea mays* to artificial selection for high or low oil content. Over 80 generations the former had almost quadrupled oil content and the latter reduced it by about 90%. (Redrawn from Ridley, 1993.)

be changed. For instance, if herbivores preferentially graze taller grasses because they are easier to eat, the proportion of genes for shortness that are passed to the next generation will be increased and the population will become shorter. A long-term experiment aimed at altering the oil content of maize seeds (Fig. 1.2b) has shown that selection over many

generations can produce extremely large changes very rapidly.

1.3.3 Cytogenetics and sex

Of course, we now know that genes are not just abstract ideas but are real entities which are located in the **chromosomes** which are found in almost all cells. At the molecular scale, following the discoveries of Crick and Watson, we also now know that the genes are coded regions of the molecule **deoxyribonucleic acid (DNA)** which occurs in the famous double helix. However, the ways in which the DNA is packaged within cells differs between the simple **prokaryotes** such as bacteria and the larger, more complex **eukaryotes**, which include unicellular and multicellular algae and all land plants.

Prokaryotes

The prokaryotes have only a single copy of each gene, all of which are encoded onto a single long circular strand of DNA, often referred to as a bacterial **chromosome**, which floats free in the cytoplasm. Additional shorter circular **plasmids** may also be present. Prokaryotes divide asexually by the process of **mitosis** (Fig. 1.3) which produces two nearly identical daughter cells. If the copying mechanism for DNA was perfect, there would be a limit to evolution; selection would reduce the variation within the population and eventually all the surviving organisms would be identical. Instead, rare mistakes in the copying process, which are known as **mutations**, maintain the genetic variation and ensure that evolution can continue. Limited transfer of genetic material is also possible between individuals.

Eukaryotes

In the larger and more slowly reproducing eukaryotes, rare mutations would not be sufficient to ensure rapid enough evolution. One way of increasing the rate of evolution might be to increase the mutation rate of the genes. Unfortunately, though, this has the drawback that, because most mutations are harmful, few of the offspring would survive. Instead, eukaryotes have evolved a much more

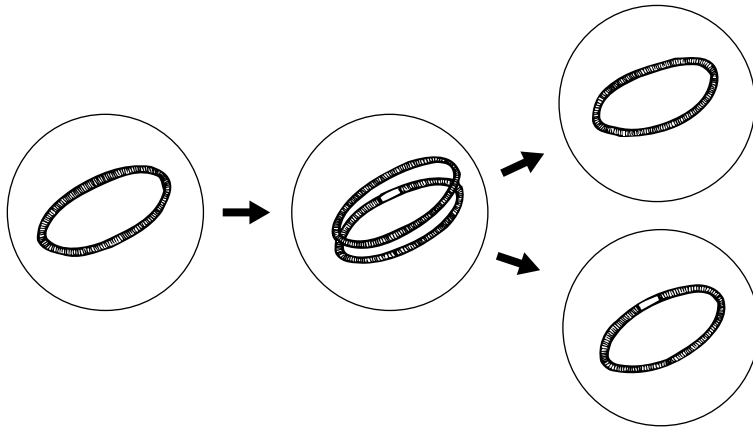


Fig. 1.3 Mitosis in a prokaryote cell. The bacterial chromosome is replicated and the cell then divides, one copy of the chromosome moving into each of the daughter cells. Note that the copying mechanism is not exact, so that one daughter chromosome has a mutation (white area).

sophisticated (and enjoyable!) way of maintaining variability—sex.

The cells of eukaryotic organisms can typically be found in two different states: the cells may be either **haploid**, in which case they contain a single copy of each gene; or **diploid** in which case they contain *two* copies. Each gene is found in a linear chromosome, several of which are usually found within the nucleus, but while haploid cells contain one copy of each chromosome, diploid cells contain two. Both haploid and diploid cells can divide, like bacteria, by mitosis, but mutations are mostly eliminated by special **restriction enzymes** which correct any mistakes that have been made. The variability is produced by allowing genetic information to be transferred between homologous chromosomes when diploid cells divide in a special process called **meiosis** (Fig. 1.4). This process actually involves two separate divisions of the cells. In the first division, each chromosome doubles up, as in mitosis. Then, however, something odd occurs. Instead of splitting, the two pairs of chromosomes line up with each other and may exchange some genetic material. Only then does cell division occur to produce two diploid cells with pairs of mixed chromosomes. Finally these cells divide again to leave four haploid cells each with a single totally original copy of each chromosome.

Meiosis can produce an almost infinite number of new combinations of genes on which natural selection can operate without the drawback of an overly high mutation rate. But meiosis always produces haploid cells. To reform diploid cells which can go

through the process again, two haploid cells need to go through another process, **fusion**, in which two cells meet, join together and the nuclei fuse to produce a nucleus with two copies of each chromosome. Sex therefore requires alternate meiosis and fusion.

1.4 LIFE CYCLES OF EUKARYOTES

Apart from its effect on the variability of the offspring an organism produces, the process of sex has important implications for the life cycles of eukaryotic organisms. Because meiosis and fusion must alternate, producing haploid and diploid cells in turn, the life cycles of these organisms are necessarily complex. And the process is made even more complex because both haploid and diploid cells can also divide by mitosis. Haploid cells can either fuse immediately after they have been formed by meiosis, or may divide by mitosis many times first. Similarly diploid cells can undergo meiosis immediately to form new haploid cells or they may divide by mitosis many times first. The different life cycles seen in eukaryotes (Fig. 1.5) are the result simply of different patterns of meiosis, mitosis and fusion.

1.4.1 Zygotic meiosis

If the diploid **zygote** splits by meiosis immediately after it has been formed (Fig. 1.5a), a process known as **zygotic meiosis**, the organism will spend most of

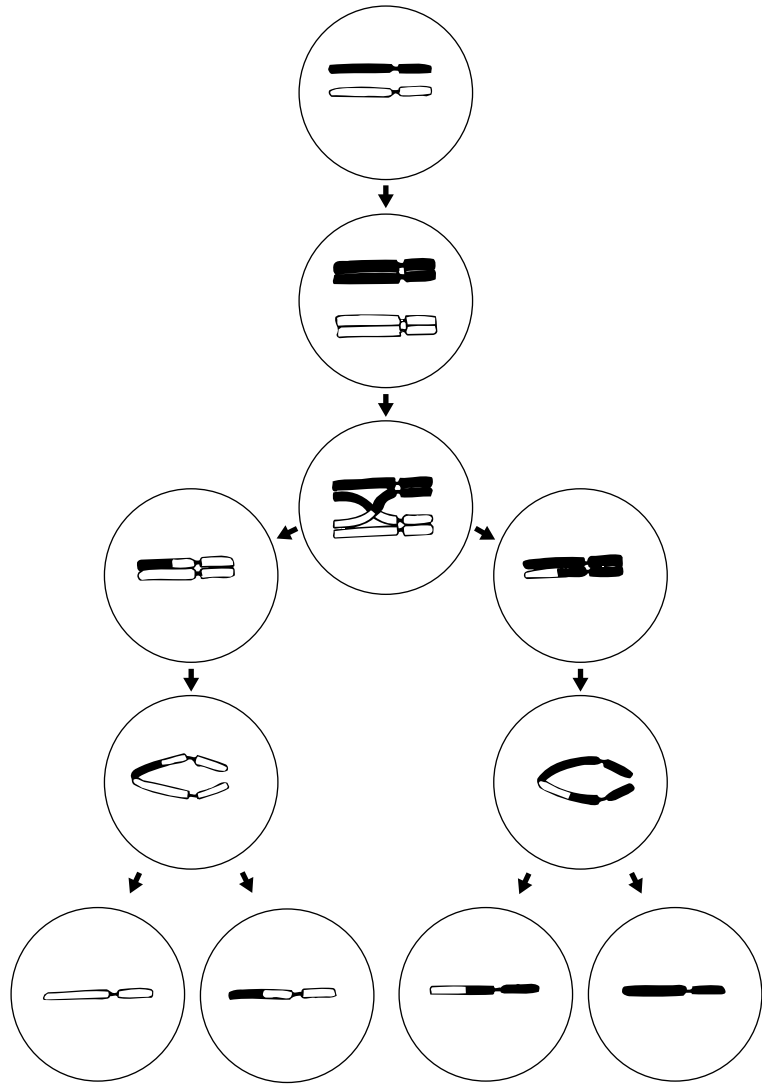


Fig. 1.4 Meiosis in a eukaryote cell. The first stage is a doubling up of each homologous chromosome in the diploid cell. The next involves the lining up of the homologous pairs and exchange of material. The cell then splits to give two diploid cells with pairs of mixed chromosomes. The final cell division produces four haploid cells, each with a single novel copy of the chromosome.

its life in the haploid state. The haploid cells can divide in two different ways which will produce very different sorts of haploid organisms.

The daughter cells of the meiosis can divide and separate from each other to produce generations of single-celled organisms. Eventually some of these organisms may fuse to recreate the **zygote**. Alternatively the daughter cells can remain attached to each other after cell division to create a multicellular organism. Eventually some of the cells of this

organism will form gametes which will fuse with gametes from a different organism to re-create the **zygote**. In both cases the zygote is the only diploid cell.

Life cycles involving zygotic meiosis were probably the first to evolve, since the earliest eukaryotes, like prokaryotes, must have been haploid. Zygotic meiosis is found today in algae, such as the unicellular *Chlamydomonas* (Chapter 3), and the multicellular *Chara* (Chapter 4). Fungi also use this method.

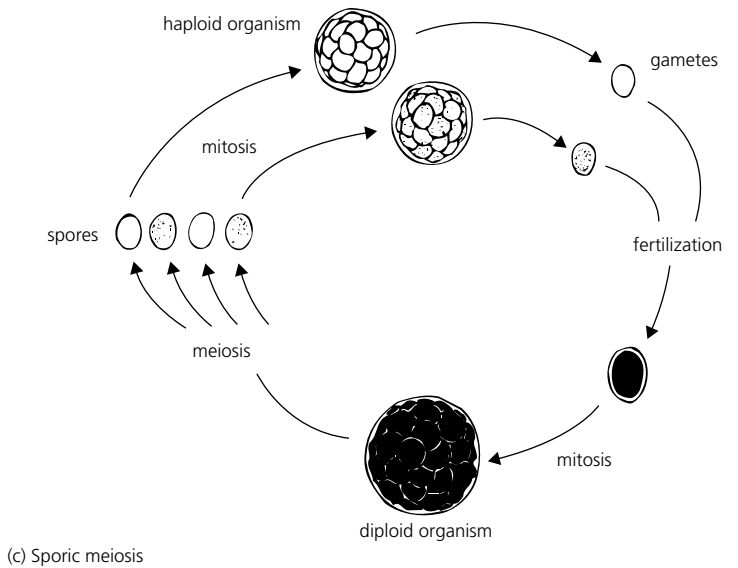
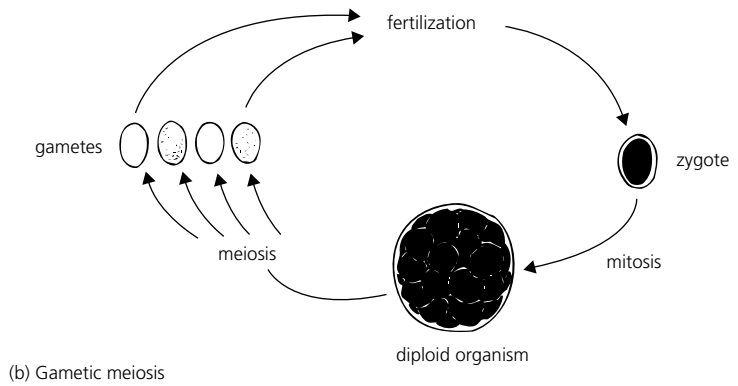
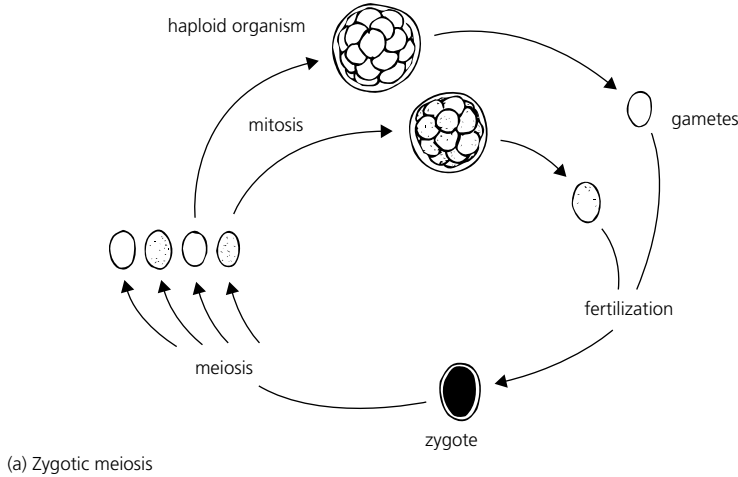


Fig. 1.5 Diagrams of the three types of eukaryote life cycle. In these diagrams the diploid phase is black, while the male and female haploid stages are white and light grey. Some green algae and fungi undergo **zygotic meiosis** (a) in which the zygote divides by meiosis immediately after being formed to give haploid cells. These divide by mitosis to produce multicellular haploid organisms or more single-celled haploid organisms. These eventually produce gametes which fuse to reform the zygote. Some brown algae and animals undergo **gametic meiosis** (b) in which the haploid gametes are formed by meiosis from a multicellular diploid organism. These gametes fuse immediately after they are formed to produce a zygote which divides by mitosis to produce another diploid organism. Some algae and all plants undergo **sporic meiosis** (c) in which both gametes and zygotes divide by mitosis to produce multicellular organisms. The diploid **sporophyte** produces haploid spores by meiosis, and these divide to produce the multicellular **gametophyte** which eventually produces gametes. Because this produces two different generations of adult organisms this sort of life cycle is often known as **alternation of generations**.

1.4.2 Gametic meiosis

If the haploid **gametes** fuse together immediately after they have formed (Fig. 1.5b), the organism will spend most of its life in the diploid state. Again, the form of the diploid organism that forms will depend on the pattern of cell division.

If the diploid cells separate after each cell division, generations of unicellular organisms will be produced. Alternatively if the cells remain attached a multicellular organism will be produced. Eventually, some of the cells will undergo **gametic meiosis** to recreate gametes which fuse with ones from other organisms. In both cases the gametes are the only haploid cells.

Gametic meiosis is characteristic of both multicellular animals such as ourselves and some unicellular protists. It has also developed in some brown algae such as *Fucus* (Chapter 4).

1.4.3 Sporic meiosis

The most complex sort of life cycles occur when both haploid and diploid cells can undergo mitosis (Fig. 1.5c). In this case meiosis of diploid cells produces haploid **spores** rather than gametes. These are released and divide mitotically many times to produce a **haploid organism**. Eventually this produces gametes which fuse to produce a diploid zygote. This in turn divides by mitosis to produce a **diploid organism**. Eventually some of this organism's cells will undergo **sporic meiosis** to recreate the **spores**. In life cycles with this pattern of meiosis therefore there are two **alternating generations** of organisms: one haploid, the other diploid.

Sporic meiosis is characteristic of many algae and all the higher plants. The two generations: the haploid **gametophyte** (so called because it produces gametes) and the diploid **sporophyte** (so called because it produces spores) often look similar in algae, and are then said to be **isomorphic**. However, in many algae and in all plants mutations have occurred which are expressed in only one of the generations. As a result the gametophyte and sporophyte have come to be very different from each other and are said to be **heteromorphic**.

Different generations have become dominant in

different groups, as we shall see. In mosses and liverworts (Chapter 5) the gametophyte is dominant, and the sporophyte is usually dependent on it for nutrition. In vascular plants such as ferns (Chapter 6), in contrast, it is the sporophyte that is dominant. This process has been taken to such an extreme in the seed plants, for instance the conifers and angiosperms (Chapter 7), that the gametophytes are microscopic and totally dependent on the sporophyte for nutrition. The females are minute organisms which are held within the ovary of the flower, while the male gametophytes are held within the even tinier pollen grains. As a result, most seed plants seem at first sight to reproduce in a very similar way to animals, but the processes are very different.

1.4.4 Implications of life cycles

The success of organisms depends just as much on their reproductive efficiency as on the factors that affect survival of the existing organisms. The efficiency of reproduction is greatly affected by environmental conditions. It is particularly difficult for unicellular gametes to disperse on dry land, for instance, because desiccation becomes a big problem. As we shall see, therefore, plants' life cycles greatly influence which environments they can effectively colonize. For this reason the evolution of plant life cycles will be discussed throughout this book as we encounter each new group of organisms.

1.5 MECHANISMS OF ADAPTATION

1.5.1 Evolution of complex characters

It is at first glance hard to imagine how the small-scale changes in gene frequency which are caused by natural selection could have produced the vast array of sophisticated adaptations possessed by modern plants. The process must be very slow. It must be remembered, however, that photosynthetic organisms first appeared over 3 billion years ago, and the first eukaryotic organisms over a billion years ago. Natural selection has therefore had plenty of time over which to operate.

Bearing in mind that each stage in evolution has to be an improvement on the previous one, it is also difficult to see how complex organs such as flowers could be produced by the gradual process of evolution by natural selection. Surely half a flower would not be any use to a plant? However, careful thought can allow us to put forward quite plausible ideas about how natural selection could have generated flowers. Many species of insect eat pollen because it is an excellent source of protein. Presumably early flying insects such as beetles would have inadvertently spread pollen from one reproductive structure to another as a result. More insects could also have been attracted by sugar within the pollen drop of early seed plants. Plants that produced this sugar solution would get improved pollen transfer both because it would attract more insects and because each insect would eat less pollen. They would consequently be more likely to pass on their genes.

A change that might improve the efficiency of the pollen transfer process would be the evolution of a signal to the insects that pollen and sugar solution were available. The leaves that surrounded the reproductive parts of the plant could have become more prominent by gradually replacing their chlorophyll with other pigments. The flowers with the more visible leaves would have been visited more frequently by insects and would be more likely to have their pollen transferred and hence to have more offspring. The genes for prominent leaves would therefore become more common, so over time the leaves might become brighter, change shape and so evolve into petals. Similarly, the amount of sugar solution produced by the plant would also gradually increase, because plants with larger amounts of sugar would also be more frequently visited. The end result would be the evolution of sophisticated nectaries. Over time therefore the competition between flowers to attract pollinating insects could produce the beautifully adapted flowers we see today.

1.5.2 Preadaptations

Frequently, large changes in evolution can be brought about when the function of an existing organ is changed. The flower petals, which attract insects, for instance, are probably modified leaves.

Similarly, the tendrils which are used by many climbing plants to grip supports (Fig. 1.6) have evolved from petioles, which were used to bear leaves. Structures that become used in a different way from their original function are known as **preadaptations**. They frequently show extensive evolutionary change after the alteration in function to ‘fine tune’ them to their new role.

It is often easy to detect when such changes have occurred. One way is to use a comparative approach and examine a range of organisms. Related species may retain the ancestral character. Magnolias, for instance, have flowers that look much more like simple leaf stalks than other flowering plants. Similarly, some climbing plants like *Clematis* climb using tendrils (Fig. 1.6b) which still bear leaves. A second way is to examine mutant forms of the plant, since the original genes may still be present, only masked by later additions. In many mutant peas, for instance, the tendrils can be replaced by fully leafed petioles, showing that the two structures are **homologous**. No structure or organ has yet been found whose evolution cannot be explained by the process of evolution by natural selection. Until one has, therefore, it is safe to assume that evolution by natural selection is the cause of **adaptation**.

1.6 MECHANISMS OF SPECIATION

1.6.1 Reproductive isolation and speciation

A second puzzle for botanists is how so many separate species of plants could have evolved. This is because although natural selection might drive plants of a single species to become different, when they mate with each other, meiosis would constantly be mixing up their genes again and would keep the population uniform. Therefore in a single interbreeding population, although change and adaptation are possible, the evolution of diversity would not be.

The crucial step that allows a species to split up into two or more new ones is for its population to be split up into **reproductively isolated** subpopulations. Once they no longer breed with each other

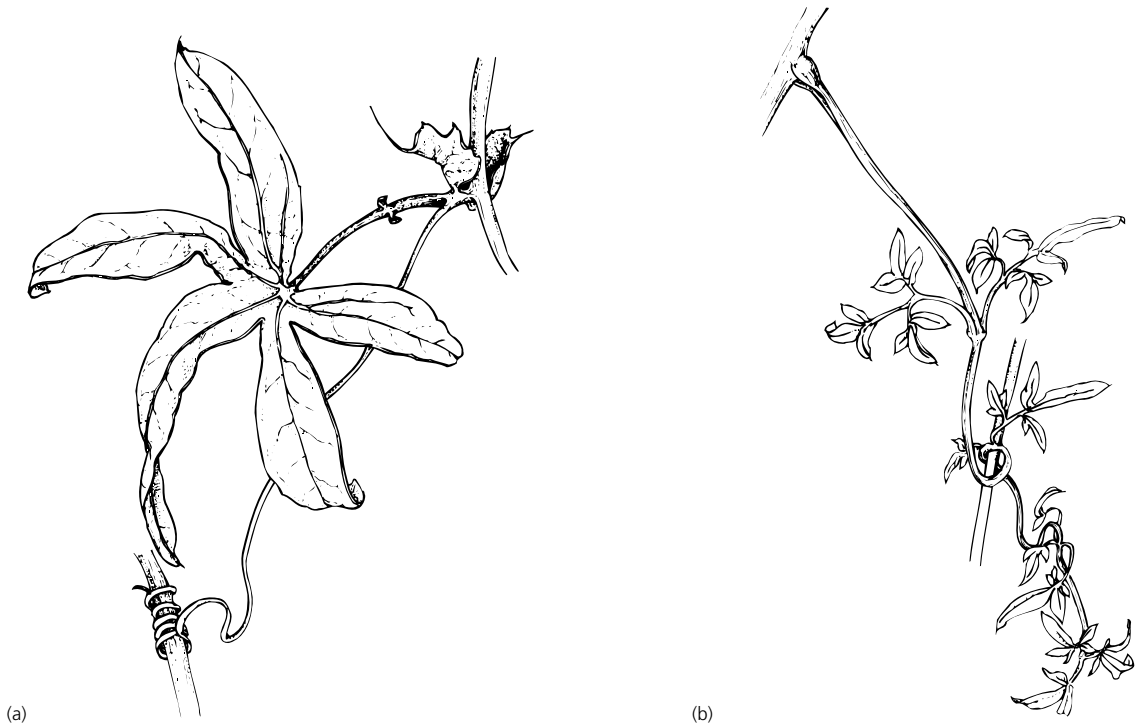


Fig. 1.6 Many tendrils such as those of the passion flower *Passiflora caerulea* (a) are modified petioles. This ancestry is shown up by plants such as *Clematis tibetica* (b) in which the tendrils still bear leaves.

they will be able to alter independently and start to become different. If they breed apart for long enough they may be so different when they meet again that they are unable to breed with each other. Fertilization may be prevented or the hybrids produced between the two forms may be inviable or sterile. If so, **speciation** will have occurred; two or more isolated breeding populations (or **species**) will have been produced where only one existed before.

1.6.2 Allopatric speciation

Clearly the easiest way for populations to become isolated from each other is geographically: populations may be isolated on islands within an ocean; in lakes within a continent; on mountains separated by valleys; in valleys separated by mountains; or in isolated patches of one habitat within another. Much of the speciation of plants probably did take place

as a result of such isolation, particularly in the small populations which often survive at the extreme edges of a species' range. Speciation that occurs as a result of this form of isolation is known as **allopatric speciation**.

There are many examples of plant species that were almost certainly formed in this way. Isolated oceanic islands contain many **endemics**, species found only on that island but similar to forms that grow on the mainland. These species probably formed by allopatric speciation. Often whole groups of closely related plants are found in chains of recently formed volcanic islands, just like Darwin's finches on the Galapagos islands. A good example are the silver-swords of Hawaii: originally small daisy-like flowers which must have speciated within the last few million years, as the islands emerged. They have evolved into plants as diverse as large rosette plants, shrubs, lianas, and even trees.